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Comments

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Experimental Evolution and Economics

Terence C. Burnham[1], Aimee Dunlap[2], and David W. Stephens[3]

Abstract

This is a theory paper that advocates experimental evolution as a novel approach to study economic preferences. Economics could benefit because preferences are exogenous, axiomatic, and contentious. Experimental evolution allows the empirical study of preferences by placing organisms in designed environments and studying their genotype and phenotype over multiple generations. We describe a number of empirical studies on different aspects of preferences. We argue that experimental evolution has the potential to improve economics.

Keywords

preferences, natural selection, evolution, microeconomics

Introduction

We advocate using experimental evolution as a novel approach to study economic preferences.

Preferences are statements about human nature. What do people want? How do people make risky decisions? How do people trade-off today versus tomorrow? Do people make good decisions? Are people altruistic?

Until recently, investigations into the origin of preferences have been backward-looking and theoretical. Advances in the field of experimental evolution create the possibility of an empirical approach to the origins, and nature, of economic preferences.

The current state of economics is that preferences are exogenous, axiomatic, and contentious.

Preferences are exogenous in that they are taken as given by some unspecified, implicitly biological, process. Economics imposes no limitations on some aspects of preferences; people are left unconstrained in the sources of their pleasure, in their attitudes toward risk, and in their level of patience. While economics allows considerable freedom in these aspects of preferences, standard theory imposes structural constraints and assumes high levels of consistency.

Preferences are axiomatic in that economics attempts to derive all results from a small, coherent set of preferences. The rigor of models based on a small set of axioms allows economics to make unequivocal statements such as the well-known, and widely-accepted, economic conclusion that “free trade is good.”

Axiomatic approaches are fragile, however, in that small problems at the foundation create much more significant problems in other parts of the edifice. For example, “free trade is good” primarily follows from two premises. First, trade can improve the wealth of all trading parties, and second, people care about their absolute wealth, and not their relative wealth.

If, however, preference theory mischaracterizes human nature, then economic conclusions are suspect. For example, if people are envious by caring about relative wealth, then free trade may make all parties richer, but may cause envious people to be less happy.

If economics misunderstands human nature, then free trade may simultaneously increase wealth and unhappiness. Similarly, all economic theorems rest upon assumptions about human nature reified in preference theory. A graduate microeconomics text states, “Substantial portions of economic theory would not survive if economic agents could not be assumed to have transitive preferences” (Mas-Collell, Whinston, & Green, 1995, p. 7).

Preferences are contentious. Neoclassical and behavioral economics are sharply divided in their views on preferences. For every axiom of neoclassical economics, there is a behavioral economic literature that documents divergences between actual human behavior and standard economic theories of behavior (Kahneman, Slovic, & Tversky, 1982; Kahneman & Tversky, 1972, 1979; Thaler, 1988).

Consequently, economics is built on a fragile foundation. Its core assumptions: (a) come from outside the field, (b) are necessary for the theorems of economics, and (c) are disputed.

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Experimental evolution is a promising new approach to improving the economic theory of preferences.

Experimental evolution is a shorter version of the organic process that created all species on earth, extant and extinct. Experimental evolution studies populations of organisms over multiple generations in replicable, constructed environments (Rose & Garland, 2009). The populations are maintained, without any external breeding, in these environments for many generations.

Laboratory applications of experimental evolution commonly create test and control environments that differ in exactly one attribute. The populations undergo genetic evolution, and it is possible to study the genotypic and phenotypic effects of evolution.

Experimental evolution is complementary to other approaches. It is, however, unique in its ability to use precisely defined control and test environments to understand events that occurred in the past. Proponents of experimental evolution argue,

> It satisfies all the elements of the classical scientific method and provides, therefore, the most unarguable and convincing empirical analysis of evolutionary processes . . . it can provide rigorous testing of evolutionary hypotheses and theories that formerly were matters only of assumption or speculation. (Futuyama, Bennett, Garland, & Rose, 2009, pp. 26-27)

Experimental evolution uses organisms with lifespans that are short, relative to the human lifespan. A 50-generation experiment using an organism with a 2-week lifespan requires 2 years or about 2.5% of the human experimenters' lifespan. Organisms of study have included plants, viruses, bacteria, rodents, and fruit flies.

Experimental evolution is related to, but different from, artificial selection. Artificial selection is the process where humans choose which organisms replicate based on particular traits. Artificial selection has, for example, created agricultural plants with desirable properties for humans. Artificial selection, in the form of pigeon breeding, helped shape Darwin's evolutionary views (these influences can be seen in the *Origin of Species*).

To see the differences between artificial selection and experimental evolution, consider how selection might act on the beak of a seed-eating bird. To study beak size via artificial selection, the investigator could select the largest beaked individuals in the population and allow them to interbreed. We expect the average beak size of these new lineages (plural because experimental evolution uses replicate lines) to exceed the average beak size of the ancestral population.

The nature of the response to this selection tells us something about genetic control of beak size; however, it probably tells us little about the selective forces that act on beak size in nature. Suppose we hypothesize that in nature, the selective forces on beak size flow from the sizes of seeds in the environment. Environments with big seeds select for big beaks and so on. To test this hypothesis via experimental evolution, we would experimentally create large seed and small seed environments, and expose populations of birds to these "selective environments" over many generations. We predict that big seed environments will produce bigger beaked birds over many generations. In this case, the experimenter does not select which individuals reproduce. Instead, experimental evolution tests our hypothesis about the selective forces that act on beak size.

Artificial selection remains useful (Fuller, Baer, & Travis, 2005; Garland, 2003; Hill & Caballero, 1992), while experimental evolution allows more avenues for organismic change. Darwin noted the difference between artificial and natural selection: "Man can act only on external and visible characters; nature . . . can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life" (Darwin, 1859, ch. 4).

Early selection experiments (Lynch, 1980; Wattiaux, 1968) motivated subsequent researchers. There are now hundreds of published experimental evolution studies addressing varied questions while utilizing varied types of organisms (Garland & Rose, 2009). However, experimental evolution is still in a growth phase within the natural sciences with some relatively recent papers urging more adoption of the approach (Garland, 2003; Swallow & Garland, 2005).

While experimental evolution is a relatively uncommon approach even in the natural sciences, the idea of linking biological selection and economic preferences dates back at least to Adam Smith. Roughly a century before Darwin wrote *The Origin of Species*, Smith wrote, "Thus self-preservation, and the propagation of the species, are the great ends which nature seems to have proposed in the formation of all animals . . . endowed with a desire of those ends, and an aversion to the contrary" (p. 86, the Theory of Moral Sentiments).

In modern terminology, Adam Smith argued that preferences were shaped by biological payoffs to induce behaviors that lead to survival and reproduction. More recently, Gary Becker (1976) made the connection between preferences and natural selection more explicit: "The preferences taken as given by economists and vaguely attributed to 'human nature' . . . may be largely explained by the selection over time of traits having greater genetic fitness and survival value" (p. 826).

Until the advent of experimental evolution, the role of selection in shaping economic preferences was focused on the past. However, experimental evolution now allows the empirical study of preferences. We suggest three reasons that experimental evolution can become important for economics.

First, experimental evolution is a shorter version of a similar process that created humans. This provides a conceptual motivation for using experimental evolution. Restated, one approach to investigate the nature of preferences is to utilize the same natural process that created those preferences.

Second, experimental evolution can investigate questions that are both important and unanswered by economics. Do people discount the future exponentially or hyperbolically? Are people altruistic? Do people use expected choice theory or prospect theory in making decisions under uncertainty? In each of these cases, there is a behavioral economic literature that began decades ago; hyperbolic discounting (Ainslie, 1974; Thaler, 1981), "altruism" (Guth, Schmittberger, & Schwarze, 1982), and prospect theory (Kahneman & Tversky, 1979). After decades of work, and thousands of papers, economics remains divided on these questions.

It is possible to design experiments that investigate these important questions that have remained contentious for decades. Later in this article, we propose experiments to investigate unanswered questions about preferences.

Third, we find valuable, economic insight in some of the already completed experimental evolution studies. These studies are not presented by their authors as being economic studies, but they cover topics that are important to economics. Here are three lines of research that we feel have significant implications for economics:

First, experimental evolution has been able to increase the lifespan of fruit flies (Rose, 1984). In this work, subsequent generations are derived from eggs laid late in the mother's life. The result is that, after many generations, the average female fly lives 42.81 days versus 33.28 days for control flies, average male longevity increases to 44.14 days from 38.49 days. Furthermore, it is possible to study the genotypic and phenotypic changes that accompany longer life. The longer-lived flies develop reproductive physiology later in their lives; there is a trade-off between early reproduction and long life (Kirkwood & Rose, 1991).

Lifespan connects to preferences via discount rates; the bias to current consumption assumed within economics is often justified by invoking mortality: "The chance of death may be said to be the most important rational factor tending to increase impatience; anything that would tend to prolong human life would tend, at the same time, to reduce impatience" (I. Fisher, 1930, pp. 84-85).

If discounting is caused by mortality, it is important to understand that lifespan is endogenous to an evolutionary process. In addition, there is a well-developed biological theory of aging with implications both for discount rates and for future changes in average human lifespan caused by medical technology (Charlesworth, 1980; R. Fisher, 1930; Haldane, 1941; Hamilton, 1966; Medawar, 1946, 1952; Williams, 1957).

Second, experimental evolution studies report that the ability to learn is selected for in particular environments. A pioneering study demonstrated that experimental evolution could produce flies with improved ability to learn (Mery & Kawecki, 2002). A related study, using a refined framework, created environments that both selected for, and against, learning; there are some environments where learning has negative reproductive consequences (Dunlap & Stephens, 2009). Furthermore, greater capacity to learn is not free; flies that had evolved to be better learners were less successful in competing for survival against other flies (Mery & Kawecki, 2003).

Education is a large topic within economics with many different themes, including human capital formation (Heckman, 2000), payoffs to education (Lundvall & Johnson, 1994; Magnuson, Ruhm, & Waldfogel, 2007), rewards to different types of abilities (Hanushek & Woessmann, 2008), and the impact of technological change (Acemoglu, 2000; Goldin & Katz, 2009; Levy & Murnane, 2003). Experimental evolution provides the ability to run controlled experiments on learning.

