Abstract. This paper, prepared for the forthcoming *The Social Economics Handbook* (Jess Benhabib, Alberto Bisin and Matthew Jackson, editors, Elsevier Press), surveys recent work on the evolutionary origins of preferences. We are especially interested in the circumstances under which evolution would push preferences away from the self-interested perfectly-rational expected utility maximization of classical economic theory in order to incorporate environmental or social considerations.

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1 Introduction

This essay on the evolutionary foundations of preferences is best introduced with an example. The example in turn requires some notation, but this seemingly technical beginning will set the stage for a more intuitive ensuing discussion.

We are interested in a setting in which consumption must be distributed across periods in the face of uncertainty. Suppose that time is discrete, indexed by \( \{0,1,2,\ldots\} \). In each period \( t \), a state \( z_t \) is drawn from the finite set \( Z \), independently and identically across periods, with \( \rho(z_t) \) giving the probability of state \( z_t \). The consumption bundle in each period is drawn from the set \( C \). A consumption plan \( \{c_t(z_t)\}_{z_t \in Z, t \in \{0,1,\ldots\}} \) thus identifies the bundle to be consumed in each period, as a function of the realized state in that period. Let \( c \) denote a typical such consumption plan and \( C \) the set of such plans. How do we model preferences over the set \( C \)?

The most common approach in economics is to assume there exists an increasing utility function \( u : C \to \mathbb{R} \) allowing preferences over \( C \) to be represented by the discounted-sum-of-expected-utility function \( U : C \to \mathbb{R} \), given by

\[
U(c) = \sum_{t=0}^{\infty} \sum_{z_t \in Z} D^t u(c_t(z_t)) \rho(z_t),
\]

where \( D \in (0,1) \) is the discount factor.

Why is this a useful representation? From an analytic point of view, (1) is compelling for its tractability. The additive separability across time and states, the stationarity of the discounting, and the stationarity of the function \( u \) over time and states all make analysis and computation easier. For example, this maximization problem exhibits the consistency property that lies at the heart of dynamic programming. If (1) is maximized by a consumption plan \( c \), then once \( t \) periods have passed, the continuation of the plan \( c \) maximizes the sum corresponding to (1) but beginning with period \( t \). Computationally, a single function \( u \) is much easier to simulate or estimate than one such function for each period or state. At the very least, one might view (1) as an ideal point of departure for a study of behavior, however unrealistic it turns out to be, perhaps with the goal of subsequently
examining the robustness of its more interesting implications to more flexible specifications.

From a normative point of view, (1) can be viewed as an expression of rationality. Within periods, the expected utility formulation is implied by Savage’s [123] axioms, often defended as foundations of rationality (with Allais [3] and Ellsberg [35] giving rise to a vast literature questioning their positive applicability). For example, a person whose behavior is characterized by (1) can never fall prey to a money pump, a criterion typically regarded as essential for rationality (cf. Nau and McCardle [88]). Looking across periods, it is once again reassuring that the resulting behavior is consistent, in the sense that the optimal consumption plan at time \( t \) is the continuation of the optimal plan at time \( t' < t \). This ensures that recommendations based on (1) cannot lead to conflicting advice.

From a positive point of view, (1) is less convincing, doing both too little and too much. This representation does too little in the sense that it leaves important questions open. What is the shape of the function \( u \)? Are people risk neutral, risk averse, risk seeking, or something more complicated? How are risk attitudes related to observable characteristics of either the decision maker or her environment? The representation does too much in the sense that it places a great deal of structure on preferences. Do people really discount in such a stationary fashion? Are their preferences linear in probabilities? Do they think in terms of probabilities at all? Are their preferences really so separable? Once we go beyond these points to open the question of what enters the utility function, all sorts of questions arise. Are their preferences really concerned only with their own consumption and nothing else? How might their preferences be affected by various aspects of their environment, including perhaps the consumption of others?

One possible response to these questions is empirical. Bolstered by ever-more-plentiful data as well as more powerful experimental techniques, we can simply observe behavior and infer the corresponding preferences. In doing so, one could usefully draw on the rich revealed-preference literature in psychology as well as economics.\(^1\)

Our thinking on this point is that empirical work on preferences and behavior is essential. However, the specification of preferences is sufficiently complicated, and poses sufficient identification issues, that we have little hope of in pursuing a purely empirical approach. However much data we have, we can hope to make sense of it only in the context of theoretical

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\(^1\)See Rabin [102] for an introduction to work at the intersection of psychology and economics.
models. But where do we find these models? Building models is something at which economists excel, and economists are seldom idle when there are new models to be produced. As one might expect, models of preferences are no exception. The difficulty is that if we do not restrict ourselves to some simple form such as (1), it seems that anything goes. How do we impose discipline on the resulting theoretical exercise?

