

# The Origin of Behavior<sup>\*</sup>

Thomas J. Brennan<sup>†</sup> and Andrew W. Lo<sup>‡</sup>

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## Abstract

We propose a single evolutionary explanation for the origin of several behaviors that have been observed in organisms ranging from ants to human subjects, including risk-sensitive foraging, risk aversion, loss aversion, probability matching, randomization, and diversification. Given an initial population of individuals, each assigned a purely arbitrary behavior with respect to a binary choice problem, and assuming that offspring behave identically to their parents, only those behaviors linked to reproductive success will survive, and less reproductively successful behaviors will disappear at exponential rates. This framework generates a surprisingly rich set of behaviors, and the simplicity and generality of our model suggest that these behaviors are primitive and universal.

**Keywords:** Probability Matching; Loss Aversion; Risk Aversion; Risk Preferences; Behavioral Finance; Evolution.

**JEL Classification:** G00, D81, D01, D03, C73

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<sup>†</sup>Assistant Professor, School of Law, Northwestern University, East Chicago Avenue Chicago, IL 60611–3069, [t-brennan@law.northwestern.edu](mailto:t-brennan@law.northwestern.edu) (email).

<sup>‡</sup>Harris & Harris Group Professor, MIT Sloan School of Management, and Chief Scientific Officer, AlphaSimplex Group, LLC. Please direct all correspondence to: MIT Sloan School, 50 Memorial Drive, E52-454, Cambridge, MA 02142–1347, (617) 253–0920 (voice), [alo@mit.edu](mailto:alo@mit.edu) (email).

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# 1 Introduction

The events surrounding the Financial Crisis of 2007–2008 have brought into sharp focus the inconsistencies between the hypothetical behavior of *Homo economicus* and the observed behavior of *Homo sapiens*. Those who insist that U.S. housing prices were rational prior to 2006 are hard-pressed to explain the 33% decline since then, and those who believe that markets are obviously irrational are equally challenged by the surprising difficulty in “arbitraging” away such behavioral anomalies. This state of affairs suggests that human behavior may not be solely determined by economic considerations, but is the amalgam of multiple decisionmaking faculties—including instinct, emotion, and logic—that yield a particular observed action. And because the relative importance of these faculties vary across time and circumstances, even for a given individual, it is no wonder that despite centuries of intense analysis and debate, there is still remarkably little consensus among economists, psychologists, and biologists as to how to model behavior. In particular, while the expected-utility and rational-expectations framework is still the dominant paradigm among economists, critics point to empirical and experimental counter-examples that are inconsistent with rational optimizing agents and economic equilibrium (Kahneman, Slovic, and Tversky, 1982; Thaler, 1993), and biologists have observed similar behavioral anomalies in other animal species.

In this paper, we propose an evolutionary explanation for these anomalies in a model that is simple enough to solve analytically, but general enough to explain commonly observed behavior in animal species ranging from ants to human subjects. We show that risk aversion, risk-sensitive foraging, loss aversion, probability matching, and more general forms of randomizing behavior can all be derived from evolutionary forces acting on an arbitrary set of behaviors over an extended period of time.

Some of these behaviors have been the subject of significant controversy, and “biases” are especially pronounced when elements of risk and probability are involved. Two of the most ubiquitous biases are loss aversion (Tversky and Kahneman, 1974; Kahneman and Tversky, 1979) (the tendency to take greater risk when choosing between two potential losses, and less risk when choosing between two potential gains) and probability matching (Grant, Hake, and Hornseth, 1951; Hake and Hyman, 1953; Herrnstein, 1997; Vulkan, 2000) (the tendency to choose randomly between heads and tails when asked to guess the outcomes of

a series of biased-coin tosses, where the randomization matches the probability of the biased coin). Both biases clearly imply individually sub-optimal choices, yet these behaviors have been observed in thousands of geographically diverse human subjects over several decades, as well as in other animal species.

Our model consists of an initial population of individuals (not necessarily human) that live for one period of unspecified length, and engage in a single binary decision that has implications for the random number of offspring they will generate. To the extent that their behavior is linked to fecundity, only the most reproductively successful behaviors will flourish due to the forces of natural selection. Although obvious from an evolutionary biologist's perspective, this observation yields surprisingly specific implications for the types of behavior that are sustainable over time, behaviors that are likely to be innate to most living organisms.

A simple numerical example of one of our results will illustrate our approach. Consider a population of individuals, each facing a binary choice between one of two possible actions,  $a$  and  $b$ . 60% of the time, environmental conditions are positive, and action  $a$  leads to reproductive success, generating 3 offspring for the individual. 40% of the time, environmental conditions are negative, and action  $a$  leads to 0 offspring. Suppose action  $b$  has exactly the opposite effect of  $a$ —whenever  $a$  yields 3 offspring,  $b$  yields 0, and whenever  $a$  yields 0,  $b$  yields 3. From the individual's perspective, always choosing  $a$  will lead to more reproductive success on average, given  $a$ 's higher probability of producing offspring. However, if all individuals in the population behaved in this manner, the first time that a negative environmental condition occurs, the entire population will become extinct. Assuming that offspring behave identically to their parents, the behavior “always choose  $a$ ” cannot survive over time. For the same reason, “always choose  $b$ ” is also unsustainable. In fact, we show below that the behavior with the highest reproductive success over time is for each individual to choose  $a$  60% of the time and  $b$  40% of the time, matching the probabilities of reproductive success and failure. Eventually, this behavior will dominate the entire population.

Probability matching behavior has long puzzled economists and psychologists because of its apparent inconsistency with basic self interest.<sup>1</sup> However, probability matching is perfectly consistent with evolution, arising purely from the forces of natural selection and

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<sup>1</sup>One of the earliest papers to document this phenomenon is Grant, Hake, and Hornseth (1951), and as recently as 2007, Kogler and Kühberger (2007) report that: “Experimental research in simple repeated risky choices shows a striking violation of rational choice theory: the tendency to match probabilities by allocating the frequency of response in proportion to their relative probabilities”.

population growth. Moreover, we derive more general types of behavior that involve randomization but not necessarily probability matching, which may explain the inconsistency with which such behavior is observed. Whether or not randomizing behavior matches environmental probabilities depends on the relative reproductive success of the outcomes, and our framework yields a simple and specific condition for such behavior. Our results do not depend on how individuals arrive at their choices, whether they learn over time, or whether individuals possess a theory of mind or a self-awareness of the consequences of their actions. In fact, our results do not even require individuals to possess central nervous systems.

We also show that the concepts of risk aversion and risk-sensitive foraging behavior emerge from the same framework. Because populations grow geometrically, a sequence of 50/50 gambles yielding 2 or 4 offspring each generation will yield a slower average growth rate than sure bets of 3 offspring (the product of 2 and 4 is smaller than the product of 3 and 3). While this principle of “geometric mean fitness” is well known among population biologists, its implications for risk-bearing activity in economic settings has not been fully explored. For example, the fact that those preferences most likely to survive over time are those that require a higher expected fecundity in return for taking risk implies the existence of a positive evolutionary “risk premium”, which we are able to derive explicitly and quantify as a function of environmental conditions.

Finally, our model also generates asymmetric risk preferences for gains and losses, i.e., loss aversion, resolving a longstanding debate among disciples of von Neumann and Morgenstern expected-utility theory (von Neumann and Morgenstern, 1944; Schoemaker, 1982) and proponents of behavioral alternatives such as prospect theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1981). Both perspectives are capturing certain aspects of the same behavior shaped by natural selection and population growth.

## 2 Literature Review

The literature on evolution and behavior is overwhelming, spanning the disciplines of evolutionary biology, ecology, evolutionary and social psychology, and economics, with myriad branches of relevant citations within each of these broad fields. While a comprehensive survey is well beyond the scope of this section, we attempt to provide a representative sampling of the many related strands of this vast body of research.