Third, experimental evolution demonstrates the evolution of risk strategies. In one experiment, risky strategies arose by imposing a selective regime that favored novel phenotypic states. The result was that some of the populations evolved the ability to "bet-hedge" by stochastically producing different phenotypes (Beaumont, Gallie, Kost, Ferguson, & Rainey, 2009). In this study, risk attitudes are not taken as fixed but seen as an adaptive outcome of selection.

Risk attitudes and decision under uncertainty play central roles in many areas of economics. The ability to fit experimental results with standard risk aversion is debated (Rabin, 2000). One of the first behavioral economic papers introduces prospect theory as an alternative to expected utility theory (Kahneman & Tversky, 1979). Experimental evolution provides an experimental system to test theories about the nature of risk preferences and risky decision making.

There are, however, important questions regarding the ability of experimental evolution to inform economics. We address two issues here—the ability to extrapolate from non-human species to humans, and the relatively small number of generations possible in experiments.

First, can we extrapolate studies on mice, bacteria, viruses, and fruit flies to human economic behavior? If humans are sufficiently different from other species, then experimental evolution may not inform economic views of human nature.

This is not a purely theoretic view; there is evidence that humans are different in ways that argue against experimental evolution as a tool to study economic behavior. For example, chimpanzees appear to be qualitatively less capable of overriding impulses than humans. When experimenters present chimpanzees with symbolic representations of food, the animals are able to make good strategic choices. When actual food is used, however, the chimpanzees do not learn, and grab for the food, even when it is not in their strategic interest (Boysen, Mukobi, & Berntson, 1999).

Chimpanzees, along with Bonobos, are the extant species phylogenetically closest to humans (Hasegawa, Kishino, & Yano, 1985). If our closest genetic relatives are very different from humans on tasks that appear related to economic choices, what can we learn about human economic behavior from bacteria in a Petri dish?

Second, can we run experiments for enough generations to learn about human evolution? Consider that the fossil specimen of "Lucy" classified as *Australopithecus afarensis*. Lucy is estimated to have lived approximately 2.9 to 3.8 million years ago (Johanson & White, 1979). If we use a 20-year generation, and 2.9 million years before present, then Lucy preceded us by 145,000 generations. While some experiments on bacteria have continued for thousands of generations (Lenski, Rose, Simpson, & Tadler, 1991), for sexually reproducing organisms (e.g., mice, fruit flies) it is challenging to run experiments for 100 generations.

Furthermore, as compared with extant primates and other animals, Lucy is a relatively recent ancestor to modern humans (Nei & Kumar, 2000). Thus, experimental evolution is a very short version of the process that created humans. Because of these issues, macroevolutionary events may be sufficiently rare as to not be seen in experiment (Garland & Rose, 2009; Oakley, 2009), and this leads some to argue that simulations are better for such issues (Gavrilets & Vose, 2005).

In short, can experimental evolution studies using (a) short-lived organisms, (b) which are phylogenetically distant from modern humans, (c) for a relatively small number of generations inform our views of human economic behavior?

While these concerns have merit, we believe that they can be addressed. We know that animal models can inform human issues because of successes in other fields. In medicine, for example, animal tests are a standard part of the regulatory and scientific approval process. No human drug is approved based solely on non-human tests; however, animal tests are an important part of the process.

At the physiological level, human processes can be identical to that found in organisms that are phylogenetically distant from humans. For example, basic cell transport appears to be highly conserved with common genes involved in vesicle traffic (Novick, Field, & Schekman, 1980), common protein machinery for fusion to target (Rothman, 1994), and common, specific signals for cargo release (Südhof & Jahn, 1991). This research on cell transport was performed on organisms far from humans, including yeast, and it garnered the 2013 Nobel Prize in medicine or physiology.

Non-human models are useful not just for basic cell function but also for mental processes, including Alzheimer's disease and dementia (Götz & Ittner, 2008; Smith, 1988). Beyond disease, there are many aspects of human minds where science has found animal models to be productive (Cryan & Holmes, 2005; Dobbing, 1970; Lang, Davis, & Öhman, 2000; D. Rice & Barone, 2000). We believe that animals can help us understand human economic behavior.

The second argument against experimental evolution is that the studies are too short. A related idea has been labeled "Darwin's other mistake" by Michael Rose and Ted Garland (Rose & Garland, 2009). Darwin's first mistake was his belief in blended inheritance, and his second mistake was the idea, repeated many times in the Origin of Species, that evolution is slow and gradual.

Contrary to what Darwin believed, evolution can be rapid and the rate of change can be uneven (Eldredge & Gould, 1972). Existing experimental evolutionary studies have demonstrated rapid enough evolution to be useful in a wide range of areas and species (Garland & Rose, 2009). In the wild, modern studies of "Darwin's finches" document significant evolutionary changes with a relatively small number of generations (Grant & Grant, 2002).

Finally, there is evidence of relatively recent and rapid human evolution in the form of "selective sweeps." In a selective sweep, a new genetic variant arises and is strongly selected for, often because of some change in the environment. While there is debate about the number of such recent sweeps in humans, there is a broad agreement that they have occurred (Akey, 2009; Akey et al., 2004; Hernandez et al., 2011; Voight, Kudaravalli, Wen, & Pritchard, 2006).

Selective sweeps are argued to have occurred relatively recently in humans in the areas of malarial resistance (Sabeti et al., 2002; Tishkoff et al., 2001), salt preferences (Thompson et al., 2004), and the ability to digest lactose in adult humans (Bersaglieri et al., 2004).

In summary, we believe that animal models can be informative for human behavior, and that evolution can be rapid enough to be observed in experiments.

We argue for a program of economically motivated, experimental evolution studies. Experimental evolution is a promising approach that has yielded benefits in other areas. It is one of the few approaches that can address the important topic of economic preferences.

The rest of the article is structured as follows: The section "Experimental Evolution" provides a primer on experimental evolution for social scientists with economists as a particular audience. The section "Methodology for Experimental Evolution and Economics" contains a methodology for performing experimental evolution and economics studies. The section "Experiments on Economic Preferences" describes studies using experimental evolution to inform economics. These experiments cover attitudes toward goods, risk, time, and the decision process. The article ends with the "Discussion" on a possible future for experimental evolution and economics.

Experimental Evolution

Introduction

Experimental evolution is a well-developed methodology where the experimenter designs one or more test environments and measures the impact of the test environment(s) on genotype and phenotype relative to the control environment (Garland & Rose, 2009; Lenski et al., 1991).

Organisms, derived from a common stock, are randomly selected to be placed in the different environments. Commonly, test and control environments differ in precisely one aspect. Statistical inference is used to attribute the differences between the groups of organisms to evolution in

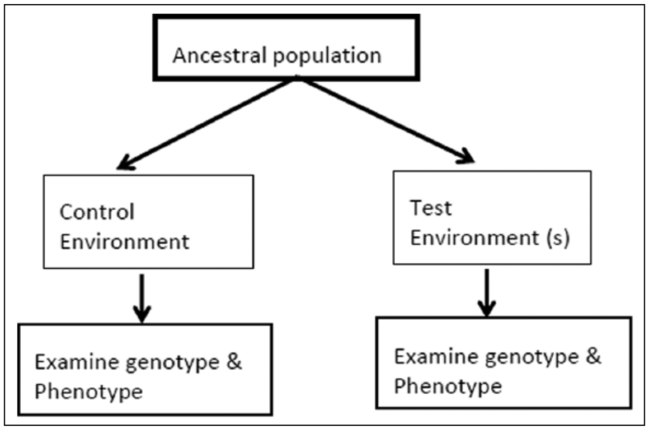

Figure 1. Experimental evolution.

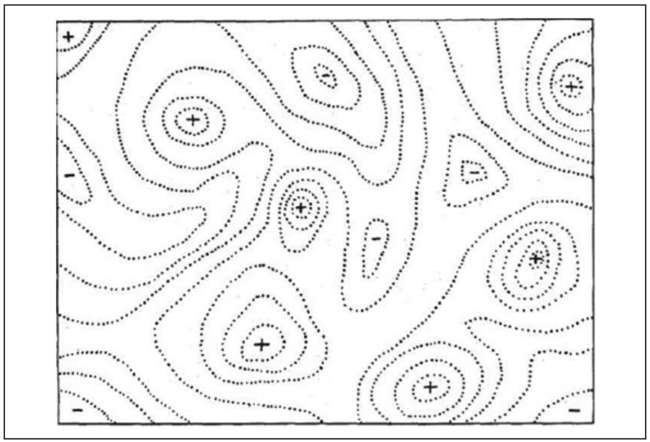

Figure 2. Adaptive landscape.
Source. Adapted from Wright (1932, p. 358).

the different environments. Figure 1 provides a summary of experimental evolution.

Environmental Design

Experimental evolution examines the genetic evolutionary trajectory of groups of organisms in different environments. The idea of an "adaptive landscape" is central to experimental evolution.

Sewall Wright (1932) invented the adaptive landscape concept, and Figure 2 (above) is Figure 2 from his original paper on the topic. The *x*- and *y*-axes represent the genetic variants of two genes. The third dimension represents adaptive value, or fitness, in modern evolutionary terminology.

Areas marked with "+" are peaks or relative maxima, while "–" represent valleys or relative minima. All the points on one contour line have the same fitness value. Within an actual organism, the adaptive landscape will be of much higher dimension (and would be very difficult to illustrate graphically).

At any given time, each individual can be placed at a single location in the landscape, determined by the alleles at the two loci that are represented by the axes. In general, the individuals within a population will not be evenly distributed around the landscape but more likely to be near one location. In equilibrium, Wright states, "The species will occupy a certain field of variation about a peak in our diagram" (p. 360).