The quest for discipline is perhaps the ultimate motivation for (1). Whatever its disadvantages, it clearly imposes a great deal of structure on the analysis. As a result, when faced with behavior seemingly inconsistent with (1), a common reaction is to preserve (1) while searching for features of the environment to rationalize the proposed behavior. Postlewaite [101] states the case for doing so quite clearly. In particular, by opening up departures from (1) as explanations, we allow ourselves the freedom to explain anything. This not only robs the resulting exercise of any power, but the ease with which we can accommodate observed behavior by altering (1) distracts attention from aspects of the environment that lie behind the behavior. If allowed to work freely with models in which people simply prefer to not purchase used durable goods such as automobiles, we may never have discovered the lemons phenomenon (Akerlof [2]). It may thus be better to stick with (1), trading the constraints it imposes and its potential lack of realism for the concreteness it brings to our inquiry.

The point of departure for this essay is the belief that we must sometimes impose more structure on (1) and sometimes move beyond this formulation, and that we require solid theoretical foundations for both. We suggest seeking the required theoretical discipline in evolutionary models. In particular, we view human preferences as having been shaped by years of evolutionary selection. When thinking about whether (1) is a reasonable representation of preferences, or which more specific or more general models might be useful alternatives, our first step is to ask what sorts of preferences are likely to emerge from this evolutionary process. The more readily can we provide evolutionary foundations for a model of preferences, the more promise do we see in using this model in theoretical and applied economic analyses.

This approach to preferences raises a collection of methodological issues that are discussed in Section 2. Sections 3 and 4 provide illustrations from the literature. Section 3 concentrates on the functional form assumptions built into (1), including the expected-utility criterion that is applied within periods and the exponentially-discount summation that aggregates utility across periods. Section 4 examines arguments that are likely to appear in

\footnote{Camerer, Loewenstein and Rabin [19] provide a good point of entry into this literature.}
the utility function beyond an agent’s own consumption. Section 5 very briefly concludes.

2 Evolutionary Foundations

2.1 Evolution and Economic Behavior

Is it reasonable to talk about evolution and human behavior at all? A large literature, referred to as evolutionary game theory, has grown around evolutionary models of behavior.\(^3\) The presumption behind evolutionary game theory is that human behavior, whether in games (and hence the name) or decision problems, typically does not spring into perfect form from a process of rational reasoning. Instead, it emerges from a process of trial and error, as people experiment with alternatives, assess the consequences, and try new alternatives. The resulting adaptive processes have been modeled in a variety of ways, from Bayesian to reinforcement learning, from cognitive to mechanical processes, from backward to forward looking processes, all collected under the metaphor of “evolutionary game theory.”

This literature has provided valuable insights into how we interpret equilibria in games, but we have a fundamentally different enterprise in mind when talking about the evolution of preferences in this essay. We take the word “evolution” literally to mean the biological process of evolution, operating over millions of years, that has brought us to our present form.\(^4\) The driving force behind this evolution is differential survival. Some behavior makes its practitioners more likely to survive than others, and those behaviors most conducive to survival are the ones we expect to prevail. Our task is to identify these behaviors.

This view would be uncontroversial if we were talking about the evolution of physical characteristics. A giraffe who can reach more leaves on a tree is more likely to survive, and hence evolution gives us giraffes with long necks.

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\(^3\)See, for example, Fudenberg and Levine [49], Hofbauer and Sigmund [65], Mailath [80], Samuelson [119], van Damme [139, Chapter 9], Vega Redondo [141], Weibull [143] and Young [150].

\(^4\)We have no doubts that cultural evolution is also vitally important. We expect the techniques we examine to transfer readily to models of cultural evolution, often with simply a reinterpretation. We find interpretations in terms of biological evolution more straightforward, and hence tend to adopt them. Joseph Henrich, Robert Boyd, Samuel Bowles, Colin Camerer, Ernst Fehr, Herbert Gintis AND Richard McElreath [64] and Joseph Henrich, Robert Boyd, Samuel Bowles, Colin Camerer, Ernst Fehr and Herbert Gintis [63] provide interesting points of departure into the study of cultural evolution and economic behavior.
A bat that can detect prey is more likely to survive, and so evolution gives us bats capable of echolocation. Porcupines are more likely to survive if they are not eaten, and so have evolved to be covered with sharp quills. The list of such examples is virtually endless.

