Economic Behavior from an Evolutionary Perspective

by

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Abstract

The conflict between rational models of economic behavior and their systematic deviations, often referred to as behavioral economics, is one of the most hotly debated issues in social sciences. This thesis reconciles the two opposing perspectives by applying evolutionary principles to economic behavior and deriving implications that cut across species, physiology, and genetic origins.

In the context of a binary-choice model, we first show that risk aversion emerges via natural selection if reproductive risk is “systematic”, i.e., correlated across individuals in a given generation. The degree of risk aversion is determined by the stochastic nature of reproductive rates, and different statistical properties lead to different utility functions. More generally, irrational behaviors are not just mere divergence from rationality, but seeds necessary for successfully coping with environmental transformations. Furthermore, there is an optimal degree of irrationality in the population depending on the degree of environmental stochasticity.

When applied to evolutionary biology, we show that what appears to be group selection may, in fact, simply be the consequence of natural selection occurring in stochastic environments with “systematic” risks. Those individuals with highly correlated risks will appear to form “groups”, even if their actions are totally autonomous, mindless, and, prior to selection, uniformly randomly distributed in the population.

Evolutionary principles can also be used to model the dynamics of financial markets. In a multiperiod model of the contagion of investment ideas, we show that heterogeneous investment styles can coexist in the long run, implying a wider variation of diverse strategies compared to traditional theories. These results may provide new insights to the survival of a wide range of hedge funds. In a model that investors maximize their relative wealth, the initial wealth plays a critical role in determining how the optimal behavior deviates from the Kelly Criterion, regardless of whether the investor is myopic or maximizing the infinite-horizon wealth.

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Chapter 1

Introduction

1.1 Background

Rationality is the key assumption behind standard economic models of human behavior. The idea that individuals maximize their own self-interest subject to resource constraints has led to numerous breakthroughs, including the expected utility theory (von Neumann and Morgenstern 1944), game theory (von Neumann and Morgenstern 1944, Nash 1950), rational expectations (Lucas Jr 1972), and the option pricing theory (Black and Scholes 1973, Merton 1973). The influence of this paradigm goes far beyond academia—it underlies current macroeconomic and monetary policies, and has also become an integral part of the rules and regulations that govern financial markets today (Kocherlakota 2010, Hu 2012).

Two of the theories that are particularly relevant for this thesis are the modern portfolio theory (Markowitz 1952) and the Efficient Markets Hypothesis (Samuelson 1965, Fama 1970). Ever since Markowitz's groundbreaking work, the mean variance approach has remained the cornerstone of modern portfolio theory, which has led to the famous Capital Asset Pricing Model (Sharpe 1964, Treynor 1965, Lintner 1965b, Lintner 1965a, Mossin 1966). As one of the most influential ideas in all the social sciences, the Efficient Markets Hypothesis argues that market prices “fully reflect all available information”; agents with incorrect beliefs will be driven out of the market by agents with correct beliefs (Fama 1965), and market pressure would eventually
result in behavior consistent with maximization (Alchian 1950, Friedman 1953).

However, accumulating evidence from psychology, cognitive science, behavioral economics and finance has documented significant inconsistencies to the rationality assumption. These systematic deviations from rational behaviors are hard to reconcile with the standard economic models, and are therefore considered “irrational”. Representatives of these cognitive biases include probability matching (Grant et al. 1951, Herrnstein 1961) (the tendency to choose randomly between heads and tails when asked to guess the outcomes of a series of independent biased-coin tosses, where the randomization matches the probability of the biased coin), loss aversion (Tversky and Kahneman 1974, Tom et al. 2007) (the tendency to take greater risk when choosing between two potential losses, and less risk when choosing between two potential gains), uncertainty effect (Gneezy et al. 2006) (a risky prospect is valued less than its worst possible outcome), and confirmation bias (Mahoney 1977) (the tendency to search for or interpret information in a way that confirms one’s preconceptions). Such anomalous behaviors have also been observed in many non-human subjects ranging from bacteria to primates (Harder and Real 1987, Pasteels et al. 1987, Kirman 1993, Smallwood 1996, Chen et al. 2006, Ben-Jacob 2008, Santos and Chen 2009), which suggests that they may have a common and ancient origin, and an evolutionary role that belies their apparent shortcomings.


This thesis applies evolutionary principles to human economic behavior and reconciles the two opposing perspectives. The idea of natural selection in economics can
be traced back to 1950s (Alchian 1950, Penrose 1952, Friedman 1953). Since then the Darwinian selection perspective has been applied to a variety of economic behaviors and concepts including altruism (Alexander 1974, Becker 1976, Hirshleifer 1977, Almenberg and Dreber 2013), evolutionary game theory (Maynard Smith 1982), the rate of time preference (Rogers 1994, Robson and Samuelson 2009), and utility functions (Campbell 1986, Robson 1996a, Robson 1996b, Dekel and Scotchmer 1999, Samuelson 2001). In particular, irrational behavior—as opposed to utility-maximizing behavior—has been found useful and persistent in a variety of environments in evolution (Belavkin 2006, Houston et al. 2007, Waksberg et al. 2009, Ross and Wilke 2011, Okasha and Binmore 2012). However, it is still unclear how these behaviors relate to standard economic theories of individual rationality, and why they emerge in some instances and not others.

In the context of financial markets, evolutionary models have also been proposed to understand market selection (Blume and Easley 1992, Luo 1995, Kogan et al. 2006a, Hirshleifer and Toch 2009) and the geometric mean principle or “Kelly criterion” (Kelly Jr. 1956). In recent years, the Adaptive Markets Hypothesis (Lo 2004) provides an evolutionary perspective and reconciles economic theories based on the Efficient Markets Hypothesis with behavioral economics: the neoclassical models of rational behavior can coexist with behavioral models, and what was cited as counterexamples to rationality—loss aversion, overconfidence, overreaction, and other behavioral biases—are, in fact, consistent with an evolutionary model of human behavior.

More recently, Brennan and Lo (2011) have proposed a binary choice model that provides an evolutionary framework for generating a variety of behaviors that are considered “anomalous” from the perspective of traditional economic models, i.e., loss aversion, probability matching, and bounded rationality. In this framework, natural selection yields standard risk-neutral optimizing economic behavior when reproductive risk is idiosyncratic, i.e., uncorrelated across individuals within a given generation. But when reproductive risk is systematic, i.e., correlated among individuals within a given generation, some seemingly irrational behaviors such as probability
matching and loss aversion become evolutionarily dominant.

This thesis extends the binary choice model in various aspects. Next section summarizes the main results, and more specific backgrounds are given in the beginning of each chapter.

1.2 Overview of the Thesis

The main results in this thesis are divided into five chapters. Each chapter is self-contained and, therefore, can be read in isolation.

Chapter 2 studies the origin of risk aversion. Risk aversion is one of the most basic assumptions of economic behavior, but few studies have addressed the question of where risk preferences come from and why they differ from one individual to the next. Here we propose an evolutionary explanation for the origin of risk aversion. In the context of a simple binary-choice model, we show that risk aversion emerges via natural selection if reproductive risk is “systematic”, i.e., correlated across individuals in a given generation. In contrast, risk neutrality emerges if reproductive risk is “idiosyncratic”, i.e., uncorrelated across each given generation. More generally, our framework implies that the degree of risk aversion is determined by the stochastic nature of reproductive rates, and we show that different statistical properties lead to different utility functions. The simplicity and generality of our model suggest that these implications are primitive and cut across species, physiology, and genetic origins. From a policy perspective, our results underscore the importance of addressing systematic risk through insurance markets, capital markets, and government policy. However, our results also highlight the potential dangers of sustained government intervention, which can become a source of systematic risk in its own right.

Chapter 3 shows that irrational behaviors are evolutionary adaptations to stochastic environments. The debate between rational models of behavior and their systematic deviations, often referred to as “irrational behavior”, has attracted an enormous amount of research. Here we reconcile the debate by proposing an evolutionary explanation for irrational behavior. In the context of a simple binary choice model, we
show that irrational behaviors are necessary for evolution in stochastic environments. Furthermore, there is an optimal degree of irrationality in the population depending on the degree of environmental stochasticity. In this process, mutation provides the important link between rational and irrational behaviors, and hence the variety in evolution. Simulation confirms the generality of these implications in a wide range of stochastic environments. Our results yield widespread implications for science, management, and public policy.

Chapter 4 applies the binary choice model to group selection, one of the most important concepts in evolutionary biology. Despite many compelling applications in economics, sociobiology, and evolutionary psychology, group selection is still one of the most hotly contested ideas in evolutionary biology. Here we propose a simple evolutionary model of behavior and show that what appears to be group selection may, in fact, simply be the consequence of natural selection occurring in stochastic environments with reproductive risks that are correlated across individuals. Those individuals with highly correlated risks will appear to form “groups”, even if their actions are, in fact, totally autonomous, mindless, and, prior to selection, uniformly randomly distributed in the population. This framework implies that a separate theory of group selection is not strictly necessary to explain observed phenomena such as altruism and cooperation. At the same time, it shows that the notion of group selection does capture a unique aspect of evolution—selection with correlated reproductive risk—that may be sufficiently widespread to warrant a separate term for the phenomenon.

Chapter 5 turns to the application of the binary choice model in financial context. This chapter studies the contagion of investment ideas in a multiperiod model where each investor has a propensity to invest in one of the two strategies with general distributions of returns. Investors with higher realized payoffs are more likely to transmit their ideas to other investors from social interaction and, therefore, generate more “offspring”. We show that when returns are endogenous, heterogeneous investment styles can coexist in the long run, implying a wider variation of diverse strategies compared to traditional theories. In addition, our model gives a characterization of
which strategies survive in relation to security return characteristics. These results may provide new insights to the survival of investment strategies and, more broadly, the survival of a wide range of hedge funds.

Chapter 6 adds to the literature of the optimal portfolio growth theory. We propose an evolutionary framework for portfolio growth where investors allocate their wealth between two assets. By considering criteria with both absolute wealth and relative wealth, we show that different investor behaviors survive under different environments. In the case that investors maximize their relative wealth, conditions under which the Kelly Criterion is optimal are identified. It is shown that the initial relative wealth plays a critical role in determining how the optimal behavior deviates from the Kelly Criterion, regardless of whether the investor is myopic or maximizing the infinite-horizon wealth.

Chapter 2-4 are joint work with Andrew W. Lo and Thomas J. Brennan, and are derived from Zhang et al. (2014b), Zhang et al. (2015), and Zhang et al. (2014a). Chapter 5 is joint work with Andrew W. Lo and David Hirshleifer. Chapter 6 is joint work with Andrew W. Lo and H. Allen Orr. Proofs of the main results for all chapters are given in Appendix A.
Chapter 2

The Origin of Risk Aversion

2.1 Introduction

Risk aversion is one of the most fundamental properties of human behavior. Ever since Bernoulli’s pioneering work in gambling and the St. Petersburg Paradox in the 17th century (Bernoulli 1954), considerable research has been devoted to understanding human decision making under uncertainty. Two of the most well-known theories are expected utility theory (von Neumann and Morgenstern 1944) (an axiomatic formulation of rational behavior under uncertainty) and prospect theory (Kahneman and Tversky 1979) (a behavioral theory of decision making under uncertainty). Several measures of risk aversion have been developed, including curvature measures of utility functions (Arrow 1971, Pratt 1964), human-subject experiments and surveys (Rabin and Thaler 2001, Holt and Laury 2002), portfolio choice for financial investors (Guiso and Paiella 2008), labor-supply behavior (Chetty 2006), deductible choices in insurance contracts (Szpiro 1986, Cohen and Einav 2007), contestant behavior on game shows (Post et al. 2008), option prices (Aït-Sahalia and Lo 2000), and auction behavior (Lu and Perrigne 2008).

Despite its importance and myriad applications in the past several decades, few economists have addressed the question: where does risk aversion come from? Biologists and ecologists have documented risk aversion in non-human animal species—often called “risk-sensitive foraging behavior”—ranging from bacteria to primates...
(Harder and Real 1987, Pasteels et al. 1987, Kirman 1993, Smallwood 1996, Ben-
Jacob 2008). Recently, the neural basis of risk aversion has also received much atten-
tion as researchers discovered that the activity of a specific brain region correlates
with risk-taking and risk-averse behavior (Knoch et al. 2006, Fecteau et al. 2007, Tom
et al. 2007).

Evolutionary principles have been applied by economists to a variety of eco-
nomic behaviors and concepts including altruism (Becker 1976, Hirshleifer 1977),
the rate of time preference (Robson and Samuelson 2009), and utility functions
(Robson 1996a, Robson 1996b, Dekel and Scotchmer 1999, Samuelson 2001, Robatto
and Szentes 2013). In particular, Robson (1996a) proposes an evolutionary model of
risk preferences in which he assumes an increasing concave relation between an indi-
vidual’s number of offspring and the amount of resources available to that individual,
and given this concave “biological production function”, he shows that expected utility
arises from idiosyncratic environmental risk and non-expected utility arises from sys-
tematic risk. In the context of financial markets, evolutionary models have also been
proposed to capture market selection (Blume and Easley 1992) and the geometric
mean principle or “Kelly criterion” (Kelly Jr. 1956). And as an alternative to the tra-
ditional view that markets are always and everywhere efficient and that “prices fully
reflect all possible information” (Samuelson 1965, Fama 1970), the Adaptive Markets
Hypothesis (Lo 2004) provides an evolutionary perspective of financial markets.

More recently, Brennan and Lo (2011) have proposed a binary choice model that
provides an evolutionary framework for generating a variety of behaviors that are
considered “anomalous” from the perspective of traditional economic models, i.e., loss
aversion, probability matching, and bounded rationality. In this framework, natural
selection yields standard risk-neutral optimizing economic behavior when reproduc-
tive risk is idiosyncratic, i.e., uncorrelated across individuals within a given gener-
ation. But when reproductive risk is systematic, i.e., correlated among individuals
within a given generation, some seemingly irrational behaviors such as probability
matching and loss aversion become evolutionarily dominant.

In this chapter, we extend the binary choice model (Brennan and Lo 2011) and
focus on the origin of utility and risk aversion. We show that risk aversion emerges as a consequence of systematic risk and risk neutrality emerges as a consequence of idiosyncratic risk, regardless of the species and without the need for any biological production function, concave or otherwise. This result suggests that the degree and type of risk aversion are determined by the stochastic nature of reproductive risk, and we show how different environments lead to different stable utility functions over time. This approach provides an alternate and more fundamental explanation of risk aversion, and the fact that our results do not depend on any exogenously specified production function suggests that risk aversion is a much more primitive feature of all organisms. Moreover, the simplicity of our framework and the direct relation between reproductive success and risk aversion provides an equally simple explanation for the large amount of heterogeneity in risk aversion observed in empirical studies (Holt and Laury 2002, Guiso and Paiella 2008, Chetty 2006, Szpiro 1986, Cohen and Einav 2007): variation in the amount of systematic risk in reproductive success.

When applied to economic contexts, our results imply a link between the expected returns of risky assets such as equities and systematic reproductive risk which, in turn, is correlated with aggregate financial risk. This relation is consistent with the well-known equilibrium risk/reward trade-off first proposed by Sharpe (1964). However, our theoretical derivation of this relation does not depend on preferences or general equilibrium, but is solely a consequence of natural selection under systematic reproductive risk.

Our model consists of an initial population of individuals, each assigned a purely arbitrary behavior with respect to a binary choice problem and where it is assumed that offspring behave in an identical manner to their parents. Therefore, those behaviors leading to greater reproductive success will lead to higher growth rates and become more representative in the general population. Environments with different types of reproductive risks will lead to different optimal behaviors and in the limit, only certain types of behaviors—corresponding to specific types of preferences or “utility functions”—will survive in such environments.

By studying the impact of selection on behavior rather than on genes, we are able
to derive evolutionary implications that cut across species, physiology, and genetic origins. In the same way that different magnifications of a microscope reveal different details of a specimen, applying evolutionary principles to behavioral variations leads to different insights that may be more relevant for economics, psychology, and behavioral ecology. Our focus on behavior as the object of selection is a different lens through which the effects of evolution may be studied.

2.2 The Binary Choice Model

Consider a population of individuals that live for one period, produce a random number of offspring asexually, and then die. During its life (we use the pronoun “it” since the individual need not be human), individual $i$ makes only one decision: choose one of two possible actions $a$ and $b$, which results in one of two corresponding random numbers of offspring, $x_{a,i}$ and $x_{b,i}$. These two random variables summarize the impact of the environment on the reproductive success of the individual, and they are assumed to be the weighted sum of two components:

$$
\begin{align*}
  x_{a,i} &= \lambda z_a + (1 - \lambda)y_{a,i} \\
  x_{b,i} &= \lambda z_b + (1 - \lambda)y_{b,i}.
\end{align*}
$$

(2.1)

The first component of the weighted sum, $(z_a, z_b)$, is assumed to be independently and identically distributed (IID) over time and identical for all individuals in a given generation, hence we refer to it as “systematic” risk since one individual experiences the same reproductive outcome as others that choose the same action. The second component, $(y_{a,i}, y_{b,i})$, is assumed to be IID both over time and across individuals $i$ in a given generation, hence we refer to it as “idiosyncratic”. Both components are described by some well-behaved probability distributions (Assumption 1), and $\lambda$ is a real number between 0 and 1.

**Assumption 1.** $(z_a, z_b)$, $(y_{a,i}, y_{b,i})$, $\log(f z_a + (1 - f) z_b)$, and $\log(f y_{a,i} + (1 - f) y_{b,i})$ have finite moments up to order 2 for all $f \in [0,1]$ and $i$. 

24
Each individual chooses $a$ with some probability $f \in [0, 1]$ and $b$ with probability $1-f$. We shall henceforth refer to $f$ as the individual's behavior since it completely determines how the individual chooses between $a$ and $b$. Note that $f$ can be 0 or 1, hence we are not requiring individuals to randomize—this will be derived as a consequence of natural selection under certain conditions. Denote by $x_i^f$ the random number of offspring produced by individual $i$ of type $f$, then $x_i^f = I_i^f x_{a,i} + (1 - I_i^f) x_{b,i}$, where $I_i^f$ is the Bernoulli random variable that equals 1 with probability $f$ and 0 otherwise.

Furthermore, offspring behave in a manner identical to their parents, i.e., they choose between $a$ and $b$ according to the same $f$, hence the population may be viewed as being segmented into groups of distinct types $f$. This assumption is tantamount to assuming perfect genetic transmission of traits from one generation to the next, which provides a clearer analysis of the interaction between natural selection and the stochastic properties of reproduction implicit in the environment. However, mutation can easily be incorporated into this framework at the expense of analytical simplicity (see Chapter 3). We also assume that the initial population contains an equal number of all types, and we normalize this common initial population to be 1 for each type without loss of generality.

We wish to emphasize the difference between reproductive success with systematic risk $(z_a, z_b)$ and idiosyncratic risk $(y_{a,i}, y_{b,i})$, which points to the central role that systematic risk plays in shaping the evolution of behavior and preferences. In the case of systematic risk, the number of offspring is given by the same two random variables $(z_a, z_b)$, for all individuals. If two individuals choose the same action $a$, both will generate the same number of random offspring $z_a$, i.e., their reproductive success is perfectly correlated. In this sense, fecundity is systematic. On the other hand, for $(y_{a,i}, y_{b,i})$, the randomness in the number of offspring is strictly idiosyncratic in the sense that the correlation between the number of offspring for two individuals $i$ and $j$ is 0, even if both individuals choose the same course of action. Idiosyncratic fecundity implies that even if all individuals in a given population choose the same action, there will still be considerable cross-sectional variability in the number of offspring produced in any generation.
Using (2.1) we can rewrite $x^f_i$ as a combination of systematic and idiosyncratic risk:

$$
x^f_i = \lambda z^f_i + (1 - \lambda)y^f_i
$$

where

$$
\begin{align*}
  z^f_i &= I_t^f z_a + \left(1 - I_t^f\right) z_b \\
y^f_i &= I_t^f y_{a,i} + \left(1 - I_t^f\right) y_{b,i}.
\end{align*}
$$

The coefficient $\lambda \in [0, 1]$ indicates the proportion of systematic risk in the environment. When $\lambda = 1$, all reproductive risk is systematic; when $\lambda = 0$, all reproductive risk is idiosyncratic; and when $0 < \lambda < 1$, both types of risk are present. In a particular environment described by $\lambda$, denote by $n^f_T$ the total number of offspring of type $f$ in generation $T$. It is easy to show that the average of the log-population $T^{-1} \log n^f_T$ converges in probability to the log-geometric-average growth rate:

$$
\alpha \lambda(f) = \mathbb{E}_z \left[ \log \left( \Lambda z^f + (1 - \lambda)\mathbb{E}_y[y^f] \right) \right] \tag{2.2}
$$

where $\mathbb{E}_z$ denotes the expectation taken with respect to $z^f$ and $\mathbb{E}_y$ denotes the expectation taken with respect to $y^f$. Equation (2.2) can also be written as

$$
\alpha \lambda(f) = \mathbb{E}_z \left[ \log \left( f \omega_a^\lambda + (1 - f)\omega_b^\lambda \right) \right] \tag{2.3}
$$

where

$$
\begin{align*}
  \omega_a^\lambda &= \lambda z_a + (1 - \lambda)\mathbb{E}_y[y_a], \\
  \omega_b^\lambda &= \lambda z_b + (1 - \lambda)\mathbb{E}_y[y_b].
\end{align*}
$$

Maximizing (2.3) yields the evolutionarily dominant or “growth-optimal” behavior in environment $\lambda$ (Brennan and Lo 2011):

$$
\begin{cases}
  1 & \text{if } \mathbb{E}_z[\omega_a^\lambda/\omega_b^\lambda] > 1 \text{ and } \mathbb{E}_z[\omega_b^\lambda/\omega_a^\lambda] < 1 \\
  \text{solution to (2.5)} & \text{if } \mathbb{E}_z[\omega_a^\lambda/\omega_b^\lambda] \geq 1 \text{ and } \mathbb{E}_z[\omega_b^\lambda/\omega_a^\lambda] \geq 1 \\
  0 & \text{if } \mathbb{E}_z[\omega_a^\lambda/\omega_b^\lambda] < 1 \text{ and } \mathbb{E}_z[\omega_b^\lambda/\omega_a^\lambda] > 1,
\end{cases}
$$

(2.4)
where $f_*^\lambda$ is defined implicitly in the second case of (2.4) by:

$$0 = \mathbb{E}_x \left[ \frac{\omega_a^\lambda - \omega_b^\lambda}{f\omega_a^\lambda + (1 - f)\omega_b^\lambda} \right]. \tag{2.5}$$

The three possible behaviors described in (2.4) reflect the relative reproductive success of the two choices. Choosing $a$ deterministically will be optimal if choice $a$ exhibits unambiguously higher expected relative fecundity; choosing $b$ deterministically will be optimal if the opposite is true; and randomizing between $a$ and $b$ will be optimal if neither choice has a clear-cut reproductive advantage. This last outcome is perhaps the most counter-intuitive because it is sub-optimal from an individual’s perspective (Brennan and Lo 2011).

When $\lambda = 0$ (pure idiosyncratic risk), the optimal behavior $f_*^\lambda$ can only be 0 or 1, corresponding to purely deterministic choice. In this case, the individually optimal choice—to select the action that yields the highest expected number of offspring—coincides with the evolutionarily dominant strategy (see Section 2.6 for further discussion and examples). However, when $\lambda > 0$ (a portion of reproductive risk is systematic), the evolutionarily dominant behavior $f_*^\lambda$ can be between 0 and 1, in which case individuals exhibit randomizing behavior. Although mixed strategies are well known in the evolutionary game theory literature (Maynard Smith 1982), those strategies emerge from sophisticated strategic interactions between rational optimizing players—in our framework, randomization is “mindless” behavior produced solely through natural selection. Section 2.6 provides several examples for common distributions of relative fecundity $\omega_a^\lambda/\omega_b^\lambda$.

Now imagine a large population with individuals who are exposed to different reproductive risks—some individuals are only exposed to idiosyncratic risk ($\lambda = 0$), some individuals are only exposed to systematic risk ($\lambda = 1$), and some individuals are exposed to a mix of both. The same parameters apply to their offspring. These different groups of individuals have different behaviors in terms of (2.4), as well as different growth rates.
2.3 Individual Preferences

We assume there exists an objective function $V(z, y)$ that describes an individual's preference, where $z$ represents systematic risk and $y$ represents idiosyncratic risk, in the sense that $(z_1, y_1)$ is favored over $(z_2, y_2)$ if and only if $V(z_1, y_1) > V(z_2, y_2)$. In other words, the individual maximizes $V(z, y)$ to determine its choice over random outcomes.

The objective function $V(z, y)$ can take any form. For example, $V(z, y) = \max_{z+y} \mathbb{E}[U(z+y)]$ corresponds to expected utility that does not distinguish between systematic and idiosyncratic risk. However, some functions will give individuals an evolutionary advantage over others in the population; we derive the evolutionarily dominant function in environments with varying proportions of systematic risk.

When $\lambda = 1$, the individual faces only systematic risk. The evolutionarily dominant behavior $f^*$ is given by $f^* = \arg \max_{f} \mathbb{E}_{\mathbb{P}} [\log(z/f)]$, hence the evolutionarily implied individual maximization criterion is:

$$V_{\lambda=1}(z, y) = \mathbb{E}_{\mathbb{P}} [\log(z)].$$

This is simply expected log-utility of the total number of offspring, which Bernoulli (1954) proposed in 1738 to resolve the St. Petersburg Paradox.

When $\lambda = 0$, the individual faces only idiosyncratic risk. The dominant behavior $f^*$ in this case is given by $f^* = \arg \max_{f} \log (\mathbb{E}_{\mathbb{P}} [y/f])$. Therefore, the evolutionarily implied individual maximization criterion is

$$V_{\lambda=0}(z, y) = \mathbb{E}_{\mathbb{P}} [y].$$

This is expected linear utility of the total number of offspring. In other words, the optimal criterion for an individual is simply the expected value—individuals are risk neutral in this environment.

In the general case in which $0 < \lambda < 1$, reproductive risk contains both systematic and idiosyncratic components. The implied individual maximization criterion from
the evolutionary perspective is therefore:

\[ V_\lambda(z, y) = \mathbb{E}_z \left[ \log (\lambda z + (1 - \lambda)\mathbb{E}_y[y]) \right]. \] (2.6)

This objective function does not conform to the traditional expected utility framework in which the individual’s behavior can be represented as the outcome of a constrained optimization of the expected value of a concave function of the total number of offspring, \( \lambda z + (1 - \lambda)y \). The idiosyncratic component gives rise to a linear expectation in \( y \), and the systematic component gives rise to a logarithmic function of \( z \) and the expectation in \( y \). Risk aversion emerges as a consequence of systematic risk and risk neutrality emerges as a consequence of idiosyncratic risk, regardless of the species. This is a novel implication of natural selection that has not appeared in prior studies of human or animal risk preferences. We explore this further in the next section.

### 2.4 Risk Aversion and Systematic Risk

From Equation (2.6) it is clear that the level of risk aversion is determined by natural selection as a function of the level of systematic risk in the environment. Suppose an individual is faced with a random number of offspring \( \lambda z + (1 - \lambda)y \) and \( (1 - \lambda)\mu = \mathbb{E}_y[(1 - \lambda)y] \) is the expectation of the idiosyncratic component. As a function of \( z \), (2.6) can be written as the expected utility function \( V_\lambda(z, y) = \mathbb{E}_z[U_{\lambda,\mu}(z)] \) where

\[ U_{\lambda,\mu}(z) = \log (\lambda z + (1 - \lambda)\mu). \] (2.7)

This expression defines a class of utility functions with utility measured as a function of the number of offspring arising from the systematic component. Different amounts of systematic risk in the environment correspond to different evolutionarily dominant utility functions. Figure 2-1 shows nine example utility functions with \( \lambda = 0.1, 0.5, 0.9 \) and \( \mu = 1, 2, 3 \) respectively. All nine utility functions are normalized by an affine transformation that sets \( U_{\lambda,\mu}(0) = 0 \) and \( U_{\lambda,\mu}(10) = 10 \).

We can see from Figure 2-1 that variation in the proportion (\( \lambda \)) of systematic risk
Figure 2-1: Utility functions implied by environments with different portion of systematic risk and different level of idiosyncratic risk. \( \lambda = 0.1 \) represents a low level of systematic risk; \( \lambda = 0.9 \) represents a high level of systematic risk. \( \mu = 1 \) represents a low level of idiosyncratic risk; \( \mu = 3 \) represents a high level of idiosyncratic risk. All nine utility functions are normalized by setting \( U_{\lambda,\mu}(0) = 0 \) and \( U_{\lambda,\mu}(10) = 10 \).

...drives the concavity of utility functions, while variation in the level of idiosyncratic risk (\( \mu \)) also plays a role in determining the level of risk aversion. More specifically, we consider the Arrow-Pratt measure of absolute risk aversion (ARA) of \( U_{\lambda,\mu}(\cdot) \):

\[
A_{\lambda,\mu}(z) = -\frac{U''_{\lambda,\mu}(z)}{U'_{\lambda,\mu}(z)} = \frac{1}{z + \left(\frac{1}{\lambda} - 1\right) \mu},
\]

and the Arrow-Pratt-De Finetti measure of relative risk aversion (RRA) of \( U_{\lambda,\mu}(\cdot) \):

\[
R_{\lambda,\mu}(z) = z A_{\lambda,\mu}(z) = \frac{1}{1 + \left(\frac{1}{\lambda} - 1\right) \frac{\mu}{z}}.
\]

As the number of offspring gets larger, ARA gets smaller while RRA gets larger:

\[
\begin{cases} 
A_{\lambda,\mu}(z_1) \geq A_{\lambda,\mu}(z_2) & \text{if } z_1 \leq z_2, \\
R_{\lambda,\mu}(z_1) \leq R_{\lambda,\mu}(z_2) & \text{if } z_1 \leq z_2.
\end{cases}
\]
Moreover, both measures of risk aversion are increasing functions of the proportion $\lambda$ of systematic risk:

\[
\begin{align*}
A_{\lambda_1,\mu}(z) &\leq A_{\lambda_2,\mu}(z) \quad \text{if} \quad \lambda_1 \leq \lambda_2, \\
R_{\lambda_1,\mu}(z) &\leq R_{\lambda_2,\mu}(z) \quad \text{if} \quad \lambda_1 \leq \lambda_2,
\end{align*}
\]

and decreasing functions of the level of idiosyncratic risk $\mu$:

\[
\begin{align*}
A_{\lambda,\mu_1}(z) &\geq A_{\lambda,\mu_2}(z) \quad \text{if} \quad \mu_1 \leq \mu_2, \\
R_{\lambda,\mu_1}(z) &\geq R_{\lambda,\mu_2}(z) \quad \text{if} \quad \mu_1 \leq \mu_2.
\end{align*}
\]

In other words, risk aversion arises from natural selection in environments with systematic risk. More generally, the degree of risk aversion is determined by the stochastic nature of environment: the more systematic risk is in the environment, the more risk averse are the evolutionarily dominant utility functions.

### 2.5 Testable Implications

Although our theory of the evolutionary origin of risk aversion is a highly simplified mathematical caricature of reality, its implications should be empirically verifiable if the theory has captured the most relevant features of decision making under uncertainty, as we claim. While formal tests of these implications are beyond the scope of this study, in this section we describe several methods for conducting such tests so as to illustrate the potential practical relevance of the theory.

**Biology and Behavioral Ecology.** Because the individuals in our theory are not assumed to be intelligent beings—they need not even possess central nervous systems—the theory’s implications should apply to the full cross section of the animal kingdom for which risk-sensitive foraging behavior has been observed (Harder and Real 1987, Pasteels et al. 1987, Kirman 1993, Smallwood 1996, Ben-Jacob 2008). Therefore, one direct test of our theory is to perform controlled experiments on non-human animal species in which the amount of systematic and idiosyncratic reproductive risk is var-
icd and the impact of these variations on behavior is documented and compared to the theory’s predictions (2.4).

A particularly promising species with which to conduct such experiments is bacteria, which engage in remarkably varied and sophisticated behaviors (Ben-Jacob et al. 1994, Shapiro and Dworkin 1997, Ben-Jacob et al. 2004, Ben-Jacob 2008, Ingham and Ben-Jacob 2008, Dunny et al. 2008, Be’er et al. 2009, Sirota-Madi et al. 2010, Kenett et al. 2011). Although an individual bacterium is clearly “mindless”, colonies of bacteria such as *Paenibacillus vortex* have been observed to engage in seemingly intelligent behavior such as competition, collaborative foraging, and cell-to-cell chemotactic and physical communication (Ben-Jacob 2008). Moreover, this setting most closely matches two key assumptions of our theory: asexual reproduction (bacteria reproduce via binary fission and other forms of cellular division), and no environmental resource constraints (unless purposely imposed by the experimenter).

A direct test of our theory may be constructed by focusing on a simple behavior such as chemotaxis—cell movement in response to gradients in the concentration of a specific chemical agent, usually a food source—and manipulating the environment to generate systematic or idiosyncratic risk. Given the speed with which bacteria reproduce, the growth-optimal chemotactic behavior should be observable within a short time span. Although such behavior can ultimately be traced to genetic structures (Sirota-Madi et al. 2010), our complementary approach of linking behavior directly to reproductive outcomes may yield additional insights into the common evolutionary origins of risk preferences.