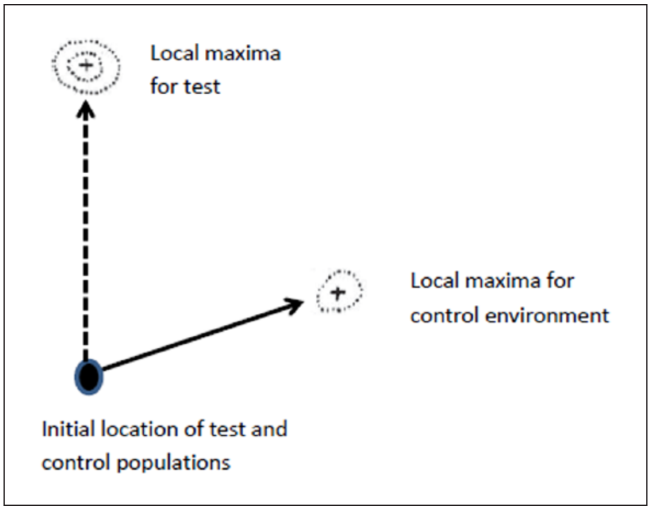

Figure 3. Adaptive landscapes representation of an experiment.

When populations are not in equilibrium, the individuals are not expected to be clustered around local maxima. In such cases, Sewall Wright argued, "A species whose individuals are clustered about some combination other than the highest would move up the steepest gradient toward the peak" (pp. 357-358). Selection favors evolution toward areas with higher fitness values—uphill in the adaptive landscape.

In addition to selection, which favors fitness increasing evolution, there are three non-adaptive evolutionary forces (Gould & Lewontin, 1979; Slatkin, 1977): genetic drift (Lande, 1976), mutation, and gene flow. In the history of evolutionary thought, the relative importance of non-adaptive evolution has had more or less emphasis at various times (see, for example, Gould, 2002, pp. 522-526).

Control and Test Environments in the Adaptive Landscape Framework

For selection to produce differences in an experimental evolution study, the test and control environments must have different adaptive landscapes. The test and control populations are expected to start at the same average coordinates in the landscape. If the topology of the two environments is different at these initial coordinates, then selection will favor divergence between the control and test groups.

Figure 3 is a representation of the adaptive landscapes in an experimental evolution study. The test and control populations are randomly selected from an initial stock; thus, both are expected to begin the experiment from the same location on the adaptive landscape.

If the initial stock is in equilibrium with the control environment, then the populations might both start at local maxima for the control environment. In such cases, stabilizing selection is expected to keep the control organisms in the initial location. The diagram illustrates a case where the control and test environments' local maxima are not the same as the beginning location.

For selection to create differences between the test and control organisms, the direction of selective pressure must be different. In Figure 3, the test and control organisms start at the same location in the lower left of the diagram, and over evolutionary time move toward the local maxima in their respective fitness landscapes.

In most, and possibly all, experimental evolution studies conducted to date, the experimenter does not know the topology of the adaptive landscape. Selection works on phenotype, while the adaptive landscape is a representation of genotype (Lewontin, 1974). For example, in a study of desiccation resistance in *Drosophila*, the test environment has less moisture than the control environment (Gibbs, Chippindale, & Rose, 1997). The experimenter may have some idea about which genes may be favored in the test environment, but to date, not enough is known to have any specific idea of the fitness landscape.

Population Is the Unit of Study in Experimental Evolution

Experimental evolution studies changes between test and control at the population level. In general, individuals will vary in their genotype. Variations between individuals exist because non-adaptive change prevents all individuals from converging to the same genetic sequence and because the fitness of an allele depends on the distribution of genes at other loci (R. Fisher, 1930; Hartl & Clark, 1997; Lewontin, 1970).

In addition, some equilibria will not be a unique location in the adaptive landscape, but rather a stable distribution of genes. This occurs when different phenotypes have fitness that is dependent on relatively frequencies. In such cases, equilibrium may not be a single allele but a stable distribution of alleles (Hardy, 1908; Stern, 1943; Weinberg, 1908). For example, in geographic areas with malaria, the allele that causes sickle cell anemia is selected for because of its beneficial effect in people who are heterozygous (Allison, 1954; Pauling, Itano, Singer, & Wells, 1949).

A population is a group of individuals that has no gene flow with other populations. Experimental evolution uses replicate populations in each treatment. In practice, several different test and control populations are created, and the organisms within each population only interact and breed with each other. We apply our experimental treatments to populations and replicate treatments on different populations.

Summary of Experimental Evolution for Economists

Experimental evolution allows the empirical investigation of the axioms of economics. Replicate populations are maintained in a control environment and one or more test environments. Over multiple generations, the phenotype and genotype of the populations can be studied. Because the adaptive landscapes are designed, experimental evolution allows control and can be replicated.

Methodology for Experimental Evolution and Economics

Design a Fitness Landscape

The experiments in the subsequent section are described in terms of a fitness landscape. Table 1 describes the simplest, non-degenerate fitness landscape for experimental evolution. With sufficient experimental creativity, selection can be applied to any aspect of phenotype. Table 1 shows the following attributes:

- There is a test environment and a control environment.
- The control environment imposes no selective pressure on phenotype A versus phenotype B.
- The test environment creates selective pressure for phenotype B over phenotype A.

If experimental selection creates evolution, B will become more frequent in the test populations. A and B can be associated with a wide variety of areas of interest, including behavior toward goods, risk, or time. This setting can be extended by adding phenotypes or environments. The relative fitness of different phenotypes can be adjusted arbitrarily subject to the experimental methods used to create the fitness landscape (see subsequent discussion).

Create the Fitness Landscape Experimentally

There are some important considerations in creating a fitness landscape that are difficult to describe in the abstract. For most of this article, we have purposely not specified any species, nor have we described the method of creating the fitness landscape.

In this section, we discuss some specifics of using *Drosophila* to induce preferences. One specific approach to creating such an experimental landscape is to use *Drosophila* and their oviposition (the location of egg laying) as a means of creating selection on phenotype. In this case, A and B represent physical areas where the *Drosophila* lay eggs that are distinct geographically and/or temporally. The distinct areas may be associated with attributes such as color, odor, and temperature.

Table 1. Fitness Landscape Where Phenotype B Has Higher Fitness for Test Populations.

	Phenotype	
	A	B
Test environment	1	2
Control environment	1	1

To create a fitness landscape, the experimenter must create different probabilities of an egg getting to the next generation ("hazard rate" hereafter). To impose the landscape in Table 1, one simple approach would be to use a hazard rate of 100% for B in the test condition, and 50% for eggs laid in Choice A in both conditions and 50% for eggs laid in Choice B in the control condition. Table 2 contains a hypothetic example implementing this simple approach.

The method described in Table 2 creates the correct, relative hazard rates to create the fitness landscape in Table 1 (in practice, the number of eggs will always be an integer). However, there is a practical problem with the example shown in Table 2, as there are population density effects in *Drosophila*. Thus, the population that begins the generation with 211 eggs will be subject to different forces than the population that begins with 77 eggs. The goal of the experiment was to create control and test environments that differ in exactly one aspect. For *Drosophila*, it is important to keep initial populations to the same or similar sizes.

A method to address density dependence in *Drosophila* is to start every generation with the same number of eggs. Table 3 shows the same example in terms of number of eggs laid as Table 2 but constrains each condition to start the subsequent generation with 50 eggs.

The correct fitness landscape is created using the process shown in Table 3. In the control environment, the hazard rate is the same for A and B (32.47%). In the test environment, there is selective pressure for B as the hazard rate for B (24.88%) is two times that of A (12.44%).

This solution creates the correct relative hazard rates, and it creates equivalent starting population sizes, thus removing density dependent effects. Operationally, this process requires the experimenter to use different hazard rates depending on the number of eggs laid. This adds an addition level of complexity to the step where eggs are harvested to start the next generation.

The message here is that expertise regarding the specifics of the experimental species is required. To create an experiment, the goal is to associate aspects of phenotype, with engineered, relative hazard rates. Furthermore, the creation of the relative hazard rates ought to be performed in a manner that does not produce any other differences between test and control environments beyond the aspect(s) of planned study.

Measure Evolution

Once the experiment commences, it is possible to study phenotype and genotype. For example, Figure 4 shows a hypothetical outcome where organisms in the text condition evolve to exhibit more of Phenotype B.

The test environment can be the same as the selective environment, or it can be different. Consider, for example, a *Drosophila* experiment where, during selection, flies can lay eggs on one of two surfaces. One surface is associated with a level of added odor, the second surface with no added odor.

One environment that could be used to evaluate the experiment would be to present flies with the exact same two odor levels and measure percentage of eggs laid on the surface with the added odor. We describe this by saying that the test environment is the same as the selective environment.

There are, however, additional types of test environments. For example, if the test environment with two levels of odor is labeled (high, none), it might be interesting to observe flies in an environment both higher levels of odor and intermediate. For example, these could be labeled very high, high, medium, none, or very high, medium.

Using a test environment that differs from the selective environment may provide insight into the mechanistic details of the phenotype. For example, including additional odor levels beyond those used in selection may differentiate between mechanisms that favor a particular level from others that select based on relative levels.

Experiments on Economic Preferences

Introduction

In this section, we sketch out some experimental ideas that we believe could be useful for economics. There are benefits and costs to laying out part of an experimental agenda. The benefit of describing some experiments is to make the proposition of this article more concrete. In addition, people may want to pursue these specific experimental ideas, and we encourage people to perform experiments motivated by these sketches.

The cost of laying out some specific experiments is that the list is necessarily incomplete. Furthermore, each individual experiment may appear poorly designed. The planning stage for a single experiment can take several years. Thus, describing multiple experiments, even at a high level, in one paper may not do justice to the power of the approach.

Weighing these costs and benefits, we proceed to sketch some experiments. We believe that this is an ambitious experimental list in addressing some of the most important issues in economics. However, this list only scratches the surface of the possible research program of experimental evolution and economics.

Table 2. Creating a Fitness Landscape.

	A No. harvested /no. eggs laid, hazard rate	B No. harvested /no. eggs laid, hazard rate	No. of eggs to start next generation
Test	63 / 126, 50%	138 / 138, 100%	63 + 138 = 211
Control	26.5 / 53, 50%	50.5 / 101, 50%	26 + 51 = 77

Table 3. Creating a Fitness Landscape With Constant Initial Starting Population.