Behavior can also confer an evolutionary advantage, with a similarly long list of examples. African wild dogs enlarge their set of eligible prey, and hence their chances of survival, by hunting in packs. Vampire bats reduce their likelihood of starvation by sharing food. Humans enhance the survival prospects of their offspring by providing food for their young. If different members of a population behave differently, then those whose behavior enhances their survival can be expected to dominate the population. The relentless process of differential survival will thus shape behavior as well as characteristics.

Doesn’t this commit us to a strong form of biological determinism? Is our behavior really locked into our genes? We think the answer is no on both counts. Nature does not dictate behavior. However, there is a huge gap between the assertion that genetic factors determine every decision we will ever make and the assertion that biological considerations have no effect on our behavior. We need only believe that there is some biological basis for behavior, however imprecise and whatever the mechanics, for the issues raised in this essay to be relevant.\footnote{The evidence that there is some such connection is both wide-ranging and fascinating. For two examples, see Dreber and Hoffman [30] and Knafo, Israel, Darvasi, Bachner-Melman, Uzeovsky, Cohen, Feldman, Lerer, Laiba, Raz, Nemanov, Gritsenko, Dina, Agam, Dean, Bronstein, and Ebstein [70].}

2.2 The Rules of Evolution

We will often refer to “evolution” as if referring to a conscious being. We will use phrases such as “evolution selects” or “evolution prefers” or “evolution maximizes” or even “evolution believes.” It is important to be clear at the beginning that we attribute no consciousness and no purpose to evolution. We have in mind throughout the standard, mindless process of mutation and selection studied by biologists. We suppose that individuals in a population may have different types, whether these are manifested as different physical characteristics or different behavior. These different types reflect genetic endowments that arose initially from undirected, random mutations. Some of these types will make their possessors more likely to survive, others will be detrimental. Over time, this process of differential survival will cause a larger proportion of the population to be characterized by the former
types, and it is this process that lies behind our analysis. It is therefore often convenient to model the outcome of a dynamic evolutionary process as the solution to a maximization problem. This convention is familiar to economists, who routinely model consumers, firms, governments, and other entities as maximizers, bolstered by the view that this maximization may be the outcome of an adaptive process rather than conscious calculation. We proceed similarly here when talking about evolution, without any illusions that there is purposeful behavior behind this maximization.

The idea that an evolutionary perspective might be helpful in studying behavior is by no means unique to economists. The field of evolutionary psychology has grown around this perspective on behavior. We can learn not only from the successes of evolutionary psychology, but also its difficulties. Gould and Lewontin [53] criticize evolutionary psychology as being an exercise without content. In their view, a clever modeler can produce an evolutionary model capable of producing any behavior. To reinforce their point, they refer to the resulting models as “just-so” stories. Of course, an analytical approach capable of explaining everything in fact explains nothing. If an evolutionary approach is to be useful, we must address the just-so critique.

Economists are also adept at constructing models, and the criticism that we can concoct models rationalizing any imaginable sort of behavior is not a new one. How do we reconcile Gould and Lewontin’s argument with our assertion that evolutionary models are designed to impose discipline on our study of preferences? In our view, the ability to fix a characteristic of behavior and then construct an evolutionary rationale for that behavior is only the first step. If we can go no further, we have typically learned very little. An obvious next step is to fit the model into its place in the existing body of evolutionary theory. Simple and direct models constructed from familiar and inherently-plausible evolutionary principles tend to be convincing, while convoluted models taking us well beyond the usual evolutionary considerations are reasonably greeted with skepticism. Moving beyond this informative but subjective evaluation, our goal should be to construct models that generate predictions beyond those of the target behavior, especially predictions that we could take to data. The more fruitful is a model in doing so, the more useful will it be.

\[6\] We suggest Dawkins [29], Ridley [105] and Williams [144] as accessible introductions to evolutionary theory, and Hofbauer and Sigmund [65] for a more precise examination of the conditions under which the outcome of an evolutionary process can be modeled as the solution to an optimization problem.