**Financial Economics.** A less direct test of our theory may be performed by applying statistical inference to retrospective data on human behavior. Although the outcome is likely to be considerably noisier and more difficult to interpret because of the complexity of human cognitive abilities, the simplicity of our evolutionary framework suggests that risk aversion is an extremely primitive adaptation possessed by most animal species. Nevertheless, human evolutionary biology is at odds with several of our theory’s assumptions, including asexual semelparous reproduction and no resource constraints. Moreover, current human lifespans make controlled experiments
with humans subjects impractical. However, our theory’s growth-optimal behavior may be a reasonable approximation to human decision making over long timespans, in which case a statistical hypothesis test of the theory can be conducted using historical data involving financial risk and reward. The challenge is to identify scenarios in which human decision making is driven primarily by this adaptation and no other cognitive mechanisms such as strategic, cooperative, altruistic, or ethical behaviors, and to distinguish between systematic and idiosyncratic reproductive risk in these scenarios.

One possible context is the stock markets of developed economies, which reflect the decisions of many investors facing both systematic and idiosyncratic risk (though we are using these terms in a different sense than Sharpe (1964) who focused on systematic and idiosyncratic financial risk, but it is not hard to see how this type of risk might be related to reproductive risk over long timespans). The impact of economy-wide shocks such as natural disasters, technological hazards, and financial crises can proxy for systematic risk (World Bank 2013), and low-frequency high-impact events have been used in the financial economics literature to explain a variety of asset-pricing anomalies including high equity risk premia, low risk-free rates, and excess volatility in stock returns (Barro 2006, Barro 2009), all of which yield a high level of implied risk aversion in expected-utility rational expectations equilibrium models. On the other hand, an example of idiosyncratic reproductive risk is infant mortality due to accidental suffocation (Shapiro-Mendoza et al. 2009), preterm birth (Kramer et al. 2000, MacDorman and Mathews 2008), and congenital malformations (Rosano et al. 2000). While each of these risks may contain a systematic component, e.g., birth defects due to environmental pollutants in a given geographical region, this component should become less influential in country-level data.

An indirect hypothesis test of our theory can then be performed by comparing the estimated risk aversion of populations with varying exposures to systematic risk—those populations with greater systematic risk should be more risk averse. Measures of risk aversion can be obtained from several sources including human-subject experiments and surveys (Rabin and Thaler 2001, Holt and Laury 2002), portfolio choice
for financial investors (Guiso and Paiella 2008), labor-supply behavior (Chetty 2006), deductible choices in insurance contracts (Szpiro 1986, Cohen and Einav 2007), contestant behavior on game shows (Post et al. 2008), option prices (Aït-Sahalia and Lo 2000), and auction behavior (Lu and Perrigne 2008).

By comparing aggregate risk aversion across countries with high and low amounts of systematic reproductive risk, an indirect econometric test of the evolutionary origin of risk aversion may be constructed.

2.6 Additional Results and Examples

On top of the binary choice model, we assume further that:

Assumption 2. For all \( f \in [0, 1] \), \( \mathbb{E}[f z_a + (1 - f) z_b] = \mathbb{E}[f y_{a,i} + (1 - f) y_{b,i}] \) for all \( i \).

With Assumption 2, one can compare growth rates of population in different environments. More specifically, the optimal log-geometric-average growth rate increases as the portion of idiosyncratic risk increases:

\[
\alpha_{\lambda_1}(f^*_1) \geq \alpha_{\lambda_2}(f^*_2) \quad \text{if} \quad 0 \leq \lambda_1 \leq \lambda_2 \leq 1.
\]

To prove this, for any given \( f \), take the first derivative of \( \alpha_{\lambda}(f) \) to \( \lambda \):

\[
\frac{\partial \alpha_{\lambda}(f)}{\partial \lambda} = \mathbb{E}_z \left[ \frac{z^f - \mathbb{E}[y^f]}{\lambda z^f + (1 - \lambda)\mathbb{E}[y^f]} \right].
\]

Evaluate the first derivative at \( \lambda = 0, 1 \), and note that Assumption 2 says that \( \mathbb{E}_z[z^f] = \mathbb{E}_y[y^f] \):

\[
\left. \frac{\partial \alpha_{\lambda}(f)}{\partial \lambda} \right|_{\lambda=0} = \mathbb{E}_z \left[ \frac{z^f - \mathbb{E}_y[y^f]}{\mathbb{E}_y[y^f]} \right] = 0,
\]

\[
\left. \frac{\partial \alpha_{\lambda}(f)}{\partial \lambda} \right|_{\lambda=1} = \mathbb{E}_z \left[ \frac{z^f - \mathbb{E}_y[y^f]}{z^f} \right] = 1 - \mathbb{E}_y[y^f]\mathbb{E}_z \left[ \frac{1}{z^f} \right] \leq 0
\]

where the last step uses Jensen’s Inequality. Now take the second derivative of \( \alpha_{\lambda}(f) \)
to $\lambda$:

$$\frac{\partial^2 \alpha(\lambda)}{\partial \lambda^2} = \mathbb{E}_x \left[ \frac{- (z^f - \mathbb{E}[y^f])^2}{(\lambda z^f + (1 - \lambda)\mathbb{E}[y^f])^2} \right] \leq 0.$$  

Therefore, for any given $f$, $\alpha(\lambda)$ is a non-increasing concave function in the interval $0 \leq \lambda \leq 1$. Because $\alpha(\lambda)$ is the maximum of $\alpha(f)$ over all $f$, it follows that $\alpha_1(f_1^*) \geq \alpha_2(f_2^*)$ whenever $\lambda_1 \leq \lambda_2$, as desired.

Next, we provide several examples for common distributions of relative fecundity. Define $R = \omega_A^\lambda / \omega_B^\lambda$ to be the relative fecundity of two actions. We can characterize the growth-optimal behavior $f^*$ for common distribution of $R$. Figure 2-2 plots $f^*$ for five distributions of $R$, as a function of distribution parameters.

Figure 2-2: Optimal behavior $f^*$ for several distributions of relative fecundity $R = \omega_A^\lambda / \omega_B^\lambda$. In each subfigure, different color corresponds to deterministic ($f^* = 0$ or 1) or randomizing ($0 < f^* < 1$) behavior given particular parameters of the distribution.

Lognormal distribution. Let $R$ follow the lognormal distribution $\text{log}N(\Delta \alpha, \Delta \beta^2)$.
The expectation of $y$ and $1/y$ is:

$$E[y] = \exp\left(\Delta \alpha + \frac{\Delta \beta^2}{2}\right)$$

$$E[1/y] = \exp\left(-\Delta \alpha + \frac{\Delta \beta^2}{2}\right).$$

Therefore the optimal behavior $f^*$ is given by:

$$f^* = \begin{cases} 
1 & \text{if } \Delta \beta^2/2 < \Delta \alpha \\
\text{between } 0 \text{ and } 1 & \text{if } \Delta \beta^2/2 \geq |\Delta \alpha| \\
0 & \text{if } \Delta \beta^2/2 < -\Delta \alpha.
\end{cases}$$

*Gamma distribution.* Let $R$ follow the gamma distribution $\Gamma(\alpha, \beta)$ where $\alpha > 0, \beta > 0$. The expectation of $1/y$ exists only for $\alpha > 1$, so the parameter space is restricted to $\alpha > 1, \beta > 0$:

$$E[y] = \frac{\alpha}{\beta}$$

$$E[1/y] = \frac{\beta}{\alpha - 1}.$$ 

Therefore the optimal behavior $f^*$ is given by:

$$f^* = \begin{cases} 
1 & \text{if } \beta < \alpha - 1 \\
\text{between } 0 \text{ and } 1 & \text{if } \alpha - 1 \leq \beta \leq \alpha \\
0 & \text{if } \beta > \alpha.
\end{cases}$$

As special cases of gamma distribution, we automatically have the results for exponential, chi-squared, and Erlang distribution.

*Pareto distribution.* Let $R$ follow the Pareto distribution $\text{Parcto}(x_m, \alpha)$ where $x_m > 0, \alpha > 0$. The expectation of $y$ exists only for $\alpha > 1$, so the parameter space is
restricted to $x_m > 0, \alpha > 1$:

$$E[y] = \frac{\alpha x_m}{\alpha - 1}$$

$$E[1/y] = \frac{\alpha}{(\alpha + 1) x_m}.$$

Therefore the optimal behavior $f^*$ is given by:

$$f^* = \begin{cases} 1 & \text{if } x_m > 1 - \frac{1}{\alpha+1} \\ \text{between 0 and 1} & \text{if } 1 - \frac{1}{\alpha} \leq x_m \leq 1 - \frac{1}{\alpha+1} \\ 0 & \text{if } x_m < 1 - \frac{1}{\alpha}. \end{cases}$$

**Beta Prime distribution.** Let $R$ follow the beta prime distribution $BetaPrime(\alpha, \beta)$ where $\alpha > 0, \beta > 0$. The expectation of $y$ exists only for $\beta > 1$, and the expectation of $1/y$ exists only for $\alpha > 1$, so the parameter space is restricted to $\alpha > 1, \beta > 1$:

$$E[y] = \frac{\alpha}{\beta - 1}$$

$$E[1/y] = \frac{\beta}{\alpha - 1}.$$

Therefore the optimal behavior $f^*$ is given by:

$$f^* = \begin{cases} 1 & \text{if } \beta < \alpha - 1 \\ \text{between 0 and 1} & \text{if } \alpha - 1 \leq \beta \leq \alpha + 1 \\ 0 & \text{if } \beta > \alpha + 1. \end{cases}$$

**Weibull distribution.** Let $R$ follow the Weibull distribution $Weibull(k, \lambda)$ where $k > 0, \lambda > 0$. The expectation of $1/y$ exists only for $k > 1$, so the parameter space is
restricted to $k > 1, \lambda > 0$:

$$E[y] = \lambda \Gamma \left(1 + \frac{1}{k}\right)$$

$$E[1/y] = \frac{1}{\lambda} \Gamma \left(1 - \frac{1}{k}\right)$$

where $\Gamma(.)$ is the gamma function. Therefore the optimal behavior $f^*$ is given by:

$$f^* = \begin{cases} 1 & \text{if } \lambda > \Gamma \left(1 - \frac{1}{k}\right) \\ \text{between } 0 \text{ and } 1 & \text{if } \frac{1}{\Gamma(1+\frac{1}{k})} \leq \lambda \leq \Gamma \left(1 - \frac{1}{k}\right) \\ 0 & \text{if } \lambda < \frac{1}{\Gamma(1+\frac{1}{k})}. \end{cases}$$

### 2.7 Discussion

Risk aversion is one of the most widely observed behaviors in the animal kingdom, hence it stands to reason that it must confer certain evolutionary advantages. This intuition is confirmed in our simple but general binary-choice model of behavior in which risk aversion emerges from mindless behavior as the evolutionarily dominant behavior in stochastic environments with correlated reproductive risk across the population. Our evolutionary framework shows how the stochastic properties of the environment shapes preferences, yielding specific utility functions that depend on the nature of reproductive risk. Logarithmic utility and linear utility arise as special cases for the two extremes of pure systematic and idiosyncratic risk, respectively. However, for environments containing a mixture of both types of risk, there is a continuum of evolutionarily dominant behaviors that does not conform to expected utility theory. The simplicity of our framework suggests that our results are likely to apply across species and that the degree of risk aversion in animal behavior is significantly influenced by the stochastic properties of the environment as it affects fecundity.

These results are closely related to, but distinct from, those in the extant literature on evolution and economic behavior (Robson 1996a, Dekel and Scotchmer 1999, Samuelson 2001, Robson and Samuelson 2009, Robatto and Szentes 2013). In
particular, Robson (1996a)'s seminal paper on the evolutionary origins of utility functions specifies an increasing concave relation between the number of offspring and the amount of resources available to a given individual, from which the relation between expected/non-expected utility and systematic/idiosyncratic risk follows naturally. In particular, Robson shows that “properties of risk aversion or risk preference for gambles over commodities derive from a biological production function relating expected offspring to commodities” (Robson 1996a, p.405), where this “biological production function” is exogenously specified to be increasing and concave (the “concavity hypothesis”).

Our model highlights a different and simpler origin of risk aversion—the stochastic nature of the environment—without reference to any biological production function. By developing a formal theory of the evolution of preferences in stochastic environments in the context of the simplest possible nontrivial choice problem, a binary choice, we show that the origin of risk aversion is considerably more primitive than previously thought. Moreover, we derive a class of utility functions that emerges from natural selection as the proportion of systematic risk $\lambda$ in the environment is varied (equation (2.7)-(2.9)), which may explain the large amount of heterogeneity in risk preferences observed in empirical studies (Holt and Laury 2002, Guiso and Paiella 2008, Chetty 2006, Szpir 1986, Cohen and Einav 2007).

Other studies have also made use of the concavity hypothesis to generate risk aversion (Robson 1996b, Dekel and Scotchmer 1999), and this specification can also be incorporated into our binary-choice framework to yield similar results (Brennan and Lo 2011). There is no doubt that the concavity hypothesis provides one explanation for risk aversion, simply because decreasing marginal returns is a common pattern found in Nature. However, the economics literature is also replete with examples of non-decreasing marginal returns both in consumption and production. For example, early research on non-convex preferences (which implies non-concave utility functions) (Farrell 1959, Bator 1961, Koopmans 1961, Rothenberg 1960) have motivated a large and diverse literature on general equilibrium with non-convexities (e.g., the Shapley Folkman Lemma (Starr 1969) that guarantees existence of “approximate” general
equilibria with many consumers). From the producer perspective, non-decreasing marginal returns have been considered since Sraffa (1926), giving rise to an extensive literature on monopolies, oligopolies, externalities, and regulatory policy designed to correct such market failures. In fact, the concavity hypothesis is necessarily restrictive in “hardwiring” a particular degree of risk aversion, i.e., curvature, once a particular concave function is specified. No single function can explain the large degree of heterogeneity observed in human risk preferences, or the state-dependent nature of risk aversion, unless these features are also exogenously specified in multiple time-varying state-dependent biological production functions.

We have purposely avoided the use of any such function because we wish to highlight the more fundamental role that stochastic environments play in generating risk aversion. Our simple binary-choice framework shows that a concave biological production function is unnecessary for generating risk aversion which, in our setting, is simply a consequence of natural selection operating in stochastic environments with systematic risk, irrespective of any additional functional transformations. Moreover, a by-product of our simpler framework is a natural explanation for the large heterogeneity in risk preferences observed in empirical studies: natural variation in the proportion of systematic risk across a geographically diverse population. Because our binary choice model is so simple and its results follow from a minimal set of assumptions, its implications are likely to apply much more generally across species, time, and contexts.

The evolutionary origins of strategic behavior have also been considered (Robson 1996b, Dekel and Scotchmer 1999), and natural selection can also produce overconfidence (Johnson and Fowler 2011) and altruism (Becker 1976), both of which emerge as a result of more complex environmental conditions. In contrast, our framework does not require any strategic interactions and individual decision making is deliberately mindless, allowing us to determine the most fundamental links between stochastic environments and adaptive behavior.

Extensions of the binary choice framework include regime-switching environmental conditions (Chapter 3), mutation through sexual reproduction (Chapter 3), resource-
constrained environments (which generates strategic interactions), and the emergence of intelligent behavior and bounded rationality (Brennan and Lo 2012). A recent study (Robatto and Szentes 2013) considers an evolutionary framework in continuous time and distinguishes between systematic variations that are instantaneous drops in population size and future shifts in death and birth rates. The former corresponds to the systematic environmental risk in our model while the latter is closely related to extensions to regime-switching environments (Chapter 3).

Our results have several broader implications for financial economics and public policy. The role of systematic risk in shaping individual and aggregate behavior provides a more fundamental channel through which Sharpe (1964)'s relation between systematic financial risk and expected asset returns can arise (as long as systematic reproductive risk is positively correlated with systematic financial risk, which is implied by Robson (1996a)'s concave reproduction function). However, unlike the fixed preferences assumed in Sharpe's Capital Asset Pricing Model, our framework implies that preferences vary over time and across environmental conditions, hence large systematic financial shocks can lead to more risk aversion over time, and vice versa.

From a policy perspective, our results underscore the importance of addressing systematic risk through insurance markets, capital markets, and government policy to allow individuals to transfer or mitigate such risks. If not properly managed, systematic risk can lead to increases in risk aversion, implying higher risk premia, borrowing costs, and lower economic growth. However, our results also highlight the potential dangers of sustained government intervention, which can become a source of systematic risk in its own right (Acharya et al. 2011, Lucas 2011).
Chapter 3

Variety Is the Spice of Life: Irrational Behavior as Adaptation to Stochastic Environments

3.1 Introduction

Rationality is the key assumption behind standard economic models of human behavior. The idea that individuals maximize their own self-interest subject to resource constraints has led to numerous breakthroughs, including expected utility theory (von Neumann and Morgenstern 1944), game theory (von Neumann and Morgenstern 1944, Nash 1950), rational expectations (Lucas Jr 1972), the efficient markets hypothesis (Samuelson 1965, Fama 1970), and the option pricing theory (Black and Scholes 1973, Merton 1973). The influence of this paradigm goes far beyond academia — it underlies current macroeconomic and monetary policies, and has also become an integral part of the rules and regulations that govern financial markets today (Kocherlakota 2010, Hu 2012).

On the other hand, psychologists and economists have documented many violations of rational models in human behavior, often referred to as “cognitive biases”. These systematic deviations from rational behaviors are hard to reconcile
with the standard economic models, and are therefore considered irrational behaviors. Representatives of these cognitive biases include probability matching (Grant et al. 1951, Herrnstein 1961) (the tendency to choose randomly between heads and tails when asked to guess the outcomes of a series of independent biased-coin tosses, where the randomization matches the probability of the biased coin), loss aversion (Tversky and Kahneman 1974, Tom et al. 2007) (the tendency to take greater risk when choosing between two potential losses, and less risk when choosing between two potential gains), uncertainty effect (Gneezy et al. 2006) (a risky prospect is valued less than its worst possible outcome), and confirmation bias (Mahoney 1977) (the tendency to search for or interpret information in a way that confirms one's preconceptions). Such anomalous behaviors have also been observed in many non-human subjects ranging from bacteria to primates (Harder and Real 1987, Pasteels et al. 1987, Kirman 1993, Smallwood 1996, Chen et al. 2006, Ben-Jacob 2008, Santos and Chen 2009), which suggests that they may have a common and ancient origin, and an evolutionary role that belies their apparent shortcomings.

The debate between rational models of behavior and their systematic deviations has attracted an enormous amount of research in economics, psychology, and evolutionary biology (Becker 1962, Stanovich and West 2000, Rabin and Thaler 2001, McKenzie 2003, Burnham 2013, Gneezy and List 2013). For instance, bounded rationality (Simon 1955) and prospect theory (Kahneman and Tversky 1979, Tversky and Kahneman 1992) provide alternative perspectives for understanding human behavior beyond the maximization of expected utility. At the same time, numerous empirical studies are devoted to understanding the relationship between individual rationality and decision-making in the real world (Hsu et al. 2005, Camerer and Fehr 2006, Gneezy and List 2006, Apicella et al. 2008, Dreber et al. 2009, Chen and Chen 2011, Bednar et al. 2012, Fershtman et al. 2012, Gneezy and Imas 2014).

Evolutionary principles have been adopted by economists and psychologists to explain these counterintuitive behaviors (Cooper and Kaplan 1982, McDermott et al. 2008, Kenrick et al. 2009, Brennan and Lo 2011), as well as altruism and sociobiology (Alexander 1974, Becker 1976, Hirshleifer 1977, Almenberg and Dreber 2013),
the biological origin of utility functions and time preference (Campbell 1986, Rogers 1994, Waldman 1994, Robson 1996a, Samuelson 2001), and the dynamics of financial markets (Blume and Easley 1992, Luo 1995, Lo 2004, Kogan et al. 2006a, Hirshleifer and Teoh 2009). In particular, irrational behavior—as opposed to utility-maximizing behavior—has been found useful and persistent in a variety of environments in evolution (Belavkin 2006, Houston et al. 2007, Waksberg et al. 2009, Ross and Wilke 2011, Okasha and Binmore 2012). However, it is unclear how these behaviors relate to standard economic theories of individual rationality, and why they emerge in some instances and not others.


In this chapter, we reconcile the rationality debate by proposing an evolutionary explanation for irrational behavior. The rational behavior is a function of the particular environment, and different environments lead to different rational behaviors in evolution. As a result, irrational behaviors not only persist in evolution, but are also necessary for robust growth of population in stochastic environments. Furthermore, we show that there is an optimal degree of irrationality in the entire population depending on the degree of environmental stochasticity. This is a novel implication of natural selection that has not appeared in prior studies of human or animal rationality.

Much of the rationality debate among economists and psychologists focuses on whether the rational models can help people make better inferences and decisions in the real world (McKenzie 2003). Instead, our framework provides an evolutionary explanation of seemingly irrational behaviors and different degrees of irra-
tionality in the population. The results have widespread implications for science, management, and public policy. For example, our framework has a different explanation for the entry of new firms and technologies in an industry, a well-studied phenomenon in industrial economics (Klepper and Graddy 1990, Audretsch and Mahmood 1994, Geroski 1995, Mata et al. 1995, Campbell 1998). Even if new entrants appear to be suboptimal with respect to their current context, they facilitate more robust growth of the entire industry in the face of a stochastically shifting environment. Furthermore, our results yield the optimal amount of entrants as a function of environmental stability.

Our model consists of an initial population of individuals, each assigned a purely arbitrary behavior with respect to a binary choice problem. Assuming that offspring have behaviors identical to their parents, only those behaviors linked to reproductive success will survive. The key is the interaction between individual behavior and the stochastic environment in which reproductive success is determined. On the other hand, by assuming that a small fraction of offspring have behaviors different from their parents, irrational behavior emerges as a result of mutation. Mutation provides diversity of behaviors in the entire population, and therefore, the important link between rational and irrational behaviors. Over time, only a certain degree of mutation and irrationality in the population will persist in the limit.

By studying the impact of selection on behavior rather than on genes, we are able to derive evolutionary implications that cut across species, physiology, and genetic origins. In the same way that different magnifications of a microscope reveal different details of a specimen, applying evolutionary principles to behavioral variations leads to different insights that may be more relevant for economics, psychology, and behavioral ecology. Our focus on behavior as the object of selection is a different lens through which the effects of evolution may be studied.

In the remainder of this chapter, we describe the binary choice model with mutation in Section 3.2. Section 3.3 shows that mutation and irrational behaviors are essential in evolution. Furthermore, the degree of irrationality is determined by evolution to match the degree of environmental stochasticity. We provide additional
results and technical details in Section 3.4 and conclude with a brief discussion in Section 3.5.

3.2 Binary Choice Model with Mutation

We begin with the binary choice model (Brennan and Lo 2011). Consider a population of individuals that live for one period, produce a random number of offspring asexually, and then die. During their lives, individuals make only one decision: they choose from two actions $a$ and $b$, and this results in one of two corresponding random numbers of offspring $x_a$ and $x_b$, described by some well-behaved probability distribution function $\Phi(x_a, x_b)$. We assume that $x_a$ and $x_b$ are not perfectly correlated, and

**Assumption 3.** $x_a$ and $x_b$ are bounded non-negative random variables, and $\mathbb{P}(x_a = x_b = 0) = 0$.

**Assumption 4.** $(x_a, x_b)$ is IID over time and identical for all individuals in a given generation.

Note that Assumption 3 simply rules out the degenerate case that no offspring is produced at all. Now suppose that each individual chooses $a$ with some probability $f \in [0, 1]$ and $b$ with probability $1 - f$, denoted by the Bernoulli variable $I^f$, hence the offspring of an individual is given by:

$$x^f = I^f x_a + (1 - I^f) x_b, \quad I^f = \begin{cases} 1 & \text{with prob } f \\ 0 & \text{with prob } 1 - f. \end{cases}$$

We shall henceforth refer to $f$ as the individual's behavior since it completely determines how the individual chooses between $a$ and $b$. Assume for the moment that there is no mutation, so that offspring from a type $f$ individual are still of type $f$. The following proposition (Brennan and Lo 2011) summarizes the population dynamics of the binary choice model without mutation.
Proposition 1. Under Assumptions 3-4, suppose that the total number of type $f$ individuals in generation $T$ is $n_T^f$. As both the number of generations and the number of individuals in each generation increases without bound, $T^{-1} \log n_T^f$ converges almost surely to the log-geometric-average growth rate

$$\mu(f) = \mathbb{E} [\log (f x_a + (1 - f) x_b)]. \quad (3.1)$$

Furthermore, the growth-optimal behavior $f^*$ is given by:

$$f^* = \begin{cases} 
1 & \text{if } \mathbb{E} [x_a/x_b] > 1 \text{ and } \mathbb{E} [x_b/x_a] < 1 \\
\text{solution to (3.3)} & \text{if } \mathbb{E} [x_a/x_b] \geq 1 \text{ and } \mathbb{E} [x_b/x_a] \geq 1 \\
0 & \text{if } \mathbb{E} [x_a/x_b] < 1 \text{ and } \mathbb{E} [x_b/x_a] > 1
\end{cases} \quad (3.2)$$

where $f^*$ is defined implicitly in the second case of (3.2) by

$$\mathbb{E} \left[ \frac{x_a}{f^* x_a + (1 - f^*) x_b} \right] = \mathbb{E} \left[ \frac{x_b}{f^* x_a + (1 - f^*) x_b} \right], \quad (3.3)$$

and the expectations in (3.1)-(3.3) are with respect to $\Phi(x_a, x_b)$.

The growth-optimal behavior $f^*$ is a function of the particular environment $\Phi(x_a, x_b)$. The role of $\Phi$ is critical in our framework, as it represents the entirety of the implications of an individual’s actions for reproductive success. Embedded in $\Phi$ is the biological machinery that is fundamental to evolution, i.e., genetics. However, this machinery is of less interest to economists than the link between behavior and reproductive success, which is summarized compactly by $\Phi$. The specification of $\Phi$ also captures the fundamental distinction between traditional models of population genetics (Levins 1968, Wilson and Bossert 1971, Dawkins 1976) and more recent applications of evolution to behavior (Hamilton 1964, Trivers 1971, Wilson 1975a, Maynard Smith 1982); the former focuses on the natural selection of traits (determined by genetics), whereas the latter focuses on the natural selection of behavior. Although behavior is obviously linked to genetics, the specific genes involved, their loci, and
the mechanisms by which they are transmitted from one generation to the next are of less relevance to economic analysis than the ultimate implications of behavior for reproduction, i.e., $\Phi$. In the jargon of econometrics, $\Phi$ may be viewed as a "reduced form" representation of an individual’s biology.

This simple and general model generates a remarkably rich set of behaviors. For example, the three possible behaviors in (3.2) reflect the relative reproductive success of the two choices and is a generalization of the “adaptive coin-flipping” strategies of Cooper and Kaplan (1982). The behavior $f^*$ that emerges through the forces of natural selection is quite distinct from the neoclassical economic framework of expected utility in one important respect: expected utility theory implies deterministic behavior. Furthermore, intelligence has a natural definition in our framework—any type of behavior that is positively correlated with reproductive success—and bounds on the level of intelligence arise organically from physiological and environmental constraints on this correlation (Brennan and Lo 2012). By considering different sources of randomness in reproductive success, risk aversion can be derived in this framework as a consequence of systematic reproductive risks (Zhang et al. 2014b). Proposition 1 may also be interpreted as a primitive form of group selection, in which natural selection appears to operate at the group level instead of, or in addition to, the level of individuals, traits, or genes (Zhang et al. 2014a).

3.2.1 Mutation: a link between optimal and sub-optimal behavior

Now we add mutation to the binary choice model to provide a link between optimal and sub-optimal behaviors in evolution. In general, mutation implies that the offspring of type-$f$ individuals are not necessarily of type-$f$, but assume a probability distribution over all possible types. We consider a simple form of mutation, namely that an offspring of type-$f$ mutates equally likely to all types.

To be more specific, consider a discrete type space. Let $f$ takes value in a finite set \{\(f_1, f_2, \cdots, f_{K+1}\)\} (for example, \(\{0, \frac{1}{K}, \frac{2}{K}, \cdots, \frac{K-1}{K}, 1\}\)) where $K$ is a positive integer.
The world has \( K + 1 \) types in total. In addition to Assumptions 3-4, we further assume that:

**Assumption 5.** Each type \( f \) individual mutates with a small probability \( \epsilon > 0 \) to type \( g \neq f \). Once it mutates, it mutates with equal probability \( \frac{\epsilon}{K} \) to any type \( g \in \{f_1, f_2, \ldots, f_{K+1}\} \setminus \{f\} \).

Note that Assumption 5 is a simple and special form of mutation. From the behavioral point of view, it is general enough to capture the most important characteristics of mutation, which is to provide the link between different behaviors. With this particular structure, we are able to parametrize the degree of mutation with a single parameter \( \epsilon \).

We would like to emphasize that each individual lives for only one period in our model, and therefore its mutant offspring may be viewed as “new entrants” in the next generation’s population because they represent different behaviors than their predecessors. Also, there is no intelligence or volition ascribed to the behavior \( f \); we are simply providing a formal representation for it, and then investigating its evolutionary implications. To that end, individuals choosing between \( a \) and \( b \) according to the same \( f \) may be viewed as consisting of the same “type”, where types are indexed by \( f \) and range continuously from 0 to 1, including the endpoints. In this manner, we are able to study the evolutionary dynamics of each type of individual over many generations.

Once mutation is introduced into the population, it is no longer possible to analyze the population dynamics of each type \( f \) separately. The entire system is a multi-type branching process in random environments (Smith and Wilkinson 1969, Tanny 1981). Let \( n_t = (n_{t}^{f_1}, \ldots, n_{t}^{f_{K+1}})' \) be the column vector of number of individuals of all \( K + 1 \) types in generation \( t \). The following proposition describes the population dynamics between two generations.

**Proposition 2.** Under Assumptions 3-5, as \( n_{t-1}^q \) increases without bound for all
where \( A_t := M \cdot F_t \). Here \( M \) is a constant mutation matrix:

\[
M = \begin{pmatrix}
1 - \epsilon & \frac{\epsilon}{K} & \cdots & \frac{\epsilon}{K} \\
\frac{\epsilon}{K} & 1 - \epsilon & \cdots & \frac{\epsilon}{K} \\
\vdots & \vdots & \ddots & \vdots \\
\frac{\epsilon}{K} & \frac{\epsilon}{K} & \cdots & 1 - \epsilon
\end{pmatrix},
\]

and \( F_t \) is a stochastic fecundity matrix:

\[
F_t = \begin{pmatrix}
f_1 x_{a,t} + (1 - f_1) x_{b,t} & \cdots & 0 \\
\vdots & \ddots & \vdots \\
0 & \cdots & f_{K+1} x_{a,t} + (1 - f_{K+1}) x_{b,t}
\end{pmatrix},
\]

with \( 0 = f_1 < f_2 < \cdots < f_{K+1} = 1 \).

Equation (3.4) gives the fundamental relationship between individuals in two consecutive generations. With probability \( 1 \), \( n_t \) can be written as the product of two matrices and \( n_{t-1} \). \( F_t \) represents the reproducibility of different types of individuals, and \( M \) represents a re-distribution of types because of mutation. Then the natural question is: how does \( n_t \) behave in the limit? We summarize the asymptotic behavior of population with mutation in the following proposition.

**Proposition 3** (Growth rate). Under Assumptions 3-5, there exists a number \( \mu_\epsilon \) such that:

\[
\mu_\epsilon = \lim_{T \to \infty} \frac{1}{T} \log c' n_T = \lim_{T \to \infty} \frac{1}{T} \log \| A_t A_{t-1} \cdots A_1 \|
\]

almost surely, where \( \| \cdot \| \) is any matrix norm, \( c \) is any vector of bounded non-negative numbers (\( c \neq 0 \)).

In particular, when \( c \) is a vector of 1's, we get the growth rate of total population; when \( c = e_i \) (the vector with \( i \)-th coordinate equals to 1 and 0 otherwise), we get
the growth rate of the \( i \)-th type individuals. A direct corollary is that all types of behaviors grow at the same exponential rate \( \mu_c \). This is an important difference of population with mutation compared to non-mutation populations. To understand this fact, suppose a long time has elapsed, because the positive mutation rate is fixed, any behavior that is not favored by the current environment still gets a fixed proportion of the offspring from the behavior that grows the fastest. Therefore the ratio of the individuals of any two behaviors can be lower bounded by some positive constant, and no single behavior can grow exponentially faster than any other behaviors. Note that \( \mu_c \) is called the maximum Liapunov characteristic exponent of matrix \( A_t \) in the probability literature, and Corollary 1 in the next section gives an estimate of \( \mu_c \).