Evolutionary principles are now routinely used to derive implications for animal behavior.

While each species may have developed unique responses for addressing particular environmental challenges, the most critical of these have been shaped by the forces of mutation, competition, and natural selection. Beginning with the pathbreaking work of Hamilton (1964), Trivers (1971, 1985, 2002), Wilson (1975), and Maynard Smith (1982, 1984), many evolutionary models have been proposed to explain a variety of counter-intuitive behaviors including altruism, cooperation, kin selection, reciprocity, and other social customs. More recently, the field of evolutionary psychology (Cosmides and Tooby, 1994; Barkow, Cosmides, and Tooby, 1992; Tooby and Cosmides, 1995; Pinker, 1979; Pinker, 1991; Pinker, 1994; Gigerenzer, 2000; Buss, 2004; Ehrlich and Levin, 2005) has expanded the reach of evolution to even broader domains such as language, culture, and religion.

Evolutionary ideas have also played an important role in economics. Thomas Malthus (1826) used a simple biological argument—the fact that populations increase at geometric rates whereas natural resources increase at only arithmetic rates (at least in the nineteenth century)—to arrive at the dire economic consequences that earned the field the moniker “dismal science”. Both Darwin and Wallace were aware of and apparently influenced by these arguments (see Hirshleifer (1977) for further details). Also, Schumpeter’s (1939) view of business cycles, entrepreneurs, and capitalism have an unmistakable evolutionary flavor to them; in fact, his notions of “creative destruction” and “bursts” of entrepreneurial activity are similar in spirit to natural selection and Eldredge and Gould’s (1972) notion of “punctuated equilibrium”.

More recently, economists and biologists have begun to explore these connections in several veins: economic extensions of sociobiology (Becker, 1976; Hirshleifer, 1977), evolutionary game theory (Maynard Smith 1982, 1984; Weibull, 1995); an evolutionary interpretation of economic change (Nelson and Winter, 1982); economies as complex adaptive systems (Anderson, Arrow, and Pines, 1988), and the impact of uncertainty regarding the number of offspring on current consumption patterns (Arrow and Levin, 2009).

Evolutionary concepts have also appeared in the finance literature. For example, Luo (1995) explores the implications of natural selection for futures markets, Hirshleifer and Luo (2001) consider the long-run prospects of overconfident traders in a competitive securities market, and Kogan, Ross, Wang, and Westerfield (2006) show that irrational traders can influence market prices even when their wealth becomes negligible. The literature on agent-based modeling pioneered by Arthur, Holland, LeBaron, Palmer, and Tayler (1997), in which

interactions among software agents programmed with simple heuristics are simulated, relies heavily on evolutionary dynamics. And at least two prominent investment professionals have proposed Darwinian alternatives to explain market behavior. In a chapter titled “The Ecology of Markets”, Niederhoffer (1997, Ch. 15) likens financial markets to an ecosystem with dealers as “herbivores”, speculators as “carnivores”, and floor traders and distressed investors as “decomposers”. And Bernstein (1998) makes a compelling case for active management by pointing out that the notion of equilibrium is rarely realized in practice and that market dynamics are better explained by evolutionary processes.

But in our specific context, the two most relevant lines of research—one from biology and the other from economics—involve direct applications of evolutionary principles to individual behavior and preferences. In the evolutionary biology literature, Maynard Smith (1982) has developed the concept of an “evolutionarily stable strategy” (ESS), 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 terms of maximizing geometric growth rates) in the face of random 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, 1972; Seger and Brockmann, 1987). Frank and Slatkin (1990) propose a framework that highlights the importance of correlations among individual reproductive success in determining the path of evolution. And 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 mammals (Real and Caraco, 1986; Stephens and Krebs, 1986; Mangel and Clark, 1988), and seed dispersal strategies in plants (Levin, Cohen, and Hastings, 1984; Levin, Muller-Landau, Nathan, and Chave, 2003).

In the economics literature, evolutionary principles have been used to justify the existence of utility functions and develop implications for their functional form, as in Hansson and Stuart (1990) and Robson (1996a, 2001b) (see, Robson, 2001a, and Robson and Samuelson, 2008, for comprehensive reviews of this literature). For example, in an equilibrium model of economic growth, Hansson and Stuart (1990) derive restrictions on individual preferences for

consumption, savings, and labor-supply arising from the forces of natural selection. Robson (1996a) investigates expected and non-expected utility behaviors, and finds that idiosyncratic risk-seeking may be optimal from a population perspective even though it is suboptimal from an individual perspective (see, also, Grafen, 1999, and Curry, 2001). And Robson (2001b) 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. Specifically, early exploration in choice-making (which is the primary focus of our analysis), coupled with a utility-based rule of thumb for deciding when to cut exploration off and stick with a particular choice, leads to evolutionarily optimal adaptation to unknown underlying distributions of outcomes. Robson and Samuelson (2007) find that exponential discounting in utility functions is consistent with evolutionarily optimal growth of a population, and the emergence of time preference is derived by Rogers (1994), Samuelson (2001), Robson and Samuelson (2007), and Robson and Szentes (2008).

However, as Waldman (1994, p. 483) observed, individually optimal behavior predicted by expected utility—even when utility functions are derived from evolutionary principles—may not always coincide with behavior that maximizes fitness:

Another possible outcome is that preferences do not equate utility maximization with fitness maximization, and correspondingly evolution then does not favor humans who are efficient utility-maximizers. Instead what happens in this case is that evolution favors a systematic bias in the decision-making process which moves behavior away from the maximization of utility and toward the maximization of fitness.

Waldman (1994) provides a compelling illustration of this insight through the comparison between asexual and sexual reproduction in which the latter yields evolutionarily stable second-best adaptations. In our binary choice framework, we show that even with asexual reproduction, systematic “errors” such as probability matching can persist and become dominant despite the fact that such behavior is sub-optimal from the individual’s perspective.

Our approach builds on the insights of Fretwell (1972), Maynard Smith (1982), Waldman (1994), and Robson (1996a, 2001a) in applying the well-known principle of geometric-mean fitness (Dempster, 1955) to the actions of a heterogeneous population of individuals and deriving the subset of behaviors that survive.<sup>2</sup> However, our framework is considerably

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<sup>2</sup>Geometric-mean fitness has also appeared in the financial context as the “Kelly criterion” for maximizing



simpler, involving only a single binary choice for each individual during its lifetime, a choice that has implications for the individual’s reproductive success. One virtue of such simplicity is the universality with which this framework’s derived behaviors are likely to be found among living organisms.<sup>3</sup> Our model is simple enough to solve analytically, but remarkably rich in its implications for behavior, yielding risk aversion, probability matching, loss aversion, and more general forms of randomization. Also, as with most other models in the population biology literature, the individual behaviors that survive in our framework need not be optimal from the individual’s perspective, and may appear irrational. In fact, such behavior is merely adaptive, a product of natural selection that is likely to be more primitive on an evolutionary timescale than the more sophisticated learned behaviors captured by Rogers (1994), Robson (1996a, 2001a), and Robson and Samuelson (2007). In this respect, our analysis complements those of the existing literature on evolutionary foundations of utility theory, providing additional evidence for the link between behavior and natural selection at the most basic level of choice.

### 3 The Binary Choice Model

We begin with a population of individuals that live for one period, produce a random number of offspring asexually, and then die (“asexual semelparous” organisms, in the jargon of evolutionary biology). During their lives, individuals make only one decision: they choose one of two possible courses of action, denoted  $a$  and  $b$ , which 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, otherwise for all intents and purposes, individuals have only one action available to them. We also require  $\Phi$  to have finite moments up to order 2, and assume it is independent and identical

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the geometric growth rate of a portfolio (Kelly, 1956; Cover and Thomas, 1991). However, the motivation for geometric-mean fitness in population biology is considerably more compelling than in financial investments, as Samuelson (1971) has argued (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).