\[7\] Barkow, Cosmides and Tooby [8] provide a wide-ranging introduction.
2.3 Evolution and Utility Functions

The preceding subsections have referred frequently to the evolution of behavior, while our title refers to the evolution of preferences. How should we think about evolution shaping out behavior? In one view, evolution would simply program or “hard-wire” us with behavior, equipping us with a rule indicating what to do in each possible circumstance. Alternatively, we might think of evolution as equipping us with utility functions and instructions to maximize utility whenever called upon to make a choice. Most of what we discuss in this essay requires no choice between these alternatives, and requires us to take no stand on the countless intermediate models that combine aspects of both types of behavior. Our focus will primarily be to identify behavior that confers evolutionary advantage. We will then frequently describe this behavior in terms of the preferences with which it is consistent. However, this description is a matter of convenience rather than an assertion about causality.

Taking this approach keeps us squarely within the revealed-preference approach to behavior. Among the fundamental building blocks of economic theory is an assumption that behavior satisfies the consistency conditions captured by the revealed-preference axioms. However, it is often insightful to describe this behavior in terms of preferences, and then convenient to use these preferences as the point of departure for subsequent models of behavior. Similarly, it is behavior that matters to evolution, but there often will be much to be gained by describing this behavior in terms of preferences.\(^8\)

We are convinced of one thing: no amount of introspection will tell us the extent to which our behavior is hard-wired and the extent to which we have discretion. Reading a restaurant menu and choosing a meal makes us feel as if we have conscious control over our actions. However, there is no particular reason why that same feeling could not accompany an inevitable action, or why we might not make choices without being aware of what we are doing. Pursuing these distinctions runs the risk of recreating a long-running discussion of whether we have free will, and how we would know whether we have. This is a fascinating topic, but one that has bedevilled philosophers for centuries and that would only be a hopeless diversion here.

As the same time, we think there are good a priori grounds for thinking of evolution as designing us to be utility maximizers rather than simply hard-
wiring us with behavior. Robson [112] offers an argument beginning with
the assumption that environments fluctuate more quickly than evolution
can respond. Simply telling people to hunt rabbits is risky because they
may encounter situations in which deer are more readily available. With
hard-wired behavior, an evolutionary response would require a deer-hunting
mutation, or perhaps several if the first few such mutations are unlucky. This
must then be followed by a process of selection that may be fast compared
to length of time humans have been developing, but may be quite slow
compared to the length of time it takes for a shock to the weather or to
the population of predators to once again make rabbits relatively plentiful.
By the time the new hard-wired behavior has spread into the population, it
may well be out of step with the environment. A more effective approach is
to endow the agent with a goal, such as maximizing caloric intake or simply
feeling full, along with the ability to learn which behavior is most likely to
achieve this goal in a given environment. Under this approach, evolution
would equip us with a utility function that would provide the goal for our
behavior, along with a learning process, perhaps ranging from trail-and-error
to information collection and Bayesian updating, that would help us pursue
that goal.9

If this is the case, however, why would we attach utility to activities
such as eating? Evolution selects for that behavior which leads to the most
effective propagation, so why don’t we have preferences solely over offspring,
or some appropriate trade-off between the quantity and quality of offspring?
One difficulty is that giving us preferences simply over offspring gives rise
to a small-sample learning process. Human offspring come relatively rarely
and provide relatively sparse feedback. Opportunities to eat are much more
frequent and provide a much richer flow of information. An agent designed
with the goal of producing healthy adult offspring, and then left to learn
the details of doing so by trail-and-error, may not learn soon enough to do
any good. An agent whose goal is to be well nourished may acquire enough
experience soon enough to make good use of this information. Defining

9There are, of course, other aspects of our preferences that evolution may prefer
to place outside our learning. Many people have a deep-seated fear of snakes (cf. Mineka
and Cook [85] and Pinker [98, pp. 388–389]), but few of us are afraid of mushrooms. Since
both can be potentially fatal and both can be eaten, this is puzzling. To see why, imagine
that being bitten by a poisonous snake is very unlikely to happen but likely to be fatal if it
does, while ingesting a poisonous mushroom more likely to occur but less likely to be fatal.
Then evolution may be optimally leave it to her agents to sort out which mushrooms are
dangerous, while being unwilling to take chances on encounters with snakes. In general,
evolution should make us fear not simply things that are bad for us, but rather things
whose danger we may underestimate without discovering our error before they kill us.
utilities in terms of offspring thus gives us an objective that quite faithfully captures the relevant evolution criterion, but gives us little means of learning how to accomplish this objective. Defining utilities in terms of intermediate goods such as consumption gives us an objective that only approximates evolution’s—in some environments we will mechanically pursue additional consumption even though circumstances are such that doing so retards reproduction—in return for giving us the means to effectively learn how to accomplish this objective. The choice of which arguments to place in a utility function thus reflects a delicate evolutionary balancing act, one that we believe merits further study. There is much to be learned in this respect simply from observing how evolution has solved this problem, i.e., observing what enters our utility functions.