	A No. harvested / no. eggs laid, % harvested	B No. harvested / no. eggs laid, % harvested	No. of eggs to start next generation
Test	15.7 / 126, 12.44%	34.3 / 138, 24.88%	15.7 + 34.3 = 50
Control	17.2 / 53, 32.47%	32.8 / 101, 32.47%	17.2 + 32.8 = 50

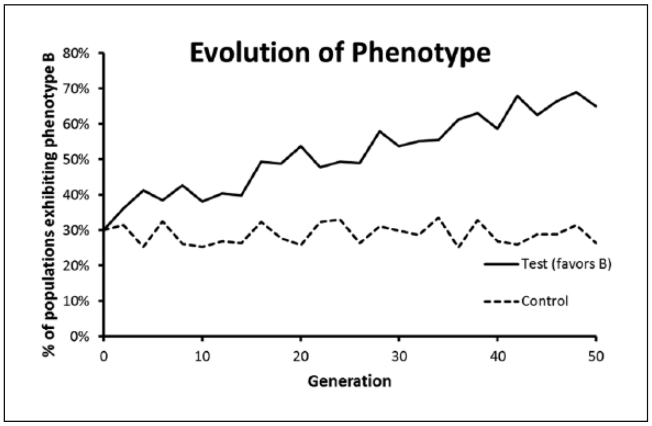

Figure 4. Hypothetical results where selective pressure favors Phenotype B.

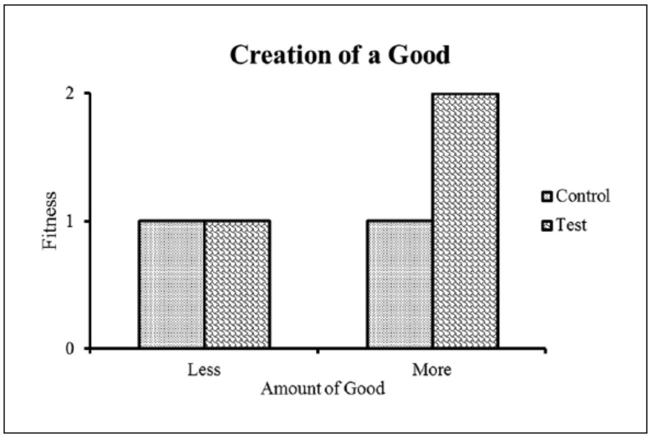

Figure 5. Selective environment for creating a good.

Experiment 1: Creation of a Good

Can an economic good be created?

Economics is silent about the origin of attitudes toward goods. "*De gustibus non est disputandum*" is an important paper about preferences (Stigler & Becker, 1977). The authors explain that economics take preferences as given, and research on the origin of preferences is left to "whoever studies and explains tastes (psychologists? Phrenologists? Sociobiologists?)" (p. 76).

We expect pleasure to be associated with behaviors that led to evolutionary success (higher inclusive fitness) for ancestral humans. Experimentally, to create selective pressure for a good, construct a test environment that associates higher fitness with more of some attribute (Figure 5).

Any number of attributes could be used to create a fitness landscape where more is better. These include temperature, odors, visual cues, or food of various types. It will be important to select an attribute that the organism can perceive and one where there may be genetic variation regarding the attribute.

This simple experiment where more of an attribute/good is favored by selection may inform a number of important issues within economics.

Variation between individuals.

The standard economic model is silent on the nature of goods, and it does not constrain different individuals to like similar goods. Thus, the standard economic framework allows an individual to prefer cyanide to food. It also allows one person to prefer cocaine to pasta, and another individual (even the individual's identical twin) to have the reverse taste. Empirically, experimental evolution can investigate the sources and extent of variation.

Time scale.

If preferences are shaped by the environment, and the environment is changing, possibly rapidly relative to genetic evolution, how do preferences change over time? If preferences were shaped by evolution to produce fitness maximizing behavior, what happens when the payoffs to behavior change? How does the organism change, and how long does it take? For example, it is hypothesized that the human taste for high fat food and calories was an adaptation for our ancestors who were frequently hungry (Irons, 1998). In industrialized societies, however, many people would live longer if they had different preferences. Experimental evolution allows empirical measurement of rates of change in preferences.

Self-destructive preferences and will power.

Why do many humans engage in behaviors that lead to both unhappiness and low biological fitness? For example, many people get intense pleasure from cigarettes and a number of other drugs, including alcohol. The economic approach takes these preferences as given and then asks how a person would maximize happiness, given their tastes.

Self-control issues arise when an individual desires something, yet wants to control its consumption. Some economic models assume internal conflict (Fudenberg & Levine, 2006), an aspect not contained in the rational view of addiction. Self-control remains an active area of economic research (DellaVigna & Malmendier, 2004) decades after earlier work (Schelling, 1984; Thaler & Shefrin, 1981).

An evolutionary perspective might explain why certain substances are both pleasurable and unhealthful. A changing adaptive landscape might produce organisms with preferences for fitness decreasing behaviors. Of particular relevance is the notion that humans began changing the world quite rapidly relative to the pace of human genetic change with the invention of agriculture (Barkow, Cosmides, & Tooby, 1992; Bowlby, 1969; Wilson, 1978).

Dietary preferences are a specific manifestation of this idea of "mismatch" between human genes and modern industrialized conditions. As noted previously, the human taste for fat, salt, and excess calories is hypothesized to reflect positive fitness payoffs in ancestral conditions (Irons, 1998). In the ancestral environment, the marginal value of an additional gram of dietary fat is hypothesized to be positive. For many people today, the marginal fitness value of dietary fat is negative. Our self-control struggles may be productively viewed as the product of a mismatch between ancestral and modern fitness landscapes.

Experiment 2: Non-Monotonic and Other-Shaped Preferences

Is more always better? Standard economic models assume that preferences are monotonic, with more being better than less. If preferences are not monotonic, then some of the most important conclusions of economics would not hold. For example, the First Fundamental Welfare Theorem states that, under certain conditions, all market outcomes are pareto optimal. This welfare theorem can be viewed as a mathematical version of Adam Smith's famous invisible hand argument. However, the First Fundamental Welfare Theorem is proved by assuming that preferences are monotonic.

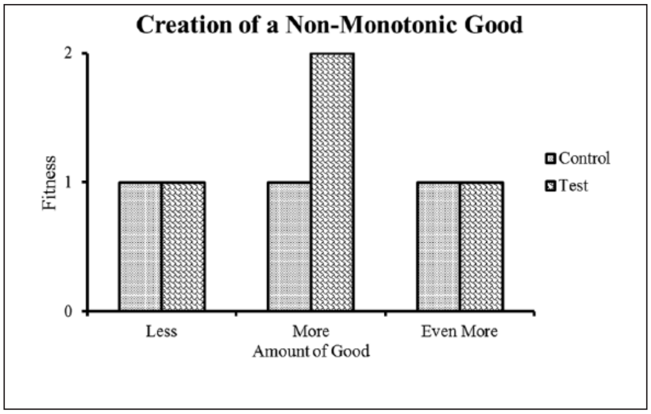

Figure 6. Fitness landscape for creating non-monotonic preferences.

In natural settings, there is no such expectation that preferences will be monotonic. For example, intermediate temperatures are preferred to extremes for all animals.

A simple adaptive landscape for the evolution of non-monotonic preferences is shown in Figure 6.

The test environment produces selective pressure for non-monotonic preferences. Over evolutionary time, the behavior can be observed to determine if intermediate levels are preferred to extremes. If a "taste for moderation" arises in the selective environment, it would then be informative to look at levels that are not included in selective environment. If non-monotonic preferences can arise, there would be fundamental implications for economics.

Many other experiments on the shape of preferences can be conducted. For example, it is possible to construct convex and concave preferences (Figure 7). Any combination of shapes is also possible with linear areas, convex, concave, and so on.

Finally, it would also be informative to impose no selection over certain levels of an attribute, and then observe preferences in those regions. There is a literature in biology on one-sided decision rules. Herring gulls, for example, have "bigger is better" decision rules with regard to caring for their eggs. Bigger appears to be better in natural settings (Parsons, 1970) but can produce very strange outcomes in experimentally modified settings (Baerends & Drent, 1982a, 1982b; Baerends & Krujit, 1973).

One of the central paradoxes in human behavior is that people seem to have a one-sided decision rule with regard to wealth, even though there appear to be no fitness or happiness benefits from more money above some level.

Ancestral humans could not accumulate any substantial wealth until the invention of pottery for storage, perhaps beginning as early as 30,000 years before present (P. M. Rice, 1999). To the extent that human tastes for resources were importantly shaped in the Pleistocene (the epoch that

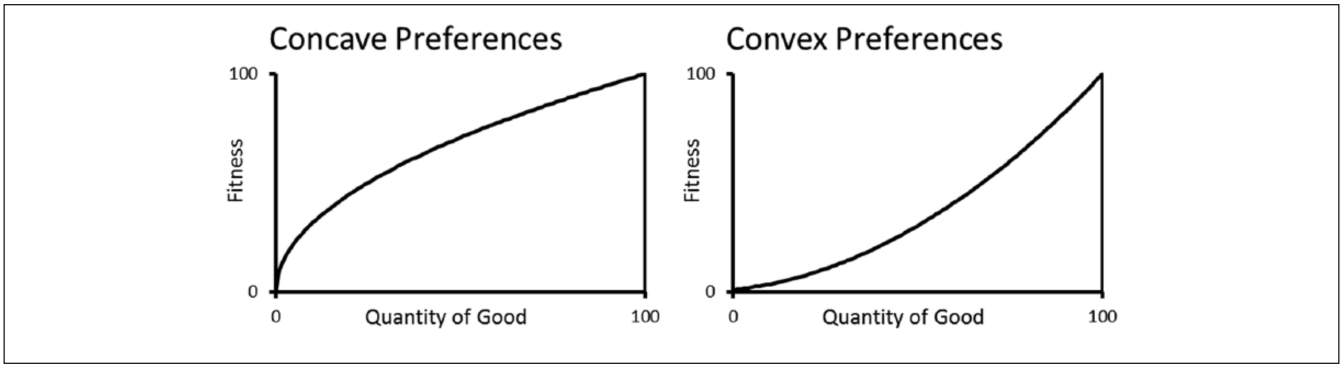

Figure 7. Creating concave and convex preferences.