Another difference between the mutation and non-mutation population is the asymptotic ratio between different types of population. Without mutation, \( \mu(f) \) is different for different \( f \), and therefore the ratio \( n_T^f / n_T^{f*} \) converges to 0 for any \( f \neq f^* \) (see Proposition 1). However, \( \mu_c \) is the same with mutation for all types \( f \), and the ratio \( n_T^f / n_T^{f*} \) is typically stochastic even in the long run as \( T \) increases without bound. Fortunately, we have ergodic theorems to characterize the asymptotic behavior of this ratio.

### 3.2.2 Asymptotic population dynamics

Under Assumptions 3-5, let \( P_t = 1' n_t \) be the total population size at time \( t \) and

\[
y_t := \frac{n_t}{P_t} = \left( \frac{n_T^1}{\sum_g n_T^g}, \ldots, \frac{n_T^{K+1}}{\sum_g n_T^g} \right)'
\]

be the normalized population vector in generation \( t \). Because of the dynamics between two consecutive generations (3.4), \( \{y_t\}_{t=0}^{\infty} \) is a vector-valued Markov process, with a compact state space:

\[
\mathcal{Y} := \left\{ y = (y_1, \cdots, y_{K+1}) \mid y \geq 0, \sum_{i=1}^{K+1} y_i = 1 \right\}.
\]

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The 1-step transition probability for $y \in \mathcal{Y}$ and $B \subseteq \mathcal{Y}$ is:

$$p_1(y, B) := \mathbb{P}_{\Phi} \left( \frac{Ay}{\|Ay\|} \in B \right).$$  \hfill (3.6)

Without mutation, because different behaviors grow at different exponential rates, $y_t$ converges almost surely to a basis vector $e_i = (0, \ldots, 1, \ldots, 0)$ as $T \to \infty$. In the case of positive mutation rates, similar result exists only for non-random matrices $F_t$ in (3.4), in which case the long run proportion vector converges to the eigenvector of $F_t$ (see models in Robson (1996a) and Gaal et al. (2010) for example). In the case of positive mutation rates when $F_t$ are random matrices, environmental uncertainty implies that $y_t$ is typically stochastic even in the long run (see simulation results in Section 3.4). However, we have the following ergodic theorem (Tuljapurkar 1990) to characterize the asymptotic behavior of $y_t$:

**Proposition 4** (Stochastic ergodic theorem). Under Assumptions 3-5, let $\mathcal{L}_t(\cdot)$ be the distribution of $y_t$, then $\mathcal{L}_t(\cdot)$ converges to a stationary distribution $\mathcal{L}(\cdot)$ pointwisely as $T$ increases without bound:

$$\lim_{T \to \infty} \mathcal{L}_T = \mathcal{L}.$$

Proposition 4 asserts that the proportion vector $y_t$ converges weakly as $T \to \infty$. In addition, by basic properties of Markov chains, the stationary distribution $\mathcal{L}$ satisfies the following equation:

$$\mathcal{L}(B) = \int_{\mathcal{Y}} p_1(y, B) \mathcal{L}(dy)$$

for any $B \subseteq \mathcal{Y}$. An important application of Proposition 4 is that it provides a formula to estimate the exponential growth rate $\mu_e$. Note that the total population size

$$P_t = 1' n_t = 1' M F_t n_{t-1} = 1' F_t n_{t-1} = P_{t-1} 1' F_t y_{t-1},$$

so the log-geometric-average growth rate $\mu_e$ can be expressed as:

$$\mu_e = \mathbb{E} \left[ \log(1' F_t y_{t-1}) \right] \hfill (3.7)$$

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where the expectation is taken over the joint stationary distribution of \((F_t, y_{t-1})\).

**Corollary 1** (Bounds of growth rate). Let \(f^*\) be the optimal behavior without mutation (see Proposition 1). Under Assumptions 3-5, if the type space is dense enough such that \(f^* \in \{f_1, f_2, \ldots, f_{K+1}\}\), then:

\[
\mu(f^*) - |\log(1 - \epsilon)| \leq \mu_e \leq \mu(f^*). \tag{3.8}
\]

Corollary 1 asserts that the growth rate \(\mu_e\) is slightly less than the optimal growth rate of population without mutation. Note that this is different from the mutation modeled in Robson (1996a), where population growth could be increased by randomizing between different types of individuals to create a new “behavior”. We will identify the case where mutation does speed up growth in non-stationary environments in Section 3.3.

Section 3.4 gives additional results for population dynamics with mutation. In particular, Proposition 7 gives the asymptotic distribution of total population size \(P_t\). Proposition 8 provides the rate of convergence for the limit distribution \(\mathcal{L}(\cdot)\) in Proposition 4. Proposition 9 (Robson 1996a) gives the optimal behavior with mutation in the probabilistic sense.

### 3.2.3 Extinction probability

When the population is extinct in evolution, the stochastic processes \(n_t\) and \(y_t\) become degenerate. Therefore, all results so far are implicitly conditional on non-extinction sample paths. However, extinction is important in evolution, and particularly of interest with mutation. In this section, we investigate the extinction probability of different behaviors \(f\) in different environments \(\Phi(x_a, x_b)\).

Consider a specific behavior \(f \in \{f_1, f_2, \ldots, f_{K+1}\}\) starting with an initial population \(n_0^f > 0\), we define that the type \(f\) is **extinct** if \(n_T^f = 0\) for some \(T > 0\), and **surviving** otherwise. There are two scenarios in terms of extinction when the number of generation \(T\) increases without bound:
(i) \( \lim_{T \to \infty} P \left( n_T^f > 0 \right) = 0 \): the population is extinct with probability 1;

(ii) \( \lim_{T \to \infty} P \left( n_T^f > 0 \right) > 0 \): the population survives with positive probability.

Note that in case (ii), if \( \lim_{T \to \infty} P \left( n_T^f > 0 \right) < 1 \), then the extinction probability depends on the initial population \( n_0 \). However, when \( n_0 \) is relatively large, the survival probability is close to 1. To be more specific, we define that the type \( f \) is immortal if the extinction probability is strictly less than 1 as \( T \to \infty \), and the extinction probability goes to 0 as the initial number of individuals \( n_0 \) increases without bound. Mathematically, A type \( f \) is immortal if \( P(n_T^f = 0) < 1 \) as \( T \to \infty \), and \( P(n_T^f = 0) \to 0 \) as \( T \to \infty \) and \( n_0 \to \infty \).

For an immortal population, case (ii) can be essentially treated as almost sure survival with a large initial population. Proposition 1-4 are implicitly conditional on non-extinction sample paths. The probability of non-extinction in these results is close to 1 for a large initial population, because immortality is a common feature for non-degenerate populations, as we will see in:

**Proposition 5** (Immortality with mutation). *Suppose that the number of initial population of any behavior \( f \in \{f_1, f_2, \ldots, f_{K+1}\} \) is \( n_0 \),

(i) Consider the model without mutation. Under Assumptions 3-4, any behavior \( f \) with \( \mu(f) < 0 \) is extinct with probability 1, and any behavior \( f \) with \( \mu(f) > 0 \) is immortal.

(ii) Consider the model with mutation rate \( \epsilon > 0 \). Under Assumptions 3-5, all behaviors \( f \in \{f_1, f_2, \ldots, f_{K+1}\} \) are immortal if \( \mu_\epsilon \) in Proposition 3 is positive. In particular, if there exists a behavior \( f \in \{f_1, f_2, \ldots, f_{K+1}\} \) such that \( \mu(f) > |\log(1 - \epsilon)| \) without mutation, then all behaviors are immortal.

Proposition 5 asserts that positive mutation rates make all behaviors in the population immortal, and help preserve all behaviors even if some of them are inferior in the current environment. In other words, mutation provides robustness to evolution by avoiding extinction.
So far we have considered stationary environments generating IID fecundities across time. In this case, mutation does not help increase the speed of population growth (Corollary 1). This brings us to the next topic, where non-stationary environments are considered and mutation can indeed speed up growth.

### 3.3 Results: Optimal Degree of Irrationality

The binary choice model with mutation provides a framework of evolution of behaviors. Given a particular environment $\Phi(x_a, x_b)$, we define rational behavior as the evolutionarily optimal behavior $f^*$ that achieves the maximum log-geometric-average growth rate. We would like to emphasize that the rational behavior depends on the particular environment, and therefore rational behaviors might change over time because the environment $\Phi(x_a, x_b)$ could change. In contrast to the rational behavior $f^*$, all the other sub-optimal behaviors with slower growth rates are irrational.

Mutation provides the link between rational and irrational behaviors. Positive mutation rates and irrational behaviors are necessary because environmental shocks could happen unexpectedly. In this sense, a population with irrational behaviors is favored in order to maintain robust growth under possible environmental shocks. We further elaborate this idea by considering a simple example with one-time environmental change.

Following the binary choice model with mutation, suppose that the fecundity is specified by the joint distribution $\Phi^1(x_a, x_b)$ before generation $T^1$, and after generation $T^1$ the environment suddenly changes and the distribution becomes $\Phi^2(x_a, x_b)$. To be more precise, let $\Phi_t(x_a, x_b)$ be the joint distribution of $(x_a, x_b)$ in generation $t$, and

$$\Phi_t(x_a, x_b) = \begin{cases} 
\Phi^1(x_a, x_b) & \text{if } t = 1, 2, \ldots, T^1 \\
\Phi^2(x_a, x_b) & \text{if } t = T^1 + 1, T^1 + 2, \ldots.
\end{cases}$$

Denote by $\mu^1(\cdot)$ and $\mu^2(\cdot)$ the log-geometric-average growth rate without mutation for $\Phi^1$ and $\Phi^2$ respectively. Furthermore, denote by $f^*_1$ and $f^*_2$ the optimal behavior under
Φ₁ and Φ² respectively. Suppose that the optimal behavior in a given environment is extinct almost surely in the other. More specifically,

\[ \mu^1(f^*_1) > |\log(1 - \epsilon)|, \quad \mu^1(f^*_2) < 0; \quad \mu^2(f^*_2) > |\log(1 - \epsilon)|, \quad \mu^2(f^*_1) < 0 \]

for some fixed mutation rate \( \epsilon > 0 \).

Without mutation, \( f^*_2 \) is extinct with probability 1 as the number of generations before the shock \( T^1 \) increases without bound. After the shock, the long-term optimal behavior and optimal growth rate are therefore given by \( \max_{\{f \mid \mu^1(f) > 0\}} \mu^2(f) \).

On the other hand, with mutation rate \( \epsilon > 0 \), as a direct corollary of Proposition 5 and Corollary 1, all behaviors are immortal under both Φ₁ and Φ². The long-term optimal behavior is \( f^*_2 \), and optimal growth rate is at least \( \mu^2(f^*_2) - |\log(1 - \epsilon)| \), which is greater than the optimal growth rate without mutation as long as the mutation rate \( \epsilon \) is sufficiently small.

In this simple example, irrational behaviors and positive mutation rates are seemingly inefficient because they slow down the growth rate of the individually rational behavior. However, as long as the environment \( \Phi(x_a, x_b) \) and rational behavior \( f^* \) change, it is the irrational behaviors that provide a variety of diversified possibilities in the population, so that new rational behaviors can emerge and thrive. In other words, certain behaviors that are growth-optimal under Φ² might become extinct under Φ₁ in the absence of mutation. Mutation ensures a constant flow of new entrants into the population each generation; hence when the regime shifts to Φ², these new entrants reproduce more quickly than others, and \( f^*_2 \) emerges as the new dominant behavior. As a result, the very notion of "optimality" is ill-defined in isolation, and must be interpreted with respect to a given environment. This is consistent with Simon (1955)'s notion of bounded rationality. Note that the individuals are mindless and need not know whether they are behaving optimally or not—natural selection is sufficient for determining what is optimal for a given environment.
3.3.1 Regime-switching environments

As a generalization of the example of one-time environmental change, a more realistic world has multiple environmental changes and possibly cycles. In this case, not only the irrational behaviors are necessary in terms of providing robustness, but also the degree of irrationality in the population is determined by how often the environment changes. In other words, the degree of mutation is selected by the nature, and there is an optimal degree of irrationality in the entire population. We formalize this idea by considering the following regime-switching environments.

Suppose that the nature switches randomly between two regimes, in which the fecundities are specified by \( \Phi^1(x_a, x_b) \) and \( \Phi^2(x_a, x_b) \) respectively. The lengths of regime 1 and regime 2 are positive integer random variables \( T^1 \) and \( T^2 \) specified by some well-behaved probability distribution function \( F(T^1, T^2) \). The nature draws IID samples from \( F(T^1, T^2) \) to generate lengths of consecutive regimes \( T^1_1, T^2_1, T^1_2, T^2_2, \ldots \). Note that the superscript denotes the regime number and the subscript indicates the number of cycle, where a cycle is defined as the two consecutive changes of regime:

\[
0 \xrightarrow{\Phi^1} T^1_1 \xrightarrow{\Phi^2} T^2_1 \xrightarrow{\Phi^1} T^1_2 \xrightarrow{\Phi^2} T^2_2 \ldots
\]

We would like to emphasize that the environment within each regime is still stochastic, this is an important distinction to the existing literature where the environment is usually assumed to be approximately constant between changes or within a period (Ishii et al. 1989, Acar et al. 2008, Kussell and Leibler 2005, Gaal et al. 2010). For general \( \Phi^1(x_a, x_b) \) and \( \Phi^2(x_a, x_b) \), the exact population dynamics is hardly computable after a few regime switches. However, a simple example suffices to illustrate the optimal degree of irrationality in the population.

3.3.2 An example of two behaviors

For simplicity, we consider a world with only two behaviors \( f \in \{0, 1\} \). Suppose that the fecundities in the two regimes are given by \( \Phi^1(x_a, x_b) \) and \( \Phi^2(x_a, x_b) \) that satisfy
the following condition:

\[ P_{\Phi^1}(x_b = 0) = P_{\Phi^2}(x_a = 0) = 1. \]

That is, one choice in each regime results in no offspring for sure. Note that in regime 1, \( x_a \) is still a random variable; in regime 2, \( x_b \) is still a random variable. In this world, during regime 1, only action \( a \) generates positive offspring; during regime 2, only action \( b \) generates positive offspring. Therefore, both behaviors die out without mutation after a few regime switches.

A positive mutation rate \( \epsilon \) helps preserve the irrational behaviors in the current environment to prepare for possible environmental shocks, at the cost of slowing down the growth of the rational behavior. In other words, a positive mutation rate implies that there is always a fixed positive fraction of new entrants into the population in each generation, even if their behavior may be suboptimal with respect to the current environment.

**Proposition 6.** With a positive mutation rate \( \epsilon > 0 \), let \( n_k^{\text{Total}} \) be the total number of individuals in the entire population at the end of \( k \)-th cycle. Under Assumptions 3-5 and the regime-switching model described above where the fecundities \( \Phi^1(x_a, x_b) \) and \( \Phi^2(x_a, x_b) \) satisfy

\[ P_{\Phi^1}(x_b = 0) = P_{\Phi^2}(x_a = 0) = 1, \]

as \( k \) increases without bound, \( k^{-1} \log n_k^{\text{Total}} \) converges almost surely to

\[ \pi(\epsilon) = 2 \log \frac{\epsilon}{1 - \epsilon} + \mathbb{E}[T^1 + T^2] \log(1 - \epsilon) + \mathbb{E}[T^1] \mathbb{E}_{\Phi^1} \log x_a + \mathbb{E}[T^2] \mathbb{E}_{\Phi^2} \log x_b \]  

(3.9)

for \( 0 < \epsilon < 1 \). The growth optimal mutation rate \( \epsilon^* \) that maximizes (3.9) is

\[ \epsilon^* = \frac{2}{\mathbb{E}[T^1 + T^2]}. \]

As a special case of Proposition 6, we have the following result when the lengths of each regime are all IID.
Corollary 2. Under the assumptions of Proposition 6, if in addition the lengths of both regime 1 and regime 2 are drawn IID from a single distribution $F(T)$, then the growth optimal behavior that maximizes (3.9) is

$$
\epsilon^* = \frac{1}{E[T]}.
$$

By Proposition 6 and Corollary 2, the optimal mutation rate is simply the reciprocal of the expected length of a regime. In the long run, the more stable the environment is, the less irrational behaviors are present in the population; the more frequently environmental changes happen, the more irrational behaviors prevail in the population. The mutation rate and the amount of irrational behaviors are not exogenous variables given by the nature. They are not only necessary, but also important quantities that are selected by the nature in evolution to match the degree of environmental instability. In this sense, natural selection shapes the degree of irrationality in the population.

This also implies that the optimal amount of new entrants into the population is determined by the degree of environmental stability. For example, one would expect relatively small amount of new entrants in areas with relatively stable market conditions, such as the automobile industry; and relatively high turnover rates in areas with relatively volatile market conditions such as the hedge fund industry.

### 3.3.3 Generalization and simulation experiments

The implications from the above two-behavior example with a special fecundity structure can be generalized to any number of types and any fecundity structures. We use simulation to demonstrate the generality of the optimal degree of mutation and irrationality. In this section, we consider eight different pairs of environments and different lengths of regimes. We calculate the optimal degree of mutation for each of them.

In the following experiments, the lengths of regimes $T^1$ and $T^2$ are independent random variables with expectation $E[T^1]$ and $E[T^2]$ respectively, ranging from 10
to 37. For a given expectation $\mathbb{E}[T^1]$, $T^1$ is uniformly distributed in the interval $[0.8 \times \mathbb{E}[T^1], 1.2 \times \mathbb{E}[T^1]]$, rounding to the nearest integer. $T^2$ is distributed in the same way.

For a given pair of $(\mathbb{E}[T^1], \mathbb{E}[T^2])$, 11 types of behavior from $\{0, \frac{1}{10}, \frac{2}{10}, \ldots, 1\}$ starting with one individual each evolve for 700 to 1000 generations. The optimal degree of mutation in each pair of environment is calculated by taking the average over 200 to 500 simulation paths.

Table 3.1 gives eight different environmental conditions, for which we plot the optimal degree of mutation and the optimal log-geometric-average growth rate as a function of $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$ in Figure 3-1. In these figures, the colored plane with colorbar shows the optimal mutation rates; the transparent surface of which the height is indicated by the $z$-axis shows the optimal log-geometric-average growth rate associated with that optimal mutation rate.

Symmetric regimes. Environment 1 assumes that one of the actions in each regime leads to no offspring. Results are consistent with the example of two behaviors: the optimal degree of mutation is inversely proportional to $\mathbb{E}[T^1] + \mathbb{E}[T^2]$. However, the growth rate is proportional to $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$: the longer the length of a regime is, the faster the population grows.

Environment 2 considers the case where both action $a$ and $b$ produce positive number of offspring. As expected, the growth rates are much higher than those in environment 1. The optimal degree of mutation is inversely proportional to the length of a regime, except for two regions where the length of one regime is much larger than that of the other (the region $\mathbb{E}[T^1] > 25, \mathbb{E}[T^2] < 12$, and the region $\mathbb{E}[T^1] < 12, \mathbb{E}[T^2] > 25$). In these two regions, the optimal degree of mutation drops to nearly 0 because one regime is significantly shorter than the other and therefore it is not worth sacrificing growth in one regime for the other by mutation, as long as the inferior behavior does not die out in the shorter regime.

Environment 3 adds dependence of $x_a$ and $x_b$ in each regime. In this case the optimal behavior in each regime is the perfect probability matching behavior: $f_1^* = 0.8, f_2^* = 0.2$. Simulation results are similar to environment 1.
Table 3.1: Probability table for the simulation of optimal mutation rates: environment 1-8

<table>
<thead>
<tr>
<th></th>
<th>Regime 1</th>
<th>Regime 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Environment 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.</td>
<td>$\frac{1}{3}$</td>
<td>$\frac{1}{3}$</td>
</tr>
<tr>
<td>$x_a$</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>$x_b$</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(b) Environment 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.</td>
<td>$\frac{1}{3}$</td>
<td>$\frac{1}{3}$</td>
</tr>
<tr>
<td>$x_a$</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>$x_b$</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>(c) Environment 3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td>$x_a$</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>$x_b$</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>(d) Environment 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td>$x_a$</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>$x_b$</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>(e) Environment 5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td>$x_a$</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>$x_b$</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>(f) Environment 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td>$x_a$</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>$x_b$</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>(g) Environment 7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td>$x_a$</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>$x_b$</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>(h) Environment 8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td>$x_a$</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>$x_b$</td>
<td>1</td>
<td>3</td>
</tr>
</tbody>
</table>
Figure 3-1: Optimal degree of mutation and optimal log-geometric-average growth rate as a function of regime lengths $\mathbb{E}[T^1]$ and $\mathbb{E}[T^2]$. Eight subfigures show simulation results of eight different environments in Table 3.1. The colored plain with the colorbar shows the optimal mutation rates; the transparent surface of which the height is indicated by the $z$-axis shows the optimal log-geometric-average growth rate associated with that optimal mutation rate.
Environment 4 considers a different kind of dependence of \( x_a \) and \( x_b \) in each regime. In this case the optimal behavior in each regime is deterministic: \( f_1^* = 1, f_2^* = 0 \). Simulation results are similar to environment 1.

Asymmetric regimes. The four experiments considered so far are all symmetric in terms of the two regimes. In other words, the second regime is simply a copy of the first regime with \( x_a \) and \( x_b \) reversed. As a consequence, all results are expected to be symmetric with respect to the line \( \mathbb{E}[T^1] = \mathbb{E}[T^2] \). In this part we consider asymmetric regimes and investigate how this changes the optimal mutation rates and growth rates.

Environment 5 is a mixture of environment 3 and 4 in the symmetric regime case: regime 1 is from environment 3 and regime 2 is from environment 4. In this case the optimal behavior is \( f_1^* = 0.8 \) in regime 1 and \( f_2^* = 0 \) in regime 2. There are several interesting observations. First of all, both the optimal degree of mutation and the growth rate are no longer symmetric with respect to \( \mathbb{E}[T^1] \) and \( \mathbb{E}[T^2] \). Secondly, the growth rate increases as \( \mathbb{E}[T^2] \) increases; decreases as \( \mathbb{E}[T^1] \) increases. This is because regime 2 has a larger geometric-mean fitness than regime 1, and the growth rate increases as the proportion of generations in regime 2 increases. Thirdly, similar phenomenon to environment 2 of zero-mutation appears when \( \mathbb{E}[T^1] \) is large and \( \mathbb{E}[T^2] \) is small.

Environment 6 makes the two regimes more asymmetric. The optimal behavior is \( f_1^* = 1 \) in regime 1 and \( f_2^* = 0 \) in regime 2. This time regime 1 has an edge in terms of geometric-mean fitness. Results are similar to environment 5 except that \( \mathbb{E}[T^1] \) and \( \mathbb{E}[T^2] \) are reversed.

When mutation is not desirable. Mutation is desirable because the environment is unstationarily stochastic and the two regimes favor different actions. When these conditions change, mutation is no longer desirable.

Environment 7 reverses action \( a \) and \( b \) in the second regime of environment 5. The shape of the transparent surface indicating growth rates is similar to environment 5. However, the optimal degree of mutation is 0 for any combination of \( \mathbb{E}[T^1] \) and \( \mathbb{E}[T^2] \), because the optimal behavior is \( f_1^* = 0.8 \) in regime 1 and \( f_2^* = 1 \) in regime 2. They
are close to each other, and both of them grow relatively fast in both regimes.

Environment 8 reverses action $a$ and $b$ in the second regime of environment 6. The shape of the transparent surface indicating growth rates is similar to environment 6, and the optimal degree of mutation is 0 for the same reason as in environment 7. The optimal behavior is $f^* = 1$ in both regime 1 and regime 2.

### 3.3.4 Optimal degree of irrationality

It is clear that there exists a balance between growth without mutation and robustness with mutation. The simulation results confirm the inverse relation between the optimal degree of mutation and expected lengths of regimes derived analytically in the simple two-behavior model with special fecundity structure (Proposition 6 and Corollary 2). The relation is robust across a variety of environmental conditions.

For symmetric regimes, the optimal degree of mutation is inversely proportional to $E[T^1] + E[T^2]$; the growth rate is proportional to both $E[T^1]$ and $E[T^2]$. For asymmetric regimes, the growth rate increases as the proportion of the regime that has a larger geometric-mean fitness increases. The relative magnitude of the two regimes matters.

The optimal degree of mutation could be zero if one regime is significantly shorter than the other, because it is not worth sacrificing growth in one regime for the other as long as the inferior behavior does not die out in the shorter regime. The optimal degree of mutation could also be zero if the optimal behaviors in two regimes are similar to each other, and both of them grow relatively fast in both regimes.

The length of regime, or equivalently the frequency of change, is one aspect of the nature of environmental change. The intensity of each environmental change is another aspect. In our framework, the intensity of environmental change is reflected by the difference in optimal behaviors in the two regimes: $|f_1^* - f_2^*|$. When the optimal behaviors in the two regimes are similar to each other, the optimal degree of mutation is relatively low; when the optimal behaviors in the two regimes are wildly different, the optimal degree of mutation must be high to compensate for the slow growth of the suboptimal behaviors in each regime.
In general, the evolutionarily optimal degree of irrationality in the population is influenced by both the frequency and intensity of environmental change. A higher frequency or intensity of change would imply a higher degree of irrationality. Equivalently, markets and industries with more volatile environments should attract more entrants over time.

3.4 Additional Results and Technical Details

3.4.1 Birkhoff’s contraction coefficient

The definition and properties of the Birkhoff’s contraction coefficient can be found in Caswell (2001, p.370-372) or Ipsen and Selee (2011, p.159). Let \( x \) and \( y \) be positive vectors. The Hilbert pseudo-metric distance between \( x \) and \( y \) is defined as:

\[
d(x, y) := \log \left( \frac{\max_i \frac{x_i}{y_i}}{\min_i \frac{x_i}{y_i}} \right) = \max_{i,j} \log \left( \frac{x_i y_j}{x_j y_i} \right).
\]

It measures the distance between two vectors in a way that depends only on their proportional composition, independent of their absolute size. It satisfies the following conditions:

\[
\begin{align*}
d(x, y) &\geq 0 \\
d(x, y) &= d(y, x) \\
d(x, y) &\leq d(x, z) + d(z, y) \\
d(x, y) &= 0 \quad \text{iff} \quad x = ay \\
d(x, y) &= d(ax, by) \quad \text{for} \quad a, b > 0.
\end{align*}
\]

The Birkhoff’s contraction coefficient of a non-negative matrix \( A \) is defined as:

\[
\tau(A) = \sup \frac{d(Ax, Ay)}{d(x, y)} \quad (3.10)
\]
where the supremum is taken over all vectors $x > 0$ and $y > 0$ that are not multiples of each other. Note that because $d$ is invariant with respect to the absolute magnitude of vectors, the supremum can be taken over a compact subset equivalently, say $||x||_1 = ||y||_1 = 1$.

If $A$ is a strictly positive matrix, then $\tau(A) < 1$ (see Caswell (2001, p.372) for example). Under Assumptions 3-5, the matrix $A_t$ might not be strictly positive. However, there is at least one positive entry in each row of $A_t$, so $\tau(A_t) \leq 1$ (see Hajnal (1976)'s discussion on “row allowable” matrices). We will prove in Lemma 1 that $\tau(A_t)$ is indeed strictly less than 1.

**Lemma 1** (Contraction properties of $A_t$). Under Assumptions 3-5, the Birkhoff’s contraction coefficient $\tau$ of $A_t$ is strictly less than 1 almost surely:

$$P(\tau(A_t) < 1) = 1.$$  

Because of Assumption 3, there are only finitely many possible random matrices $A_t$ if $x_a$ and $x_b$ are integers. Therefore, the Birkhoff’s contraction coefficient $\tau(A_t)$ is uniformly less than some positive constant $\delta < 1$. But Lemma 1 is enough for the analysis henceforth.

### 3.4.2 Additional results for population dynamics

**Lemma 2** (Decomposition of population vector). Under Assumptions 3-5, starting from $n_0 = 1$ to be a $(K + 1)$-dimensional column vector of 1’s. Write $P_t = 1'n_t$ for total population size at time $t$. Then the population vector at time $t$ can be written as:

$$n_t = \tilde{F}_t\tilde{F}_{t-1} \cdots \tilde{F}_1n_0 + \frac{\epsilon}{K} \left( \tilde{F}_t \cdots \tilde{F}_2P_11 + \tilde{F}_t \cdots \tilde{F}_3P_21 + \cdots + \tilde{F}_tP_{t-1}1 + P_t1 \right)$$

almost surely, where $\tilde{F}_t = \left( 1 - \left( 1 + \frac{1}{K} \right) \epsilon \right) F_t$ is the “mutation-adjusted” fecundity matrix.

Lemma 2 provides a decomposition of the population vector $n_t$ into a linear com-
bination of non-mutation vector and \( t \) vectors for shorter generational spans, each of which is weighted by \( \frac{1}{K} \) and stands for evolution starting from a certain time in evolution.

**Proposition 7** (Asymptotic population distribution). *Under Assumptions 3-5, there exists some \( \sigma \) such that the total population size \( P_t = 1' n_t \) at time \( t \) satisfies:

\[
\frac{\log P_t - t \mu_e}{\sigma \sqrt{t}} \Rightarrow \text{Normal}(0, 1)
\]

in distribution as \( t \to \infty \).

By Proposition 7, the asymptotic distribution of total population is lognormal, and the mean and variance of \( \log P_t \) both increase linearly with time.

**Proposition 8** (Rate of convergence). *Under Assumptions 3-5, the Markov chain \( \{y_t\}_{t=0}^\infty \) is uniformly ergodic if the support of \( \mathcal{L}(\cdot) \) has nonempty interior\(^1\). By uniformly ergodic we mean that \( \mathcal{L}_T \) converges to the stationary distribution \( \mathcal{L} \) geometrically fast:

\[
||\mathcal{L}_T(\cdot) - \mathcal{L}(\cdot)||_{TV} \leq M \rho^T, \quad T = 1, 2, 3, \ldots
\]

for some \( \rho < 1 \) and \( M < \infty \), where \( ||\cdot||_{TV} \) is the total variation distance between two probability measures.

Proposition 8 asserts that the rate of convergence in Proposition 4 is exponential. Therefore, one would expect that the convergence of \( \mathcal{L}_T(\cdot) \) to the stationary distribution \( \mathcal{L}(\cdot) \) is very fast in evolution.

**Proposition 9** (Selection of the optimal behavior (Robson 1996a)). *Suppose the optimal behavior without mutation is \( f^* \) and \( \mu(f^*) > 0 \) (see Proposition 1). Under Assumptions 3-5, suppose the corresponding element of \( f^* \) in the vector \( y_t \) is \( y^* \). For any all small probability \( \bar{p} > 0 \), positive constant \( \bar{\delta} > 0 \), there exists \( \epsilon \in (0, 1) \) such

\(^{1}\)The support of \( \mathcal{L}(\cdot) \) is defined to be the set of all points \( y \in \mathcal{Y} \) for which every open neighborhood of \( y \) has positive measure.
that, for all mutation rates $\epsilon \in (0, \overline{\epsilon})$, we have:

$$\mathbb{P}(y^* \geq 1 - \delta) > 1 - \bar{p}$$

with respect to the limit distribution $\mathcal{L}$.

Proposition 9 asserts an important property of $\mathcal{L}$: $f^*$ without mutation again dominates the population in evolution with mutation with arbitrarily high probability, provided that the mutation rate is small enough. However, explicit calculation of the stationary distribution is difficult. Next we provide a simulation experiment to understand the limit stationary distribution $\mathcal{L}$.

### 3.4.3 Simulation for the limit distribution of population proportions

Let’s consider an example to show how the limit distribution of population proportions behaves. Let $\Phi(x_a, x_b)$ be given in Table 3.2 and we study a system with 6 behaviors $f \in \{0, \frac{1}{5}, \frac{2}{5}, \ldots, 1\}$.

Table 3.2: Probability table for the simulation of asymptotic population dynamics

<table>
<thead>
<tr>
<th>Action</th>
<th>State 1</th>
<th>State 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$x_a = 3$</td>
<td>$x_a = 0$</td>
</tr>
<tr>
<td>$a$</td>
<td>$x_b = 0$</td>
<td>$x_b = 3$</td>
</tr>
</tbody>
</table>

Figure 3-2a, 3-2b, and 3-2c show the proportion of each behavior in the entire population as the number of generation increases in one simulation. Without mutation, the proportion of different behaviors converges almost surely. With positive mutation rates, the population proportion vector is stochastic even in the long run.

Figure 3-2d and 3-2e show the limit distribution of population proportions for mutation rates $\epsilon = 0.01$ and 0.05. Each subplot shows the histogram of three behaviors in the last generation $T = 500$ with 1000 simulation paths: the optimal behavior $f^* = 0.8$, and two suboptimal behaviors $f = 0.6, f = 1$. We only plot three representative behaviors for simplicity. From the histogram, it is clear that $f^* = 0.8$ (purple
Figure 3-2: Simulation for the limit distribution of population proportions. (3-2a): simulation of one evolution path without mutation. (3-2b): simulation of one evolution path with mutation $\epsilon = 0.01$. (3-2c): simulation of one evolution path with mutation $\epsilon = 0.05$. (3-2d): simulation of limit distribution of 1000 evolution paths with mutation $\epsilon = 0.01$; only $f = 0.6, 0.8, 1$ are shown. (3-2e): simulation of limit distribution of 1000 evolution paths with mutation $\epsilon = 0.05$; only $f = 0.6, 0.8, 1$ are shown. 3-2f): sample paths averaged over 1000 simulation with mutation $\epsilon = 0.01$. 3-2g): sample paths averaged over 1000 simulation with mutation $\epsilon = 0.05$. 
bar) corresponds to the optimal behavior. As the mutation rate gets smaller, the probability that $f^* = 0.8$ dominates the entire population gets closer to 1.