<sup>3</sup>For example, the fact that probability matching behavior has been observed in non-human subjects—including ants (Deneubourg, Aron, Goss, and Pasteels, 1987; Pasteels, Deneubourg, and Goss, 1987; Kirman, 1993; Hölldobler and Wilson, 1990), bees (Harder and Real, 1987; Thuijsman, Peleg, Amitai, and Shmida, 1995; Keasar, Rashkovich, Cohen, and Shmida, 2002), fish (Bitterman, Wodinsky, and Candland, 1958; Behrend and Bitterman, 1961), pigeons (Graf, Bullock, and Bitterman, 1964; Young, 1981), and primates (Woolverton and Rowlett, 1998)—suggests that they may have a common and ancient origin, and an evolutionary role that belies their apparent shortcomings.

across individuals and over time.

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, but which is of less direct interest to economists than the link between behavior and reproductive success. If action  $a$  leads to higher fecundity than action  $b$  for individuals in a given population, the particular set of genes that predispose individuals to select  $a$  over  $b$  will be favored by natural selection, in which case these genes will survive and flourish, implying that the behavior “choose  $a$  over  $b$ ” will flourish as well. On the other hand, if  $a$  and  $b$  have identical implications for success, i.e.,  $x_a \equiv x_b$ , then  $\Phi$  is a degenerate distribution. By asserting that  $\Phi$  is a non-degenerate bivariate distribution, we have essentially defined two equivalence classes of actions that yield different implications for reproduction.

The specification of  $\Phi$  also captures the fundamental distinction between traditional models of population genetics (Levins, 1969; Wright, 1968; Wilson and Bossert, 1990) and more recent applications of evolution to behavior (Hamilton, 1964; Trivers, 1971; Wilson, 1975; 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, which is captured by  $\Phi$ . In the jargon of econometrics,  $\Phi$  may be viewed as a “reduced form” representation of an individual's biology, whereas the molecular biology of genetics corresponds to the “structural form”.<sup>4</sup> This terminology is more than a simple analogy—it accurately summarizes the difference between our framework and the emerging field of behavioral genomics (Plomin, 1990; Plomin, Owen, and McGuffin, 1994; McGuffin, Riley, and Plomin, 2001) which attempts to map traits and behaviors to specific genes.

Now suppose that 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 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

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<sup>4</sup>Waldman (1994) uses the same terminology in his framework in which individual traits are directly linked to reproductive success rather than specific genes.

selection under certain conditions.

We assume that 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 comprised of “types”  $f$  that range continuously from 0 to 1. We assume that the initial population contains an equal number of all types, which we normalize to be 1 each without loss of generality. In a given generation  $t$ , the total number of offspring produced by individuals of type  $f$  is simply

$$G_t(f) = \left( f x_a + (1 - f) x_b \right) G_{t-1}(f) \quad , \quad G_1(f) \equiv 1 \quad (1)$$

and for simplicity, we have assumed that  $(x_a, x_b)$  is independently and identically distributed across generations (this can be relaxed to some degree). After  $T$  generations, the total population size of this type,  $G_T(f)$ , is given by:

$$G_T(f) \approx \exp \left( T E[\log(f x_a + (1 - f) x_b)] \right) \quad (2)$$

where the approximate equality follows from the Law of Large Numbers for large  $T$  (Lewontin and Cohen, 1969). From this expression, we see that the value of  $f$  that maximizes the population size  $G_T(f)$  is the value that maximizes the expectation:

$$I(f) \equiv E[\log(f x_a + (1 - f) x_b)] \quad (3)$$

This optimal value  $f^*$ , which we call the “growth-optimal” behavior to distinguish it from behavior that may be optimal for the individual, is given by (all proofs are relegated to the Appendix):

**Proposition 1** *If  $(x_a, x_b)$  is independently and identically distributed across individuals and over time, then the growth-optimal behavior  $f^*$  is:*

$$f^* = \begin{cases} 1 & \text{if } E[x_a/x_b] > 1 \text{ and } E[x_b/x_a] < 1 \\ \text{solution to (5)} & \text{if } E[x_a/x_b] \geq 1 \text{ and } E[x_b/x_a] \geq 1 \\ 0 & \text{if } E[x_a/x_b] < 1 \text{ and } E[x_b/x_a] > 1 \end{cases} \quad (4)$$

where  $f^*$  is defined implicitly in the second case of (4) by:

$$0 = \text{E} \left[ \frac{x_a - x_b}{f^*x_a + (1 - f^*)x_b} \right] \quad (5)$$

and the expectations in (2)–(5) are with respect to the joint distribution  $\Phi(x_a, x_b)$ .

The three possible behaviors in (4) reflect the relative reproductive success of the two choices, and is a generalization of the “adaptive coin-flipping” strategies of (Cooper and Kaplan, 1982). 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, but the population perspective implies that in such cases, the individuals that have the most reproductive success over time will be those that choose randomly according to probability  $f^*$ .<sup>5</sup> If, however, one choice is significantly better than the other in terms of the expected ratio of offspring, then over time, the behavior that will survive is deterministic choice, not randomization. In these extreme cases, because of the unambiguous implications for fecundity, the deterministic choice that leads to higher reproductive success will quickly dominate the population.

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 fecundities  $\text{E}[x_a/x_b]$  and  $\text{E}[x_b/x_a]$  shift suddenly from the intermediate state in (4) to one of the deterministic states due to rapid environmental changes, and if there is sufficient diversity of behavior left in the population after the change occurs.<sup>6</sup> To an outside observer, behaviors among individuals in this population may seem heterogenous before the shift (because individuals are randomizing), but will become increasingly similar after the shift—as selective pressures begin to favor deterministic behavior over randomization—creating the appear-

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<sup>5</sup>Cooper and Kaplan (1982) 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.

<sup>6</sup>This last qualification is critical due to our assumption that offspring behave exactly as their parents, hence if individuals with behavior  $f=1$  no longer exist in the population, such behavior cannot emerge even if it becomes optimal from the population perspective. This observation underscores the importance of random mutations and the evolutionary advantages of sexual reproduction in the face of random environmental conditions.

ance (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. Considerably more sophisticated adaptations are necessary to generate true herding and synchronization behavior as in (Hamilton, 1971; Mirollo and Strogatz, 1990; Strogatz and Stewart, 1993), including sensory inputs, conditional behavior (conditioned on additional state variables), and neuroplasticity.

The growth-optimal behavior described in (4) is much simpler, but it leads to a “winner-take-all” outcome in which individuals of all other sub-optimal types  $f'$  will be rapidly overrun by individuals of type  $f^*$ , since the ratio of the population sizes of  $f'$  and  $f^*$  converges exponentially fast to 0 (due to the optimality of  $f^*$ ):

$$\lim_{T \rightarrow \infty} \frac{G_T(f')}{G_T(f^*)} = \lim_{T \rightarrow \infty} \exp(T[I(f') - I(f^*)]) = 0. \quad (6)$$

and where the magnitude of the exponent is determined by the relative fecundities implied by the two behaviors. In other words, the behavior that emerges through the forces of natural selection, and at an exponential rate, is given by (4). Accordingly, whether such behavior is deterministic or random depends entirely on the implications of such behavior for reproductive success.