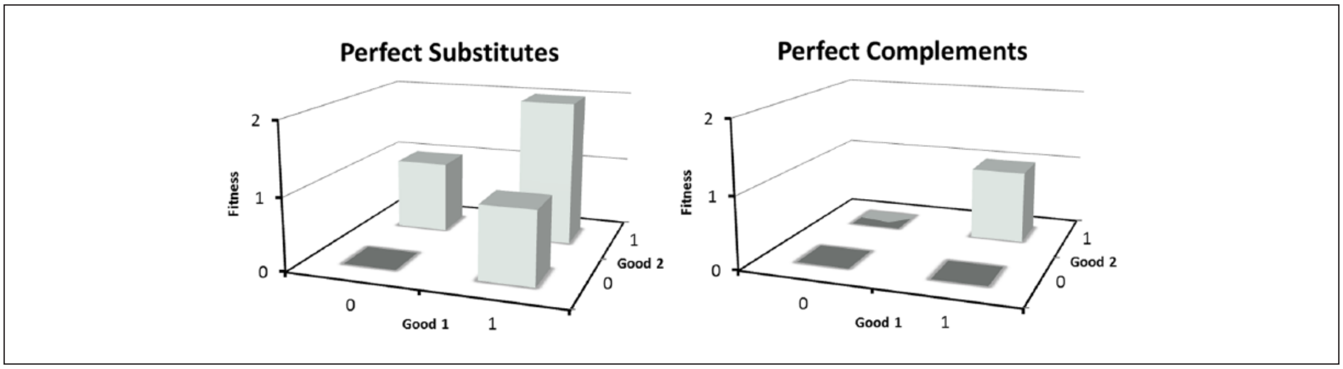

Figure 8. Creating substitutes and complements.

ended 10,000 years ago), unlimited taste for money may be an outdated, one-sided decision rule.

Experiment 3: More Than One Good—Substitutes and Complements

Substitute goods satisfy similar wants, so that more consumption of one good leads to less desire for consumption of a substitute. Conversely, more consumption of one good leads to increased desire for consumption of a complement. As with attitudes about individual goods, most economics takes attitudes toward multiple goods as exogenous.

Experimental evolution allows empirical investigation of attitudes toward more than one good. Figure 8 shows simple adaptive landscapes for perfect substitutes and complements. In the case of perfect substitutes, the fitness of a combination is equal to the sum of the levels of the two goods. In the case of perfect complements, the fitness of a combination is equal to the minimum of the two goods.

It is possible to build fitness landscapes with more than two goods. It is also possible to construct more complex landscapes. For example, goods could be substitutes in one region and complements in a second region. Finally, it is possible to layer in convex, concave, linear, or non-monotonic preferences into experiments on more than one good.

Experiment 4: Risk Premia

Some of the most important economic decisions have uncertain outcomes, including financial investments, career choice, and education level. Neoclassical economics assumes that people make such uncertain decisions to maximize expected utility, using risk tastes that vary both as a function of their personalities and as a function of their wealth.

Expected utility theory is grounded in a 1738 formulation by Daniel Bernoulli, who emphasized that monetary outcomes must be translated into utility, which varies depending on circumstances: “No valid measurement of the value of a risk can be obtained without consideration being given to its utility . . . the utility of an item may change with circumstances” (Bernoulli, 1954, p. 24). In 1947, Bernoulli’s insight was formalized, based on von-Neumann and Morgenstern’s (1947) axioms, and subsequently expected utility theory has been the standard (neoclassical) economic theory of decision under uncertainty.

The critiques of the expected utility theory began even before Bernoulli’s formulation (e.g., St. Petersburg paradox, 1713; created by Daniel Bernoulli’s cousin Nicolas Bernoulli) and continue to the modern period (Allais, 1953; de Montmort, 1713; Ellsberg, 1961; Kahneman & Tversky, 1979; Rabin, 2000; Rabin & Thaler, 2001). Many behavioral economists favor “prospect theory” over expected utility theory. Two important aspects of prospect theory are as follows: (a) "Value is assigned to gains and losses rather than to final assets." (b) "The value function is . . . generally steeper for losses than for gains" (Kahneman & Tversky, 1979, p. 263).

Prospect theory and expected utility theory have very different implications in a wide variety of important economic problems. For example, in the area of asset pricing, "The differences between our [prospect theory] framework and a . . . [expected utility framework] are highlighted by the distinct predictions of each" (Barberis, Huang, & Santos, 2001, p. 3).

In their 2001 review, Rabin and Thaler argue that economics should consign expected utility theory to the dustbin of history: "It is time for economists to recognize that expected utility is an ex-hypothesis" (p. 230). Notwithstanding the behavioral critique, expected utility theory remains the foundation of mainstream economic approaches to decisions with uncertainty.

An evolutionary model of endogenous preferences concludes that as long as there is no chance of extinction, natural selection favors risk neutrality (Robson, 1996). If there is a chance of extinction, then selection favors risk aversion (over payoffs in inclusive fitness units).

Organisms often make decision over food and other attributes with indirect translations into fitness. In such cases, if the translation between a behavior and fitness is concave, risk aversion is optimal. If the translation to fitness is convex, risk seeking (also labeled "risk prone" in the biology literature) is optimal (Caraco, Martindale, & Whittam, 1980; Stephens, 1981; for a review, see McNamara & Houston, 1992). Empirically, animals tend to be risk averse over variability in amount and risk prone over variability in delay (Kacelnik & Bateson, 1996; Kacelnik & El Mouden, 2013); there is no agreed-upon theoretical explanation for the observed regularities in uncertain decisions in non-human animals.

In summary, decision making under uncertainty is an unresolved important topic for both humans and non-human animals. Experimental evolution allows empirical investigation of these questions. In addition, experimental evolution allows for mechanistic investigations into decisions under uncertainty. If test and control populations are created, then mechanistic differences between populations can be investigated. A recent review paper underscores the need for this type of investigation for uncertain decisions: "A Tinbergian persistence of simultaneous interest in function and mechanism would be a good thing" (Kacelnik & El Mouden, 2013, p. 1128).

One experimental evolution study selected for phenotypic switching in bacteria by selecting for change (Beaumont et al., 2009). Specifically, alternate generations grew in media that was either shaken or unshaken because variants with an advantage in one environment have a disadvantage in the subsequent environment. The subsequent generation begins with the most common, novel phenotype from the prior generation. The outcome is that each generation begins with two different phenotypes, with a single genotype. This outcome is labeled bet-hedging because one genotype produces two phenotypes, and, in the experiment, one of these two phenotypes makes it to the next generation.

This pioneering study illustrates the power of experimental evolution in understanding decisions under uncertainty. Selection produced new populations better adapted to the novel environment than the ancestral population. Furthermore, it was possible to analyze the genetic changes that accompanied the evolution.

We propose an experimental evolution study of risk premia. To accomplish this study, we construct a test environment where the payoff associated with an aspect of phenotype has both different mean and variance than in the control environment. It is possible to study the risk premium in such an experiment. This allows an empirical calculation of the sign and magnitude of the risk premium.

Table 4. A Generalized Framework for Risk and Return Experiments.

	Phenotype			
	A		B	
	Mean	Variance	*Mean*	Variance
Test environment	1	1	x	y
Control environment	1	1	1	1

Table 4 describes a generalized framework for experiments on risk and return. The control environment is normalized to have a mean fitness and variance of 1. Test environments can be constructed for a variety of questions by setting x and y appropriately.

Does evolution favor risk aversion? The experimental setup for investigating this question would have $x = 1$ and $y > 1$. In this case, test and control have the same mean fitness, while the test lines have a higher risk.

What is trade-off between risk and return? A series of experiments could be conducted with $x > 1$ and $y > 1$. If higher risk increases the chance of extinction, how much additional average fitness compensates for some measured increase in risk? With this design, it would be possible to measure the trade-off between risk and return.

It is also possible to conduct experiments on skew and higher moments. For example, a skew column could be added to Table 4. One possible experiment would be to have test and control environments with identical mean and variance but different skewness.

Finally, it would be possible to contrast prospect theory preferences with expected utility preferences. The experimental approach would be to create different lines that exhibit these preferences and then use a competitive assay to measure relative success of the two sets of preferences.

Experiment 5: Evolution of Time Preference

How patient or impatient are humans, and what role did natural selection play in the evolution of time preference? Experimental evolution allows the empirical investigation of attitudes toward time.

Economists assume that later time periods have lower value—people are assumed to discount the future. As discussed in the subsequent experiment, there is disagreement whether the form of the discounting is exponential or hyperbolic, but most behavioral scientists agree that people discount.

In 1930, the famous economist Irving Fisher (1930) connected discounting with a probability of dying writing: "The chance of death may be said to be the most important rational factor tending to increase impatience; anything that would tend to prolong human life would tend, at the same time, to reduce impatience" (pp. 84-85). Presumably, Fisher's view is grounded in an implicit role of natural selection in creating preferences.

While Fisher assumed that discounting was based on the chance of death, more recent theoretical work has explicitly modeled time preference. An economic model of endogenous preferences investigates the relationship between patience and various attributes including income, mortality, and even religious beliefs (Becker & Mulligan, 1997). The payoffs in this model are not grounded in biological fitness, which produces some interesting speculation:

> If consumers expect positive utility after death—perhaps because they believe they will go to heaven—this raises their investments in future-oriented capital because their future utilities are increased. In equilibrium, therefore, consumers who expect to go to heaven will discount the future less. (p. 741)

A biological model of endogenous time preference that uses demographic parameters from human populations before the creation of birth control, argues that the discount rate ought to be around 2% per year, and that younger people should discount at higher rates (Rogers, 1994). In this model, younger people have lower chances of death, and this effect by itself would make young people more patient. However, the model uses fertility rates to estimate the value of current consumption. The higher fertility rates for young people in this model outweigh the lower chance of death, and the overall conclusion is that discount rates will be higher for young people.

Empirical studies in the evolution of senescence literature connect selection with lifespan. In a natural experiment, senescence was measured in two groups of wild opossums: a mainland group and an island population (separate for approximately 5,000 years) with reduced predation. As compared with the mainland group, the island group displayed delayed senescence (Austad, 1993). In a laboratory experimental evolution study, *Drosophila* senescence was delayed by choosing eggs that were laid by older females (Rose, 1984). These studies are consistent with the evolutionary view that senescence is an outcome of selection. Both the decreased external hazard rate for island opossum and selecting *Drosophila* eggs laid later in life increase the relative value of later periods.

Table 5. Generalized Framework for Discounting.