Furthermore, the final stationary distribution does not behave like normal because of the heavy-tailness observed in simulation. In particular, a Kolmogorov-Smirnov test of normality on the distribution of $f^* = 0.8$ proportion gives $p$-value $= 1.08 \times 10^{-50}$, rejecting the normality hypothesis.

Finally, although it is hard to show the evolution of the complete distribution of normalized population vector (3.5) in one figure, Figure 3-2f and 3-2g show the proportion of each behavior in the entire population averaged over 1000 simulation paths. It is clear that the expectation of the distribution converges quickly, and the optimal behavior without mutation again dominates the population in expectation. This supports our results in Proposition 8 and 9.

### 3.5 Discussion

Evolutionary models of behavior are important for understanding the conflicts between individual rationality and human behavior. The binary choice model (Brennan and Lo 2011) provides a framework for explanations of the deviations from the neoclassic utility-based economic theory. Building on the binary choice model, we investigate the evolution of irrational behaviors in this chapter. Mutation is the key because it provides the link between rational and irrational behaviors in an evolutionary context. Because the rational behavior is the evolutionarily optimal behavior given a particular environment, it is subject to change when the environment changes. As a result, irrational behavior is necessary to provide robustness for population growth. Furthermore, we have shown that there is an evolutionarily optimal degree of irrationality in the entire population. More unstable environments imply more irrational behaviors in the population and more new entry over time.

The evolutionary origins of strategic behavior have also been considered (Robson 1996b, Skyrms 2000, Skyrms 2014), and natural selection can also produce more sophisticated behaviors such as overconfidence (Johnson and Fowler 2011), altruism
and self-deception (Trivers 1971, Becker 1976), and state-dependent strategies like the Hawk-Dove game (Maynard Smith 1984), which emerge as a result of more complex environmental conditions. In our framework, if we assume that one individual’s action is correlated with the reproductive success of another individual, individuals engaging in strategic behavior will reproduce more quickly than those with simpler behaviors such as probability matching. If the actions of individuals in the current generation can affect the reproductive success of individuals in future generations, even more complex dynamics are likely to emerge as in the well-known overlapping generations model (Samuelson 1958). In a resource-constrained environment in which one individual’s choice can affect another individual’s reproductive success, strategic interactions such as reciprocity and cooperation will likely emerge within and across generations (Trivers 1971, Nowak and Highfield 2011).

In contrast, the model considered in this chapter does not require any strategic interactions, and individual decision-making is deliberately mindless, allowing us to determine the most primitive and fundamental links between stochastic environments and adaptive behavior. Even in such a simple setting, we find a range of behaviors—behaviors that do not always conform to common economic intuition about rationality—can arise and persist via natural selection. Simon (1981) illustrated this principle vividly with the example of a single ant traversing a mixed terrain of sand, rocks, and grass. The ant’s path seems highly complex, but the complexity is due more to the environment than the ant’s navigational algorithm.

Much of the rationality debate among economists and psychologists focuses on whether the rational models can help people make better inferences and decisions in the real world (McKenzie 2003). Instead, our framework provides an evolutionary explanation of irrational behaviors and different degrees of irrationality in the population. The results suggest that irrational behaviors are necessary even if they are seemingly inefficient in the current environment, and the nature of stochastic environment determines the degree of irrationality, and the amount of new entrants into the population.

From a policy perspective, our results underscore the importance of addressing
different human behaviors in different environments. For example, the financial mar-
ket is considered to be efficient most of the time (Samuelson 1965, Fama 1970), and
participants with irrational beliefs constitutes a minimum part in the market. How-
ever, in periods of economic turbulence and financial crisis, irrational behaviors are
much more prevalent than usual. Our results also highlight the importance of entry of
new actors into the market even if they appear suboptimal in the current context, and
suggest that the optimal amount of new entrants depends on the degree of environ-
mental stability. On the other hand, if not properly managed, volatile environments
can lead to increases in the degree of irrationality, implying higher social costs and
lower economic growth. However, our results also highlight the potential dangers of
sustained government intervention, which can become a source of systematic risk and
cause volatile environments in its own right (Acharya et al. 2011, Lucas 2011).
4.1 Introduction

Since the publication of the path-breaking work of Wynne-Edwards (1963), Hamilton (1963), and Hamilton (1964), the theory of evolution has been applied to much broader contexts than self-replicating genes. By appealing to notions of inclusive fitness and kin and group selection, compelling explanations for previously inexplicable behaviors such as altruism and cooperation have been developed. This approach has generated a number of additional insights such as reciprocity (Trivers 1971), the Price equation (Price 1970), sociobiology (Wilson 1975c, Wilson 2005), and the theory of multi-level selection (Wilson and Sober 1994). Moreover, empirical studies have lent further support to the theory of group and kin selection, including social behavior in bacteria (Ben-Jacob et al. 1994, Ben-Jacob et al. 2004, Ingham and Ben-Jacob 2008), sterility in social insects (Hamilton 1964, Queller and Strassmann 1998), and the avoidance of cannibalism in salamanders (Pfennig et al. 1999).

The behavioral implications of group selection have also received considerable attention from economists, who have used evolutionary models to explain apparent conflicts between individual rationality and human behavior (Brennan and Lo 2011, Brennan and Lo 2012), including attitudes toward risk and utility functions (Robson 1996a,
Samuelson 2001), time preference (Robson 2001b), and financial markets (Blume and Easley 1992, Kogan et al. 2006a). As an alternative to the traditional view that “market prices fully reflect all available information” (Samuelson 1965, Fama 1970), the Adaptive Markets Hypothesis (Lo 2004) provides an evolutionary interpretation of financial market dynamics.

Despite these applications, group selection is still one of the most hotly contested issues in evolutionary biology. An enormous body of research has been dedicated to understanding the relationship between genetic, organismic, and group selection (Wilson 1975b, Wright 1980, Williams 1996), and the relationship between group and kin selection (Maynard Smith 1964, Queller 1992, Wild et al. 2009, Nowak et al. 2010, Wade et al. 2010, Frank 2013). Critics over the last few decades have argued forcefully against group selection as a major mechanism of evolution, and recent attempts to revive it (Wilson and Wilson 2008, Nowak et al. 2010, Wilson 2013) have been met with swift and broad rebuke (Abbot et al. 2011, Pinker 2012).

Here we propose a reconciliation of the two opposing perspectives by arguing that what appears to be group selection may, in fact, simply be the consequence of natural selection occurring in stochastic environments with reproductive risks that are correlated across individuals. Those individuals with highly correlated risks will appear to form “groups”, even if their actions are, in fact, totally autonomous, mindless, and, prior to natural selection, uniformly randomly distributed in the population.

We illustrate our approach with the following simple example. Consider a population of individuals, each facing a binary choice between one of two possible actions, a and b, and suppose the environment consists of two possible states of nature, rain or sunshine, with probability 20% and 80%, respectively. If it rains, action a leads to 0 offspring for any given individual and action b leads to 3 offspring; if it shines, the reverse occurs and action a leads to 3 offspring while action b leads to 0 offspring. From an individual’s perspective, choosing a will lead to more reproductive success on average given the higher likelihood of sunshine. However, if all individuals in the population behaved in this manner, and rain or sunshine occurred for all individuals at the same time, the first time that a negative environment appears, the entire pop-
ulation of individuals that always choose a will become extinct. If we assume that offspring behave identically to their parents (perfect transmission of traits across generations), the behavior "always choose a" cannot survive over time. In fact, we show below that the behavior with the highest reproductive success over time in this very specialized example is to randomize between a and b using the same probability as the probability of sunshine, 80%; the group of individuals exhibiting this probability-matching behavior achieves the maximum possible growth rate. As a result, it appears as though selection operates at the group level and that this group—all individuals i who randomize their actions with probability $p_i = 80\%$—is the fittest.

The key to this outcome is the fact that the reproductive risk facing all individuals in the population, rain or sunshine, is perfectly correlated, which we refer to as systematic risk. If we had assumed, instead, that reproductive risk was idiosyncratic—that the state of nature is independently and identically distributed (IID) for each individual—then the evolutionarily dominant strategy is, in fact, the purely "selfish" one in which a is chosen all the time.

This framework demonstrates that a separate theory of group selection is not strictly necessary to explain observed phenomena such as altruism and cooperation. But our results also show that the notion of group selection does capture a unique aspect of evolution—selection with correlated reproductive risk—that may be sufficiently widespread and distinct to warrant a separate term for the phenomenon. There is no controversy around the fact that selection occurs at the genetic level because of the basic biology of reproduction. However, we show that selection can also appear to operate at coarser levels if environmental forces affect a particular subset of individuals in similar fashion, i.e., if their reproductive risks are highly correlated. We use the term "appear" intentionally because in our framework, selection does not occur at the level of the group, but the behavior that is evolutionarily dominant is consistent with some of the empirical implications of group selection.

By studying the impact of selection on behavior rather than on genes, we are able to derive evolutionary implications that cut across species, physiology, and genetic origins. In the same way that different magnifications of a microscope reveal differ-
ent details of a specimen, applying evolutionary principles to behavioral variations leads to different insights that may be more relevant for economics, psychology, and behavioral ecology. Because evolution is essentially a passive “process of elimination” (Mayr 2001), selection and adaptation operate at all levels, from genes to populations, depending on the nature of the corresponding environmental challenges. Our focus on behavior as the object of selection is a different lens through which the effects of evolution may be studied.

Because of the extensive literature involved in this topic, we first provide a review of the work that are closed related to our discussion. Then we introduce the binary choice model with two systematic environmental factors. In this framework, we derive a behavioral adaptation to stochastic environments with systematic risk in which groups seem to be the unit of selection, but which is purely the result of natural selection operating on individuals in the population. A generalization of the binary choice model to the multinomial case with multiple factors is then provided. We conclude with a brief discussion of the results.

4.1.1 Literature review

The literature on evolution and behavior can be overwhelming, spanning the disciplines of evolutionary biology, ecology, evolutionary and social psychology, and economics. While a comprehensive survey is well beyond the scope of this chapter, we attempt to provide a representative sampling of the many strands that are most relevant to our focus.

The role of stochastic environments in evolution has been investigated extensively by biologists and ecologists. Stochastic environments cause high genetic variation and, in the extreme cases, extinction (Lynch and Lande 1993, Burger and Lynch 1995, Burger and Gimelfarb 2002, Pekalski 1998, Pekalski 1999, Pekalski 2002, De Blasio 1999). Environmental uncertainty that is associated with stochasticity over time (Cohen 1966, Oster and Wilson 1979, Bergstrom 2014) or heterogeneity across space (Levins 1968) can cause natural selection to favor a gene that randomizes its phenotypic expression. Gillespie and Guess (1978) describe a heuris-
tic method to study selection in random environments. Frank (2011a) analyzes how variability in reproductive success affects fitness and relates it to the geometric mean principle. Geometric-mean fitness has also appeared in the financial context as the "Kelly criterion" for maximizing the geometric growth rate of a portfolio (Kelly Jr. 1956, Samuelson 1971, Thorp 1971, Thorp 2006). However, the motivation for geometric-mean fitness in population biology is considerably more compelling than in financial investments because maximizing the geometric-mean return of a portfolio is optimal only for individuals with a very specific risk preference, i.e., those with logarithmic utility functions (Samuelson 1971).

In the evolutionary biology literature, Maynard Smith (1982) has developed the concept of an "evolutionarily stable strategy", specific behaviors that survive over time by conferring reproductive advantages or "fitness", typically measured by the rate of population growth. Using this notion of fitness, Fretwell (1972), Cooper and Kaplan (1982), and Frank and Slatkin (1990) observe that randomizing behavior can be advantageous in the face of stochastic environmental conditions. The impact of variability in reproductive success among individuals in a population has been shown to yield a kind of risk aversion (which increases average reproductive success) and "bet-hedging" (which reduces the variance of reproductive success) (Slatkin 1974, Caraco 1980, Real 1980, Rubenstein 1982, Seger and Brockmann 1987, Beaumont et al. 2009, Childs et al. 2010, Bergstrom 2014). Frank and Slatkin (1990) propose a framework that highlights the importance of correlations among individual reproductive success in determining the path of evolution.

Similar results have been derived in the behavioral ecology literature, in which the maximization of fitness via dynamic programming has been shown to yield several observed behaviors, including risk-sensitive foraging in non-human animal species (Real and Caraco 1986, Stephens and Krebs 1986, Deneubourg et al. 1987, Harder and Real 1987, Pasteels et al. 1987, Mangel and Clark 1988, Hölldobler and Wilson 1990, Kirman 1993, Thuijsman et al. 1995, Smallwood 1996, Keasar et al. 2002, Ben-Jacob 2008) and seed dispersal strategies in plants (Levin et al. 1984, Levin et al. 2003). Recently, the neural basis of risk aversion has also received much attention as

The relationship between risk-spreading behavior and kin selection has also been considered. Yoshimura and Clark (1991) show that the risk-spreading polymorphism, in which a given genotype consists of a mixture of two or more forms each employing different behavioral strategies (Levins 1968, Cooper and Kaplan 1982), makes sense only for groups. Yoshimura and Jansen (1996) argue that risk-spreading adaptation is a form of kin selection (Cooper and Kaplan 1982), and the strategies of kin can be very important in stochastic environments even if there are no interactions at all. McNamara (1995) introduces the profile of a strategy and relates the geometric mean fitness to a deterministic game.

In the economics literature, evolutionary principles were first introduced to understand cooperation and altruism (Alexander 1974, Hirshleifer 1977, Hirshleifer 1978), and evolutionary game theory is considered a foundation for altruistic behavior (Samuelson 2001, Bergstrom 2002). Evolutionary models of behavior are especially important for economists in resolving conflicts between individual rationality and human behavior (Robson 2001b, Brennan and Lo 2011), including attitudes toward risk and utility functions (Waldman 1994, Robson 1996a, Robson 1996b, Robson 2001a, Samuelson 2001), time preference (Rogers 1994, Robson and Samuelson 2007, Robson and Szentes 2008, Robson and Samuelson 2009, Burnham 2013), financial markets and firm selection (Blume and Easley 1992, Luo 1995, Luo 1998, Kogan et al. 2006a), and the economic analysis of social institutions (Herrmann-Pillath 1991, van den Bergh and Gowdy 2009, Safarzyńska and van den Bergh 2010).

Evolutionary models of behavior have also been used to justify the existence of utility functions and to derive implications for their functional form (Hansson and Stuart 1990, Robson 1996a, Robson 2001a) (see Robson (2001b) and Robson and Samuelson (2009) for comprehensive reviews of this literature). For example, Robson (1996a) investigates expected and non-expected utility behaviors, and finds that randomized behavior may be optimal from a population perspective even though it
is sub-optimal from an individual perspective (Grafen 1999, Curry 2001). Robson (2001a) argues that the kind of predictable behavior capable of being captured by a utility function emerged naturally as an adaptive mechanism for individuals faced with repeated choices in a nonstationary environment. Robson and Samuelson (2007) find that exponential discounting in utility functions is consistent with evolutionarily optimal growth of a population.

### 4.2 Binary Choice Model with Systematic Risk

Consider a population of individuals that live for one period, produce a random number of offspring asexually, and then die. During their lives, individuals make only one decision: they choose from two actions, $a$ and $b$, and this results in one of two corresponding random numbers of offspring, $x_a$ and $x_b$. Now suppose that each individual chooses action $a$ with some probability $p \in [0, 1]$ and action $b$ with probability $1 - p$, denoted by the Bernoulli variable $I^p$, hence the number of offspring of an individual is given by the random variable:

$$x^p = I^p x_a + (1 - I^p) x_b,$$

where

$$I^p = \begin{cases} 
1 & \text{with probability } p \\
0 & \text{with probability } 1 - p.
\end{cases}$$

We shall henceforth refer to $p$ as the individual's behavior since it completely determines how the individual chooses between action $a$ and $b$. Note that $p$ can be 0 or 1, hence we are not requiring individuals to randomize—this will be derived as a consequence of natural selection under certain conditions.

Now suppose that there are two independent environmental factors, $\lambda_1$ and $\lambda_2$, that determine reproductive success, and that $x_a$ and $x_b$ are both linear combinations
of these two factors:

\[
\begin{align*}
    x_a &= \beta_1 \lambda_1 + (1 - \beta_1) \lambda_2 \\
    x_b &= \beta_2 \lambda_1 + (1 - \beta_2) \lambda_2
\end{align*}
\]

where \( \lambda_i \geq 0, 0 \leq \beta_i \leq 1, i = 1, 2 \). Examples of such factors are weather conditions, the availability of food, or the number of predators in the environment. Because these factors affect the fecundity of all individuals in the population, we refer to them as \textit{systematic}, and we assume that:

**Assumption 6.** \( \lambda_1 \) and \( \lambda_2 \) are independent random variables with some well-behaved distribution functions, such that \((x_a, x_b)\) and \(\log(px_a + (1-p)x_b)\) have finite moments up to order 2 for all \( p \in [0, 1], \beta_1 \in [0, 1], \beta_2 \in [0, 1] \).

**Assumption 7.** \((\lambda_1, \lambda_2)\) is IID over time and identical for all individuals in a given generation.

We shall henceforth refer to \((\beta_1, \beta_2)\) as an individual’s \textit{characteristics}. For each action, individuals are faced with a tradeoff between two positive environmental factors because of limited resources.

Under this framework, an individual is completely determined by his behavior \( p \) and characteristics \((\beta_1, \beta_2)\). We shall henceforth refer to \( f \equiv (p, \beta_1, \beta_2) \) as an individual’s \textit{type}. We assume that offspring behave in a manner identical to their parents, i.e., they have the same characteristics \((\beta_1, \beta_2)\), and choose between \( a \) and \( b \) according to the same \( p \), hence the population may be viewed as being comprised of different types indexed by the triplet \( f \). In other words, offspring from a type-\( f \) individual are also of the same type \( f \), hence we are assuming perfect genetic transmission from one generation to the next (once a type \( f \), always a type \( f \)). We also assume that the initial population contains an equal number of all types, which we normalize to be 1 each without loss of generality. In summary, an individual \( i \) of type \( f = (p, \beta_1, \beta_2) \) produces a random number of offspring:

\[
x_i^{p, \beta_1, \beta_2} = P_i x_{a,i}^{\beta_1} + (1 - P_i) x_{b,i}^{\beta_2}
\] (4.1)
where
\[
\begin{align*}
   x_{a,i}^{\beta_1} &= \beta_1 \lambda_1 + (1 - \beta_1) \lambda_2 \\
   x_{a,i}^{\beta_2} &= \beta_2 \lambda_1 + (1 - \beta_2) \lambda_2.
\end{align*}
\] (4.2)

Now consider an initial population of individuals with different types. Suppose the total number of type \( f = (p, \beta_1, \beta_2) \) individuals in generation \( T \) is \( n_f^T \). Under Assumptions 6–7, it is easy to show that \( T^{-1} \log n_f^T \) converges in probability to the log-geometric-average growth rate:
\[
\mu(p, \beta_1, \beta_2) = \mathbb{E} \left[ \log \left( p x_{a,i}^{\beta_1} + (1 - p) x_{a,i}^{\beta_2} \right) \right],
\] (4.3)
as the number of generations and the number of individuals in each generation increases without bound (we provide the proof for a more general case in Section 4.5). Define
\[
\begin{align*}
   \alpha_1 &= p \beta_1 + (1 - p) \beta_2 \\
   \alpha_2 &= p(1 - \beta_1) + (1 - p)(1 - \beta_2),
\end{align*}
\]
then \( \alpha_1 + \alpha_2 = 1 \), and (4.3) can be equivalently written as
\[
\mu(p, \beta_1, \beta_2) = \mathbb{E} \left[ \log (\alpha_1 \lambda_1 + (1 - \alpha_1) \lambda_2) \right].
\] (4.4)

We shall henceforth refer to \((\alpha_1, \alpha_2)\) as the *factor loadings* of type-\( f \) individuals, and (4.3) and (4.4) characterize the log-geometric-average growth rate of individuals as a function of their type \( f \) in terms of both behavior \( p \) and characteristics \((\beta_1, \beta_2)\).

Over time, individuals with the largest growth rate will dominate the population geometrically fast (Brennan and Lo 2011). The optimal factor loading \( \alpha_1^* \) that maximizes (4.4) is given by:
\[
\alpha_1^* = \begin{cases} 
1 & \text{if } \mathbb{E}[\lambda_1/\lambda_2] > 1 \text{ and } \mathbb{E}[\lambda_2/\lambda_1] < 1 \\
\text{solution to (4.6)} & \text{if } \mathbb{E}[\lambda_1/\lambda_2] \geq 1 \text{ and } \mathbb{E}[\lambda_2/\lambda_1] \geq 1 \\
0 & \text{if } \mathbb{E}[\lambda_1/\lambda_2] < 1 \text{ and } \mathbb{E}[\lambda_2/\lambda_1] > 1
\end{cases}
\] (4.5)
where $\alpha_1^*$ is defined implicitly in the second case of (4.5) by

$$E\left[\frac{\lambda_1}{\alpha_1^* \lambda_1 + (1 - \alpha_1^*) \lambda_2}\right] = E\left[\frac{\lambda_2}{\alpha_1^* \lambda_1 + (1 - \alpha_1^*) \lambda_2}\right].$$

(4.6)

As a result, the growth-optimal type is $f^* = (p^*, \beta_1^*, \beta_2^*)$, which is given explicitly in Table 4.1.

Table 4.1: Optimal type $f^* = (p^*, \beta_1^*, \beta_2^*)$ for the binary choice model with different factor loadings $\alpha_1^*$

<table>
<thead>
<tr>
<th>Optimal characteristics</th>
<th>Optimal behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>If $\alpha_1^* = 1$</td>
<td>${(\beta_1, \beta_2) : \beta_1 = 1 \text{ or } \beta_2 = 1}$</td>
</tr>
<tr>
<td></td>
<td>$p^* = \begin{cases} \frac{\alpha_1^* - \beta_2^<em>}{\beta_1^</em> - \beta_2^<em>} = 1 &amp; \text{if } \beta_1^</em> = 1, \beta_2^* \neq 1 \ \frac{\alpha_1^* - \beta_2^<em>}{\beta_1^</em> - \beta_2^<em>} = 0 &amp; \text{if } \beta_1^</em> \neq 1, \beta_2^* = 1 \ \text{arbitrary} &amp; \text{if } \beta_1^* = \beta_2^* = 1 \end{cases}$</td>
</tr>
<tr>
<td>If $\alpha_1^* = 0$</td>
<td>${(\beta_1, \beta_2) : \beta_1 = 0 \text{ or } \beta_2 = 0}$</td>
</tr>
<tr>
<td></td>
<td>$p^* = \begin{cases} \frac{\alpha_1^* - \beta_2^<em>}{\beta_1^</em> - \beta_2^<em>} = 1 &amp; \text{if } \beta_1^</em> = 0, \beta_2^* \neq 0 \ \frac{\alpha_1^* - \beta_2^<em>}{\beta_1^</em> - \beta_2^<em>} = 0 &amp; \text{if } \beta_1^</em> \neq 0, \beta_2^* = 0 \ \text{arbitrary} &amp; \text{if } \beta_1^* = \beta_2^* = 0 \end{cases}$</td>
</tr>
<tr>
<td>If $0 &lt; \alpha_1^* &lt; 1$</td>
<td>${(\beta_1, \beta_2) : (\beta_1 - \alpha_1^<em>)(\beta_2 - \alpha_1^</em>) \leq 0}$</td>
</tr>
<tr>
<td></td>
<td>$p^* = \begin{cases} \frac{\alpha_1^* - \beta_2^<em>}{\beta_1^</em> - \beta_2^<em>} &amp; \text{if } \beta_1^</em> \neq \beta_2^* \ \text{arbitrary} &amp; \text{if } \beta_1^* = \beta_2^* \end{cases}$</td>
</tr>
</tbody>
</table>

The optimal characteristics and associated optimal behaviors in Table 4.1 show that, when $\alpha_1^*$ is 1 or 0, one of the factors, $\lambda_1$ or $\lambda_2$, is significantly more important than the other, and the optimal strategy places all the weight on the more important factor. However, when $\alpha_1^*$ is strictly between 0 and 1, a combination of factors $\lambda_1$ and $\lambda_2$ is necessary to achieve the maximum growth rate. Individual characteristics ($\beta_1^*, \beta_2^*$) need to be distributed in such a way that one of the two choices of action puts more weight on one factor, while the other choice puts more weight on the other factor. Eventually, the behavior $p^*$ randomizes between the two choices and therefore achieves the optimal combination of factors. This is a generalization of the "adaptive coin-flipping" strategies of Cooper and Kaplan (1982), who interpret this behavior as a form of altruism because individuals seem to be acting in the interest of the population at the expense of their own fitness. However, Grafen (1999) provides a different interpretation by proposing an alternate measure of fitness, one that reflects the growth rate of survivors.
This result may be viewed as a primitive form of herding behavior—where all individuals in the population choose to act in the same manner—especially if the relative environmental factors, $E[\lambda_1/\lambda_2]$ and $E[\lambda_2/\lambda_1]$, shift suddenly due to rapid environmental changes. To an outside observer, behaviors among individuals in this population may seem heterogenous before the shift, but will become increasingly similar after the shift, creating the appearance (but not the reality) of intentional coordination, communication, and synchronization. If the reproductive cycle is sufficiently short, this change in population-wide behavior may seem highly responsive to environmental changes, giving the impression that individuals are learning about their environment. This is indeed a form of learning, but it occurs at the population level, not at the individual level, and not within an individual’s lifespan.

4.3 Individually Optimal versus Group Optimal Behavior

It is instructive to compare the optimal characteristics and behavior in Table 4.1 that maximize growth with the behavior that maximizes an individual’s reproductive success. According to (4.1) and (4.2), the individually optimal behavior maximizes

$$E[x^p,\beta_1,\beta_2] = E[p x_{a_1}^{\beta_1} + (1 - p)x_{a_2}^{\beta_2}] = \alpha_1 E[\lambda_1] + \alpha_2 E[\lambda_2]$$

over $p, \beta_1, \beta_2$. Therefore, the individually optimal factor loading, denoted by $\hat{\alpha}_1$, is simply:

$$\hat{\alpha}_1 = \begin{cases} 
1 & \text{if } E[\lambda_1] > E[\lambda_2] \\
0 & \text{if } E[\lambda_1] < E[\lambda_2] \\
\text{arbitrary} & \text{if } E[\lambda_1] = E[\lambda_2].
\end{cases}$$

Given a particular environment $(\lambda_1, \lambda_2)$, the individually optimal behavior depends only on the expectation of two factors, and this selfish behavior is generally sub-optimal for the group.

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In contrast, individuals of type $f^* = (p^*, \beta_1^*, \beta_2^*)$ described in Table 4.1 are optimal in the group sense, attaining the maximum growth rate as a group by behaving differently than the individually optimal behavior. We shall refer to $f^*$ henceforth as the growth-optimal behavior to underscore the fact that it is optimal from the population perspective, not necessarily from the individual's perspective. This provides a prototype of group selection as a consequence of stochastic environments with systematic risk. We define groups to be individuals with the same characteristics. More precisely, in our model, individuals with the same $(\beta_1, \beta_2)$ are considered a group. Nature selects the groups with optimal characteristics $(\beta_1^*, \beta_2^*)$, and $p^*$ is a reflection of different behaviors for each group.

Like altruism, cooperation, trust, and other behaviors that do not immediately benefit the individual, the growth-optimal characteristics and behaviors derived in our framework flourish because they allow these individuals to pass through the filter of natural selection. However, unlike theories of group selection that are based on sexual reproduction and genetic distance, our version of group selection is based on behavior itself. Those individuals with types other than $f^*$ will not reproduce as quickly, hence from an evolutionary biologist's perspective, group selection is operating at the level of those individuals with characteristics $(\beta_1^*, \beta_2^*)$ and behaving according to $p^*$. Of course, we cannot measure all forms of characteristics and behavior as readily as we can measure genetic make-up, but in the stark case of the binary choice model, it is clear that selection can and does occur according to groups defined by characteristics and behavior.

Section 4.5 contains a generalization of the binary choice model to multinomial choices with multiple environmental factors. In general, it is possible that the optimal growth rate $\mu^*$ corresponds to multiple groups, and each group corresponds to multiple optimal behaviors. In terms of group selection, this fact means that several different groups—each defined by a specific combination of characteristics—could simultaneously be optimal from an evolutionary perspective. Within each group, natural selection will determine the behavior that achieves the optimal growth rate. The optimal behavior is not necessarily unique for each group. Also, the optimal behaviors
for different groups might overlap.

### 4.4 A Numerical Example

Consider an island that is isolated from the rest of the world, and suppose $\lambda_1$ is a measure of weather conditions of the local environment, and $\lambda_2$ is a measure of the local environment's topography where, without loss of generality, we assume that larger values of each factor are more conducive to reproductive success. Moreover, $\lambda_1$ and $\lambda_2$ are independent random variables and described by:

\[
\lambda_1 = \begin{cases} 
1 \text{ with probability } \frac{1}{2} \\
2 \text{ with probability } \frac{1}{2}, 
\end{cases} \\
\lambda_2 = \begin{cases} 
1 \text{ with probability } \frac{1}{2} \\
2 \text{ with probability } \frac{1}{2}. 
\end{cases}
\]

An individual on this island lives for one period, has one opportunity to choose one of two actions—farming (action $a$) or mining (action $b$)—which determines its reproductive success, and then dies immediately after reproduction. The number of offspring is given by $x_a^{\beta_1}$ if action $a$ is chosen and $x_b^{\beta_2}$ if $b$ is chosen, where $x_a^{\beta_1}$ and $x_b^{\beta_2}$ are given by:

\[
\begin{cases} 
x_a^{\beta_1} = \beta_1 \lambda_1 + (1 - \beta_1) \lambda_2 \\
x_b^{\beta_2} = \beta_2 \lambda_1 + (1 - \beta_2) \lambda_2.
\end{cases}
\]

Here, $\beta_1$ captures an individual’s farming ability as determined by the two factors, weather and topography; $\beta_2$ captures an individual’s mining ability as determined by the same two factors. According to Table 4.1, the optimal factor loadings are $\alpha_1^* = \alpha_2^* = 1/2$, which indicates that individuals should have a balanced exposure to both weather and topography. The optimal characteristics are

\[
\left\{(\beta_1^*, \beta_2^*) \mid (\beta_1^* - \frac{1}{2})(\beta_2^* - \frac{1}{2}) \leq 0 \right\}, \tag{4.7}
\]
and each group is associated with the optimal behavior:

\[
p^* = \begin{cases} 
\frac{1}{\beta_1^* - \beta_2^*} & \text{if } \beta_1^* \neq \beta_2^* \\
\text{arbitrary} & \text{if } \beta_1^* = \beta_2^* = \frac{1}{2}.
\end{cases}
\] (4.8)

For example, \( (\beta_1^*, \beta_2^*) \bigg| \beta_1^* = \frac{1}{2} \) is an optimal group associated with \( p^* = 1 \). These are individuals who can perfectly balance the output of farming with respect to weather and topography. Therefore, they choose farming with probability 1 and appear as a “group” of farmers.

On the other hand, \( (\beta_1^*, \beta_2^*) \bigg| \beta_2^* = \frac{1}{2} \) is another optimal group, but associated with the optimal behavior \( p^* = 0 \). These individuals can perfectly balance the output of mining with respect to weather and topography. Therefore, they choose mining with probability 1 and appear as a “group” of miners.

Finally, there are also other optimal groups, described by (4.7) in general, in which individuals randomize their choices between farming and mining according to (4.8), to achieve the optimal exposure to weather and topography.

Figure 4-1 shows the optimal behavior for each group. The optimal groups described by (4.7) correspond to the upper-left and lower-right blocks. Randomized behaviors are optimal for these groups. Interestingly, all the sub-optimal groups (upper-right and lower-left blocks) correspond to deterministic behaviors (\( p^* = 0 \) or \( 1 \)) except when \( \beta_1 = \beta_2 \). Figure 4-2 shows the optimal log-geometric-average growth rate for each group. It is clear that all groups described by (4.7) have the largest growth rate.

We can see that multiple optimal groups co-exist through natural selection, and within each group, individuals share the same characteristics. A particular behavior must be paired with a particular set of characteristics to achieve the optimal growth rate. Note that the individuals in (4.7) are optimal only in the group sense. As a single entity, a group possesses survival benefits above and beyond an individual, and in our framework, these benefits arise purely from stochastic environments with systematic risk.
Figure 4-1: The optimal behavior for each group in the numerical example of group selection. The optimal groups described by Equation (4.7) correspond to the upper-left and lower-right blocks. Randomized behaviors are optimal for these groups.

Figure 4-2: The optimal log-geometric-average growth rate for each group in the numerical example of group selection. All groups described by Equation (4.7) have the largest growth rate.