This evolutionary basis of behavior is the same as Seger and Brockmann’s (1987) geometric-mean fitness criterion, but applied directly to reproductive success  $x$ , not to specific genes. The basic logic of (4) is similar to the ESS of (Maynard Smith, 1982) in which mixed strategies are shown to be evolutionarily stable, but our approach is more parsimonious and, by design, yields broader implications for behavior that represented by  $\Phi$ . Our derived behaviors are also distinct from those of Hansson and Stuart (1990), Robson (1996a, 1996b, 2001a,b), Grafen (1999), Curry (2001), Samuelson (2001), Robson and Samuelson (2007) in which evolutionary arguments are used to justify specific types of utility functions and risk preferences—in the latter cases, two individuals with identical utility functions will behave identically, whereas in our case, two individuals with identical  $f^* \in (0, 1)$  may make difference choices at any point in time (see, also, Waldman, 1994).

In the sections to follow, we show that this simple binary choice framework and growth-optimal behavior can explain a surprisingly rich set of behavioral anomalies that have been a source of controversy in economics, psychology, and evolutionary biology, including more general forms of probability matching, loss aversion, and risk aversion.

## 4 Probability Matching

To develop further intuition for the binary choice model, consider the special case in which the number of offspring  $x_i$  are simply Bernoulli random variables that are perfectly out of phase in each of two possible environmental states:

$$\begin{aligned} \text{Prob}(x_a = m, x_b = 0) &= p \\ \text{Prob}(x_a = 0, x_b = m) &= 1 - p \\ \text{Prob}(x_a = 0, x_b = 0) &= 0 \\ \text{Prob}(x_a = m, x_b = m) &= 0. \end{aligned} \tag{7}$$

With probability  $p$ , one environmental state is realized in which choice  $a$  yields  $m > 0$  offspring and choice  $b$  yields none, and with probability  $1 - p$  the other environmental state is realized in which the reverse is the case. Without loss of generality, assume that  $p \in (\frac{1}{2}, 1]$  so that the environmental state in which choice  $a$  produces offspring is more likely.

In this simple case of 0 or  $m$  offspring, the expectation in (3) can be evaluated explicitly as:

$$I(f) = \log m + p \log f + (1 - p) \log(1 - f) \tag{8}$$

and the value of  $f$  that maximizes this expression is  $p$ . Despite the fact that setting  $f = 1$  would maximize the likelihood than an individual is able to reproduce, such “selfish” behavior is not sustainable from a population perspective because if all individuals were to behave in this way, the entire population would be wiped out the first time  $x_a = 0$ . Since such an extinction is almost sure to occur eventually,<sup>7</sup> the behavior  $f = 1$  will ultimately be eliminated from the population. In contrast, the randomizing behavior  $f^* = p$  yields the highest possible growth rate  $I(p) = \log(mp^p(1-p)^{(1-p)})$ . This is classic probability matching, documented over half a century ago in human subjects (Grant, Hake, and Hornseth, 1951), and still the

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<sup>7</sup>If all individuals always choose  $a$ , and if  $x_i$  is independently and identically distributed over time, the probability of extinction by time  $t$  is  $1 - p^t$ , which approaches 1 as  $t$  increases without bound.

subject of controversy and analysis (Kogler and Kühberger, 2007).

The Bernoulli example above can be easily generalized to any arbitrary number of offspring for both choices:

$$\begin{aligned}\text{Prob}(x_a = c_{a1}, x_b = c_{b1}) &= p \in [0, 1] \\ \text{Prob}(x_a = c_{a2}, x_b = c_{b2}) &= 1 - p \equiv q\end{aligned}\tag{9}$$

where we assume that  $c_{ij} \geq 0$  and  $c_{aj} + c_{bj} \neq 0$ ,  $i = a, b$  and  $j = 1, 2$ . The condition  $c_{aj} + c_{bj} \neq 0$  rules out the case where both  $c_{aj}$  and  $c_{bj}$  are 0, in which case the binary choice problem becomes degenerate because both actions lead to extinction hence the only choice that has any impact of fecundity is in the non-extinction state, and the only behavior that is sustainable is to select the action with the higher number of offspring.

The growth-optimal behavior in this case will depend on the relation between the probability  $p$  and the relative-fecundity variables  $r_j \equiv c_{aj}/c_{bj}$  for each of the two possible states of the world  $j = 1, 2$ .<sup>8</sup> Specifically, we have:

**Proposition 2** *If  $(x_a, x_b)$  is independently and identically distributed across individuals and over time and given by (9), then the growth-optimal behavior  $f^*$  is:*

$$f^* = \begin{cases} 1 & \text{if } r_2 \in [q + \frac{pq}{r_1 - p}, \infty) \text{ and } r_1 > p \\ \frac{p}{1-r_2} + \frac{q}{1-r_1} & \text{if } \begin{cases} r_2 \in (\frac{1}{q} - \frac{p}{q}r_1, q + \frac{pq}{r_1 - p}) \text{ and } r_1 > p, \text{ or} \\ r_2 \in (\frac{1}{q} - \frac{p}{q}r_1, \infty) \text{ and } r_1 \leq p \end{cases} \\ 0 & \text{if } r_2 \in [0, \frac{1}{q} - \frac{p}{q}r_1] \end{cases}\tag{10}$$

Figure 1 illustrates the values of  $r_1$  and  $r_2$  that yield each of the three types of behaviors in (10). If  $r_1$  and  $r_2$  are not too different—implying that the ratio of fecundities of choices  $a$  and  $b$  is not that different between the two states of the world—then random behavior yields no evolutionary advantage over deterministic choice. In this case, the individually optimal behavior ( $f^* = 0$  or 1) will prevail in the population. If, on the other hand, one of the  $r$  variables is large while the other is small, then random behavior will be more advantageous from the population perspective than a deterministic one. In such cases, there are times

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<sup>8</sup>Since  $c_{ij}$  may be 0, the ratios  $r_j$  may be infinite if a finite numerator is divided by 0, which poses no issues for any of the results in this paper as long as the usual conventions involving infinity are followed. The ambiguous case of  $r_j = 0/0$  is ruled out by the condition  $c_{aj} + c_{bj} \neq 0$ .

in which each choice performs substantially better than the other, hence it is evolutionarily optimal for a population to diversify between the two choices rather than to always choose the outcome with the highest probability of progeny in a single generation. This case is summarized in:

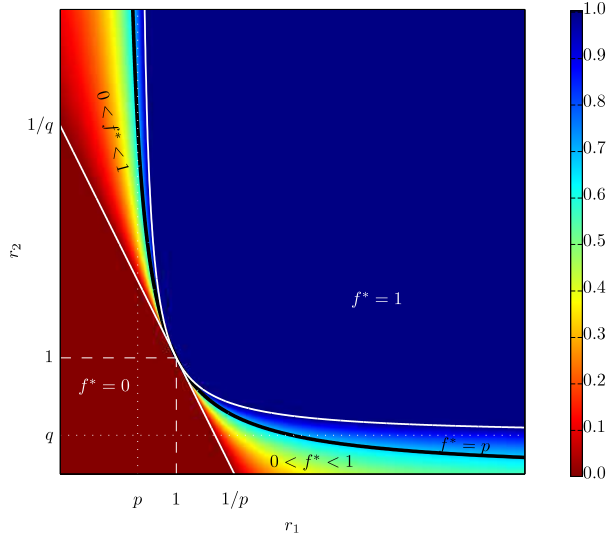


Figure 1: Regions of the  $(r_1, r_2)$ -plane that imply deterministic ( $f^* = 0$  or  $1$ ) or randomizing ( $0 < f^* < 1$ ) behavior, where  $r_j = c_{aj}/c_{bj}$  measures the relative fecundities of action  $a$  to action  $b$  in the two states  $j = 1, 2$ . The asymptotes of the curved boundary line occur at  $r_1 = p$  and  $r_2 = q$ . Values of  $r_1$  and  $r_2$  for which exact probability matching is optimal is given by the solid black curve.