	Relative fitness	
	Now	Future
Control	1	1
Test	1	A

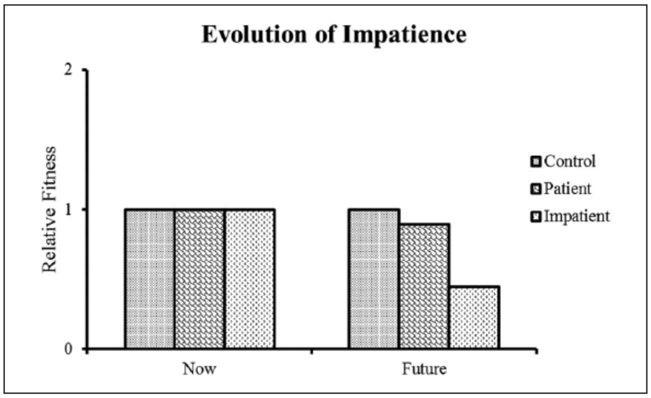

Figure 9. Evolution of discounting.

Experimental evolution in the aging literature has already provided empirical insight into the evolution of time preference. Table 5 contains fitness payoffs for further experimental evolution on time preference.

An experiment with A < 1 creates selective pressure to value the present over the future. Maintaining the value of A below 1 but varying its value allows investigation of relative pressure for impatience. For example, an experiment could contrast two test environments with A = 0.9 and 0.45, respectively (Figure 9).

Mathematically, an experiment with A > 1 would create pressure to value the future over the present. While economics assumes that discount rates will always be positive (the present has higher value than the future), there is no reason to believe that this is always favored by selection.

There are myriad natural examples where animals prefer later over now; for example, a wide variety of animals, including squirrels, birds, cache nuts, seeds, and other foods (Vander Wall, 1990). These animals often retrieve much of the food they cache. However, they always retrieve less than 100% of the food they store, thus earning a negative return on their savings.

Cicadas demonstrate a different form of patience also present broadly in non-human animals. Some cicada species mate only once every 13 or 17 years (Williams, Smith, &

Stephen, 1993). The cicadas live for long periods in the soil and only mate after morphing and emerging above ground. By synchronizing their emergence, the cicadas overwhelm the ability of predators to consume them. The prime numbers between mating periods are thought to make it more difficult for predators to also breed cyclically but with higher frequency, thereby facilitating higher than average predator population sizes on cicada hatching years. These cicadas exhibit a form of patience by waiting for so long to mate.

In summary, discounting is a vitally important topic within economics. For the most part, economics takes as given that people value the present more than the future. There is no theoretical framework within economics to predict discount rates, how discount rates will vary as a function of circumstances (e.g., sex, age, wealth), or variation in discount rates between individuals. There is limited, theoretical work on connected discounting with biological payoffs. Experimental evolution allows a wide range of empirical studies into the evolution of patience (and impatience).

Experiment 6: Structure of Time Preferences

Experimental evolution provides an empirical tool to study the role of natural selection in shaping the structure of intertemporal decision making.

Economics is divided about how people make intertemporal decisions (also known as discounting). Neoclassical economists assume that people are patient and consistent. In contrast, behavioral scholars argue that people are impatient and inconsistent. Intertemporal decisions are among the most important areas in economics as they include education, savings, investments, productivity, and these decisions affect the wealth of both individuals and nations.

Neoclassical economics assume that humans use "exponential discounting" where consumption in each period has lower value than consumption in earlier periods. Furthermore, exponential discounting assumes that adjacent periods have constant, relative weights. Exponential discounting dates back to 1937: "We assume in the first instance that the rate of discount of future utilities is a constant" (Samuelson, 1937, p. 156).

Behavioral economists argue that people discount hyperbolically (Ainslie & Haslam, 1992; Frederick, Loewenstein, & O'Donoghue, 2002; Laibson, 1997). Hyperbolic discounting models allow the discount between today and tomorrow to be larger than the discount between other adjacent periods. This creates a bias toward current consumption, and it also creates inconsistency (Figure 10).

In laboratory experiments, non-human animals exhibit the high value on today that is consistent with hyperbolic discounting (Frederick et al., 2002). Pigeons, for example, will chose a smaller, sooner reward over a later, larger reward even if the larger reward is much bigger (Ainslie & Herrnstein, 1981; Green, Fischer, Perlow, & Sherman, 1981).

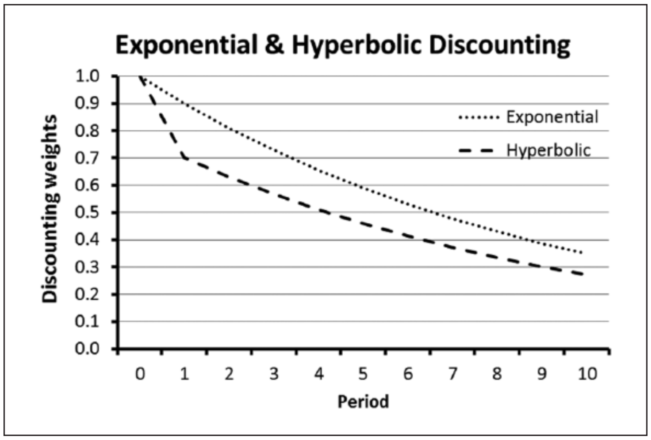

Figure 10. Exponential (neoclassical) and hyperbolic (behavioral) weights.

A biological model of time preference concludes that selection should not favor the reversals of hyperbolic discounting (Robson, 2001). However, with some level of uncertainty, hyperbolic discounting is argued to be optimal (Dasgupta & Maskin, 2005).

Economics has not resolved the issues about intertemporal decision making, and this is important. Most theories rest upon assumptions of exponential discounting, yet the data suggest that this is not a good description of human behavior. To cite one example of many for why this is important, hyperbolic savers will have different savings and consumption decisions than exponential discounters (Angeletos, Laibson, Repetto, Tobacman, & Weinberg, 2001).

Experimental evolution provides a novel, empirical approach to investigate this important economic issue. The core of experiments on intertemporal choice involved designing selective environments. For example, it is possible to run experiments that contrast exponential and hyperbolic discounting (Figure 11).

In this experiment, selection favors hyperbolic discounting in one condition and exponential discounting in another. The populations that evolve can then be tested in some form of competitive paradigm appropriate for the experimental species (Fellowes, Kraaijeveld, & Godfray, 1998; Santos, Fowler, & Partridge, 1992).

More generally, experimental evolution allows the systematic, empirical study of discounting with many different fitness landscapes. The long-term hope of such studies is to allow the neoclassical and behavior views to be merged to improve economics.

In summary, intertemporal decisions are among the most important in economics. There is an important unresolved debate over whether humans and non-humans are exponential or hyperbolic discounters. Experimental evolution is a novel approach to this important problem and may be able to improve economics.

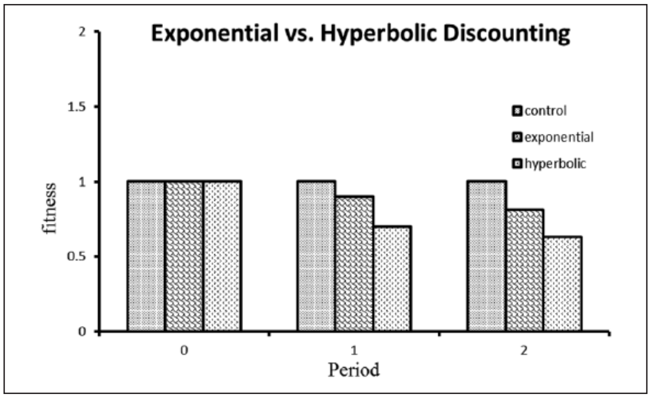

Figure 11. Creating exponential and hyperbolic discounting.

Discussion

We are enthusiastic proponents of using experimental evolution to study, and ultimately improve, economics. There are three primary reasons for our optimism.

First, economics is divided currently between the neoclassical and behavioral schools. This division is based on a profound disagreement over human nature as reified in preferences. The neoclassical versus behavioral disagreement began decades ago, and we are not optimistic that the current approaches within economics will lead to a synthesis.

Experimental evolution is an approach where preferences are endogenous. Thus, it is possible to study the role of selection in shaping the core axioms of economics. Our hope and expectation is that experimental evolution can provide a path to a synthesis of neoclassical and behavioral economics grounded in an empirically informed view of human nature.

Second, experimental evolution is consistent with a series of advances in economics that use the strong inference allowed by true experiments. Experimental economics is a well-established approach that began in modern form in the late 1940s and 1950s (historical accounts are found in the introductions of Davis & Holt, 1993; Kagel & Roth, 1995). Over the past half century or so, experimental economics has moved from a novel, fringe activity to the core of many areas of economics (Smith, 1982).

More recently, randomized experiments have been increasingly used to evaluate social policy (Banerjee & Duflo, 2008; Heckman, 1991). For example, one frequently cited paper using randomization reports that deworming of schoolchildren produced important education improvement at very low cost relative to other approaches such as decreasing student–teacher ratios (Miguel & Kremer, 2004). The success of randomized social policy studies has led to "a veritable explosion of randomized experiments in development economics" (Banerjee & Duflo, 2008, p. 1).

Third, we feel experimental evolution captures an important aspect of modern human existence. In experimental evolution, the test populations are placed in an experimentally altered adaptive landscape.

We believe that humans are productively viewed as existing in an altered adaptive landscape. This altered landscape was not produced by an experimenter but rather by rapid technological change (Barkow et al., 1992; Wilson, 1978). Many of the puzzles in economics may be resolved by viewing humans as existing in an altered adaptive landscape (Burnham & Phelan, 2000).

What might the impact on economics be of a sustained program using experimental evolution? Our informed speculation includes the following:

1. There is selective pressure for optimal behavior. In accordance with neoclassical economic views, selection favors behaviors that lead to higher fitness. There is evolutionary pressure to optimize.
2. Humans are not in equilibrium with the environment. Many neoclassical economic models assume that humans make optimal decisions over novel aspects of the environment. These range from food selection to financial instruments to technology itself. For novel products or attributes, there has been very little time for humans to evolve to be in synch with these aspects.