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The usual notion of group selection in the evolutionary biology literature is that natural selection acts at the level of the group instead of at the more conventional level of the individual, and interaction among members within each group is much more frequent than interaction among individuals across groups. In this case, similar individuals are usually clustered geographically. However, in our model, individuals do not interact at all, nevertheless, the fact that individuals with the same behavior generate offspring with like behavior makes them more likely to cluster geographically and appear as a “group”. In addition, imagine that the environment \((\lambda_1, \lambda_2)\) experiences a sudden shift. To an outside observer, behaviors among individuals in this population will become increasingly similar after the shift, creating the appearance—but not the reality—of intentional coordination, communication, and synchronization.

Here we use the phrase “appear as a group” because our derived behavior is not strictly the same as group selection as defined in the evolutionary biology literature. Instead, we show that behavior which is evolutionarily dominant through the traditional mechanism of natural selection is consistent with the implications of group selection. We purposefully model individuals in our population as mindless creatures engaging in random choices to demonstrate that group-like selection can arise purely through common factors in reproductive success. If we include more complex features such as sexual reproduction, limited resources, and competitive/cooperative interactions among individuals, even more sophisticated group dynamics can be generated.

4.5 The General Model: Multinomial Choice with Multiple Factors

In this section, we generalize the binary choice model to the general case where individuals face multinomial choices and the reproducibility is described by multiple environmental factors.

Consider a population of individuals that live for one period, produce a random number of offspring asexually, and then die. During their lives, individuals make only
one decision: they choose from \( m \) actions \( \{1, \cdots, m\} \), and this results in one of \( m \) corresponding random numbers of offspring \( (x_1, \cdots, x_m) \). Suppose each individual chooses action \( i \) with probability \( p_i \), for \( i = 1, 2, \cdots, m \). Let \( \mathbf{p} = (p_1, \cdots, p_m) \) be the probability vector that characterizes an individual’s behavior. Obviously \( p_1, \cdots, p_m \) are non-negative numbers and restricted such that \( \sum_{i=1}^{m} p_i = 1 \).

On the other hand, the environment is described by \( k \) factors \( \lambda = (\lambda_1, \cdots, \lambda_k) \). Let \( \mathbf{B} = (\beta_{ij})_{m \times k} \) be the matrix of an individual’s characteristics that satisfies the following conditions:

\[
0 \leq \beta_{ij} \leq 1, \quad \forall i = 1, \cdots, m; j = 1, \cdots, k
\]

\[
\sum_{j=1}^{k} \beta_{ij} = 1, \quad \forall i = 1, \cdots, m.
\]

Note that the second condition is a direct generalization of the binary choice model, which means that each row of \( \mathbf{B} \) sums to 1. This reflects the tradeoff between \( k \) environmental factors for each action.

In the multinomial choice model, an individual is characterized by both \( \mathbf{p} \) and \( \mathbf{B} \). The number of offspring for individual \( i \) with type \( f = (\mathbf{p}, \mathbf{B}) \) is:

\[
x_i^{\mathbf{p}, \mathbf{B}} = I_{1,i}^\mathbf{p} x_{1,i}^\mathbf{B} + \cdots + I_{m,i}^\mathbf{p} x_{m,i}^\mathbf{B}
\]

where \((I_1^\mathbf{p}, \cdots, I_m^\mathbf{p})\) is the multinomial indicator variable with probability \( \mathbf{p} = (p_1, \cdots, p_m) \):

\[
(I_1^\mathbf{p}, \cdots, I_m^\mathbf{p}) = \begin{cases} 
(1, 0, \cdots, 0) & \text{with probability } p_1 \\
(0, 1, \cdots, 0) & \text{with probability } p_2 \\
\vdots & \\
(0, 0, \cdots, 1) & \text{with probability } p_m,
\end{cases}
\]
and the number of offspring produced by taking each action is given by:

\[
\begin{align*}
\mathbf{x}_{i,t}^B &= \beta_{i1}\lambda_1 + \cdots + \beta_{iK}\lambda_K \\
&\quad \cdots \\
\mathbf{x}_{m,t}^B &= \beta_{m1}\lambda_1 + \cdots + \beta_{mk}\lambda_K.
\end{align*}
\]

We assume that

**Assumption 8.** \(\lambda_1, \cdots, \lambda_k\) are independent random variables with some well-behaved distribution functions, such that \((x_1, \cdots, x_m)\) and \(\log(p_1x_1 + \cdots + p_mx_m)\) have finite moments up to order 2 for all \(p = (p_1, \cdots, p_m)\) and \(B = (\beta_{ij})_{m \times k}\).

**Assumption 9.** \((\lambda_1, \cdots, \lambda_k)\) is IID over time and identical for all individuals in a given generation.

Similar to the binary choice model, it is convenient to define factor loadings of type \(f = (p, B)\) individuals. Define \(\mathbf{\alpha} = (\alpha_1, \cdots, \alpha_k) = pB:\)

\[
(\alpha_1, \cdots, \alpha_k) = (p_1, \cdots, p_m) \begin{pmatrix}
\beta_{11} & \cdots & \beta_{1k} \\
\vdots & \ddots & \vdots \\
\beta_{m1} & \cdots & \beta_{mk}
\end{pmatrix}.
\]

(4.9)

Note that \(\alpha_1 + \cdots + \alpha_k = 1\) by definition.

Suppose that the total number of type \(f\) individuals in generation \(T\) is \(n_T^f\), the following proposition gives us the log-geometric-average growth rate of type \(f\) in the general \(m\)-choice \(k\)-factor setting.

**Proposition 10.** Under Assumptions 8-9, as the number of generations and the number of individuals in each generation increases without bound, \(T^{-1} \log n_T^f\) converges in probability to the log-geometric-average growth rate

\[
\mu(p, B) = \mathbb{E}[\log(pB\lambda')] = \mathbb{E}[\log(\alpha\lambda')].
\]

(4.10)
Proposition 10 characterizes the log-geometric-average growth rate as a function of type $f$. The next proposition gives the optimal type $f^*$ that maximizes (4.10).

**Proposition 11.** Under Assumptions 8-9, the optimal factor loading $\alpha^* = (\alpha_1^*, \cdots, \alpha_k^*)$ that maximizes (4.10) is given by:

$$
\alpha^* = \begin{cases} 
(1, 0, \cdots, 0) & \text{if } \mathbb{E} \left[ \frac{\lambda_2}{\lambda_1} \right] < 1, \mathbb{E} \left[ \frac{\lambda_3}{\lambda_1} \right] < 1, \cdots, \mathbb{E} \left[ \frac{\lambda_k}{\lambda_1} \right] < 1 \\
(0, 1, \cdots, 0) & \text{if } \mathbb{E} \left[ \frac{\lambda_1}{\lambda_2} \right] < 1, \mathbb{E} \left[ \frac{\lambda_3}{\lambda_2} \right] < 1, \cdots, \mathbb{E} \left[ \frac{\lambda_k}{\lambda_2} \right] < 1 \\
\cdots \\
(0, 0, \cdots, 1) & \text{if } \mathbb{E} \left[ \frac{\lambda_1}{\lambda_k} \right] < 1, \mathbb{E} \left[ \frac{\lambda_2}{\lambda_k} \right] < 1, \cdots, \mathbb{E} \left[ \frac{\lambda_{k-1}}{\lambda_k} \right] < 1 \\
\text{solution to (4.12) otherwise.} 
\end{cases} 
$$

(4.11)

In the last case, suppose without loss of generality $\alpha^* = (\alpha_1^*, \cdots, \alpha_i^*, 0, \cdots, 0)$. That is, $\alpha_1, \cdots, \alpha_i$ are non-zero, $\alpha_{i+1}, \cdots, \alpha_k$ are zero. Then $\alpha^*$ in the last case of (4.11) is defined implicitly by:

$$
\mathbb{E} \left[ \frac{\lambda_1}{\alpha_1^* \lambda_1 + \cdots + \alpha_i^* \lambda_i} \right] = \cdots = \mathbb{E} \left[ \frac{\lambda_i}{\alpha_1^* \lambda_1 + \cdots + \alpha_i^* \lambda_i} \right] = 1, 
$$

(4.12)

and $\alpha^*$ satisfies:

$$
\left\{ \begin{array}{l}
\mathbb{E} \left[ \frac{\lambda_{i+1}}{\alpha_1^* \lambda_1 + \cdots + \alpha_i^* \lambda_i} \right] < 1 \\
\cdots \\
\mathbb{E} \left[ \frac{\lambda_k}{\alpha_1^* \lambda_1 + \cdots + \alpha_i^* \lambda_i} \right] < 1.
\end{array} \right. 
$$

(4.13)

As a result, the growth-optimal type $f^* = (p^*, B^*)$ is given by

$$
p^* B^* = \alpha^*.
$$

Note that in Proposition 11, it is not possible to fully characterize $\alpha^*$ simply by the ratios $\mathbb{E} [\lambda_i/\lambda_j]$. However, there is still a natural analogue to the binary choice model by (4.12) and (4.13). $\alpha^* = (\alpha_1^*, \cdots, \alpha_i^*, 0, \cdots, 0)$ is optimal if and only if the expectation of any irrelevant factor divided by the optimal combination of factor
is less than 1, and any factor in the optimal combination divided by the optimal combination is equal to 1. Intuitively, this means that any factor in the optimal combination is adding a useful degree of freedom.

When the number of factors is no more than the number of choices: \( k \leq m \), the maximization actually takes place in the \( k \) dimensional space \((\alpha_1, \cdots, \alpha_k)\). Putting it another way, there might be multiple solutions for the original probabilities \((p_1, \cdots, p_m)\) that correspond to the same factor combinations \((\alpha_1, \cdots, \alpha_k)\), and therefore the same growth rates.

It is important to reduce the dimensionality on which maximization takes place. If the dimension of the optimization problem is very large, then in practice a population won’t be large enough for there to be a reasonable initial representation of all possible types. The factor model reduces the dimensionality of the problem, however, and makes it considerably more tractable, and more possible for the population to exhibit characteristics that respond to all the lower dimensional range of environmental uncertainty.

### 4.6 Discussion

Many species have a social structure in which individuals form groups and the aggregation of individuals promotes the fitness of group members. When selection for a biological trait in such populations depends on the difference between groups rather than individual differences within a group, it is described as “group selection” in evolutionary biology.

The debate surrounding genetic, kin, and group selection began over four decades ago, but has recently become more animated thanks to Nowak et al. (2010), who challenge inclusive fitness theory in the study of social evolution by arguing that it is not a constructive theory that allows a useful mathematical analysis of evolutionary processes. Moreover, they conclude that inclusive fitness is neither useful nor necessary to explain the evolution of eusociality or other phenomena. However, this view was sharply criticized by a flurry of responses by many leading evolutionary biolo-
gists (Abbot et al. 2011, Boomsma et al. 2011, Strassmann et al. 2011, Ferriere and Michod 2011, Herre and Wcislo 2011), who observe that the more general inclusive fitness theory has stimulated the extensive empirical literature over the past 40 years in the fields of behavioral and evolutionary ecology (Abbot et al. 2011), and that kin selection is a strong, vibrant theory that forms the basis for our understanding of how social behavior has evolved (Strassmann et al. 2011).

On the other hand, a significant amount of research suggests that group selection and kin selection (inclusive fitness) are essentially one process (Queller 1992, Lehmann et al. 2007, Wild et al. 2009, Wade et al. 2010, Marshall 2011, Lion et al. 2011), both seeking to characterize the genetic structure of a population but in different ways. These authors argue that it is now time to step back from the details of the specific arguments and consider the more general question of how evolution works in structured populations. This line of inquiry has the potential to generate insights beyond areas to which it has traditionally been applied (Lion et al. 2011).

Instead of entering into this debate, we propose to reconcile these opposing perspectives by studying the impact of selection on behavior and deriving evolutionary implications that cut across species, physiology, and genetic origins. As a direct consequence of this behavioral approach, we have shown that what appears to be group selection may, in fact, simply be the consequence of natural selection occurring in stochastic environments with reproductive risks that are correlated across individuals. In particular, we provide an evolutionary model with population dynamics for the simplest form of behavior, a binary choice, and derive the implications of selection on the behavior of individuals that share certain characteristics. Not surprisingly, individuals with similar characteristics experience similar selective pressures, hence evolution in stochastic environments with systematic risk can generate empirical phenomena that are consistent with group selection. In fact, Nature does select for “groups” of individuals with optimal characteristics and the optimal behavior within selected groups is simply a reflection of optimality of the characteristics of that group with respect to the given environment. Moreover, it is possible that multiple groups achieve the same optimal growth rate but through different means,
i.e., many combinations of behavior and characteristics can be optimal, leading to considerable variation in the types of behavior and characteristics in the population.

Hamilton's great insight was that individual fitness is not maximized by social evolution; inclusive fitness is (Hamilton 1963, Hamilton 1964). The idea that something other than the individual organism could be the fitness-maximizing unit was completely revolutionary at the time and opened new research areas that are still being explored (Ferriere and Michod 2011). We have shown that, in addition to Hamilton's insight, individuals with highly correlated risks will appear to form “groups” in evolution, even if their actions are, in fact, totally autonomous, mindless, and, prior to natural selection, uniformly randomly distributed in the population. Although this result seems to eliminate the need for a separate theory of group selection, the unique and important evolutionary implications of multiple sources of correlated systematic risk suggest that a separate term for this phenomenon may be worthwhile.
Chapter 5

Contagion and the Evolutionary Survival of Diverse Investment Strategies

5.1 Introduction

One of the most influential ideas in all the social sciences is the Efficient Markets Hypothesis (Samuelson 1965, Fama 1970), the notion that market prices "fully reflect all available information". Rationality is the key assumption behind the Efficient Markets Hypothesis. It is widely believed that agents with incorrect beliefs will be driven out of the market by agents with correct beliefs (Fama 1965), and market pressure would eventually result in behavior consistent with maximization (Alchian 1950, Friedman 1953).

However, accumulating evidence from psychology, cognitive science, behavioral economics and finance has documented significant inconsistencies to the rationality assumption and the Efficient Markets Hypothesis. The Efficient Markets Hypothesis has been complemented by the Darwinian selection perspective to understand the dynamics of market selection. The idea of natural selection in economics can be traced back to 1950s (Alchian 1950, Penrose 1952, Friedman 1953). In recent years, the
Adaptive Markets Hypothesis (Lo 2004) provides an evolutionary perspective and reconciles economic theories based on the Efficient Markets Hypothesis with behavioral economics: the neoclassical models of rational behavior can coexist with behavioral models, and what was cited as counterexamples to rationality—loss aversion, over-confidence, overreaction, and other behavioral biases—are, in fact, consistent with an evolutionary model of human behavior (Brennan and Lo 2011).

In this chapter, we model the contagion of investment ideas and study its implications for the survival of investment strategies from an evolutionary perspective. Motivated by the binary choice model (Brennan and Lo 2011), we consider a world where each investor has a propensity to invest in one of the two strategies. Investors with higher realized returns produce more “offspring” in the next period by transmitting their ideas to other investors from social interaction. Selection occurs at the level of investors’ behavior: the propensity to invest in one of the two strategies.

We demonstrate that heterogeneous investment styles can coexist in the long run, implying a wider variation of diverse strategies compared to traditional portfolio theories (Markowitz 1952, Merton 1972). This is consistent with stylized facts in modern financial markets, where many competing investment “styles” or “philosophies” coexist, such as value versus growth, aggressive versus defensive, momentum versus contrarian, “buy what you know” versus diversifying, and so forth. Yet in almost all past models of evolution of investment strategies, a single strategy dominates (Blume and Easley 1992, Sandroni 2000, Evstigneev et al. 2002, Amir et al. 2005). We show that the survival of diversity is a consequence of general principles of evolution in the face of risk.

Our model provides a framework for general multiperiod dynamics of contagion of investment strategies. The vast bulk of the literature on evolutionary survival of financial trading strategies has focused on wealth accumulation of individuals, and how this interacts with trading impact (see, for example, Blume and Easley (2006) and references therein). We instead focus on evolution via contagion of financial trading strategies. Specifically, and in contrast with a few studies taking this approach (Hirshleifer and Teoh 2009, Han and Hirshleifer 2013, Burnside et al. 2014), we allow
for fairly general distributions of offspring, instead of, for example, a Moran process (Moran 1958) in which the number of adopters changes by one in each generation. This generality allows us to give a general characterization of which strategies survive in the long run in relation to security return characteristics, including mean returns, betas, systematic and idiosyncratic volatilities.

More generally, our approach may lead to additional insights for the survival of a wide range of hedge funds. The investment strategies involved in hedge funds are highly diversified and there is considerable heterogeneity in the historical characteristics of the various categories of hedge fund investment styles (Chan et al. 2006). With relatively low barriers to entry and exit, and extremely high attrition rates compared with other sectors of the financial services industry (Lo et al. 2004), the hedge fund sector is considered the “Galápagos Islands” of finance (Lo 2008). In fact, our framework suggests that diversity persists even within a single non-partitioned environment, which is surprising compared with Darwin’s observations in the Galápagos Islands\(^1\) back in 1830s. This is consistent with the survival of a diverse range of hedge funds in modern financial markets which is highly interconnected.

This chapter differs from the existing literature in several aspects. In particular, the survival of a single dominant strategy has appeared in both the classical portfolio theories (Markowitz 1952, Sharpe 1964, Merton 1972) and the evolutionary finance literature (Sandroni 2000, Sandroni 2005, Evstigneev et al. 2006). Different portfolio rules are found to survive in different studies of market selection, including the Kelly rule (Kelly Jr. 1956, Lensberg and Schenk-Hoppé 2007), the CAPM rule (Hens and Schenk-Hoppé 2005), conditional expected payoff rule (Lensberg 1999, Evstigneev et al. 2002, Amir et al. 2005), etc. Our results highlight the coexistence of a diverse set of investment strategies as a consequence of general principles of evolution in the face of risk.

The market selection dynamics for financial assets and investment strategies has been explored from a wealth accumulation perspective (Evstigneev et al. 2002, Amir

\(^1\)In biological evolution, it is an example of adaptation when a species migrates into multiple segmented environments, because the islands are distant from the mainland, have different environments, and migration between the islands is difficult.
et al. 2005, Hens and Schenk-Hoppé 2005, Evstigneev et al. 2006). Some studies found that agents with more accurate beliefs will accumulate more wealth and dominate the economy (Sandroni 2000, Sandroni 2005), while others argued that wealth dynamics need not lead to rules that maximize expected utility using rational expectations (Blume and Easley 1992), and agents with wrong beliefs may drive out agents with correct beliefs (Blume and Easley 2006). Instead of studying the dynamics of wealth accumulation, we focus on evolution via contagion of financial trading strategies.

Empirical evidence for contagion in financial markets has been collected in stock markets (Barber et al. 2003, Hong et al. 2004, Barber and Odean 2008), housing markets (Burnside et al. 2014), and hedge funds (Boyson et al. 2010). The dynamics of contagion and its implications for financial markets has been investigated by a few studies (Kyle and Xiong 2001, Han and Hirshleifer 2013). Hirshleifer and Teoh (2009) provide a review of thought and behavior contagion in capital markets. Here we provide a theoretical framework for the multiperiod dynamics of contagion of investment strategies with fairly general distributions of offspring.

Research on the performance of rational versus irrational traders has also adopted evolutionary ideas. It is shown that irrational traders can survive and diverge prices significantly from fundamental values (De Long et al. 1990, De Long et al. 1991, Biais and Shadur 2000, Hirshleifer and Luo 2001, Hirshleifer et al. 2006, Kogan et al. 2006b, Yan 2008). In our framework, the reproducing units are instances of the investment strategies or traits, not investors or traders. Our focus on contagion implies that investors with higher realized returns tend to talk about their results and persuade other individuals, and are therefore more likely to transmit their investment ideas to other individuals in the population. As a result, receivers are more likely to emulate a strategy that has resulted in high payoff.

In the remainder of this chapter, we first describe the binary choice model and introduce strategy returns into our framework. Section 5.3 solves the model and provides comparative statics effects on the optimal behavior with respect to each strategy’s return characteristics. Section 5.4 endogenizes strategy returns and considers investor behavior in equilibrium trading. We conclude in Section 5.5.
5.2 Binary Choice Model

Consider two investment strategies $a$ and $b$ in discrete-time, each generating gross returns $X_a \in (0, \infty)$ and $X_b \in (0, \infty)$ in one period. The returns in the $t$-th period are denoted by $(X_{a,t}, X_{b,t})$, which are independently and identically distributed (IID) over time $t = 1, 2, \ldots$, and described by the probability distribution function $\Phi(X_a, X_b)$. We assume that:

**Assumption 10.** $(X_a, X_b)$ and $\log(fX_a + (1-f)X_b)$ have finite moments up to order 2 for all $f \in [0, 1]$.

Consider a population of investors that live for only one period, during which they make only one decision: choose to invest in either strategy $a$ or $b$. Each investor’s propensity to invest in strategy $a$ is denoted by $f \in [0, 1]$: she chooses strategy $a$ with probability $f$ and strategy $b$ with probability $1-f$. We will refer to $f$ as the investor’s behavior henceforth. For example, if strategy $a$ is an active investment strategy and strategy $b$ is a passive one, then $f$ represents the propensity that the investor chooses the active strategy.

Depending on their choices, each investor obtains gross returns $X_a$ or $X_b$, which we assume is also the number of offspring generated by that investor. Hence individual $i$’s offspring $X_i'$ is simply given by:

$$X_i' = I_i^f X_a + (1 - I_i^f) X_b, \quad I_i^f \equiv \begin{cases} 1 & \text{with probability } f \\ 0 & \text{with probability } 1 - f. \end{cases} \tag{5.1}$$

We ascribe no intelligence or volition to each investor’s behavior; we are simply providing a formal representation for it, and then investigating its evolutionary prospects. To that end, we assume that newly infected individuals behave identically to those

---

2Some models assume a monotonic mapping from the gross returns $X_a$ and $X_b$ to the number of offspring (see Robson (1996a) for example). However, this mapping is non-essential in generating the behaviors considered in our model (Zhang et al. 2014b). In addition, strictly speaking the number of offspring should be integers, but what essentially matters in our model is the relative frequency of each type of investors. Therefore, we directly use $X_a$ and $X_b$ as the number of offspring for simplicity.
from whom they acquired the behavior\(^3\), i.e., they choose between strategy \(a\) and \(b\) according to the same \(f\). Hence the population may be viewed as being comprised of "types" of individuals indexed by \(f\) that range from 0 to 1. Equivalently from the population level, for a group of investors with the same behavior \(f\), \(f\) can also be regarded as the percentage of investors that pursue strategy \(a\) in that group.

We would like to emphasize that (5.1) represents the crucial dynamics between two periods in order to study the evolution of each type of investors over many generations. It models the contagion of investment ideas between generations\(^4\). Investors with higher realized returns tend to talk about their results and persuade other individuals, and are therefore more likely to transmit their investment ideas to other individuals in the population. As a result, receivers are more likely to emulate a strategy that has resulted in high payoff. This dynamics implies that investors with higher realized returns produce more offspring with the same behavior \((f)\) as themselves in the next period. This is an important distinction from the existing literature which primarily focus on wealth accumulation of a particular investor.

Nevertheless, our approach is closely related to the interpretation of wealth accumulation in a general sense. From the evolutionary perspective, investors with higher realized returns accumulate more wealth, and therefore tend to have more resources and become more influential among the population. This is analogous to spreading the investment ideas to more individuals. For this reason, these investors are also more likely to produce more offspring, which justifies (5.1) in an alternative perspective.

### 5.2.1 Population Dynamics

We first make a few clarifying comments regarding our notation. Individuals in a given generation \(t\) are indexed by \(i\), and generations are indexed by \(t = 1, \cdots, T\). We

---

\(^3\)We still call these individuals "offspring" of their "parents" to be consistent with the evolutionary context. But it should be emphasized that the reproducing units are instances of the investment strategies or traits, not investors.

\(^4\)Han and Hirshleifer (2013), for example, studies a model of market selection with social interactions and information flows.
occasionally omit the $t$ subscript because the randomness across time is IID, unless
we wish to emphasize the temporal ordering of the variables. Finally, a superscript $f$
will denote the particular type of investor as defined by the decision rule in (5.1).

With these notational conventions in mind, let $n_{t}^{f}$ be the total number of type-$f$
investors in period $t$, which is simply the sum of all the offspring from the type-$f$
investors of the previous period:

$$n_{t}^{f} = \sum_{i=1}^{n_{t-1}^{f}} X_{i,t}^{f} = \left( \sum_{i=1}^{n_{t-1}^{f}} I_{i,t}^{f} \right) X_{a,t}^{f} + \left( \sum_{i=1}^{n_{t-1}^{f}} (1 - I_{i,t}^{f}) \right) X_{b,t}^{f}.$$ 

Applying the Kolmogorov Law of Large Numbers to the sum $\sum_{i} I_{i,t}^{f}/n_{t-1}^{f}$ as $n_{t-1}^{f}$
increases without bound, we have the following population growth relationship from
period $t - 1$ to period $t$ almost surely:

$$n_{t}^{f} = n_{t-1}^{f} [fX_{a,t} + (1 - f)X_{b,t}] .$$

Through backward recursion, the population size of type-$f$ investors in period $T$
is given by

$$n_{T}^{f} = \prod_{t=1}^{T} [fX_{a,t} + (1 - f)X_{b,t}] = \exp \left\{ \sum_{t=1}^{T} \log [fX_{a,t} + (1 - f)X_{b,t}] \right\} ,$$

where we have assumed that $n_{0}^{f} = 1$ without loss of generality. Taking logarithm of
wealth and applying the Kolmogorov Law of Large Numbers again, we have:

$$\frac{1}{T} \log n_{T}^{f} \xrightarrow{\text{a.s.}} \mathbb{E}[\log (fX_{a} + (1 - f)X_{b})] \quad (5.2)$$

as $T$ increases without bound where "$\xrightarrow{\text{a.s.}}$" in (5.2) denotes almost sure convergence.

The expression (5.2) is simply the expectation of the log-geometric-average growth
rate of the population, and we will call it $\alpha(f)$ henceforth:

$$\alpha(f) = \mathbb{E}[\log (fX_{a} + (1 - f)X_{b})] . \quad (5.3)$$
The optimal $f$ that maximizes (5.3) is given by Brennan and Lo (2011):

**Proposition 12.** Under Assumption 10, the growth-optimal behavior $f^*$ that maximizes (5.3) is:

$$f^* = \begin{cases} 
1 & \text{if } \mathbb{E}[X_b/X_a] < 1 \\
\text{solution to (5.5)} & \text{if } \mathbb{E}[X_a/X_b] \geq 1 \text{ and } \mathbb{E}[X_b/X_a] \geq 1 \\
0 & \text{if } \mathbb{E}[X_a/X_b] < 1,
\end{cases} \tag{5.4}$$

where $f^*$ is defined implicitly in the second case of (5.4) by:

$$\mathbb{E} \left[ \frac{X_a - X_b}{f^*X_a + (1 - f^*)X_b} \right] = 0 \tag{5.5}$$

and the expectations in (5.4)-(5.5) are with respect to the joint distribution $\Phi(X_a, X_b)$.

### 5.2.2 Strategy Returns

Proposition 12 is true for any return distribution $\Phi(X_a, X_b)$ that satisfies Assumption 10. However, it is interesting to give $(X_a, X_b)$ more structure and study how that affects the optimal investment behavior $f^*$.

In the spirit of Han and Hirshleifer (2013), let $r$ be the common component of returns shared by strategy $a$ and $b$. Let $\epsilon_a$ and $\epsilon_b$ be the strategy-specific component. Let $\mu_a$ and $\mu_b$ be the mean returns of strategy $a$ and $b$.

**Assumption 11.** The gross returns to the two strategies are

$$X_a = \mu_a + \beta_a r + \epsilon_a$$
$$X_b = \mu_b + \beta_b r + \epsilon_b,$$

where $\beta_a > 0$ and $\beta_b > 0$ are the sensitivity of strategy returns to the common return component. $r$, $\epsilon_a$ and $\epsilon_b$ are independent and bounded random variables such that $X_a$ and $X_b$ are always positive. $\mathbb{E}[r] = \mathbb{E}[\epsilon_a] = \mathbb{E}[\epsilon_b] = 0$.  

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Assumption 11 is very general in the sense that no restriction is imposed on the relationship between these two investment strategies. For instance, they could be active versus passive investments, value versus growth stocks, fundamental versus quantitative strategies, etc. Different assumptions on the characteristics of $\mu_i, \beta_i, \epsilon_i, (i = a, b)$ and $r$ justify different cases. The next section studies the optimal investment behavior $f^*$ under this general assumption.

### 5.3 Optimal Investment Strategies

This section asks the question: how does the optimal investment strategy change as each strategy’s characteristics change, including the mean returns, return betas, and return variances. We first identify conditions for a single strategy to be optimal, and then study the case where the long-run optimal population consists of a mixture of investors in both strategies.

#### 5.3.1 Single Dominant Strategy

By Proposition 12, the expected value of the ratio $X_a/X_b$ and $X_b/X_a$ determines whether the optimal investment behavior involves only one strategy or a combination of the two. Let $y = X_a/X_b$, and

$$
E[y] = E \left[ \frac{X_a}{X_b} \right] = E \left[ \frac{\mu_a + \beta_a r + \epsilon_a}{\mu_b + \beta_b r + \epsilon_b} \right], \quad (5.6)
$$

$$
E[1/y] = E \left[ \frac{X_b}{X_a} \right] = E \left[ \frac{\mu_b + \beta_b r + \epsilon_b}{\mu_a + \beta_a r + \epsilon_a} \right]. \quad (5.7)
$$

We focus on the case where strategy $a$ dominates the population ($f^* = 1$). The case where strategy $b$ dominates the population ($f^* = 0$) is similar. It is obvious from (5.7) that one has the following comparative statics effects on the conditions for $f^* = 1$:

**Proposition 13** (Comparative Statics for Mean Return). Under Assumptions 10 and 11, strategy $a$-investors dominate the population if $E[1/y] < 1$, which tends to occur ($E[1/y]$ decreases) if:
• the mean return of strategy \( a, \mu_a \), increases;

• the mean return of strategy \( b, \mu_b \), decreases.

It is not surprising that a higher expected return encourages that strategy to be dominant.

To get results for other return characteristics involved in (5.6)-(5.7), we need to better understand \( \mathbb{E}[y] \) and \( \mathbb{E}[1/y] \). There is no general formula for the expected value of the ratio of two random variables, but we can use the Taylor approximation of \( y \) as a function of \( r, \epsilon_a \) and \( \epsilon_b \) to estimate (5.6)-(5.7). For example,

\[
y(r, \epsilon_a, \epsilon_b) = \frac{X_a}{X_b} = \frac{\mu_a + \beta_a r + \epsilon_a}{\mu_b + \beta_b r + \epsilon_b} = y(0, 0, 0) + \frac{\partial y_0}{\partial r} r + \frac{\partial y_0}{\partial \epsilon_a} \epsilon_a + \frac{\partial y_0}{\partial \epsilon_b} \epsilon_b + \frac{1}{2} \left( \frac{\partial^2 y_0}{\partial r^2} r^2 + \frac{\partial^2 y_0}{\partial \epsilon_a^2} \epsilon_a^2 + \frac{\partial^2 y_0}{\partial \epsilon_b^2} \epsilon_b^2 + 2 \frac{\partial^2 y_0}{\partial r \partial \epsilon_a} \epsilon_a r + 2 \frac{\partial^2 y_0}{\partial r \partial \epsilon_b} \epsilon_b r + 2 \frac{\partial^2 y_0}{\partial \epsilon_a \partial \epsilon_b} \epsilon_a \epsilon_b \right) + o(r^2, \epsilon_a^2, \epsilon_b^2).
\]

After taking expected value of \( y \), all the linear terms vanish because \( \mathbb{E}[r] = \mathbb{E}[\epsilon_a] = \mathbb{E}[\epsilon_b] = 0 \). All the second order cross terms also vanish because \( r, \epsilon_a \) and \( \epsilon_b \) are independent. Therefore, \( \mathbb{E}[y] \) can be approximated by \( y(0, 0, 0) \) and second order terms \( \text{Var}(r), \text{Var}(\epsilon_a) \) and \( \text{Var}(\epsilon_b) \). Similar approximation is also true for \( \mathbb{E}[1/y] \), which is summarized in the following:

**Lemma 3.** Under Assumptions 10 and 11, up to second order Taylor approximation with respect to \( r, \epsilon_a \) and \( \epsilon_b \),

\[
\mathbb{E}[y] = \mathbb{E}\left[\frac{X_a}{X_b}\right] \approx \frac{\mu_a}{\mu_b} + \frac{\beta_a \beta_b^2}{\mu_b^3} \left( \frac{\mu_a}{\beta_a} - \frac{\mu_b}{\beta_b} \right) \text{Var}(r) + \frac{\mu_a}{\mu_b^3} \text{Var}(\epsilon_b),
\]

\[
\mathbb{E}[1/y] = \mathbb{E}\left[\frac{X_b}{X_a}\right] \approx \frac{\mu_b}{\mu_a} + \frac{\beta_a \beta_b^2}{\mu_a^3} \left( \frac{\mu_b}{\beta_b} - \frac{\mu_a}{\beta_a} \right) \text{Var}(r) + \frac{\mu_b}{\mu_a^3} \text{Var}(\epsilon_a).
\]

The beta-adjusted mean returns \( \mu_a/\beta_a \) and \( \mu_b/\beta_b \) play a critical role in determining the direction of \( \text{Var}(r) \)’s impact on \( \mathbb{E}[y] \) and \( \mathbb{E}[1/y] \). We will discuss this further after the following results.
To gain insights into the determinants of a single dominant strategy, we describe additional comparative statics effects on the conditions for $f^* = 1$ (choose strategy $a$).