**Corollary 1** *Suppose there exists a large difference between  $r_1$  and  $r_2$ ; without loss of generality, let  $r_1 \gg 0$ ,  $r_2 \ll 1$ , and  $p > \frac{1}{2}$ . Then the growth-optimal behavior is given by:*

$$f^* = p(1 + O(1/r_1) + O(r_2)) \approx p. \quad (11)$$

The expression (11) shows that if one choice is much worse than the other choice  $p$ -percent of the time, and if the other choice is much worse than the first  $(1-p)$ -percent of the time, then the first choice should be chosen with probability  $p$  and the second choice should be chosen with probability  $1-p$ . The definition of “much worse” is made precise by specifying that the values of  $1/r_1$  and  $r_2$  are both close to zero—over time, the individuals that flourish in such a world are precisely those that engage in approximate probability matching behavior.



When  $r_1$  and  $r_2$  satisfy the condition:

$$0 = p \frac{r_2}{1-r_2} + q \frac{1}{1-r_1} \quad (12)$$

exact probability matching behavior arises and the solid black curve in Figure 1 illustrates the locus of values for which this condition holds. The horizontal asymptote of the curve occurs at  $r_2=0$ , so as  $r_2$  tends toward zero and  $r_1$  becomes relatively large, exact probability matching will be optimal (note that the asymmetry between  $r_1$  and  $r_2$  is due entirely to our requirement that  $f^* = p$  and  $p \neq \frac{1}{2}$ ). However, values of  $(r_1, r_2)$  off this curve but still within the shaded region imply random behavior that is approximately—but not exactly—probability matching, providing a potential explanation for more complex but non-deterministic foraging patterns observed in various species (Deneubourg, Aron, Goss, and Pasteels, 1987; Pasteels, Deneubourg, and Goss, 1987; Kirman, 1993; Thuijsman, Peleg, Amitai, and Shmida, 1995; Keasar, Rashkovich, Cohen, and Shmida, 2002).

It is instructive to compare the growth-optimal behavior of (10) with the behavior that maximizes an individual's reproductive success, denoted by  $\hat{f}$ :

**Proposition 3** *If  $(x_a, x_b)$  is independently and identically distributed across individuals and over time and given by (9), then the optimal behavior  $\hat{f}$  is deterministic and given by:*

$$\hat{f} = \begin{cases} 1 & \text{if } r_2 > 1 + \frac{p}{q}(1-r_1)r_3 \\ 0 & \text{if } r_2 < 1 + \frac{p}{q}(1-r_1)r_3 \end{cases}, \quad r_3 \equiv \frac{c_{b1}}{c_{b2}}. \quad (13)$$

For a fixed value of  $r_3$ , the threshold in (13) that determines the optimal individual behavior is a line that divides the  $(r_1, r_2)$ -plane into two regions; for values of  $(r_1, r_2)$  above this line,  $\hat{f} = 1$ , and for values below this line  $\hat{f} = 0$ . When  $r_3 = 1$ , this implies that any time the growth-optimal behavior involves randomization, it will always be at odds with the individually optimal behavior  $\hat{f} = 1$ . We shall return to this important special case below.

Of course, from a population perspective, the growth-optimal behavior  $f^*$  is independent of  $r_3$ , and depends only on the relative performance of the two possible choices as measured by the relative fecundities  $r_1$  and  $r_2$ .

## 5 Risk Preferences

Our binary choice model can also be used to study the evolution of risk preferences by making one of the two choices riskless. In particular, in the Bernoulli case (9), suppose that choice  $b$  yields a non-random outcome  $c_{b1} = c_{b2} = c_b$  (or  $r_3 = 1$ ). In this case, each individual is choosing between a random outcome and a certain one, where we maintain the assumption that:

$$\begin{aligned} \text{Prob}(x_a = c_{a1}, x_b = c_b) &= p \in [0, 1] \\ \text{Prob}(x_a = c_{a2}, x_b = c_b) &= 1 - p \equiv q . \end{aligned} \quad (14)$$

Without loss of generality, assume that  $c_{a1} < c_{a2}$ . To ensure that the choice between  $a$  and  $b$  is not trivial, we require that  $c_{a1} < c_b < c_{a2}$ , otherwise one choice will always dominate the other trivially. Given this inequality, we can express  $c_b$  as a weighted average of  $c_{a1}$  and  $c_{a2}$ :

$$c_b = \theta c_{a1} + (1 - \theta) c_{a2} \quad , \quad \theta \in (0, 1) \quad (15)$$

and by varying  $\theta$  from 0 to 1, we vary the attractiveness of the sure thing (choice  $b$ ) relative to the risky alternative (choice  $a$ ). In this way, we can study the evolution of risk preferences for varying risk/reward trade-offs. Applying Proposition 2 to (14) yields:

**Corollary 2** *If  $(x_a, x_b)$  is independently and identically distributed across individuals and over time and given by (14), then the growth-optimal behavior  $f^*$  is:*

$$f^* = \begin{cases} 1 & \text{if } \theta \in [\theta_o, 1) \\ (1 - \frac{p}{\theta}) \left(1 + \frac{1}{(1-\theta)(s-1)}\right) & \text{if } \theta \in (p, \theta_o) \\ 0 & \text{if } \theta \in (0, p] \end{cases} \quad (16)$$

where  $\theta_o \equiv ps/(ps + q)$ , and  $s \equiv c_{a2}/c_{a1} > 1$ .

Note that  $s$  can be viewed as a crude measure of  $a$ 's risk, and as  $\theta$  increases from 0 to 1, the number of offspring produced by the riskless choice  $b$  decreases from  $c_{a2}$  to  $c_{a1}$ , making the risky choice  $a$  relatively more attractive. However, for values of  $\theta$  from 0 to  $p$ , the risky choice is not sufficiently attractive and the optimal behavior is to select the sure thing ( $f^* = 0$ ). As  $\theta$  is increased from  $p$  to  $\theta_o$ , the optimal behavior  $f^*$  from the population perspective is to select choice  $a$  with increasingly higher probability, and when  $\theta$  exceeds the threshold  $\theta_o$ , the

risky choice becomes so attractive relative to the sure thing that individuals always choose the risky alternative ( $f^* = 1$ ). Figure 2 graphs this relation between  $f^*$  and  $\theta$  for three values of  $s$ , which is close to piece-wise linear for  $s = 2$  but nonlinear for  $s = 100$ . Figure 3 provides a more complete depiction of the trade-off between  $s$  and  $\theta$  in determining the growth-optimal behavior  $f^*$ .

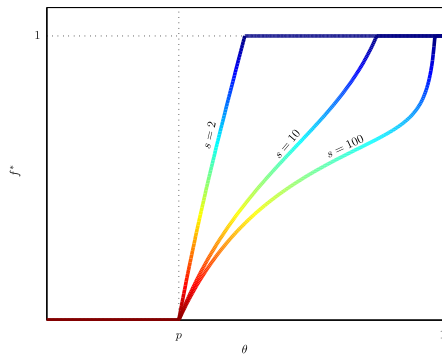


Figure 2: The growth-optimal behavior  $f^*$  as a function of  $\theta$  for  $p = 1/3$  and various levels of the ratio  $s = c_{a2}/c_{a1}$  of the two outcomes of the risky alternative  $a$ . The parameter  $\theta$  determines the magnitude of the payoff  $c_b = \theta c_{a1} + (1 - \theta) c_{a2}$ , of the riskless alternative  $b$ .

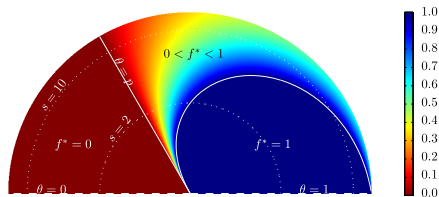


Figure 3: Radial plot of the growth-optimal behavior  $f^*$  for  $p = 1/3$  as a function of  $\theta$ , which varies from 0 to 1 clockwise around the semi-circle, and  $s = c_{a2}/c_{a1}$ , which varies from 1 to infinity from the center of the semi-circle to its perimeter. The parameter  $\theta$  determines the magnitude of the payoff  $c_b = \theta c_{a1} + (1 - \theta) c_{a2}$ , of the riskless alternative  $b$ .