Economics is currently a field divided upon itself; neoclassical and behavioral economists are at odds with each other over human nature. Economic preferences are exogenous, axiomatic, and contentious. Within an experimental evolution framework, preferences can become endogenous, non-axiomatic, and harmonious.

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References

Acemoglu, D. (2000). Technical change, inequality, and the labor market. *Journal of Economic Literature*, *40*, 7-72.

Ainslie, G. (1974). Impulse control in pigeons. *Journal of the Experimental Analysis of Behavior*, *21*, 485-489.

Ainslie, G., & Haslam, N. (1992). Hyperbolic discounting. In G. Loewenstein & J. Elster (Eds.), *Choice over time* (pp. 57-92). New York, NY: Russell Sage Foundation.

Ainslie, G., & Herrnstein, R. J. (1981). Preference reversal and delayed reinforcement. *Animal Learning Behavior*, *9*, 476-482.

Akey, J. M. (2009). Constructing genomic maps of positive selection in humans: Where do we go from here? *Genome Research*, *19*, 711-722.

Akey, J. M., Eberle, M. A., Rieder, M. J., Carlson, C. S., Shriver, M. D., Nickerson, D. A., & Kruglyak, L. (2004). Population history and natural selection shape patterns of genetic variation in 132 genes. *PLoS Biology*, *2*, 1591-1599.

Allais, M. (1953). Le comportement de l'homme rationnel devant le risque: critique des postulats et axiomes de l'école américaine. *Econometrica: Journal of the Econometric Society*, *21*, 503-546.

Allison, A. C. (1954). Protection afforded by sickle-cell trait against subtertian malarial infection. *British Medical Journal*, *1*, 290-294.

Angeletos, M., Laibson, D., Repetto, A., Tobacman, J., & Weinberg, S. (2001). The hyperbolic consumption model: Calibration, simulation, and empirical evaluation. *Journal of Economic Perspectives*, *15*, 47-68.

Austad, S. N. (1993). Retarded senescence in an insular population of Virginia opossums (*Didelphis virginiana*). *Journal of Zoology*, *229*, 695-708.

Baerends, G. P., & Drent, R. H. (1982a). The herring gull and its egg. Part I. *Behaviour*, *17*, 1-312.

Baerends, G. P., & Drent, R. H. (1982b). The herring gull and its egg. Part II. *Behaviour*, *82*, 1-415.

Baerends, G. P., & Krujit, J. P. (1973). Stimulus selection. In R. A. Hinde & J. Stevenson-Hinde (Eds.), *Constraints on learning* (pp. 23-50). New York, NY: Academic Press.

Banerjee, A. V., & Duflo, E. (2008). The experimental approach to development economics. *Annual Review of Economics*, *1*, 151-178.

Barberis, N., Huang, M., & Santos, T. (2001). Prospect theory and asset prices. *The Quarterly Journal of Economics*, *116*, 1-53.

Barkow, J. H., Cosmides, L., & Tooby, J. (1992). *The adapted mind: Evolutionary psychology and the generation of culture*. New York, NY: Oxford University Press.

Beaumont, H. J. E., Gallie, J., Kost, C., Ferguson, G. C., & Rainey, P. B. (2009). Experimental evolution of bet hedging. *Nature*, *462*, 90-93.

Becker, G. S. (1976). Altruism, egoism, and genetic fitness: Economics and sociobiology. *Journal of Economic Literature*, *14*, 817-826.

Becker, G. S., & Mulligan, C. B. (1997). On the endogenous determination of time preference. *The Quarterly Journal of Economics*, *112*, 729-758.

Bernoulli, D. (1954). Exposition of a new theory on the measurement of risk. *Econometrica*, *22*, 23-36.

Bersaglieri, T., Sabeti, P. C., Patterson, N., Vanderploeg, T., Schaffner, S. F., Drake, J. A., . . . Hirschhorn, J. N. (2004). Genetic signatures of strong recent positive selection at the lactase gene. *The American Journal of Human Genetics*, *74*, 1111-1120.

Bowlby, J. (1969). *Attachment and loss, Volume I: Attachment*. New York, NY: Basic Books.

Boysen, S. T., Mukobi, K. L., & Berntson, G. G. (1999). Overcoming response bias using symbolic representations of number by chimpanzees (*Pan troglodytes*). *Animal Learning & Behavior*, *27*, 229-235.

Burnham, T., & Phelan, J. (2000). *Mean genes: From food to sex to money, taming our primal instincts*. Cambridge, MA: Perseus.

Caraco, T., Martindale, S., & Whittam, T. S. (1980). An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour*, *28*, 820-830.

Charlesworth, B. (1980). *Evolution in age-structured populations*. Cambridge, UK: Cambridge University Press.

Cryan, J. F., & Holmes, A. (2005). The ascent of mouse: Advances in modelling human depression and anxiety. *Nature reviews Drug discovery*, *4*, 775-790.

Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London, England: John Murray.

Dasgupta, P., & Maskin, E. (2005). Uncertainty and hyperbolic discounting. *The American Economic Review*, *95*, 1290-1299.

Davis, D. D., & Holt, C. A. (1993). *Experimental economics*. Princeton, NJ: Princeton University Press.

DellaVigna, S., & Malmendier, U. (2004). Contract design and self-control: Theory and evidence. *The Quarterly Journal of Economics*, *119*, 353-402.

de Montmort, P. R. (1713). *Essay d'analyse sur les jeux de hazard*. Paris, France: Jacque Quillau.

Dobbing, J. (1970). Undernutrition and the developing brain: The relevance of animal models to the human problem. *Archives of Pediatrics & Adolescent Medicine*, *120*, 411-415.

Dunlap, A. S., & Stephens, D. W. (2009). Components of change in the evolution of learning and unlearned preference. *Proceedings of the Royal Society, Series B*, *276*, 3201-3208.

Eldredge, N., & Gould, S. J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf (Ed.), *Models in paleobiology* (pp. 82-115). San Francisco: Freeman, Cooper.

Ellsberg, D. (1961). Risk, ambiguity, and the savage axioms. *Quarterly Journal of Economics*, *75*, 643-669.

Fellowes, M., Kraaijeveld, A., & Godfray, H. (1998). Trade-off associated with selection for increased ability to resist parasitoid attack in *Drosophila melanogaster. Proceedings of the Royal Society of London, Series B: Biological Sciences*, *265*, 1553-1558.

Fisher, I. (1930). *The theory of interest as determined by impatience to spend income and opportunity to invest it*. New York, NY: Macmillan.

Fisher, R. (1930). *The genetical theory of natural selection: A complete variorum edition*. Oxford, UK: Clarendon Press.

Frederick, S., Loewenstein, G., & O'Donoghue, T. (2002). Time discounting and time preference: A critical review. *Journal of economic literature*, *40*, 351-401.

Fudenberg, D., & Levine, D. K. (2006). A dual-self model of impulse control. *American Economic Review*, *96*, 1449-1476.

Fuller, R. C., Baer, C. F., & Travis, J. (2005). How and when selection experiments might actually be useful. *Integrative & Comparative Biology*, *45*, 391-404.

Futuyama, D., Bennett, A. F., Garland, T., Jr., & Rose, M. R. (2009). The importance of experimental studies in evolutionary biology. In T. Garland Jr. & M. R. Rose (Eds.), *Experimental evolution: Concepts, methods, and applications* (pp. 15-30). Berkeley: University of California Press.

Garland, T., Jr. (2003). Selection experiments: An under-utilized tool in biomechanics and organismal biology. In V. L. Bels, J.-P. Gasc, & A. Casinos (Eds.), *Vertebrate biomechanics and evolution* (pp. 23-56). Oxford, UK: BIOS Scientific Publishers.

Garland, T., Jr., & Rose, M. R. (2009). *Experimental evolution: Concepts, methods, and applications of selection experiments*. Berkeley: University of California Press.

Gavrilets, S., & Vose, A. (2005). Dynamic patterns of adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 18040-18045.

Gibbs, A. G., Chippindale, A. K., & Rose, M. R. (1997). Physiological mechanisms of evolved desiccation resistance in *Drosophila melanogaster*. *Journal of Experimental Biology*, *200*, 1821-1832.

Goldin, C. D., & Katz, L. F. (2009). *The race between education and technology*. Cambridge, MA: Harvard University Press.

Götz, J., & Ittner, L. M. (2008). Animal models of Alzheimer's disease and frontotemporal dementia. *Nature Reviews Neuroscience*, *9*, 532-544.

Gould, S. J. (2002). *The structure of evolutionary theory*. Cambridge, MA: The Belknap Press of Harvard University Press.

Gould, S. J., & Lewontin, R. C. (1979). The Spandrels of San Marco and the Panglossian Program: A critique of the adaptationist programme. *Proceedings of the Royal Society of London*, *205*, 581-588.

Grant, P. R., & Grant, R. B. (2002). Unpredictable evolution in a 30-year study of Darwin's Finches. *Science*, *296*, 707-711.

Green, L., Fischer, E. B., Perlow, S., & Sherman, L. (1981). Preference reversal and self control: Choice as a function of reward amount and delay. *Behaviour Analysis Letters*, *1*, 43-51.

Guth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior & Organization*, *3*, 367-388.

Haldane, J. B. S. (1941). *New paths in genetics*. London, England: George Allen & Uwin.

Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, *12*, 12-45.

Hanushek, E. A., & Woessmann, L. (2008). The role of cognitive skills in economic development. *Journal of Economic Literature*, *46*, 607-668.

Hardy, G. H. (1908). Mendelian proportions in a mixed population. *Science*, *28*, 49-50.

Hartl, D. L., & Clark, A. G. (1997). *Principles of population genetics* (Vol. 116). Sunderland, MA: Sinauer Associates.

Hasegawa, M., Kishino, H., & Yano, T. (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, *22*, 160-174.

Heckman, J. J. (1991). *Randomization and social policy evaluation*. Cambridge, MA: National Bureau of Economic Research.

Heckman, J. J. (2000). Policies to foster human capital. *Research in Economics*, *54*, 3-56.

Hernandez, R. D., Kelly, J. L., Elyashiv, E., Melton, S. C., Auton, A., McVean, G., . . . Przeworksi, M. (2011). Classic selective sweeps were rare in recent human evolution. *Science*, *331*, 920-924.