**Proposition 14** (Comparative Statics for Return Beta). Under Assumptions 10 and 11, strategy $a$-investors dominate the population if $E[1/y] < 1$. Up to second order Taylor approximation with respect to $r$, $\epsilon_a$ and $\epsilon_b$, this tends to occur ($E[1/y]$ decreases) if:

- the sensitivity of strategy $b$ to the common component, $\beta_b$, increases;

- the sensitivity of strategy $a$ to the common component, $\beta_a$, increases, conditional on strategy $a$'s beta-adjusted mean return greater than twice strategy $b$'s beta-adjusted mean return: $\frac{\mu_a}{\beta_a} > 2 \cdot \frac{\mu_b}{\beta_b}$;

- the sensitivity of strategy $a$ to the common component, $\beta_a$, decreases, conditional on strategy $a$'s beta-adjusted mean return smaller than twice strategy $b$'s beta-adjusted mean return: $\frac{\mu_a}{\beta_a} < 2 \cdot \frac{\mu_b}{\beta_b}$.

We are considering the conditions for strategy $a$ to dominate in this case, and the results are not symmetric with respect to $\beta_a$ and $\beta_b$. First of all, a higher $\beta_b$ always encourages strategy $a$ to be dominant. Intuitively, this is because the log-geometric-average growth rate (5.3) is nonlinear with respect to the returns, and therefore upsides and downsides for strategy $b$'s realized returns don’t offset. As a result, high systematic risk of the competing strategy $b$ promotes success of strategy $a$ because the risk causes wipeouts of strategy $b$ in market selection.

However, this is not always the case for $\beta_a$. For the same reason described above, high systematic risk of strategy $a$ reduces its own success, but this is only true conditional on strategy $a$’s beta-adjusted mean return comparable to or smaller than strategy $b$’s. If the reverse is true—the mean return on strategy $a$ is sufficiently strong relative to its risk (strategy $a$’s beta-adjusted mean is twice or more higher than strategy $b$’s)—higher $\beta_a$ actually encourages strategy $a$ to be dominant. In other words, strategy $a$’s high beta-adjusted mean return serves as a protection from its own risk.
Proposition 15 (Comparative Statics for Return Variance). Under Assumptions 10 and 11, strategy a-investors dominate the population if \( \mathbb{E}[1/y] < 1 \). Up to second order Taylor approximation with respect to \( r, \epsilon_a \) and \( \epsilon_b \), this tends to occur (\( \mathbb{E}[1/y] \) decreases) if:

- the variance of strategy-specific component for a, \( \text{Var}(\epsilon_a) \), decreases;
- the variance of the common component, \( \text{Var}(r) \), increases, conditional on strategy a’s beta-adjusted mean return greater than strategy b’s beta-adjusted mean return: \( \frac{\mu_a}{\beta_a} > \frac{\mu_b}{\beta_b} \);
- the variance of the common component, \( \text{Var}(r) \), decreases, conditional on strategy a’s beta-adjusted mean return smaller than strategy b’s beta-adjusted mean return: \( \frac{\mu_a}{\beta_a} < \frac{\mu_b}{\beta_b} \).

Strategy a tends to dominate if its idiosyncratic variance is small, for the same reason as discussed for return betas. Intuitively, high variance tends to work against a strategy because of the nonlinearity of the long-term growth as reflected in (5.3), and therefore upsides and downsides for strategy a’s realized returns don’t offset.

Again, since we are considering the conditions for strategy a to dominate in this case, the results are not symmetric with respect to strategy a and strategy b’s idiosyncratic variances. It is interesting that strategy b’s idiosyncratic variance does not affect strategy a’s dominance, up to second order Taylor approximations.

The directional dependence on the variance of the common component is determined by the beta-adjusted mean returns. A higher variance of the common component encourages strategy a to be dominant only if its beta-adjusted mean return is higher than strategy b’s. To understand this, a higher \( \text{Var}(r) \) increases the variance of both strategies, and the overall effect therefore depends on the relative sizes of the betas of both strategies. However, the effect of risk also depends on the mean return. High mean return acts as a buffer that reduces the importance of risk. It is therefore the beta-adjusted mean return that matters, not just a comparison of betas.

Proposition 13-15 together give a complete picture of the comparative effects on the conditions for \( f^* = 1 \) (choose strategy a), with respect to mean returns, return
betas, and return variances. Parallel results can also be derived for \( f^* = 0 \) (choose strategy \( b \)) using approximations for \( E[y] \) in Lemma 3.

### 5.3.2 The Evolution of Diversity

In general, if the optimal behavior involves both strategies, \( f^* \) is given by (5.5). With Assumption 11, the first order condition becomes:

\[
E \left[ \frac{(\mu_a - \mu_b) + (\beta_a - \beta_b)r + (\epsilon_a - \epsilon_b)}{(f \mu_a + (1 - f)\mu_b) + (f \beta_a + (1 - f)\beta_b)r + (f \epsilon_a + (1 - f)\epsilon_b)} \right] = 0. \tag{5.8}
\]

Taking derivatives of (5.8) to \( \mu_a \) and \( \mu_b \), we immediately have the following obvious comparative statics effects on the optimal allocation \( f^* \).

**Proposition 16** (Comparative Statics for Mean Return). Under Assumptions 10 and 11, when the optimal behavior involves mixed strategies, the optimal frequency of strategy \( a \)-investors, \( f^* \), increases if:

- the mean return of strategy \( a \), \( \mu_a \), increases;
- the mean return of strategy \( b \), \( \mu_b \), decreases.

Not surprisingly, a higher expected return encourages investment in that strategy. To get more comparative statics effects, we again use Taylor expansion to approximate the first order condition (5.8).

**Lemma 4.** Under Assumptions 10 and 11, up to second order Taylor approximation with respect to \( r, \epsilon_a \) and \( \epsilon_b \), the first order condition (5.8) can be written as:

\[
0 = (\mu_a - \mu_b) [f\mu_a + (1 - f)\mu_b]^2 + \beta_a\beta_b [f\beta_a + (1 - f)\beta_b] \left( \frac{\mu_a}{\beta_a} - \frac{\mu_b}{\beta_b} \right) \text{Var}(r)
+ (1 - f)\mu_a\text{Var}(\epsilon_b) - f\mu_b\text{Var}(\epsilon_a).
\]

When \( E[X_a/X_b] \geq 1 \) and \( E[X_b/X_a] \geq 1 \), the optimal behavior involves mixed strategies, and \( f^* \) is given by Lemma 4, up to second order Taylor approximation. Similarly, we describe comparative statics effects on the optimal allocation \( f^* \).
**Proposition 17** (Comparative Statics for Return Beta). *Under Assumptions 10 and 11, when the optimal behavior involves mixed strategies, up to second order Taylor approximation with respect to \( r \), \( \epsilon_a \) and \( \epsilon_b \), the optimal frequency of strategy \( a \)-investors, \( f^* \), is:

- a downward quadratic function of \( \beta_a \), which is maximized when
  \[
  \beta_a = \max \left\{ 0, \frac{1}{2} \left( \frac{\mu_a}{\mu_b} - \frac{1 - f^*}{f^*} \right) \beta_b \right\};
  \]

- an upward quadratic function of \( \beta_b \), which is minimized when
  \[
  \beta_b = \max \left\{ 0, \frac{1}{2} \left( \frac{\mu_b}{\mu_a} - \frac{f^*}{1 - f^*} \right) \beta_a \right\}.
  \]

The dependency between the optimal behavior and return betas is not straightforward because it involves the optimal behavior \( f^* \) itself. Generally speaking, \( f^* \) is a downward quadratic function of \( \beta_a \), so when the systematic risk of strategy \( a \) increases, the optimal frequency of \( a \)-investors decreases, consistent with our previous discussions on the risks of returns in market selection. However, this is a conditional result that is only true when \( \beta_a \) is larger than \( \frac{1}{2} \left( \frac{\mu_a}{\mu_b} - \frac{1 - f^*}{f^*} \right) \beta_b \). Otherwise the reverse is true\(^5\).

Similarly, \( f^* \) is an upward quadratic function of \( \beta_b \), so when the systematic risk of strategy \( b \) increases, the optimal frequency of \( a \)-investors increases, also consistent with our previous discussions on the risks of returns in market selection. Again, this is a conditional result that is only true when \( \beta_b \) is larger than \( \frac{1}{2} \left( \frac{\mu_b}{\mu_a} - \frac{f^*}{1 - f^*} \right) \beta_a \). Otherwise the reverse is true.

**Proposition 18** (Comparative Statics for Return Variance). *Under Assumptions 10 and 11, when the optimal behavior involves mixed strategies, up to second order Taylor approximation with respect to \( r \), \( \epsilon_a \) and \( \epsilon_b \), the optimal frequency of strategy \( a \)-investors, \( f^* \), increases if:

\(^5\)We have assumed in Assumption 11 that \( \beta_a \) and \( \beta_b \) are always positive.
• the variance of strategy-specific component for a, \( \text{Var}(\epsilon_a) \), decreases;

• the variance of strategy-specific component for b, \( \text{Var}(\epsilon_b) \), increases;

• the variance of the common component, \( \text{Var}(r) \), increases, conditional on strategy a's beta-adjusted mean return greater than strategy b's beta-adjusted mean return: \( \frac{\mu_a}{\beta_a} > \frac{\mu_b}{\beta_b} \);

• the variance of the common component, \( \text{Var}(r) \), decreases, conditional on strategy a's beta-adjusted mean return smaller than strategy b's beta-adjusted mean return: \( \frac{\mu_a}{\beta_a} < \frac{\mu_b}{\beta_b} \).

There will be more strategy a-investors if strategy a's idiosyncratic variance is small, and if strategy b's idiosyncratic variance is large. This is consistent with our previous discussions on the risks of returns in market selection. Intuitively, a higher strategy-specific variance discourages investment in that strategy, because of the nonlinearity of the long-term growth as reflected in (5.3).

The directional dependence on the variance of the common component is again determined by the beta-adjusted mean returns. A higher variance of the common component encourages investment in the strategy with higher beta-adjusted mean return. The reason is similar to our previous discussions. A higher \( \text{Var}(r) \) increases the variance of both strategies, and the overall effect therefore depends on the relative sizes of the betas of both strategies. However, the effect of risk also depends on the mean return. High mean return acts as a buffer that reduces the importance of risk. It is therefore the beta-adjusted mean return that matters, not just a comparison of betas.

Proposition 16-18 together give a complete picture of the comparative statics effects on the optimal behavior \( f^* \), with respect to mean returns, return betas, and return variances.

\(^6\)In Han and Hirshleifer (2013) the opposite is true: variance promotes survival. This is because Han and Hirshleifer (2013) have incorporated a selection bias in what returns are reported, which is intensified by high variances. In contrast, this “self-enhancing” effect is removed here. Furthermore, the model considered here has a more general distribution in the number of offspring, which results in the long-run “evolutionary hedging” benefits to avoiding very low reproduction outcomes.
5.3.3 A Special Case

In this section we use the results derived above to study a special case where returns are further specified by:

**Assumption 12.** Strategy a and b has the same mean return. Strategy a has higher beta and higher strategy-specific variance than strategy b:

\[ \mu_a = \mu_b; \quad \beta_a > \beta_b; \quad \text{Var}(\epsilon_a) > \text{Var}(\epsilon_b). \]

To summarize these conditions, strategy a has higher systematic risk and higher volatility. This specification may suggest similar characteristics in several special cases, including active versus passive investing (Han and Hirshleifer 2013), growth versus value investing\(^7\), etc. We will call a the “riskier strategy” and b the “safer strategy”.

It immediately follows that the beta-adjusted mean return is higher for strategy b:

\[ \frac{\mu_a}{\beta_a} < \frac{\mu_b}{\beta_b}, \]

and Lemma 3 reduces to:

\[
\begin{align*}
\mathbb{E}[y] = \mathbb{E}
\left[
\frac{X_a}{X_b}
\right]
\approx 1 + \frac{\beta_a \beta_b^2}{\mu_b^3} \left( \frac{\mu_a}{\beta_a} - \frac{\mu_b}{\beta_b} \right) \text{Var}(r) + \frac{\mu_a}{\mu_b^3} \text{Var}(\epsilon_b),
\end{align*}
\]

\[
\begin{align*}
\mathbb{E}[1/y] = \mathbb{E}
\left[
\frac{X_b}{X_a}
\right]
\approx 1 + \frac{\beta_a^2 \beta_b}{\mu_a^3} \left( \frac{\mu_b}{\beta_b} - \frac{\mu_a}{\beta_a} \right) \text{Var}(r) + \frac{\mu_b}{\mu_a^3} \text{Var}(\epsilon_a) > 1.
\end{align*}
\]

Up to second order Taylor approximation, \(\mathbb{E}[1/y]\) is always greater than 1, which implies that strategy a alone is never optimal. The long-run optimal behavior is either purely strategy b (with higher beta-adjusted mean return), or a combination of both strategies, in which case the first order condition for \(f\) in Lemma 4 reduces to:

\[
0 = \left[ f \beta_a + (1 - f) \beta_b \right] (\beta_b - \beta_a) \text{Var}(r) + (1 - f) \text{Var}(\epsilon_b) - f \text{Var}(\epsilon_a),
\]

\(^7\)Although standard definition of growth versus value stock depends on the asset prices, empirical studies suggest that value and growth stocks may show similar return characteristics in Assumption 12 (see Fama and French (1993) for example).
from which the optimal $f^*$ can be solved. We summarize these observations in:

**Proposition 19.** Under Assumptions 10-12, up to second order Taylor approximation with respect to $r$, $\epsilon_a$ and $\epsilon_b$, strategy $a$ alone is never optimal. Strategy $b$ alone is optimal if

$$\text{Var}(\epsilon_b) < \beta_b(\beta_a - \beta_b)\text{Var}(r).$$

(5.9)

Otherwise the population consists of investors in both strategies in the long run, and the fraction of investors in strategy $a$ is given by:

$$f^* = \frac{\text{Var}(\epsilon_b) - \beta_b(\beta_a - \beta_b)\text{Var}(r)}{\text{Var}(\epsilon_a) + \text{Var}(\epsilon_b) + (\beta_a - \beta_b)^2\text{Var}(r)}.$$  

(5.10)

It is clear from Proposition 19 that the population tends to have only investors in strategy $b$ when the common component has a high volatility ($\text{Var}(r)$), the safer strategy has a low volatility ($\text{Var}(\epsilon_b)$), and the riskier strategy has a high beta ($\beta_a$). In the case that the population consists of investors in both strategies, the fraction of investors in strategy $a$ increases as the variance of the $a$-specific component ($\text{Var}(\epsilon_a)$) decreases, the variance of the $b$-specific component ($\text{Var}(\epsilon_b)$) increases, and the variance of the common component ($\text{Var}(r)$) decreases. This is consistent with our previous discussions that risk tends to reduce the evolutionary success of a strategy.

### 5.4 Evolutionary Survival of Diversity in Market Equilibrium

So far, we have viewed strategy returns as exogenous variables (Assumption 11). However, in a market where there is an imbalanced supply and demand for strategy $a$ and $b$, the returns will reflect this imbalance. To consider effects on supply and demand, we need to first specify the universe of investment behaviors. Let

$$U = \left\{0, \frac{1}{K}, \frac{2}{K}, \ldots, 1\right\} = \{f_1, f_2, \cdots, f_{K+1}\}$$

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be a discrete universe that consists of \( K+1 \) types of investors. Let \( q^f_T \) be the frequency of type-\( f \) investors in the population in period \( T \):

\[
q^f_T = \frac{n^f_T}{\sum_{g \in U} n^g_T}.
\]

Clearly the frequencies of all types of investors sum to 1 in any period. Now we define the aggregate interest in strategy \( a \) in period \( T \) as the frequency-weighted average investment behavior in the population:

\[
\lambda_T = \sum_{f \in U} f q^f_T. \tag{5.11}
\]

By definition the aggregate interest starts from 0.5 in the beginning and evolves between 0 and 1 as the two strategies generate different returns. For example, as strategy \( a \) generates higher returns, investors with higher \( f \) generate more offspring in the next period, driving the aggregate interest in strategy \( a \) higher. This causes higher demand and lower supply for strategy \( a \), and as a result, higher costs and lower returns for investing in strategy \( a \). Based on this observation, we make:

**Assumption 13.** The gross returns to the two strategies are given by the internal returns (Assumption 11) adjusted by the aggregate interest in that period\(^8\):

\[
R_{a,T} = X_{a,T}(1 - \lambda_T) = (\mu_a + \beta_a r_T + \epsilon_{a,T})(1 - \lambda_T)
\]

\[
R_{b,T} = X_{b,T} \lambda_T = (\mu_b + \beta_b r_T + \epsilon_{b,T})\lambda_T.
\]

Simply put, the gross returns to a strategy is higher when the aggregate interest in that strategy is lower. Assumption 13 is a very simple way to capture the market impact of investors’ behavior. In fact, the dependence of strategy returns on supply and demand is linear. Although it is a highly simplified mathematical caricature of

\(^8\)More generally, \( X_a \) and \( X_b \) can be adjusted by a function of \( \lambda_t \): \( S(\lambda_t) \), or a function of the first difference in \( \lambda_t \): \( S(\lambda_t - \lambda_{t-1}) \), as long as \( S(\cdot) \) is monotonically increasing in \([0, 1]\). However, this does not change any subsequent results essentially based on simulation results. Therefore we use this simple linear specification from which one could analytically solve the equilibrium behavior (see Proposition 20).
reality, its implications are useful if the theory has captured the most relevant features of market equilibrium.

In general, more complicated assumptions can be made on the dependence of strategy returns on supply and demand at the expense of analytical simplicity. We discuss some alternatives in Section 5.5.

5.4.1 Equilibrium Behavior

We denote the new growth-optimal behavior by \( f^e \) with "e" meaning equilibrium. It is not difficult to see that \( f^e \) is given by Proposition 12 with \( X_a \) and \( X_b \) replaced by \( R_a \) and \( R_b \), and \( \lambda \) replaced by \( f^e \). In fact, it can be explicitly characterized in this case:

**Proposition 20.** Under Assumptions 10, 11, and 13, the equilibrium behavior \( f^e \) that maximizes the investor’s growth as \( T \) increases without bound is given by

\[
f^e = \mathbb{E}\left[ \frac{X_a}{X_a + X_b} \right] \in (0, 1).
\]

(5.12)

\( f^e \) is always closer to 1/2 than \( f^* \) given in Proposition 12 without the effect of supply and demand on strategy returns:

\[
|f^e - \frac{1}{2}| \leq |f^* - \frac{1}{2}|.
\]

It is interesting to see that the “all-in” strategy \( f = 0 \) or 1 is never optimal in this case. This is because, if an investor allocates all her wealth to one strategy, the aggregate interest in that strategy will grow very high and drive down its returns.

Investors are able to diversify the risk of over-supply and over-demand in one strategy because each investor’s decision is independent of each other. As a group of type-\( f \) investors, the law of large numbers diversifies each individual’s risk and guarantees that this group of investors have the right combination of strategy \( a \) and \( b \), and therefore grow at the optimal exponential rate. Imagine that if, on the contrary, all type-\( f \) investors’ decision are perfectly correlated to each other, then this group of
investors may suffer from investing only in the over-demanded strategy in a particular period and having low realized returns. In fact, these investors would essentially act as one investor in this case, and therefore not benefit from the diversification across the population that share the same behavior \( f \).

Proposition 20 highlights the fact that both strategies coexist in market equilibrium under rather general assumptions on strategy returns, implying a wider variation of diverse investment strategies compared to traditional portfolio theories (Markowitz 1952, Sharpe 1964, Merton 1972) and the evolutionary finance literature (Blume and Easley 1992, Sandroni 2000, Evstigneev et al. 2002, Amir et al. 2005). This is consistent with stylized facts in modern financial markets, where many competing investment “styles” or “philosophies” coexist, such as value versus growth, aggressive versus defensive, momentum versus contrarian, “buy what you know” versus diversifying, and so forth.

Our framework does not depend on any form of intelligence or investor preferences, and is solely a consequence of natural selection of investment strategies in financial markets with systematic risks. In fact, preference itself may also be shaped by natural selection to maximize growth in the long run (Zhang et al. 2014b).

Next we provide some comparative statics effects for the equilibrium behavior \( f^e \).

(5.12) can be rewritten as:

\[
\begin{align*}
\hat{f}^e &= E \left[ \frac{\mu_a + \beta_a r + \epsilon_a}{(\mu_a + \mu_b) + (\beta_a + \beta_b) r + (\epsilon_a + \epsilon_b)} \right]. 
\end{align*}
\] (5.13)

It is not surprising that \( f^e \) increases as \( \mu_a \) increases and \( \mu_b \) decreases. Using Taylor approximation to (5.13) with respect to \( r \), \( \epsilon_a \) and \( \epsilon_b \), we have the following:

**Proposition 21.** Under Assumptions 10, 11, and 13, up to second order Taylor approximation with respect to \( r \), \( \epsilon_a \) and \( \epsilon_b \), the equilibrium behavior \( f^e \) is explicitly given by

\[
\begin{align*}
\hat{f}^e &= \frac{\mu_a}{\mu_a + \mu_b} + \frac{\beta_a \beta_b (\beta_a + \beta_b)}{(\mu_a + \mu_b)^3} \left( \frac{\mu_a}{\beta_a} - \frac{\mu_b}{\beta_b} \right) Var(r) - \frac{\mu_b}{(\mu_a + \mu_b)^3} Var(\epsilon_a) + \frac{\mu_a}{(\mu_a + \mu_b)^3} Var(\epsilon_b). 
\end{align*}
\]
Qualitatively these results are similar to Proposition 16-18. Strategy-specific variances discourage investment in that strategy, while variance of the common component encourages investment in the strategy with higher beta-adjusted mean return.

From Proposition 21, the equilibrium behavior \( f^e \) can also be seen as an adjustment from \( \frac{\mu_a}{\mu_a+\mu_b} \), which is simply the ratio of mean returns. \( \text{Var}(r), \text{Var}(\epsilon_a), \) and \( \text{Var}(\epsilon_b) \) serve as three terms that deviate \( f^e \) from its base value \( \frac{\mu_a}{\mu_a+\mu_b} \), and the direction and magnitude of this deviation are determined by both the mean returns and betas of the two strategies.

5.4.2 A Simulation Example

We provide a simulation example for the following two strategies in this section:

\[
X_a = \mu_a + \beta_a r + \epsilon_a \\
X_b = \mu_b + \beta_b r + \epsilon_b,
\]

where

\[
\mu_a = 3, \quad \mu_b = 2, \quad \beta_a = 2, \quad \beta_b = 1.5, \\
r \sim \text{Normal}(0, 0.25^2), \\
\epsilon_a \sim \text{Normal}(0, 0.72^2), \quad \epsilon_b \sim \text{Normal}(0, 0.52^2).
\]

All normal distributions are truncated on both sides at twice the standard deviation to make sure that \( X_a \) and \( X_b \) are positive. Figure 5-1a shows the evolution of six behaviors \( (f = 0, 0.2, \cdots, 1) \) over 500 generations with exogenous returns. The vertical axis represents the frequency of each type of investor in the population. The optimal behavior \( f^* = 1 \) quickly dominates the population. Figure 5-1b shows the same evolution with endogenous returns. The equilibrium behavior \( f^e = 0.6 \) dominates the population in a much slower fashion. In reality, the market conditions are constantly changing. Instead of looking at the long-run limit, the short-term oscillation shown here may be the prototype of market cycles.
Figure 5-1: Evolution of the optimal behavior $f^*$ with exogenous returns (5-1a) and the equilibrium behavior $f^e$ with endogenous returns (5-1b) over 500 generations. The vertical axis represents the frequency of each type of investor in the population, and the horizontal axis represents time. Different colors correspond to different behaviors.

5.5 Discussion

In the context of the binary choice model with two strategy returns, we have shown that in equilibrium, the market consists of a mixed population that invests in both strategies, implying a wider variation of coexisting strategies compared to traditional models such as the mutual fund theorems (Markowitz 1952, Merton 1972). We have also identified equilibrium behaviors with respect to the mean returns, betas, common and idiosyncratic volatilities. These results are similar for both exogenous and endogenous returns. In general, higher mean returns promote survival of the strategy, higher idiosyncratic volatilities hinder the survival of the strategy, and higher common volatility promote the survival of the strategy with higher beta-adjusted mean returns.

Our model may provide explanations for some return puzzles that are hard to reconcile with traditional asset pricing models. For example, the “beta puzzle" is the finding that high beta stocks underperform and low beta stocks overperform (Baker et al. 2011, Frazzini and Pedersen 2014). Our results suggest that stocks with high
beta and low return can stably survive, especially when the market volatility is low (see Proposition 15, 18, and 21 for example).

Another example is the "idiosyncratic volatility puzzle" that stocks with high idiosyncratic risk earn low returns (Ang et al. 2006, Ang et al. 2009). Our results suggest that the survival of an asset is determined by several factors together including its beta, average return, idiosyncratic volatility, and market volatility. Stocks with high idiosyncratic volatility and low returns can survive even in the long-run if they have low betas and therefore high beta-adjusted returns, and if the market volatility is low (see Proposition 15, 18, and 21 for example).

Our assumption on the dependence of strategy returns on supply and demand is a highly simplified mathematical caricature of reality, but it makes possible the analytical solution of the equilibrium behavior and captures the most important implications for the survival of diversity in market equilibrium. In general, different assumptions can be made to capture additional effects of investors’ impact on market. For example, non-linear dependences may capture the extreme movements of asset prices. Incorporating the full history of supply and demand in each generation could generate autocorrelated strategy returns and, therefore, lead to dynamics similar to market cycles and bubbles.

More generally, our results can help explain the survival of a wide range of hedge funds. The investment strategies involved in hedge funds are highly diversified and there is considerable heterogeneity in the historical characteristics of the various categories of hedge fund investment styles (Chan et al. 2006). For example, hedge funds are classified into 10 different investment styles in the Dow Jones Credit Suisse Hedge Fund index, and 11 different investment styles in the Lipper/TASS Hedge Fund database.

Hedge funds offer a promising domain for testing the implications of our model. The Lipper/TASS database contains an enormous amount of data of individual hedge funds, including their returns, births and deaths, assets under management, etc. Empirical tests of the implications of our model can be performed from these datasets.
Chapter 6

Growth of Relative Wealth and Kelly Criterion

6.1 Introduction

One of the key financial decisions an individual has to make is how to allocate wealth among alternative assets. Ever since Markowitz (1952)'s groundbreaking work, the mean variance theory has remained the cornerstone of modern portfolio theory, which has led to numerous breakthroughs in economic science, including the famous Capital Asset Pricing Model (Sharpe 1964, Treynor 1965, Lintner 1965b, Lintner 1965a, Mossin 1966). The influence of this paradigm goes far beyond academia and has also become an integral part of the investment management practice (Reilly and Brown 2011).

On the other hand, evolutionary principles have been adopted by economists to understand asset allocation, including the evolutionary game theory (Maynard Smith 1982), the implications of probability matching (Cooper and Kaplan 1982), the biological origin of utility functions and time preference (Rogers 1994, Waldman 1994, Robson 1996a, Samuelson 2001, Zhang et al. 2014b), and the selection of firms (Luo 1995) and traders (Blume and Easley 1992, Kogan et al. 2006a, Hirshleifer and Teoh 2009). This perspective brings new insights beyond the neoclassical economics and helps reconcile some inconsistencies between Homo economicus and Homo sapi-
ens (Kahneman and Tversky 1979, Brennan and Lo 2011). The evolutionary approach to investing is also closely related to the optimal portfolio growth theory, which is explored by, among others, Kelly Jr. (1956), Hakansson (1970), Thorp (1971), Algoet and Cover (1988), Browne and Whitt (1996), Aurell et al. (2000).

While the evolutionary frameworks often focus on the long-term performance of investment strategies, investors are sometimes concerned with the short to medium term (Browne 1999). Myopic investor behaviors have been documented in both theoretical and empirical studies (Strotz 1955, Stroyan 1983, Thaler et al. 1997, Bushee 1998). Population geneticists have applied ideas from evolutionary biology to portfolio theory in which the one-period expected wealth is maximized as much of the population genetics field focuses on short-term competition between types (Frank 1990, Frank and Slatkin 1990, Orr 2014).

Traditional portfolio growth theory has focused on absolute wealth and the Kelly Criterion (Kelly Jr. 1956, Thorp 1971). In the spirit of Orr (2014), we consider relative wealth instead in this chapter. Relative wealth or income has been considered in a number of studies (Robson 1992, Bakshi and Chen 1996, Corneo and Jeanne 1997, Hens and Schenk-Hoppé 2005, Frank 2011a), and is particularly important in the wake of the voluminous literature on behavioral economics, which provides evidence that investors sometimes assess their performance relative to a reference group (Frank 1985, Clark and Oswald 1996, Clark et al. 2008).

In this chapter, we study both the short-term and long-term investment horizon, and compare implications from maximizing relative wealth to absolute wealth. We use ideas from Orr (2014) and compare his results with an extension of the binary choice model from Brennan and Lo (2011). We consider two assets in a discrete-time model and an investor who allocates her wealth between the two assets. Instead of focusing on her absolute wealth, the investor maximizes her relative wealth to another investor with fixed behavior, in one period, multiple periods, and infinite horizon. We ask the question: what’s the optimal behavior for the investor as a function of the environment which consists of both asset returns and other participants’ behavior.

This approach leads to some interesting comparison with the Kelly Criterion. We
show that the Kelly Criterion is the optimal behavior if the investor maximizes her absolute wealth in infinite horizon (see also Brennan and Lo (2011)). In the case that the investor maximizes relative wealth, we identify conditions under which the Kelly Criterion is optimal and conditions under which the investor should deviate from the Kelly Criterion. It turns out that the initial relative wealth—which represents the investor’s market power—plays a critical role. The dominant investor’s optimal behavior is different from the minorant investor’s optimal behavior.

In the remainder of this chapter, we first consider a model with two assets where investors maximize their absolute wealth. It is shown that the long-run optimal behavior is equivalent to the behavior implied from the Kelly Criterion. Section 6.3 extends the binary choice model and considers the case of two investors who maximize their relative wealth in the population given the other investor’s behavior. The Kelly Criterion emerges as a special case with certain environmental conditions. Section 6.4 provides a numerical example to illustrate the theoretical results. We end with a discussion in Section 6.5.

### 6.2 Maximizing Absolute Wealth: the Kelly Criterion

Consider two assets $a$ and $b$ in a discrete-time model, each generating gross returns $X_a \in (0, \infty)$ and $X_b \in (0, \infty)$ in one period. For example, asset $a$ can be a risky asset whereas asset $b$ can be the riskless asset. In this case, $X_a \in (0, \infty)$ and $X_b = 1 + r$ where $r$ is the risk-free interest rate. In general, $(X_{a,t}, X_{b,t})$ are IID over time $t = 1, 2, \ldots$, and are described by the probability distribution function $\Phi(X_a, X_b)$.

Consider an investor that allocates $f \in [0, 1]$ of his wealth in asset $a$ and $1 - f$ in asset $b$. We will refer to $f$ as the investor’s behavior henceforth. We assume that:

**Assumption 14.** $(X_a, X_b)$ and $\log(fX_a + (1 - f)X_b)$ have finite moments up to order 2 for all $f \in [0, 1]$.

Note that Assumption 14 guarantees that the gross return of any investment
portfolio is positive. In other words, the investor cannot lose more than what she has. This is made possible by assuming that \( X_a \) and \( X_b \) are positive and \( f \) in between 0 and 1. In other words, the investor only allocates her money between two assets and no short-selling is allowed\(^1\).

Let \( n_t^f \) be the total wealth of investor \( f \) in period \( t \). To simplify notation, let \( \omega_t^f = fX_{a,t} + (1-f)X_{b,t} \) be the gross return of investor \( f \)'s portfolio in period \( t \). With these notational conventions in mind, the portfolio growth from period \( t-1 \) to period \( t \) is:

\[ n_t^f = n_{t-1}^f (fX_{a,t} + (1-f)X_{b,t}) = n_{t-1}^f \omega_t^f. \]

Through backward recursion, the total wealth of investor \( f \) in period \( T \) is given by

\[ n_T^f = \prod_{t=1}^T \omega_t^f = \exp \left( \sum_{t=1}^T \log \omega_t^f \right). \]

Taking logarithm of wealth and applying the Kolmogorov Law of Large Numbers, we have:

\[ \frac{1}{T} \log n_T^f = \frac{1}{T} \sum_{t=1}^T \log \omega_t^f \xrightarrow{P} \mathbb{E}[\log \omega_t^f] = \mathbb{E}[\log (fX_a + (1-f)X_b)] \]  

as \( T \) increases without bound where "\( \xrightarrow{P} \)" in (6.1) denotes convergence in probability. We have assumed that \( n_0^f = 1 \) without loss of generality.