## 6 Risk Aversion

Our binary choice model also shows that the property of risk aversion—the need to compensate individuals with a positive payment, i.e., a “risk premium”, to induce them to accept a fair gamble—arises quite naturally from natural selection. To see how, consider the risky/riskless case of (14) in Section 5 but now let the payoffs for the risky option  $a$  be

defined relative to the riskless payoff  $c_b$  of  $b$ :

$$c_{a1} \equiv c_b - d, \quad c_{a2} \equiv c_b + u, \quad u, d > 0 \quad (17)$$

and consider the case in which the optimal behavior  $f^*$  is exactly  $\frac{1}{2}$ , so that neither choice is selected more frequently than the other. This value implies that the growth-optimal behavior is indifferent between the riskless payoff of  $b$  and the risky payoff of  $a$ , which, in turn, implies that the two choices must have the same implications for population growth. In this respect,  $b$ 's sure payoff may be viewed as the ‘‘certainty equivalent’’ of  $a$ , an economic concept used to measure the dollar value of random payoffs.

Assuming that  $p=q=\frac{1}{2}$  so that  $u$  and  $d$  are equally likely outcomes, we then derive the implications of these parameter settings for  $u$  and  $d$ :

$$u = d + \frac{d^2}{c_b - d}. \quad (18)$$

When  $u=d$ , behavior is said to be ‘‘risk neutral’’ because the expected value of  $a$  is identical to the sure payoff of  $b$ . However, equation (18) shows that  $u$  must exceed  $d$  by a positive amount  $d^2/(c_b - d)$  to be consistent with the behavior  $f^* = \frac{1}{2}$ . The difference between the expected values of  $a$  and  $b$  is:

$$\pi \equiv \frac{d^2}{2(c_b - d)} \quad (19)$$

which can be considered an ‘‘evolutionary risk premium’’. However, unlike the risk premia of economic models of rational markets (Merton, 1980; Mehra and Prescott, 1985), which depend on the equalization of supply and demand,  $\pi$  arises from the fact that populations grow geometrically, and the factor by which the population grows,  $\exp(\mathbb{E}[\log(x)])$ , is always less than or equal to the expected number of offspring in a single generation,  $\mathbb{E}[x]$ , due to Jensen’s Inequality.<sup>9</sup> Therefore, risky choices will always yield lower population growth than the corresponding riskless choices with identical expected values. From an evolutionary

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<sup>9</sup>Jensen’s Inequality states that the expected value of a convex function  $g(\cdot)$  of a random variable  $x$  is greater than or equal to the function of the expected value of  $x$ , or  $\mathbb{E}[g(x)] \geq g(\mathbb{E}[x])$ . The opposite inequality holds for concave functions. In a study on risk-sensitive foraging behavior, (Smallwood, 1996) applies Jensen’s Inequality to derive risk averse behavior by first assuming that an animal’s fitness is an increasing but concave function of its energy level, and then applying Jensen’s Inequality to foraging behavior that yields random energy levels.

perspective, the only sustainable behavior in which  $a$  and  $b$  are equally likely to be chosen is if the risky choice  $a$  yields a larger expected number of offspring than the riskless choice  $b$ , i.e.,  $u$  must always be larger than  $d$ .

This result may also explain risk aversion in non-human animal species, often called “risk-sensitive foraging behavior” by ecologists, who have observed this behavior in organisms from bacteria to primates (Deneubourg, Aron, Goss, and Pasteels, 1987; Harder and Real, 1987; Pasteels, Deneubourg, and Goss, 1987; Hölldobler and Wilson, 1990; Kirman, 1993; Thuijsman, Peleg, Amitai, and Shmida, 1995; Smallwood, 1996; Keasar, Rashkovich, Cohen, and Shmida, 2002; Ben-Jacob, 2008). Regardless of the species, (18) shows that when  $c_b$  is very large relative to  $d$ , the evolutionary risk premium  $\pi$  becomes negligible since a bad outcome for  $a$  has very little impact on growth rates given the magnitude of  $c_b$ . However, when  $d$  is close to  $c_b$ , a bad outcome for  $a$  implies near sterility for that individual, hence a substantial risk premium is required to maintain the individual’s indifference between  $a$  and  $b$ .

## 7 Loss Aversion

The growth-optimal behavior can also generate loss aversion, the tendency of human subjects to take less risk when choosing between two potential gains, and to take more risk when choosing between two potential losses (Tversky and Kahneman, 1974; Kahneman and Tversky, 1979). For example, when offered the choice between investment opportunities A and B, where A generates a sure profit of \$240,000, and B is a lottery ticket paying \$1 million with a 25% probability and \$0 with 75% probability—the vast majority of MIT Sloan School of Management MBA students have chosen A in many trials over the past two decades. However, when these same subjects were offered the choice between investment opportunities C and D, where C generates a sure loss of  $-\$750,000$  and D is a lottery ticket paying  $-\$1,000,000$  with 75% probability and \$0 with 25% probability—virtually all of them chose D. Such inconsistent risk attitudes have material adverse implications: the most popular choices of A and D yield a combined outcome that is \$10,000 less than B and C, no matter how the lotteries turn out.<sup>10</sup>

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<sup>10</sup> This example is a modification of original experiments conducted by (Tversky and Kahneman, 1974) with Stanford undergraduate students using actual cash payoffs. The MIT Sloan MBA versions were based exclusively on hypothetical classroom surveys, and the primary modification was an increase in the dollar values of the outcomes, a very telling change that was necessitated by the fact that MBA students did not

More formally, suppose loss aversive behavior manifests itself when an individual engages in: (i) less risk-taking than apparently optimal when choosing between gains; and (ii) more risk-taking than apparently optimal when choosing between losses. To see how such behavior arises in our framework, consider again the situation of Section 5 in which individuals choose between risky option  $a$  and the sure thing  $b$ , and define

$$c_p \equiv pc_{a1} + qc_{a2} \tag{20}$$

which is the arithmetic average of  $c_{a1}$  and  $c_{a2}$ , weighted with the probabilities of their realization,  $p$  and  $q$ . From the individual's perspective, (13) shows that the risky choice  $a$  is optimal when  $c_b < c_p$ , and the safe choice  $b$  is optimal for the individual when  $c_b \geq c_p$ . However, the growth-optimal behavior  $f^*$  requires that an individual randomize, choosing the sure thing  $b$  with positive probability, whenever  $c_o < c_b < c_p$ , where  $c_o$  is the value of  $c_b$  defined in (15) that corresponds to the value  $\theta_o = ps/(ps + q)$  from (16). This value is simply:

$$c_o = \frac{1}{\frac{p}{c_{a1}} + \frac{q}{c_{a2}}} \tag{21}$$

which is the harmonic average of  $c_{a1}$  and  $c_{a2}$  weighted with the probabilities  $p$  and  $q$ , and always less than the corresponding arithmetic mean  $c_p$ . Therefore, if  $c_b$  is between the harmonic and arithmetic averages of the two  $c_a$  outcomes, the growth-optimal behavior takes the safe bet more often than would be individually optimal, and manifestation (i) of loss aversion is observed.