Hill, W. G., & Caballero, A. (1992). Artificial selection experiments. *Annual Review of Ecology and Systematics*, *23*, 287-310.

Irons, W. (1998). Adaptively relevant environments versus the environment of evolutionary adaptedness. *Evolutionary Anthropology*, *6*, 194-204.

Johanson, D., & White, T. (1979). A systematic assessment of early African hominids. *Science*, *203*, 321-330.

Kacelnik, A., & Bateson, M. (1996). Risky theories—The effects of variance on foraging decisions. *American Zoologist*, *36*, 402-434.

Kacelnik, A., & El Mouden, C. (2013). Triumphs and trials of the risk paradigm. *Animal Behaviour*, *86*, 1117-1129.

Kagel, J., & Roth, A. (Eds.). (1995). *The handbook of experimental economics*. Princeton, NJ: Princeton University Press.

Kahneman, D., Slovic, P., & Tversky, A. (1982). *Judgment under uncertainty: Heuristics and biases*. Cambridge, UK: Cambridge University Press.

Kahneman, D., & Tversky, A. (1972). Subjective probability: A judgment of representativeness. *Cognitive Psychology*, *3*, 430-453.

Kahneman, D., & Tversky, A. (1979). Prospect theory: An analysis of decision under risk. *Econometrica*, *47*, 263-292.

Kirkwood, T. B., & Rose, M. R. (1991). Evolution of senescence: Late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *332*, 15-24.

Laibson, D. (1997). Golden eggs and hyperbolic discounting. *The Quarterly Journal of Economics*, *112*, 443-478.

Lande, R. (1976). Natural selection and random genetic drift in phenotypic evolution. *Evolution*, *30*, 314-334.

Lang, P. J., Davis, M., & Öhman, A. (2000). Fear and anxiety: Animal models and human cognitive psychophysiology. *Journal of Affective Disorders*, *61*, 137-159.

Lenski, R. E., Rose, M. R., Simpson, S. C., & Tadler, S. C. (1991). Long-term experimental evolution in *Escherichia coli*. I. Adaptation and divergence during 2,000 generations. *The American Naturalist*, *138*, 1315-1341.

Levy, F., & Murnane, R. J. (2003). The skill content of recent technological change: An empirical exploration. *The Quarterly Journal of Economics*, *118*, 1279-1333.

Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics*, *1*, 1-18.

Lewontin, R. C. (1974). *The genetic basis of evolutionary change*. New York, NY: Columbia University Press.

Lundvall, B.-Ä., & Johnson, B. (1994). The learning economy. *Journal of Industry Studies*, *1*, 23-42.

Lynch, C. B. (1980). Response to divergent selection for nesting behavior in *Mus musculus. Genetics*, *96*, 757-765.

Magnuson, K. A., Ruhm, C., & Waldfogel, J. (2007). Does prekindergarten improve school preparation and performance? *Economics of Education Review*, *26*, 33-51.

Mas-Collell, A., Whinston, M. D., & Green, J. R. (1995). *Microeconomic theory*. Oxford, UK: Oxford University Press.

McNamara, J. M., & Houston, A. I. (1992). Risk-sensitive foraging: A review of the theory. *Bulletin of Mathematical Biology*, *54*, 355-378.

Medawar, P. B. (1946). Old age and natural death. *Modern Quarterly*, *1*, 30-56.

Medawar, P. B. (1952). *An unsolved problem of biology*. London, England: H.K. Lewis.

Mery, F., & Kawecki, T. J. (2002). Experimental evolution of learning ability in fruit flies. *Proceedings of the National Academy of Sciences*, *99*, 14274-14279.

Mery, F., & Kawecki, T. J. (2003). A fitness cost of learning ability in *Drosophila melanogaster. Proceedings of the Royal Society of London, Series B: Biological Sciences*, *270*, 2465-2469.

Miguel, E., & Kremer, M. (2004). Worms: Identifying impacts on education and health in the presence of treatment externalities. *Econometrica*, *72*, 159-217.

Nei, M., & Kumar, S. (2000). *Molecular evolution and phylogenetics*. Oxford, UK: Oxford University Press.

Novick, P., Field, C., & Schekman, R. (1980). Identification of 23 complementation groups required for post-translational events in the yeast secretory pathway. *Cell*, *21*, 205-215.

Oakley, T. H. (2009). A critique of experimental phylogenetics. In T. Garland Jr. & M. Rose (Eds.), *Experimental evolution:*

Concepts, methods, and applications of selection experiments (pp. 650-670). Berkeley: University of California Press.

Parsons, J. (1970). Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). *Nature*, *228*, 1221-1222.

Pauling, L., Itano, H. A., Singer, S., & Wells, I. C. (1949). Sickle cell anemia, a molecular disease. *Science*, *110*, 543-548.

Rabin, M. (2000). Risk aversion and expected utility theory: A calibration theorem. *Econometrica*, *68*, 1281-1292.

Rabin, M., & Thaler, R. H. (2001). Anomalies: Risk aversion. *The Journal of Economic Perspectives*, *15*, 219-232.

Rice, D., & Barone, S., Jr. (2000). Critical periods of vulnerability for the developing nervous system: Evidence from humans and animal models. *Environmental Health Perspectives*, *108*, 511-533.

Rice, P. M. (1999). On the origins of pottery. *Journal of Archaeological Method and Theory*, *6*, 1-54.

Robson, A. (1996). The evolution of attitudes to risk: Lottery tickets and relative wealth. *Games and Economic Behavior, 14*, 190-207.

Robson, A. (2001). The biological basis of economic behavior. *Journal of Economic Literature*, *39*, 11-33.

Rogers, A. R. (1994). Evolution of time preference by natural selection. *American Economic Review*, *84*, 460-481.

Rose, M. R. (1984). Laboratory evolution of postponed senescence in *Drosophila melanogaster. Evolution*, *38*, 1004-1010.

Rose, M. R., & Garland, T., Jr. (2009). Darwin's other mistake. In T. Garland Jr. & M. R. Rose (Eds.), *Experimental evolution: Concepts, methods, and applications of selection experiments* (pp. 3-13). Berkeley: University of California Press.

Rothman, J. E. (1994). Mechanisms of intracellular protein transport. *Nature*, *372*, 55-63.

Sabeti, P. C., Reich, D. E., Higgins, J. M., Levine, H. Z., Richter, D. J., Schaffner, S. F., . . . McDonald, G. J. (2002). Detecting recent positive selection in the human genome from haplotype structure. *Nature*, *419*, 832-837.

Samuelson, P. A. (1937). A note on measurement of utility. *The Review of Economic Studies*, *4*, 155-161.

Santos, M., Fowler, K., & Partridge, L. (1992). On the use of tester stocks to predict the competitive ability of genotypes. *Heredity*, *69*, 489-495.

Schelling, T. C. (1984). Self-command in practice, in policy, and in a theory of rational choice. *The American Economic Review*, *74*, 1-11.

Slatkin, M. (1977). Gene flow and genetic drift in a species subject to frequent local extinctions. *Theoretical Population Biology*, *12*, 253-262.

Smith, V. L. (1982). Microeconomic systems as an experimental science. *The American Economic Review, 72*, 923-955.

Smith, G. (1988). Animal models of Alzheimer's disease: Experimental cholinergic denervation. *Brain Research Reviews*, *13*, 103-118.

Stephens, D. W. (1981). The logic of risk-sensitive foraging preferences. *Animal Behaviour*, *29*, 628-629.

Stern, C. (1943). The Hardy-Weinberg law. *Science*, *97*, 137-138.

Stigler, G. J., & Becker, G. S. (1977). De Gustibus Non Est Disputam. *The American Economic Review*, *67*, 76-90.

Südhof, T. C., & Jahn, R. (1991). Proteins of synaptic vesicles involved in exocytosis and membrane recycling. *Neuron*, *6*, 665-677.

Swallow, J. G., & Garland, T., Jr. (2005). Selection experiments as a tool in evolutionary and comparative physiology: Insights into complex traits—An introduction to the symposium. *Integrative & Comparative Biology*, *45*, 387-390.

Thaler, R. (1981). Some empirical evidence on dynamic inconsistency. *Economic Letters*, *8*, 201-207.

Thaler, R. H. (1988). Anomalies: The ultimatum game. *The Journal of Economic Perspectives*, *2*, 195-206.

Thaler, R. H., & Shefrin, H. M. (1981). An economic theory of self-control. *The Journal of Political Economy*, *89*, 392-406.

Thompson, E., Kuttab-Boulos, H., Witonsky, D., Yang, L., Roe, B., & Di Rienzo, A. (2004). CYP3A variation and the evolution of salt-sensitivity variants. *The American Journal of Human Genetics*, *75*, 1059-1069.

Tishkoff, S. A., Varkonyi, R., Cahinhinan, N., Abbes, S., Argyropoulos, G., Destro-Bisol, G., . . . Loiselet, J. (2001). Haplotype diversity and linkage disequilibrium at human G6PD: Recent origin of alleles that confer malarial resistance. *Science*, *293*, 455-462.

Vander Wall, S. B. (1990). *Food hoarding in Animals*. Chicago, IL: University of Chicago Press.

Voight, B. F., Kudaravalli, S., Wen, X., & Pritchard, J. K. (2006). A map of recent positive selection in the human genome. *PLoS Biology*, *4*, Article e72.

von Neumann, J., & Morgenstern, O. (1947). *Theory of games and economic behavior*. Princeton, NJ: Princeton University Press.

Wattiaux, J. (1968). Cumulative parental age effects in *Drosophila subobscura. Evolution*, *22*, 406-421.

Weinberg, W. (1908). Über den nachweis der vererbung beim menschen. *Jahresh Wuertt Ver vaterl Natkd*, *64*, 368-382.

Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, *11*, 398-411.

Williams, K. S., Smith, K. G., & Stephen, F. M. (1993). Emergence of 13-yr periodical cicadas (Cicadidae: *Magicicada*): Phenology, mortality, and predators satiation. *Ecology*, *74*, 1143-1152.

Wilson, E. O. (1978). *On human nature*. Cambridge, MA: Harvard University Press.

Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proceedings of the 6th International Congress of Genetics* (Vol. 1, pp. 356-366). Brooklyn, NY: Brooklyn Botanical Garden.

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