The expression (6.1) is simply the expectation of the log-geometric-average growth rate of investor \( f \)'s wealth, and we will call it \( \mu(f) \) henceforth:

\[ \mu(f) = \mathbb{E}[\log (fX_a + (1-f)X_b)]. \]  

The optimal \( f \) that maximizes (6.2) coincides with the Kelly Criterion (Kelly Jr. 1956, Thorp 1971), and is given by

**Proposition 22.** *The optimal allocation \( f^{Kelly} \) that maximizes investor \( f \)'s absolute*  

\(^1\)One could relax this assumption by allowing short-selling, which means \( f \) can be less than 0 or greater than 1. However, \( f \) still needs to be restricted such that \( fX_a + (1-f)X_b \) is always positive. This does not change our results in any essential way, but will complicate the presentation of some results mathematically. Therefore we stick to the simple assumption that \( f \in [0, 1] \) as in Brennan and Lo (2011).
wealth as $T$ increases without bound is

$$f^{Kelly} = \begin{cases} 
1 & \text{if } \mathbb{E}[X_a/X_b] > 1 \text{ and } \mathbb{E}[X_b/X_a] < 1 \\
\text{solution to (6.4)} & \text{if } \mathbb{E}[X_a/X_b] \geq 1 \text{ and } \mathbb{E}[X_b/X_a] \geq 1 \\
0 & \text{if } \mathbb{E}[X_a/X_b] < 1 \text{ and } \mathbb{E}[X_b/X_a] > 1, 
\end{cases} \quad (6.3)$$

where $f^{Kelly}$ is defined implicitly in the second case of (6.3) by:

$$\mathbb{E} \left[ \frac{X_a - X_b}{f^{Kelly} X_a + (1 - f^{Kelly}) X_b} \right] = 0. \quad (6.4)$$

### 6.3 Maximizing Relative Wealth

In this section, we consider two investors. The first investor allocates $f \in [0, 1]$ of his wealth in asset $a$ and $1 - f$ in asset $b$. The second investor allocates $g \in [0, 1]$ of his wealth in asset $a$ and $1 - g$ in asset $b$. Investor $f$'s objective is to maximize the proportion of her wealth relative to the total wealth in the population.

In the case of maximizing relative wealth, the initial wealth plays an important role in the optimal allocation. Let $\lambda \in (0, 1)$ be the relative initial wealth of investor $f$:

$$\lambda = \frac{n^f_0}{n^f_0 + n^g_0}.$$  

Let $q^f_t$ be the relative wealth of investor $f$ in subsequent periods $t = 1, 2, \ldots$. $q^f_t$ and $q^g_t$ are defined similarly:

$$q^f_t = \frac{n^f_t}{n^f_t + n^g_t} = \frac{1}{1 + n^g_t / n^f_t},$$

$$q^g_t = 1 - q^f_t.$$

It is obvious that the ratio $n^g_t / n^f_t$ is sufficient to determine the relative wealth $q^f_t$. Let
be the $T$-period average log-relative-growth:

\[
R^f_T = \frac{1}{T} \log \frac{\prod_{t=1}^{T} \omega^g_t}{\prod_{t=1}^{T} \omega^g_r} = \frac{1}{T} \sum_{t=1}^{T} \log \frac{\omega^g_t}{\omega^g_r},
\]

(6.5)

Then we can write the relative wealth in period $T$ as:

\[
q^f_T = \frac{1}{1 + \frac{n^f_T}{n^r_T}} = \frac{1}{1 + \frac{(1-\lambda)\prod_{t=1}^{T} \omega^g_t}{\lambda \prod_{t=1}^{T} \omega^r_t}} = \frac{1}{1 + \frac{1-\lambda}{\lambda} \exp \left( T R^f_T \right)}.
\]

(6.6)

Equation (6.5)-(6.6) are well-known results in the population genetics literature.

### 6.3.1 One-period results

We first consider an investor who maximizes her expected relative wealth in the first period. By (6.6), the expectation of $q^f_T$ is:

\[
\mathbb{E}[q^f_T] = \mathbb{E} \left[ \frac{1}{1 + \frac{1-\lambda}{\lambda} \frac{\omega^g}{\omega^r}} \right].
\]

Here we have dropped the subscripts in $\omega^f_t$ and $\omega^g$, and instead simply use $\omega^f$ and $\omega^g$, because there is only one period to consider.

Given investor $g$, we denote $f^*_1$ as investor $f$'s optimal allocation that maximizes $\mathbb{E}[q^f_T]$. There is no general formula to compute $\mathbb{E}[q^f_T]$ because it involves the expectation of the ratio of random variables. Population geneticists use diffusion approximation to estimate similar quantities (Gillespie 1977, Frank and Slatkin 1990, Frank 2011a), which was later used by Orr (2014) in a similar model for relative wealth.

Without the diffusion approximation, one can still characterize $f^*_1$ to a certain degree:

**Proposition 23.** Investor $f$'s optimal behavior that maximizes expected relative wealth
in the first period is given by:

\[
f_1^* = \begin{cases} 
1 & \text{if } \mathbb{E} \left[ \frac{(X_a - X_b)\omega^g}{(\lambda X_a + (1-\lambda)\omega^g)^2} \right] > 0 \\
solution to (6.8) & \text{if } \mathbb{E} \left[ \frac{(X_a - X_b)\omega^g}{(\lambda X_a + (1-\lambda)\omega^g)^2} \right] \leq 0 \text{ and } \mathbb{E} \left[ \frac{(X_a - X_b)\omega^g}{(\lambda X_a + (1-\lambda)\omega^g)^2} \right] \geq 0 \\
0 & \text{if } \mathbb{E} \left[ \frac{(X_a - X_b)\omega^g}{(\lambda X_a + (1-\lambda)\omega^g)^2} \right] < 0,
\end{cases}
\]

where \( f_1^* \) is defined implicitly in the second case of (6.7) by:

\[
\mathbb{E} \left[ \frac{(X_a - X_b)\omega^g}{(\lambda \omega^f + (1-\lambda)\omega^g)^2} \right] = 0.
\]

In general, the optimal behavior \( f_1^* \) is a function of \( g \). The next proposition asserts that \( f_1^* \) is always "bounded" by \( g \).

**Proposition 24.** To maximize the expected relative wealth in period 1, investor \( f \) should never deviate more from the Kelly Criterion \( f_{Kelly} \) than investor \( g \) in the same direction:

- If \( g = f_{Kelly} \), then \( f_1^* = f_{Kelly} \).
- If \( g < f_{Kelly} \), then \( f_1^* > g \).
- If \( g > f_{Kelly} \), then \( f_1^* < g \).

The conclusion in Proposition 24 makes intuitive sense. When investor \( g \) takes a position that is riskier than the Kelly Criterion, investor \( f \) should never be even riskier than investor \( g \). Similarly, when investor \( g \) takes a position that is more conservative than the Kelly Criterion, investor \( f \) should never be even more conservative than investor \( g \).

It is interesting to compare the optimal behavior \( f_1^* \) with the Kelly Criterion \( f_{Kelly} \), which is provided in the next proposition. It shows that when \( g \) is not far from the Kelly Criterion, the relationship between \( f_1^* \) and \( f_{Kelly} \) depends on the initial relative wealth of investor \( f \).
Proposition 25. If investor $f$ is the dominant investor ($\lambda > \frac{1}{2}$), then he should be locally more/less risky than Kelly in the same way as investor $g$: for small $\epsilon > 0$,

$$g = f_{Kelly} - \epsilon \Rightarrow f_1^* < f_{Kelly},$$

$$g = f_{Kelly} + \epsilon \Rightarrow f_1^* > f_{Kelly}.$$

If investor $f$ is the minorant investor ($\lambda < \frac{1}{2}$), then he should be locally more/less risky than Kelly in the opposite way as investor $g$: for small $\epsilon > 0$,

$$g = f_{Kelly} - \epsilon \Rightarrow f_1^* > f_{Kelly},$$

$$g = f_{Kelly} + \epsilon \Rightarrow f_1^* < f_{Kelly}.$$

If investor $f$ starts with the same amount of wealth as investor $g$ ($\lambda = \frac{1}{2}$), then he should be locally Kelly:

$$g \approx f_{Kelly} \Rightarrow f_1^* \approx f_{Kelly}.$$

Note that when $g$ is far from the Kelly Criterion, the conclusions in Proposition 25 may not be true any more. Section 6.4 provides a numerical example (see Figure 6-1b) where investor $f$ is the minorant investor ($\lambda < \frac{1}{2}$), $g \ll f_{Kelly}$, but $f_1^* < f_{Kelly}$. However, Orr (2014) has shown that these results are still approximately true for any $g$ up to a diffusion approximation, which is consistent with the numerical results for maximizing one-period relative wealth in Figure 6-1a. We will provide more discussion on this point in Section 6.4.

6.3.2 Multi-period results

Previous results are based on maximizing the expected relative wealth in period $1$: $E[q_1^f]$. To generalize previous results to maximizing expected relative wealth in period $T$: $E[q_T^f]$, we have:

**Proposition 26.** Investor $f$'s optimal behavior that maximizes expected relative wealth
in the $T$-th period is given by:

$$f_T^* = \begin{cases} 
1 & \text{if } \mathbb{E} \left[ \exp \left( TR_T^f \right) \frac{T - \sum_{t=1}^T X_{at}}{X_{at} \left[ X_{at} + (1-f) X_{at} \right]} \right] > 0 \\
\text{solution to } (6.10) & \text{if } \mathbb{E} \left[ \exp \left( TR_T^f \right) \frac{T - \sum_{t=1}^T X_{at}}{X_{at} \left[ X_{at} + (1-f) X_{at} \right]} \right] \leq 0 \text{ and } \mathbb{E} \left[ \frac{\exp \left( TR_T^g \right) \left( \sum_{t=1}^T X_{at} - T \right)}{X_{at} \left[ X_{at} + (1-f) X_{at} \right]} \right] < 0, \\
0 & \text{if } \mathbb{E} \left[ \exp \left( TR_T^g \right) \frac{T - \sum_{t=1}^T X_{at}}{X_{at} \left[ X_{at} + (1-f) X_{at} \right]} \right] < 0,
\end{cases}$$

(6.9)

where $f_1^*$ is defined implicitly in the second case of (6.9) by:

$$\mathbb{E} \left[ \exp \left( TR_T^f \right) \sum_{t=1}^T \frac{X_{at} - X_{at}}{X_{at} \left[ X_{at} + (1-f) X_{at} \right]} \right] = 0. \quad (6.10)$$

We have assumed that $f$ is constant through time, which implies that the investor does not dynamically change her position from period to period. Such a passive strategy may be of interest because the information of each investor's relative wealth is difficult to get in each period, and also because it is costly to re-balance the portfolio after each period.

If the investor is indeed able to adjust $f$ dynamically at each new period as a function of her current relative wealth, clearly the expected growth of relative wealth can be increased. This is studied numerically in a similar model in Orr (2014).

Similarly, one can "bound" $f_T^*$ by $g$, and compare $f_T^*$ with $f_{Kelly}$ when $g$ is around the Kelly Criterion.

**Proposition 27.** The conclusions in Proposition 24-25 hold for $f_T^*$ in multi-period, $T = 2, 3, \ldots$.  

Simply put, when investor $g$ takes a position that is riskier than the Kelly Criterion, investor $f$ should never be even riskier than investor $g$, not matter how many horizons she is looking at. Similarly, when investor $g$ takes a position that is more conservative than the Kelly Criterion, investor $f$ should never be even more conservative than investor $g$, not matter how many horizons she is looking at. On the other hand, if investor $g$ does not deviate from the Kelly Criterion too much, then investor $f$ should deviate from the Kelly Criterion in the opposite direction than investor $g$.
provided that she has less initial wealth than investor $g$, and in the same direction provided that she has more initial wealth than investor $g$.

Note that in the multi-period case, one does not have similar results from diffusion approximation as in the one-period case (Orr 2014). Numerical results in Section 6.4 shows that the condition that $g$ is around the Kelly Criterion is essential (see Figure 6-2a).

### 6.3.3 Infinite horizon

Recall from (6.5) that the $T$-period average log-relative-growth $R_T^f$ is given by:

$$R_T^f = \frac{1}{T} \sum_{t=1}^{T} \log w_t^f - \frac{1}{T} \sum_{t=1}^{T} \log w_t^g \xrightarrow{p} \mu(g) - \mu(f)$$

as $T$ increases without bound. It is therefore easy to see from (6.6) that:

**Proposition 28.** As $T$ increases without bound, the relative wealth of investor $f$ converges in probability to a constant:

$$q_T^f \xrightarrow{p} \begin{cases} 0 & \text{if } \mu(f) < \mu(g) \\ \lambda & \text{if } \mu(f) = \mu(g) \\ 1 & \text{if } \mu(f) > \mu(g). \end{cases}$$

Proposition 28 is consistent with well-known results in the population genetics literature (see Gillespie (1973) for example) as well as the behavioral finance literature (see Brennan and Lo (2011) for example). It asserts that investor $f$’s relative wealth will converge to 1 as long as its log-geometric-average growth rate $\mu(f)$ is greater than investor $g$’s. This implies that when $T$ increases without bound, there are multiple behaviors that are all optimal in the following sense:

$$\arg\max_f \lim_{T \to \infty} q_T^f = \arg\max_f \mathbb{E} \left[ \lim_{T \to \infty} q_T^f \right] = \arg\max_f \lim_{T \to \infty} \mathbb{E} \left[ q_T^f \right] = \{ f : \mu(f) > \mu(g) \}$$

Note that the above equality uses the dominant convergence theorem ($q_T^f$ is always
bounded) to switch the limit and the expectation operator.

However, this is not equivalent to the limit of the optimal behavior $f_T^*$ as $T$ increases without bound, because one cannot switch the operator “arg max” and “lim” in general, and

$$\arg\max_f \lim_{T \to \infty} \mathbb{E} \left[ q_T^f \right] \neq \lim_{T \to \infty} \arg\max_f \mathbb{E} \left[ q_T^f \right].$$

In fact, Section 6.4 provides such an example.

### 6.4 A Numerical Example

We construct a numerical example in this section to illustrate results from Section 6.2-6.3. Let’s consider the following two simple assets:

$$X_a = \begin{cases} 
\alpha & \text{with probability } p \\
\beta & \text{with probability } 1 - p,
\end{cases} \quad X_b = \gamma & \text{with probability } 1.$$

In this case asset $a$ is risky and asset $b$ is riskless. Investor $f$’s expected relative wealth in period $T$ is explicitly given by:

$$\mathbb{E} \left[ q_T^f \right] = \sum_{k=0}^{T} \frac{\left( \frac{T}{k} \right) p^k (1 - p)^{T-k}}{1 + \frac{1 - \lambda}{\lambda} \exp \left( k \log \frac{f\alpha+(1-f)\gamma}{f\alpha+(1-f)\gamma} + (T - k) \log \frac{g\beta+(1-g)\gamma}{f\beta+(1-f)\gamma} \right)}.$$ (6.13)

Therefore, it is easy to numerically solve from (6.13) the optimal behavior $f_T^*$ for any given environment $\alpha, \beta, \gamma, p$.

For simplicity, we focus on one particular environment henceforth:

$$X_a = \begin{cases} 
2 & \text{with probability } 0.5 \\
0.5 & \text{with probability } 0.5, \\
\end{cases} \quad X_b = 1 & \text{with probability } 1.$$  

It is easy to show by Proposition 22 that $f_{\text{Kelly}}^{K} = \frac{1}{2}$ in this case. As noted after Assumption 14, to guarantee the gross return for any investment portfolio is positive,
$f$ can take value between -1 and 2. For simplicity and consistency with the theoretical results, we restrict $f$ to be between 0 and 1, which does not affect the comparisons below in any essential way.

**Maximizing one-period relative wealth.** We first consider the case of maximizing relative wealth in period 1. Figure 6-1a shows $f_1^*$ for several different cases of investor $f$'s relative wealth $\lambda$. We can see that investor $f$'s optimal behavior is always "bounded" by $g$, and the more dominant investor $f$ is, the closer $f_1^*$ is to $g$. These observations are consistent with Proposition 24-25.

Figure 6-1b zooms into one particular case of $\lambda = 0.49$, with the $f$-axis from 0.495 to 0.505. It shows that the comparison between $f_1^*$ and $f_{Kelly}$ is only valid when $g$ is close to the Kelly Criterion, as asserted in Proposition 25. However, except for this one particular case, the conclusions in Proposition 25 are true for any $g$. This provides evidence that the diffusion approximation in Orr (2014) is relatively accurate for one-period results.

**Maximizing multi-period relative wealth.** Next we consider maximizing relative wealth in multiple periods. Figure 6-2 shows the evolution of $f_T^*$ for three different initial relative wealth $\lambda = 0.2, 0.5, 0.8$. It is clear that investor $f$'s optimal behavior

![Graph](image-url)
is always "bounded" by $g$ as $T$ increases. In this example it is also clear that $f^*_T$ does not converge to $f^{Kelly}$ as $T$ increases without bound.

When investor $f$ is the minorant investor (Figure 6-2a, $\lambda = 0.2$), her optimal behavior deviates from the Kelly Criterion in the opposite direction as investor $g$ around $g = 0.5$. When investor $f$ is the dominant investor (Figure 6-2c, $\lambda = 0.8$), her optimal behavior deviates from the Kelly Criterion in the same direction as investor $g$ around $g = 0.5$. When investor $f$ has the same initial wealth as investor $g$ (Figure 6-2b, $\lambda = 0.5$), her optimal behavior is approximately equal to the Kelly Criterion around $g = 0.5$.

It is interesting to note that when investor $f$ is the minorant investor (Figure 6-2a, $\lambda = 0.2$), the comparison between $f^*_T$ and $f^{Kelly}$ is only true when $g$ is close to the Kelly Criterion. This is more true as the number of periods $T$ increases. In this case, the fact that $g$ has to be close to the Kelly Criterion becomes critical.

### 6.5 Discussion

As opposed to traditional theory on portfolio growth, this paper imports evolutionary ideas and focuses on relative wealth. Relative wealth is important because people sometimes measure their success or satisfaction in ways that are partly relative to others (Orr 2014). Our model considers the case with two investors in a non-game-theoretic framework. We showed how the investor’s optimal behavior is dependent on the other investor’s behavior, which might be far from the Kelly Criterion.

We consider both a myopic investor who maximizes the one-period expected relative wealth and an investor who focuses on the multi-period relative wealth. We showed that similar implications hold for both cases\(^2\). When investor 1 is wealthier than investor 2, investor 1 should roughly mimic investor 2 in terms of being more or less aggressive than the Kelly Criterion. Conversely, when investor 1 is poorer than investor 2, investor 1 should roughly act oppositely from investor 2.

Note that in the case of multiple investors, one can use a single aggregate $g$ to

\(^2\)Orr (2014) has considered the one-period case and come to similar conclusions.
Figure 6-2: Evolution of the optimal behavior of investor $f$: $f_T^*$, $T = 1, 11, \ldots, 101$. Different $\lambda$ corresponds to different initial relative wealth.
represent all investors besides investor $f$. However, this is only true for one period. In general, one cannot use a single $g$ to account for multiple investors. To understand this, note that an investor’s behavior $f$ implies that she always invests $f$ amount of her wealth in asset $a$, and this requires portfolio rebalancing after each period because asset $a$ and asset $b$ has different returns. With more than two investors, the amount of total wealth invested in asset $a$ is no longer a fixed quantity in multiple periods, because different investors grow at different speeds. Therefore, there does not exist a single aggregate behavior $g$ to account for more than two investors in general.
Appendix A

Proofs

A.1 Proofs for Chapter 2

Proof of Equation (2.2) and (2.3). The total number of offspring of type $f$ in generation $t$ is simply the sum of all the offspring from the type-$f$ individuals of the previous generation:

$$n^f_t = \sum_{i=1}^{n^f_{t-1}} x^f_{i,t} = \lambda \sum_{i=1}^{n^f_{t-1}} z^f_{i,t} + (1 - \lambda) \sum_{i=1}^{n^f_{t-1}} y^f_{i,t}$$

$$= \lambda \left( z_{a,t} \sum_{i=1}^{n^f_{t-1}} I^f_{i,t} + z_{b,t} \sum_{i=1}^{n^f_{t-1}} (1 - I^f_{i,t}) \right) + (1 - \lambda) \left( \sum_{i=1}^{n^f_{t-1}} I^f_{i,t} y_{a,i,t} + \sum_{i=1}^{n^f_{t-1}} (1 - I^f_{i,t}) y_{b,i,t} \right)$$

where we have added time subscripts to the relevant variables to clarify their temporal ordering. As $n^f_{t-1}$ increases without bound, the Law of Large Numbers implies that:

$$n^f_t \xrightarrow{p} n^f_{t-1} \left( \lambda (f z_{a,t} + (1 - f) z_{b,t}) + (1 - \lambda) (f \mathbb{E}[y_a] + (1 - f) \mathbb{E}[y_b]) \right)$$

$$= n^f_{t-1} \left( \lambda (f z_{a,t} + (1 - f) z_{b,t}) + (1 - \lambda) \mathbb{E}[y^f] \right)$$

where "$\xrightarrow{p}$" denotes equality in probability. Through backward recursion and assuming that $n^f_0 = 1$ without loss of generality, the population of type-$f$ individuals in
generation $T$ is given by:

$$
n_T^f = \prod_{t=1}^{T} \left( \lambda (f z_{a,t} + (1 - f) z_{b,t}) + (1 - \lambda) E_y[y'|y'] \right).
$$

Taking logarithm on both sides and again using the Law of Large Numbers, we get:

$$
\frac{1}{T} \log n_T^f = \frac{1}{T} \sum_{t=1}^{T} \log \left( \lambda (f z_{a,t} + (1 - f) z_{b,t}) + (1 - \lambda) E_y[y'] \right)
\xrightarrow{P} E_z \left[ \log \left( \lambda z^f + (1 - \lambda) E_y[y'] \right) \right]
$$

where "$\xrightarrow{P}$" denotes convergence in probability, which completes the proof of equation (2.2). Equation (2.3) simply rewrites equation (2.2).

A.2 Proofs for Chapter 3

Proof of Lemma 1. The proof generalizes the discussion in Caswell (2001, p.371-372). Let $A = (a_{ij})_{(K+1) \times (K+1)}$ be any matrix drawn under Assumptions 3-5. If $A$ is strictly positive, then $\tau(A) < 1$. If $A$ is not strictly positive, because $P(x_a > 0 \text{ or } x_b > 0) = 1$, $A$ must be a strictly positive matrix except for the 1st column or the $(K + 1)$-th column (but not both). Suppose without loss of generality that the 1st column of $A$ is 0 and the rest is strictly positive, and it suffices to prove $\tau(A) < 1$ in this case.

Now let $x(t) = (x_i(t + 1))_{i=1}^{K+1}$ and $y(t) = (y_i(t + 1))_{i=1}^{K+1}$ be positive vectors that are not proportional to each other, and $x(t + 1) = A \cdot x(t)$ and $y(t + 1) = A \cdot y(t)$. Then

$$
\frac{x_i(t + 1)}{y_i(t + 1)} = \sum_j a_{ij} x_j(t) \sum_k a_{ik} y_k(t) \sum_j \left( \frac{a_{ij} y_j(t)}{\sum_k a_{ik} y_k(t)} \right) \frac{x_j(t)}{y_j(t)} = \sum_j p_{ij} \frac{x_j(t)}{y_j(t)}
$$

where $\sum_j p_{ij} = 1$. A careful examination of $p_{ij}$ yields that for any $i$,

$$
p_{i1} = 0, \quad \text{and} \quad p_{ij} > 0 \text{ for } j = 2, 3, \ldots, K + 1.
$$
Therefore, \( \frac{x_i(t+1)}{y_i(t+1)} \) is a positive weighted average of \( \{ \frac{x_j(t)}{y_j(t)} \}^{K+1}_{j=2} \), and this is true for all \( i \).

Because \( x(t) \) and \( y(t) \) are not proportional to each other, there are two possibilities:

1. The ratios in \( \{ \frac{x_j(t)}{y_j(t)} \}^{K+1}_{j=2} \) are all the same, but different from \( \frac{x_i(t)}{y_i(t)} \). In this case exactly one of the following must be true:

   \[
   \min_j \frac{x_j(t)}{y_j(t)} < \frac{x_i(t+1)}{y_i(t+1)} < \max_j \frac{x_j(t)}{y_j(t)}, \quad \text{for all } i,
   \]

   or

   \[
   \min_j \frac{x_j(t)}{y_j(t)} = \frac{x_i(t+1)}{y_i(t+1)} = \max_j \frac{x_j(t)}{y_j(t)}, \quad \text{for all } i.
   \]

2. The ratios in \( \{ \frac{x_j(t)}{y_j(t)} \}^{K+1}_{j=2} \) are not all the same. In this case we have

   \[
   \min_j \frac{x_j(t)}{y_j(t)} < \frac{x_i(t+1)}{y_i(t+1)} < \max_j \frac{x_j(t)}{y_j(t)}, \quad \text{for all } i.
   \]

In both (1) and (2) we have

\[
d(x(t+1), y(t+1)) < d(x(t), y(t)).
\]

That is, each multiplication by \( A \) contracts the distance between the two vectors. Because the supremum in Birkhoff's contraction coefficient (3.10) can be taken over a compact set, we have \( \tau(A) < 1 \) with probability 1.

\[\square\]

**Proof of Lemma 2.** The mutation matrix \( \mathbf{M} \) can be written as

\[
\mathbf{M} = \left( 1 - \left( 1 + \frac{1}{K} \right) \epsilon \right) \mathbf{I}_{K+1} + \frac{\epsilon}{K} \mathbf{1}_{K+1} \mathbf{1}'_{K+1},
\]

where \( \mathbf{I}_{K+1} \) is the identity matrix of dimension \((K+1) \times (K+1)\). Plugging into (3.4) in Proposition 2 we get

\[
\mathbf{n}_t \overset{a.s.}{=} \mathbf{M} \mathbf{F}_t \mathbf{n}_{t-1} = \left( 1 - \left( 1 + \frac{1}{K} \right) \epsilon \right) \mathbf{F}_t \mathbf{n}_{t-1} + \frac{\epsilon}{K} \mathbf{P}_t \mathbf{1}_{K+1}. \tag{A.1}
\]
Note that the identity

\[ 1'F_t n_{t-1} = 1'MF_t n_{t-1} = P_t \]

was used in order to obtain (A.1). Proceeding inductively from (A.1), we have the desired result. \(\square\)

**Proof of Proposition 1.** See Brennan and Lo (2011, Proposition 1). Strong Law of Large Numbers implies almost sure convergence (see also Brennan and Lo (2011, Proof of Corollary 1)). \(\square\)

**Proof of Proposition 2.** The proof is a simple generalization of Brennan and Lo (2011). Let \(I^f\) be a Bernoulli variable defined same as in Brennan and Lo (2011), which equals 1 with probability \(f\) and 0 otherwise. Define “not mutation” indicator \(N\) and “mutation from \(g\) to \(f\)” indicator \(M^{g\rightarrow f}\):

\[
N = \begin{cases} 
1 & \text{with prob } 1 - \epsilon \\
0 & \text{with prob } \epsilon ,
\end{cases} \\
M^{g\rightarrow f} = \begin{cases} 
1 & \text{with prob } \frac{\epsilon}{K} \\
0 & \text{with prob } 1 - \frac{\epsilon}{K} .
\end{cases}
\]

In generation \(t\), type \(f\) individuals come from type \(f\) individuals without mutation and type \(g(\neq f)\) individuals with mutation in generation \(t - 1\). Consider them separately. From type \(f\):

\[
\sum_{i=1}^{n_{t-1}^f} x_{i,t}^{f\rightarrow f} = \left( \sum_{i=1}^{n_{t-1}^f} N_{i,t} I_{i,t}^f \right) x_{a,t} + \left( \sum_{i=1}^{n_{t-1}^f} N_{i,t} (1 - I_{i,t}^f) \right) x_{b,t}
\]

\[\overset{a.s.}{=} (1 - \epsilon)n_{t-1}^f (f x_{a,t} + (1 - f)x_{b,t})\]

as \(n_{t-1}^f\) increases without bound. From type \(g(\neq f)\):

\[
\sum_{g \neq f} \sum_{i=1}^{n_{t-1}^g} x_{i,t}^{g\rightarrow f} = \sum_{g \neq f} \left[ \left( \sum_{i=1}^{n_{t-1}^g} M_{i,t}^{g\rightarrow f} I_{i,t}^g \right) x_{a,t} + \left( \sum_{i=1}^{n_{t-1}^g} M_{i,t}^{g\rightarrow f} (1 - I_{i,t}^g) \right) x_{b,t} \right]
\]

\[\overset{a.s.}{=} \frac{\epsilon}{K} \sum_{g \neq f} n_{t-1}^g (g x_{a,t} + (1 - g)x_{b,t})\]
as $n_{t-1}^q$ increases without bound. Note that

$$n_t^f = \sum_{i=1}^{n_{t-1}^f} x_{i,t}^{f} + \sum_{g \neq f} \sum_{i=1}^{n_{t-1}^q} x_{i,t}^{q}$$

$$\overset{\text{as}}{=} (1 - \epsilon)n_{t-1}^f(f x_{a,t} + (1 - f)x_{b,t}) + \frac{\epsilon}{K} \sum_{g \neq f} n_{t-1}^q(g x_{a,t} + (1 - g)x_{b,t}).$$

(3.4) simply rewrites the above equation in matrix form.

Proof of Proposition 3. By Lemma 1 and Caswell (2001, p. 386, 14.22), demographic weak ergodicity\(^1\) holds. In addition, $E \log_+ ||A_1|| < \infty$ because $x_a$ and $x_b$ are bounded, where $\log_+ ||A_1|| = \max\{0, \log ||A_1||\}$. Therefore, assumption 4.2.1 in Tuljapurkar (1990) is satisfied, and Proposition 3 follows from Tuljapurkar (1990, p. 26, (A)).

Proof of Proposition 4. Because the random matrices $A_t$ are IID, assumption 4.2.1, 4.2.3, and 4.2.6 in Tuljapurkar (1990) are satisfied, and the conclusion follows directly from Tuljapurkar (1990, p.29 (J)).

Proof of Proposition 5. Part (i) is standard result for single type branching process in random environments (see Smith and Wilkinson (1969, Theorem 3.1) for example). Part (ii) follows from Proposition 3 and Corollary 1.