Next, consider the manner in which the  $c$  values are determined. When subjects are presented with a binary choice in an experimental setting, the monetary payoffs are *incremental* to their net worth, yet their decision-making abilities have presumably evolved to deal with trade-offs involving total reproductive fitness. Therefore, the size of monetary gains and losses *relative* to a subject's benchmark total wealth,  $w$ , may be critical in determining how the subject will determine the  $c$  values. If choice  $b$  and the lower realization of choice  $a$  both represent relatively significant losses as a fraction of wealth, the values of  $c_{a1}$  and  $c_b$  may be small and relatively close, while the value of  $c_{a2}$  may be substantially larger. Provided that

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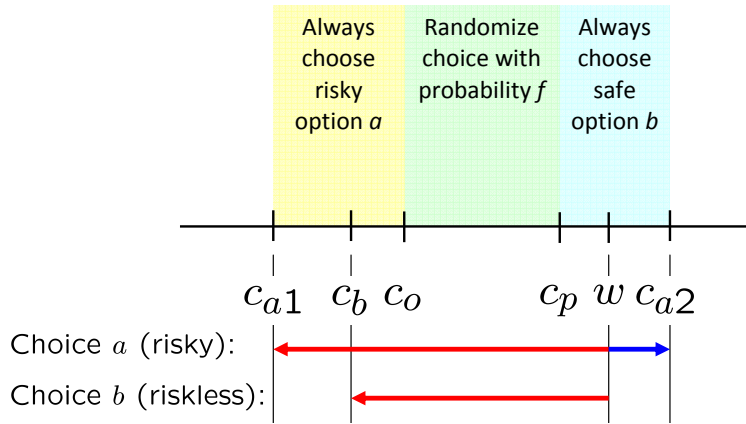
exhibit loss aversion with smaller payoffs. See the text for an explanation of this interesting difference.

$c_{a1} < c_b < c_o$ , the growth-optimal behavior will be risk-taking with probability one ( $f^* = 1$ ). This result follows even if the actual dollar payoff of choice  $b$  is higher than the expected dollar payoff of choice  $a$ , because it is the implicit impact on fecundity—not the absolute dollar amounts—that determines the  $c$  values. In such cases, the individual appears to take too much risk in terms of dollar amounts, rather than  $c$  values, and manifestation (*ii*) of loss aversion is observed.

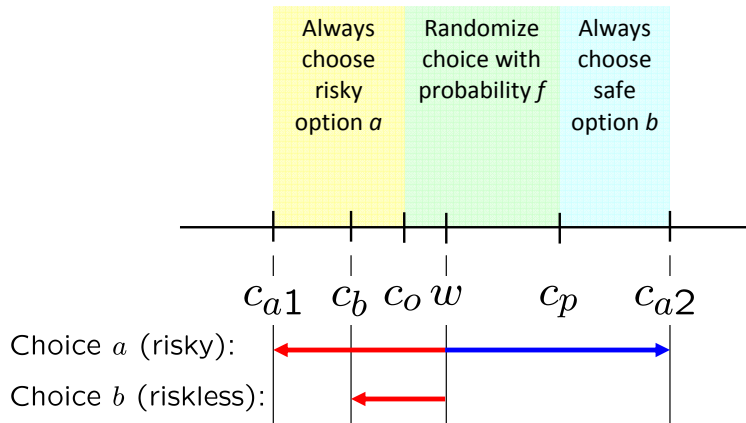
In summary, loss aversion emerges in our framework due to the fact that: (1) rational choice theory may not apply if the individually optimal behavior  $\hat{f}$  is at odds with the growth-optimal behavior  $f^*$ ; and (2) the apparent shift in risk attitude between gains and losses is an artifact of the focus on incremental payoffs (which are the only kind of payoffs easily made in experimental settings) rather than total payoffs (which is ultimately what affects reproductive success). Figure 4 provides a graphical illustration of how loss aversion arises when outcomes are calibrated in a particular manner.

Our framework clarifies the role of the reference point  $w$  in generating loss aversion, which may explain why some subjects do not exhibit such behavior in certain experiments, and why others may exhibit only one of the two manifestations of loss aversion. When subjects are offered incremental gains and losses, these translate into different values of  $c_{a1}$ ,  $c_{a2}$ , and  $c_b$  for individuals with different net worths. For subjects with less wealth and income, those increments are significant enough to affect reproductive success, and we should observe the behavior described by  $f^*$ . For those subjects with higher incomes and total net worth, the potential incremental loss will be low and  $f^*$  may not be relevant. The inconsistency of loss aversion in experimental data may have less to do with behavior than with unobservable differences in the relevant parameters across test subjects, implying cross-sectional differences in how losses and gains affect fecundity.

However, the fact that loss aversion emerges from an evolutionary process does not imply that  $f^* = 1$  is optimal from an individual investor’s perspective. In fact, loss-averse behavior is routinely singled out by professional traders as counter-productive to their objectives (“cut your losses, ride your gains” is common Wall Street wisdom that has the effect of counter-balancing loss aversion). This is another illustration of the evolutionary principle that individually optimal behavior need not coincide with the growth-optimal behavior.



(a) Larger potential incremental loss.



(b) Smaller potential incremental loss.

Figure 4: The loss-aversion anomaly is the result of measuring individual choices relative to a fixed reference point  $w$ . When the riskless payoff  $c_b$  lies in the interval  $[c_{a1}, c_o]$ , the growth-optimal behavior is to choose the risky option  $a$  and reject the riskless option  $b$ . However, when this behavior is cast in terms of gains and losses relative to a reference point  $w$  as in (a), it seems anomalous because  $a$  involves the possibility of losing  $w - c_{a1}$  which is an even greater amount than the sure loss of  $w - c_b$ . The anomaly disappears when a different reference point is used as in (b).  $c_p = p c_{a1} + (1-p) c_{a2}$  is the threshold above which the growth-optimal behavior is to always choose the riskless option  $b$ .



## 8 Qualifications and Extensions

The link between behavior and reproductive success in a binary choice model is the key to an evolutionary explanation for several commonly observed behaviors in many animal species. While risk aversion, loss aversion, probability matching, and more general forms of randomizing behavior may seem sub-optimal for the individual, these behaviors persist over time and across many species precisely because they are optimal from a population perspective. Moreover, as environmental conditions change, the growth-optimal behavior may also change in response to new selective pressures, hence the inexplicably erratic actions of certain species may well be adaptive rather than simply irrational.

These considerations may seem more relevant for the foraging behavior of ants and bees than for human challenges such as investing in the stock market. After all, most decisions we face each day have little to do with our reproductive success, hence the relevance of  $f^*$  for economic and social behavior may be questioned. The answer lies in the degree to which evolutionary pressures have any bearing on behavior, which is summarized by the specification of  $\Phi(x_a, x_b)$ . For example, if the choice between  $a$  and  $b$  has no impact on fecundity, e.g., monetary prizes that are small in comparison to an individual's net worth, then  $x_a$  and  $x_b$  will be statistically identical because either choice leaves the individual with the same reproductive prospects. In this case, the bivariate distribution  $\Phi(x_a, x_b)$  reduces to a univariate distribution  $\Phi(x)$ , natural selection is indifferent to the choice between  $a$  and  $b$ , and  $f^*$  is indeterminate. Therefore, whether  $f^*$  is applicable to a given context is fully captured by the relation between the individuals' behaviors and their impact on reproductive success, i.e.,  $\Phi$ .

One concrete illustration of how  $\Phi$  plays this role is the case of loss aversion. When the dollar amounts offered to subjects in the standard loss-aversion experiments are too low, loss aversion is not observed (see footnote 10). This result can be easily understood in the context of  $\Phi$ : when the stakes are high, the outcomes have measurable impact on reproductive fitness (broadly defined), hence one aspect of loss aversion may be observed ( $f^* = 1$ ). But when the stakes are too low, the implications of both choices for fitness are identical, hence the growth-optimal behavior has nothing to say about the outcome of the experiment.

It should be emphasized that the behaviors derived in our simple framework are primitive, both conceptually and from an evolutionary perspective. We have purposefully abstracted

from more sophisticated aspects of biology and behavior such as sexual reproduction, random mutations, neuroplasticity, learning, communication, and strategic behavior to focus on those behaviors that are primordial and common to most living organisms. Not surprisingly, those common behaviors are, in fact, evolutionarily advantageous in the face of random environmental conditions, hence they will survive and become universal over time.

Of course, more complex behaviors will arise as new species emerge and evolve. Although the specific biological manifestations of behavior are beyond the scope of our analysis, recent imaging and neurophysiological studies of decisionmaking under uncertainty in humans and primates (Breiter, Aharon, Kahneman, Anders, and Shizgat, 2001; Smith, Dickhaut, McCabe, and Pardo, 2002; Gold and Shadlen, 2007; Yang and Shadlen, 2007; Fehr and Camerer, 2007; Spitzer, Fischbacher, Herrnberger, Grön, and Fehr, 2007; Resulaj, Kiani, Wolpert, and Shadlen, 2009), including studies of loss aversion (Kuhnen and Knutson, 2005; De Martino, Kumaran, Seymour, and Dolan, 2006; Tom, Fox, Trepel, and Poldrack, 2007), are beginning to identify the neural mechanisms involved in these adaptations. From these studies, it is not difficult to see how sensory inputs, memory, and other neural substrates can yield a much greater variety of behaviors from which Nature selects the most advantageous, including the ability to avoid probability matching altogether (Shanks, Tunney, and Mccarthy, 2002).

To see how such mechanisms might have arisen through the forces of natural selection, our simple binary-choice model can easily be extended to allow for sexual reproduction, random mutations, and an arbitrary number  $n$  of possible actions, each with its own implications for the number of offspring, and these actions can, in turn, depend on a vector of auxiliary “state variables”  $\mathbf{z}$ . This more complex framework can generate considerably more sophisticated types of behavior, including learning, memory and, ultimately, the emergence of intelligence. We are currently exploring such extensions, however, economists have implicitly incorporated these more sophisticated decisionmaking mechanisms through utility theory (Robson, 1996a; Grafen, 1999; Robson, 2001a; Robson, 2001b), and have argued convincingly that utility functions are also shaped by the pressures of natural selection (Hansson and Stuart, 1990; Rogers, 1994; Robson, 1996b; Curry, 2001; Samuelson, 2001; Robson and Samuelson, 2007). Our current framework may be viewed as a bridge between the more sophisticated utility-based models of human behavior and the primitive decisionmaking components that we share with other animal species.

## 9 Conclusion

The evolutionary origin of behavior has important implications for economics, not only in resolving the loss-aversion/efficient-markets debate, but in providing a broader framework in which conflicts between rationality and human behavior can be resolved in an intellectually satisfying manner. Specifically, much of neoclassical economic theory is devoted to deriving the aggregate implications of individually optimal behavior, i.e., maximization of expected utility or profits subject to budget or production constraints. By documenting departures from individual rationality, behavioral critics argue that rational expectations models are invalid and irrelevant. Both perspectives are valid but incomplete.

Animal behavior is, in fact, the outcome of multiple decisionmaking components—in many cases involving different neural substrates—that each species has developed through the course of evolution. What economists consider to be individually rational behavior is likely to emanate from the prefrontal cortex, a relatively new component of the brain on the evolutionary timescale, and one that exists only in *Homo sapiens* and certain great apes. However, the human brain also contains other components such as the amygdala, a considerably older structure that is responsible for the “fight-or-flight” response. In the face of life-threatening circumstances, even the most disciplined individual may not be able to engage in individually rational behavior thanks to adaptive “hard-wired” neural mechanisms that conferred survival benefits to the species (and not necessarily to any given individual).

Our framework may be useful in differentiating primitive behaviors from more refined decisionmaking faculties, providing a clearer map of the boundaries of rational economic theory versus instinctive behavior. For example, our results show that loss aversion is not a stable phenomenon, but depends on the relation between incremental risks and total net worth. As aggregate wealth in the economy declines, loss-averse behavior is likely to be more prevalent in the population, but during periods of prosperity, other behaviors will emerge. A better understanding of this pattern may allow consumers, investors, and policymakers to manage their risks more effectively.

While species with more highly developed nervous systems exhibit greater behavioral variation, even in these cases, primitive behaviors are still likely to be available, if not always chosen. We conjecture that such behaviors are most readily actuated under conditions similar to those of our binary choice model, namely, when outcomes are significant enough to impact

reproductive fitness, broadly defined, and the effects of other variables on fitness is relatively small. These primitive behaviors may also be the basis of more modern adaptations such as boredom, thrill-seeking behavior, rebellion, innovation, and most recently, financial market bubbles and crashes. From an evolutionary perspective, financial markets are neither efficient nor irrational—they are merely adaptive (Farmer and Lo, 1999; Lo, 2004; Lo, 2005). In short, the behaviors derived in our evolutionary framework may well be the “animal spirits” that Keynes (Keynes, 1936) singled out seven decades ago, and which is apparently still a force to be reckoned with today.

# A Appendix

In this Appendix, we provide proofs for the main results of the paper.

## A.1 Proof of Proposition 1

This follows from the first and second derivatives of (3). Because the second derivative is strictly negative, there is exactly one maximum value obtained in the interval  $[0, 1]$ . The values of the first derivative of  $I(f)$  at the endpoints are given by:

$$I'(0) = E[x_a/x_b] - 1, \quad I'(1) = 1 - E[x_b/x_a]. \quad (\text{A.1})$$

If  $I'(0)$  and  $I'(1)$  are both positive or both negative, then  $I(f)$  increases or decreases, respectively, throughout the interval and the maximum value is attained at  $f = 1$  or  $f = 0$ , respectively. Otherwise,  $f = f^*$  is the unique point in the interval for which  $I'(f) = 0$ , where  $f^*$  is defined in (5), and it is at this point that  $I(f)$  attains its maximum value. The expression (4) summarizes the results of these observations for the various possible values of  $E[x_a/x_b]$  and  $E[x_b/x_a]$ . Note that the case  $E[x_a/x_b] \leq 1$  and  $E[x_b/x_a] \leq 1$  is not considered because this set of inequalities implies that  $I'(0) \leq 0$  and  $I'(1) \geq 0$ , which is impossible since  $I''(f)$  is strictly negative.

## A.2 Proof of Proposition 2

This result follows from the fact that the expectation (3) is given by:

$$I(f) = p \log(fc_{a1} + (1-f)c_{b1}) + q \log(fc_{a2} + (1-f)c_{b2}) \quad (\text{A.2})$$

and taking the derivative of this function and solving for  $I'(f) = 0$  yields the unique solution  $f = f^*$ , where  $f^*$  is as defined in the second case of (10). Whenever this value of  $f^*$  lies in the interval  $[0, 1]$ , it is the optimal value of  $f$ . Otherwise, analysis of the sign of the first derivative of  $I(f)$  at each endpoint of the interval  $[0, 1]$  shows that the optimal value  $f^*$  is either 0 or 1 as described in the first and third cases of (10).

### A.3 Proof of Corollary 1

Observe that the intermediate expression for  $f^*$  in (10) can be rewritten as:

$$f^* = p + p \left( \frac{r_2}{1-r_2} \right) + q \left( \frac{1}{1-r_1} \right) .$$

The second term on the right is  $O(r_2)$ , and the third term on the right is  $O(1/r_1)$ .

### A.4 Proof of Proposition 3

In particular, because an individual's expected number of offspring  $E[x_i]$ :

$$E[x_i] = p(fc_{a1} + (1-f)c_{b1}) + q(fc_{a2} + (1-f)c_{b2}) \tag{A.3}$$

is a monotone function of  $f$ , an individual seeking to maximize  $E[x_i]$  will select  $f$  to be 0 or 1, depending on which of these two extremes yields a higher expectation, as specified in (13).

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