Proof of Proposition 6. To clarify notation, let $x_{a,j}^1$ be the number of offspring generated by $\Phi^1$ for action $a$ in the $j$-th generation; $x_{b,j}^2$ the number of offspring generated by $\Phi^2$ for action $b$ in the $j$-th generation. Table A.1 calculates the number of individuals of both behaviors along evolution, starting with one individual of each type. From the last line of Table A.1 we have:

$$n_k^\text{Total} = \epsilon^{2k-1}(1 - \epsilon)\sum_{i=1}^k (T_1^1 T_2^2)^{2k-2k} \prod_{j=1}^k x_{a,j}^1 \prod_{j=1}^k x_{b,j}^2.$$  

---

\(^1\)The definition of demographic weak ergodicity is given in Caswell (2001, p. 383) and Tuljapurkar (1990, p. 17). Essentially it means that the difference between the probability distributions of normalized population vectors resulting from any two initial populations, exposed to independent sample paths of the stochastic environment, decays to zero.
Therefore,

\[
\frac{1}{k} \log n_{k,\text{Total}}^\epsilon = \frac{2k - 1}{k} \log \epsilon + \left( \frac{1}{k} \sum_{i=1}^{k} (T_i^1 + T_i^2) - 2 \right) \log(1 - \epsilon) + \frac{1}{k} \sum_{i=1}^{k} T_i^1 \log x_{a,i} + \frac{1}{k} \sum_{i=1}^{k} T_i^2 \log x_{b,i}
\]

\[
\overset{\text{a.s.}}{\longrightarrow} 2 \log \epsilon + (E[T^1 + T^2] - 2) \log(1 - \epsilon) + E[T^1]E[\log x_a] + E[T^2]E[\log x_b] = 2 \log \frac{\epsilon}{1 - \epsilon} + E[T^1 + T^2] \log(1 - \epsilon) + E[T^1]E[\log x_a] + E[T^2]E[\log x_b]
\]

where "\(\text{a.s.}\)" denotes almost sure convergence and follows from Strong Law of Large Numbers as \(k\) increases without bound. Since the value of \(\epsilon\) that maximizes the population size \(n_{k,\text{Total}}^\epsilon\) is also the value of \(\epsilon\) that maximizes \(k^{-1} \log n_{k,\text{Total}}^\epsilon\), the above analysis implies that this maximum converges in probability to the maximum of

\[
\pi(\epsilon) = 2 \log \frac{\epsilon}{1 - \epsilon} + E[T^1 + T^2] \log(1 - \epsilon) + E[T^1]E[\log x_a] + E[T^2]E[\log x_b]
\]

where \(0 < \epsilon < 1\). Take the first and second derivatives of the above equation:

\[
\pi'(\epsilon) = \frac{2}{\epsilon} - \frac{E[T^1 + T^2] - 2}{1 - \epsilon},
\]

\[
\pi''(\epsilon) = -\frac{2}{\epsilon^2} - \frac{E[T^1 + T^2] - 2}{(1 - \epsilon)^2}.
\]

Note that \(T^1\) and \(T^2\) are positive integers, so \(E[T^1 + T^2] \geq 2\). Therefore, the second derivative is always negative for \(0 < \epsilon < 1\). In addition, \(\pi'(0^+) > 0, \pi'(1^-) < 0\), which implies that \(\pi(\epsilon)\) has a unique maximum in \((0, 1)\) at \(\pi'(\epsilon) = 0\). Solve for \(\epsilon\) we get the desired result. \(\square\)
Table A.1: Population dynamics for the two-behavior regime-switching model

<table>
<thead>
<tr>
<th>Cycle</th>
<th>Regime</th>
<th>Generation</th>
<th># of individuals $f = 0$</th>
<th># of individuals $f = 1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td></td>
<td></td>
<td>$1$</td>
<td>$1$</td>
</tr>
<tr>
<td>1</td>
<td>$\Phi^1$</td>
<td>$q \cdot x_{a,1}^1$</td>
<td>$e \cdot x_{a,1}^1$</td>
<td></td>
</tr>
<tr>
<td>$T_1^1$</td>
<td></td>
<td>$q^{T_1^1 \sum_{i=1}^{T_1^1} x_{b,j}^1}$</td>
<td>$e^{T_1^1 - 1 \sum_{j=1}^{T_1^1} x_{a,j}^1}$</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>$\Phi^2$</td>
<td>$e^{T_1^1 - 1 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1$</td>
<td>$e^{T_1^1 - 1 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1$</td>
<td></td>
</tr>
<tr>
<td>$T_1^1 + 1$</td>
<td></td>
<td>$e^{2q^{T_1^1 - 1 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td>$e^{T_1^1 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1$</td>
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</tr>
<tr>
<td>$T_1^1 + T_1^2$</td>
<td></td>
<td>$e^{2q^{T_1^1 - 1 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td>$e^{T_1^1 + T_1^2 - 1 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1$</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>$\Phi^1$</td>
<td>$e^{2q^{T_1^1 + T_1^2 - 2 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td>$e^{3q^{T_1^1 + T_1^2 - 2 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td></td>
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<tr>
<td>$T_1^1 + T_1^2 + T_1^3$</td>
<td></td>
<td>$e^{2q^{T_1^1 + T_1^2 + T_1^3 - 2 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td>$e^{3q^{T_1^1 + T_1^2 + T_1^3 - 2 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
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<tr>
<td>$T_1^1 + T_1^2 + T_1^3 + 1$</td>
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<td>$e^{2q^{T_1^1 + T_1^2 + T_1^3 - 3 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td>$e^{3q^{T_1^1 + T_1^2 + T_1^3 - 3 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
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<tr>
<td>$T_1^1 + T_2^1 + T_2^2$</td>
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<td>$e^{2q^{T_1^1 + T_1^2 + T_1^3 - 4 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td>$e^{3q^{T_1^1 + T_1^2 + T_1^3 - 4 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
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<tr>
<td>2</td>
<td>$\Phi^2$</td>
<td>$e^{2q^{T_1^1 + T_1^2 + T_1^3 - 3 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td>$e^{3q^{T_1^1 + T_1^2 + T_1^3 - 3 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td></td>
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<tr>
<td>$T_1^1 + T_2^1 + T_2^2 + T_2^3$</td>
<td></td>
<td>$e^{2q^{T_1^1 + T_1^2 + T_1^3 - 4 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
<td>$e^{3q^{T_1^1 + T_1^2 + T_1^3 - 4 \sum_{j=1}^{T_1^1} x_{a,j}^1} \cdot x_{b,1}^1}$</td>
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<td>:</td>
</tr>
<tr>
<td>$k$</td>
<td>$\Phi^2$</td>
<td>$e^{2k \sum_{i=1}^{k} \sum_{j=1}^{T_i^1} x_{a,j}^i} \cdot x_{b,1}^i$</td>
<td>$e^{2k \sum_{i=1}^{k} \sum_{j=1}^{T_i^1} x_{a,j}^i} \cdot x_{b,1}^i$</td>
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</table>
Proof of Proposition 7. Because the random matrices $A_t$ are IID, assumption 4.2.1 and 4.2.3 in Tuljapurkar (1990) are satisfied, and the conclusion follows directly from Tuljapurkar (1990, p. 27,(F)).

Proof of Proposition 8. We use Meyn and Tweedie (2009, p. 411, Theorem 16.2.5):

If $\{y_t\}_{t=0}^\infty$ is a $\psi$-irreducible\(^2\) and aperiodic T-chain\(^3\), and if the state space $\mathcal{Y}$ is compact, then $\{y_t\}_{t=0}^\infty$ is uniformly ergodic.

The uniqueness of the stationary distribution $\mathcal{L}$ in Proposition 4 implies that $\{y_t\}_{t=0}^\infty$ is aperiodic, so it suffices to prove that $\{y_t\}_{t=0}^\infty$ is a $\psi$-irreducible T-chain.

Take $\psi = \mathcal{L}$ to be the stationary distribution of $\{y_t\}_{t=0}^\infty$, then for all $y \in \mathcal{Y}$ and $B \subseteq \mathcal{Y}$, whenever $\psi(B) > 0$, there exists some $n > 0$, possibly depending on both $y$ and $B$, such that the $n$-step transition probability $p_n(y, B) > 0$. Then it follows from Meyn and Tweedie (2009, p. 82, Proposition 4.2.1(ii)) that $\{y_t\}_{t=0}^\infty$ is $\psi$-irreducible.

Furthermore, the 1-step transition probability $p_1(\cdot, O)$ is a lower semicontinuous function for any open set $O \subseteq \mathcal{Y}$. Remember that the support of $\psi$ is assumed to have non-empty interior. Then it follows from Meyn and Tweedie (2009, p. 124, Theorem 6.0.1(iii)) that $\{y_t\}_{t=0}^\infty$ is a T-chain.

Finally, the uniform ergodicity of the Markov chain $\{y_t\}_{t=0}^\infty$ follows from Meyn and Tweedie (2009, p. 411, Theorem 16.2.5). \(\square\)

Proof of Proposition 9. This Proposition is essentially due to Robson (1996a, p. 413, Theorem 2(iii)). \(\square\)

Proof of Corollary 1. The lower bound is obvious by simply considering the growth of non-mutated type $f^*$ individuals. To prove the upper bound, first note that

$1'F_{t-1}y_{t-1} = 1'\begin{pmatrix} f_{i}x_{a,t} + (1-f_i)x_{b,t} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & f_{K+1}x_{a,t} + (1-f_{K+1})x_{b,t} \end{pmatrix} \begin{pmatrix} y_{t-1}(1) \\ \vdots \\ y_{t-1}(K+1) \end{pmatrix}$

$= \sum_{i=1}^{K+1} y_{t-1}(i) (f_i x_{a,t} + (1-f_i)x_{b,t}) = (\alpha_{t-1}x_{a,t} + \beta_{t-1}x_{b,t})$

\(^2\)The definition of $\psi$-irreducibility can be found in Meyn and Tweedie (2009, p. 82).

\(^3\)The definition of T-chains can be found in Meyn and Tweedie (2009, p. 124).
where
\[ \alpha_{t-1} = \sum_{i=1}^{K+1} y_{t-1}(i) f_i, \quad \beta_{t-1} = \sum_{i=1}^{K+1} y_{t-1}(i)(1 - f_i), \]
and \( \alpha_{t-1} + \beta_{t-1} = 1 \). Note that \( F_t \) and \( y_{t-1} \) are independent in (3.7), and \( \alpha_{t-1} \) and \( \beta_{t-1} \) are constants conditioning on \( y_{t-1} \), so one have:
\[
\mu_t = E_{\mathcal{X}'} \left\{ E_{\Phi} \left[ \log (f^* x_{a,t} + (1 - f^*) x_{b,t}) \right] \ \left| \ y_{t-1} \right. \right\} = E_{\mathcal{X}'} \left\{ E_{\Phi} \left[ \log (\alpha_{t-1} x_{a,t} + \beta_{t-1} x_{b,t}) \right] \ \left| \ y_{t-1} \right. \right\} \\
\leq E_{\mathcal{X}'} \left\{ E_{\Phi} \left[ \log (f^* x_{a,t} + (1 - f^*) x_{b,t}) \right] \ \left| \ y_{t-1} \right. \right\} = E_{\mathcal{X}'} \left\{ \mu(f^*) \ \left| \ y_{t-1} \right. \right\} = \mu(f^*)
\]
where the following fact is used for the inequality:
\[
f^* = \arg \max_{0 \leq f \leq 1} E_{\Phi} \left[ \log (f x_{a,t} + (1 - f) x_{b,t}) \right].
\]

**Proof of Corollary 2.** The conclusion follows immediately from Proposition 6 by replacing \( E[T^1 + T^2] \) by \( 2 \cdot E[T] \). \( \square \)

### A.3 Proofs for Chapter 4

**Proof of Table 4.1.** Note that by definition \( \alpha^*_1 = p^* \beta^*_1 + (1 - p^*) \beta^*_2 \), so \( \alpha^*_1 \) is a convex combination of \( \beta^*_1 \) and \( \beta^*_2 \). If \( \alpha^*_1 = 1 \), at least one of \( \beta^*_1 \) and \( \beta^*_2 \) must be 1. If \( \alpha^*_1 = 0 \), at least one of \( \beta^*_1 \) and \( \beta^*_2 \) must be 0. If \( 0 < \alpha^*_1 < 1 \), \( \beta^*_1 \) and \( \beta^*_2 \) cannot be both greater than or both smaller than \( \alpha^*_1 \). \( p^* \) can be solved accordingly given \( \alpha^*_1, \beta^*_1, \) and \( \beta^*_2 \). \( \square \)

**Proof of Proposition 10.** The total number of type \( f = (p, B) \) individuals in generation \( T \) is
\[
n_T^f = \sum_{i=1}^{n_{T-1}^f} x_i^p B = \sum_{i=1}^{n_{T-1}^f} I_{1,i}^p x_1^B + \cdots + I_{m,i}^p x_m^B \\
= n_{T-1}^f \left( \frac{1}{n_{T-1}^f} \sum_{i=1}^{n_{T-1}^f} I_{1,i}^p x_1^B + \cdots + I_{m,i}^p x_m^B \right).
\]
As \( n_{T-1}^f \) increases without bound, by Law of Large Numbers, it converges in probability to
\[
\lim_{T \to \infty} n_{T-1}^f (p_1 x_1^B + \cdots + p_n x_n^B) = n_{T-1}^f \cdot p B \lambda_T^f.
\]
Through backward recursion, the total number of type \( f = (p, B) \) individuals in generation \( T \) is
\[
n_T^f = n_0^f \cdot \prod_{t=1}^T p B \lambda_t^f = \exp \left( \sum_{t=1}^T \log (p B \lambda_t^f) \right).
\]
Therefore,
\[
\frac{1}{T} \log n_T^f \xrightarrow{p} \frac{1}{T} \sum_{t=1}^T \log (p B \lambda_t^f) \xrightarrow{p} E \left[ \log (p B \lambda_t^f) \right]
\]
as \( T \) increases without bound. Here \( \xrightarrow{p} \) denotes equality in probability and \( \xrightarrow{p} \) denotes convergence in probability.

Proof of Proposition 11. We first prove the following lemma and then prove Proposition 11.

Lemma 5. \((\alpha_1^*, \cdots, \alpha_k^*)\) maximizes (4.10) if and only if
\[
E \left[ \frac{\alpha_1 \lambda_1 + \cdots + \alpha_k \lambda_k}{\alpha_1^* \lambda_1 + \cdots + \alpha_k^* \lambda_k} \right] \leq 1, \quad \forall (\alpha_1, \cdots, \alpha_k).
\]

Proof of Lemma 5. Note that (4.10) is a concave function with respect to \( \alpha_1, \cdots, \alpha_k \), so a local maximum is the global maximum. Now suppose \( \alpha^* = (\alpha_1^*, \cdots, \alpha_k^*) \) is a local maximum, then a necessary and sufficient condition is that if we move \( \alpha^* \) toward a direction of any \( \alpha = (\alpha_1, \cdots, \alpha_k) \), the growth rate decreases. Formally, let
\[
\alpha^\delta = (1 - \delta) \alpha^* + \delta \alpha
\]
where \( \alpha \) is arbitrary and \( 0 \leq \delta \leq 1 \), and
\[
\mu(\alpha^\delta) = E \left[ \log ((1 - \delta) \alpha_1^* + \delta \alpha_1) \lambda_1 + \cdots + ((1 - \delta) \alpha_k^* + \delta \alpha_k) \lambda_k) \right] - \mu(\alpha)
\]

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Then,

\[ \alpha^* = (\alpha_1^*, \ldots, \alpha_k^*) \text{ maximizes (4.10)} \]

\[ \iff \frac{\partial \mu(\alpha^\delta)}{\partial \delta} \bigg|_{\delta=0} \leq 0, \text{ for any } \alpha = (\alpha_1, \ldots, \alpha_k) \]

\[ \iff \mathbb{E} \left[ \frac{(\alpha_1 - \alpha_1^*)\lambda_1 + \cdots + (\alpha_k - \alpha_k^*)\lambda_k}{\alpha_1^*\lambda_1 + \cdots + \alpha_k^*\lambda_k} \right] \leq 0, \text{ for any } \alpha = (\alpha_1, \ldots, \alpha_k) \]

\[ \iff \mathbb{E} \left[ \frac{\alpha_1\lambda_1 + \cdots + \alpha_k\lambda_k}{\alpha_1^*\lambda_1 + \cdots + \alpha_k^*\lambda_k} \right] \leq 1, \text{ for any } \alpha = (\alpha_1, \ldots, \alpha_k) \]

which completes the proof of the lemma. \[\square\]

Now we go back to the proof of Proposition 11. The first \(k\) conditions in (4.11) follow directly from the lemma. As of the last case, note that \(\alpha_1 = 1 - \alpha_2 - \cdots - \alpha_k\) and we can write \(\mu(\cdot)\) as a function of \((\alpha_2, \ldots, \alpha_k)\). Therefore \(\alpha^*\) is given by the following equations:

\[
\begin{align*}
\left. \frac{\partial \mu(\alpha_2, \ldots, \alpha_k)}{\partial \alpha_2} \right|_{\alpha_2+1=\cdots=\alpha_k=0} &= 0 \\
\left. \frac{\partial \mu(\alpha_2, \ldots, \alpha_k)}{\partial \alpha_3} \right|_{\alpha_2+1=\cdots=\alpha_k=0} &= 0 \\
& \vdots \\
\left. \frac{\partial \mu(\alpha_2, \ldots, \alpha_k)}{\partial \alpha_1} \right|_{\alpha_2+1=\cdots=\alpha_k=0} &= 0.
\end{align*}
\]

(A.3)

Also, the following partial derivatives must be negative:

\[
\begin{align*}
\left. \frac{\partial \mu(\alpha_2, \ldots, \alpha_k)}{\partial \alpha_{i+1}} \right|_{\alpha^*} &< 0 \\
& \vdots \\
\left. \frac{\partial \mu(\alpha_2, \ldots, \alpha_k)}{\partial \alpha_k} \right|_{\alpha^*} &< 0.
\end{align*}
\]

(A.4)

(A.3) yields

\[ \mathbb{E} \left[ \frac{\lambda_1}{\alpha_1\lambda_1 + \cdots + \alpha_i\lambda_i} \right] = \cdots = \mathbb{E} \left[ \frac{\lambda_i}{\alpha_1\lambda_1 + \cdots + \alpha_i\lambda_i} \right]. \]
Suppose that the above value is \( C \), then

\[
1 = \mathbb{E} \left[ \frac{\alpha_1 \lambda_1 + \cdots + \alpha_l \lambda_l}{\alpha_1 \lambda_1 + \cdots + \alpha_l \lambda_l} \right] = (\alpha_1 + \cdots + \alpha_l)C = C.
\]

(A.4) yields

\[
\mathbb{E} \left[ \frac{\lambda_j}{\alpha_1 \lambda_1 + \cdots + \alpha_l \lambda_l} \right] < \mathbb{E} \left[ \frac{\lambda_1}{\alpha_1 \lambda_1 + \cdots + \alpha_l \lambda_l} \right] = 1
\]

for \( j = l + 1, l + 2, \cdots, k \). which completes the proof.

A.4 Proofs for Chapter 5


Proof of Proposition 13. \( \mathbb{E}[1/y] \) as given in (5.7) is clearly a decreasing function of \( \mu_a \) and an increasing function of \( \mu_b \).

Proof of Lemma 3. According to the discussions proceeding to Lemma 3, calculations of second order derivatives of \( y(r, \epsilon_a, \epsilon_b) \) suffice. For simplicity we use \((0,0,0)\) to represent \( r = \epsilon_a = \epsilon_b = 0 \).

\[
\frac{\partial y}{\partial r} = \frac{\beta_a (\mu_b + \beta_b r + \epsilon_b) - \beta_b (\mu_a + \beta_a r + \epsilon_a)}{(\mu_b + \beta_b r + \epsilon_b)^2} = \frac{\beta_a \mu_b - \beta_b \mu_a + \beta_a \epsilon_b - \beta_b \epsilon_a}{(\mu_b + \beta_b r + \epsilon_b)^2}
\]

\[
\frac{\partial^2 y}{\partial r^2} = \frac{-2\beta_b (\beta_a \mu_b - \beta_b \mu_a + \beta_a \epsilon_b - \beta_b \epsilon_a)}{(\mu_b + \beta_b r + \epsilon_b)^3} \overset{(0,0,0)}{=} \frac{2\beta_b (\beta_b \mu_a - \beta_a \mu_b)}{\mu_b^3}
\]

\[
\frac{\partial y}{\partial \epsilon_a} = \frac{1}{\mu_b + \beta_b r + \epsilon_b}, \quad \frac{\partial^2 y}{\partial \epsilon_a^2} = 0
\]

\[
\frac{\partial y}{\partial \epsilon_b} = \frac{\mu_a + \beta_a r + \epsilon_a}{(\mu_b + \beta_b r + \epsilon_b)^2}
\]

\[
\frac{\partial^2 y}{\partial \epsilon_b^2} = \frac{2(\mu_a + \beta_a r + \epsilon_a)}{(\mu_b + \beta_b r + \epsilon_b)^3} \overset{(0,0,0)}{=} \frac{2\mu_a}{\mu_b^3}
\]

Therefore,

\[
\mathbb{E}[y] \approx \frac{\mu_a}{\mu_b} + \frac{\beta_b (\beta_b \mu_a - \beta_a \mu_b)}{\mu_b^3} \mathbb{E}[r] + \frac{\mu_a}{\mu_b^3} \mathbb{E}[\epsilon_b^2]
\]

\[
= \frac{\mu_a}{\mu_b} + \frac{\beta_a \beta_b^2}{\mu_b^3} \left( \frac{\mu_a}{\beta_a} - \frac{\mu_b}{\beta_b} \right) \text{Var}(r) + \frac{\mu_a}{\mu_b^3} \text{Var}(\epsilon_b),
\]

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which completes the proof of the first part. The approximation for $E[1/y]$ follows from similar calculations.

**Proof of Proposition 14.** According to Lemma 3, $E[1/y]$ is a decreasing function of $\beta_b$; it is a quadratic function of $\beta_a$ and therefore turns at its vertex.

**Proof of Proposition 15.** It follows directly from Lemma 3.

**Proof of Proposition 16.** The first order condition as given in (5.8) is an increasing function of $\mu_a$ and a decreasing function of $\mu_b$.

**Proof of Lemma 4.** For notational convenience, we define:

$$F(r, e_a, e_b) \equiv \frac{(\mu_a - \mu_b) + (\beta_a - \beta_b)r + (\epsilon_a - \epsilon_b)}{(f \mu_a + (1 - f) \mu_b) + (f \beta_a + (1 - f) \beta_b)r + (f \epsilon_a + (1 - f) \epsilon_b)}$$

and therefore the first order condition reduces to $E[F(r, e_a, e_b)] = 0$, and it suffices to calculate the second order derivatives of $F(r, e_a, e_b)$.

$$\frac{\partial F}{\partial r} = \frac{(\beta_a - \beta_b)((f \mu_a + (1 - f) \mu_b) + (f \epsilon_a + (1 - f) \epsilon_b)) - (f \beta_a + (1 - f) \beta_b)((\mu_a - \mu_b) + (\epsilon_a - \epsilon_b))}{((f \mu_a + (1 - f) \mu_b) + (f \beta_a + (1 - f) \beta_b)r + (f \epsilon_a + (1 - f) \epsilon_b))^2}$$

$$\frac{\partial^2 F}{\partial r^2} = \frac{-2f(\beta_a + (1 - f) \beta_b)((\mu_a - \mu_b) + (\epsilon_a - \epsilon_b))}{((f \mu_a + (1 - f) \mu_b) + (f \beta_a + (1 - f) \beta_b)r + (f \epsilon_a + (1 - f) \epsilon_b))^3}$$

$$\frac{\partial F}{\partial e_a} = \frac{\mu_a + \beta_a r + \epsilon_a}{((f \mu_a + (1 - f) \mu_b) + (f \beta_a + (1 - f) \beta_b)r + (f \epsilon_a + (1 - f) \epsilon_b))^2}$$

$$\frac{\partial^2 F}{\partial e_a^2} = \frac{-2f(\mu_a + \beta_a r + \epsilon_a)}{((f \mu_a + (1 - f) \mu_b) + (f \beta_a + (1 - f) \beta_b)r + (f \epsilon_a + (1 - f) \epsilon_b))^3}$$

$$\frac{\partial F}{\partial e_b} = \frac{-2(1 - f)(\mu_a + \beta_a r + \epsilon_a)}{((f \mu_a + (1 - f) \mu_b) + (f \beta_a + (1 - f) \beta_b)r + (f \epsilon_a + (1 - f) \epsilon_b))^2}$$

$$\frac{\partial^2 F}{\partial e_b^2} = \frac{2(1 - f)(\mu_a + \beta_a r + \epsilon_a)}{((f \mu_a + (1 - f) \mu_b) + (f \beta_a + (1 - f) \beta_b)r + (f \epsilon_a + (1 - f) \epsilon_b))^3}$$

Therefore,

$$E[F(r, e_a, e_b)] \approx \frac{\mu_a - \mu_b}{f \mu_a + (1 - f) \mu_b} + \frac{1}{2} \frac{\partial^2 F_0}{\partial r^2} E[r^2] - \frac{f \mu_b E[e_a^2]}{(f \mu_a + (1 - f) \mu_b)^3} + \frac{(1 - f) \mu_a E[e_b^2]}{(f \mu_a + (1 - f) \mu_b)^3}.$$

Rearranging terms, we get Lemma 4.

**Proof of Proposition 17.** The condition described in Lemma 4 is a quadratic function of both $\beta_a$ and $\beta_b$. Simple calculations of the vertex suffice to prove the result.
Proof of Proposition 18. It follows directly from Lemma 4.

Proof of Proposition 19. It follows directly from Lemma 3-4 and Assumption 12.

Proof of Proposition 20. The equilibrium behavior \( f^e \) is given by Proposition 12 with \( X_a \) and \( X_b \) replaced by \( R_a \) and \( R_b \), and \( \lambda_t \) replaced by \( f^e \). Therefore we have the first order condition:

\[
0 = E \left[ \frac{R_a - R_b}{f^e R_a + (1 - f^e) R_b} \right] = E \left[ \frac{(1 - f^e) X_a - f^e X_b}{f^e (1 - f^e) (X_a + X_b)} \right]
\]

\[
= 1 - 2 f^e \frac{1}{2 f^e (1 - f^e)} + \frac{1}{2 f^e (1 - f^e)} E \left[ \frac{X_a - X_b}{X_a + X_b} \right].
\]

Solving for \( f^e \) one immediately get (5.12). The second part is trivial given Assumption 13.

Proof of Proposition 21. For notational convenience, we define:

\[
Q(r, \epsilon_a, \epsilon_b) = \frac{X_a}{X_a + X_b} = \frac{\mu_a + \beta_a r + \epsilon_a}{(\mu_a + \mu_b) + (\beta_a + \beta_b) r + (\epsilon_a + \epsilon_b)}.
\]

It suffices to calculate the second order derivatives of \( Q \).

\[
\frac{\partial Q}{\partial r} = \frac{\beta_a \mu_b - \beta_b \mu_a + \beta_a \epsilon_b - \beta_b \epsilon_a}{((\mu_a + \mu_b) + (\beta_a + \beta_b) r + (\epsilon_a + \epsilon_b))^2}
\]

\[
\frac{\partial^2 Q}{\partial r^2} = -2(\beta_a + \beta_b) \frac{(\beta_a \mu_b - \beta_b \mu_a + \beta_a \epsilon_b - \beta_b \epsilon_a)}{((\mu_a + \mu_b) + (\beta_a + \beta_b) r + (\epsilon_a + \epsilon_b))^3}
\]

\[
\frac{\partial^2 Q}{\partial \epsilon_a} = \frac{(\mu_a + \mu_b) + (\beta_a + \beta_b) r + (\epsilon_a + \epsilon_b)}{((\mu_a + \mu_b) + (\beta_a + \beta_b) r + (\epsilon_a + \epsilon_b))^3} - \frac{2 \mu_b}{(\mu_a + \mu_b)^3}
\]

\[
\frac{\partial^2 Q}{\partial \epsilon_a \partial \epsilon_b} = \frac{(\mu_a + \mu_b) + (\beta_a + \beta_b) r + (\epsilon_a + \epsilon_b)}{((\mu_a + \mu_b) + (\beta_a + \beta_b) r + (\epsilon_a + \epsilon_b))^3} - \frac{2 \mu_a}{(\mu_a + \mu_b)^3}.
\]
Therefore,

\[ f^e = \mathbb{E}[Q(r, \epsilon_a, \epsilon_b)] \]

\[
\approx \frac{\mu_a}{\mu_a + \mu_b} + \frac{\beta_a \beta_b (\beta_a + \beta_b)}{(\mu_a + \mu_b)^3} \left( \frac{\mu_a}{\beta_a} - \frac{\mu_b}{\beta_b} \right) \mathbb{E}[r^2] - \frac{\mu_b}{(\mu_a + \mu_b)^3} \mathbb{E}[\epsilon_a^2] + \frac{\mu_a}{(\mu_a + \mu_b)^3} \mathbb{E}[\epsilon_b^2]
\]

which completes the proof. \qed

A.5 Proofs for Chapter 6

**Proof of Proposition 22.** See Brennan and Lo (2011). \qed

**Proof of Proposition 23.** The first partial derivative of \( \mathbb{E}[q_1^f] \) to \( f \) is:

\[
\frac{\partial \mathbb{E}[q_1^f]}{\partial f} = \lambda(1 - \lambda)\mathbb{E} \left[ \frac{(X_a - X_b)\omega^g}{(\lambda \omega f + (1 - \lambda)\omega g)^2} \right].
\]

The second partial derivative of \( \mathbb{E}[q_1^f] \) to \( f \) is:

\[
\frac{\partial^2 \mathbb{E}[q_1^f]}{\partial f^2} = -2\lambda^2(1 - \lambda)\mathbb{E} \left[ \frac{(X_a - X_b)^2\omega^g}{(\lambda \omega f + (1 - \lambda)\omega g)^3} \right] \leq 0,
\]

which indicates that \( \mathbb{E}[q_1^f] \) is a concave function of \( f \). Therefore, it suffices to consider the value of the first partial derivative at its endpoints 0 and 1.

\[
f_1' = \begin{cases} 
1 & \text{if } \left. \frac{\partial \mathbb{E}[q_1^f]}{\partial f} \right|_{f=1} > 0 \\
0 & \text{if } \left. \frac{\partial \mathbb{E}[q_1^f]}{\partial f} \right|_{f=0} < 0 \\
\text{solution to } \frac{\partial \mathbb{E}[q_1^f]}{\partial f} = 0 & \text{otherwise.}
\end{cases}
\]

Proposition 23 follows from trivial simplifications of the above equation. \qed

**Proof of Proposition 24.** Consider \( \frac{\partial \mathbb{E}[q_1^f]}{\partial f} \) when \( f = g \):

\[
\left. \frac{\partial \mathbb{E}[q_1^f]}{\partial f} \right|_{f=g} = \lambda(1 - \lambda)\mathbb{E} \left[ \frac{X_a - X_b}{f X_a + (1 - f) X_b} \right].
\]
Note that the right-hand side consists of a factor that also appears in the first order condition (6.4) of the Kelly Criterion. Therefore its sign is determined by whether $f$ is larger than $f_{Kelly}$:

\[
\frac{\partial \mathbb{E}[q_f]}{\partial f} \bigg|_{f=g} = \begin{cases} 
> 0 & \text{if } f = g < f_{Kelly} \\
= 0 & \text{if } f = g = f_{Kelly} \\
< 0 & \text{if } f = g > f_{Kelly}.
\end{cases}
\] (A.5)

Since $\mathbb{E}[q_f]$ is concave as a function of $f$ for any $g$, we know that:

\[
f^*_1 \begin{cases} 
> g & \text{if } g < f_{Kelly} \\
= g & \text{if } g = f_{Kelly} \\
< g & \text{if } g > f_{Kelly}
\end{cases}
\]

which completes the proof.

**Proof of Proposition 25.** The cross partial derivative of $\mathbb{E}[q_f]$ is:

\[
\frac{\partial^2 \mathbb{E}[q_f]}{\partial f \partial g} = \lambda(1 - \lambda) \mathbb{E} \left[ \frac{(X_a - X_b)^2 (\lambda \omega f - (1 - \lambda) \omega g)}{(\lambda \omega f + (1 - \lambda) \omega g)^3} \right].
\]

Consider $\frac{\partial^2 \mathbb{E}[q_f]}{\partial f \partial g}$ when $f = g = f_{Kelly}$:

\[
\frac{\partial^2 \mathbb{E}[q_f]}{\partial f \partial g} \bigg|_{f=g} = 2\lambda(1 - \lambda) \left( \lambda - \frac{1}{2} \right) \mathbb{E} \left[ \left( \frac{X_a - X_b}{fX_a + (1 - f)X_b} \right)^2 \right] \begin{cases} 
< 0 & \text{if } \lambda < \frac{1}{2} \\
= 0 & \text{if } \lambda = \frac{1}{2} \\
> 0 & \text{if } \lambda > \frac{1}{2}.
\end{cases}
\]

The first order condition (A.5) is 0 when $f = g = f_{Kelly}$, so when $g$ is around $f_{Kelly}$, the sign of the first order condition is determined by whether $\lambda$ is greater than, equal to, or less than 1/2. For example, if $\lambda < 1/2$, then the derivative of the first order condition (A.5) with respect to $g$ is negative, which implies that the first
order condition is negative when \( g = f^{Kelly} + \epsilon \) where \( \epsilon \) is a small positive quantity. Therefore, when \( g = f^{Kelly} + \epsilon, f^*_t \) is smaller than \( f^{Kelly} \). The cases when \( \lambda > 1/2 \) and \( \lambda = 1/2 \) follows similarly. 

Proof of Proposition 26. The first partial derivative of \( \mathbb{E}[q^{f^*_T}] \) to \( f \) is:

\[
\frac{\partial \mathbb{E}[q^{f^*_T}]}{\partial f} = \frac{1 - \lambda}{\lambda} \mathbb{E} \left[ \exp \left( \frac{TR^f_T}{\lambda} \sum_{t=1}^{T} \frac{X_{at} - X_{bt}}{fX_{at} + (1-f)X_{bt}} \right) \left( 1 + \frac{1-\lambda}{\lambda} \exp \left( \frac{TR^f_T}{\lambda} \right) \right)^{-2} \right].
\]

\( \mathbb{E}[q^{f^*_T}] \) is not necessarily concave, but it is unimodel. The rest follows from similar calculations to Proposition 23. 

Proof of Proposition 27. The first partial derivative of \( \mathbb{E}[q^{f^*_T}] \) to \( f \) evaluated at \( f = g \) is given by:

\[
\frac{\partial \mathbb{E}[q^{f^*_T}]}{\partial f} \bigg|_{f=g} = T\lambda(1 - \lambda) \mathbb{E} \left[ \frac{X_a - X_b}{fX_a + (1-f)X_b} \right].
\]

The cross partial derivative of \( \mathbb{E}[q^{f^*_T}] \) evaluated at \( f = g \) is given by:

\[
\frac{\partial^2 \mathbb{E}[q^{f^*_T}]}{\partial f \partial g} \bigg|_{f=g} = 2\lambda(1 - \lambda) \left( \lambda - \frac{1}{2} \right) \mathbb{E} \left[ \left( \sum_{t=1}^{T} \frac{X_{a,t} - X_{b,t}}{fX_{a,t} + (1-f)X_{b,t}} \right)^2 \right].
\]

The rest follows similarly to the proof of Proposition 24-25. 

Proof of Proposition 28. It follows directly from (6.6) and (6.11). 

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Bibliography