2.4 Evolutionary Mismatches

There are two complementary approaches to thinking about the evolutionary foundations of behavior. One is based on the observation that we currently live in an environment much different from that in which we evolved. As a result, behavior that was well suited for our evolutionary environment may fit quite awkwardly into our current one. For example, food was likely to have been in perpetually tenuous supply over the course of our evolutionary history, and the only technology for storing it was to eat it. An instruction of the form “eat all you can whenever you can” accordingly made good evolutionary sense. This presumably explains why so many of us struggle to keep our weight down in our modern world of abundance. Similarly, venomous snakes were probably not only a threat during much of our evolutionary history, but one that left little leeway for trial-and-error learning. A deep-seated fear of snakes was accordingly quite useful for survival. This presumably explains why children in our modern urban society are much more likely to fear snakes than electrical outlets, even though the latter pose a much greater threat.

We refer to these types of observations as “evolutionary mismatch” models. This is clearly a useful perspective.\(^\text{10}\) However, our interest will typically lie not in such mismatch stories, but in examining behavior that is well adapted to its environment. We will accordingly be especially interested in tracing various features of behavior to features in the environment. For example, we will examine how the nature of the competition for mates affects preferences for risk, or how the nature of the uncertainty in the environment

\(^{10}\text{See Burnham and Phelan [17] for a wealth of examples.}\)
affects intertemporal preferences. Mismatches are clearly important, but we believe that a good understanding of how preferences are tailored to the environment in which they evolved is an essential first step in understanding their effects in mismatched environments. If nothing else, allowing ourselves to indulge in mismatch explanations gives us yet one more degree of freedom in constructing our models, while the goal throughout is to use evolutionary arguments to restrict such freedom.

2.5 The Indirect Evolutionary Approach

We distinguish the work described in this essay from a body of literature that has come to be called the “indirect evolutionary approach.” It is worth making this distinction carefully. The indirect evolutionary approach grew out of evolutionary game theory. In the simplest evolutionary-game-theory model, players are characterized by the actions they take in the decision problem or game of interest. We might think of the players as being programmed to take such actions. As play progresses, a revision protocol induces a process by which the players switch their actions. For example, players may randomly choose a new action whenever their realized payoff falls below an aspiration level, or players may switch after each period to the action that would have been a best response to the previous-period average population action, or may switch only in randomly-drawn periods to actions that are best responses to an average of the play of their previous opponents, or so on. One can imagine an endless list of such revision protocols. A central question in evolutionary game theory concerns the extent to which such a revision protocol can, over the course of repeated play, induce population behavior that can be rationalized by a concept such as Nash equilibrium.

The point of departure for the indirect evolutionary approach is to note that throughout the rest of economics, we typically model people as being characterized by preferences rather than simply actions, with these preferences inducing actions through a choice procedure such as utility maximization. Taking this idea literally in an evolutionary context, we can think of people as maximizing utility given their preferences, with their preferences adjusting over time according to a revision protocol. The evolutionary process now shapes behavior through its effect on preferences, and it is this indirect link that gives rise to the name indirect evolutionary approach, pioneered by Güth [58] and Güth and Yaari [59].

The indirect evolutionary approach has been embraced by many because of its ability to explain seemingly anomalous preferences. To see what is in-
volved, it is useful to start with an example. Consider the following game:\footnote{The following discussion follows Samuelson [120].}

\[
\begin{array}{cc}
T & B \\
L & 6, 2 & 4, 4 \\
R & 5, 1 & 2, 0 \\
\end{array}
\]  \tag{2}

This game has a unique Nash equilibrium, given by \((T, R)\) for payoffs \((4, 4)\).\footnote{This is the unique rationalizable outcome, since the strategy \(T\) strictly dominates \(B\) and \(R\) is a strict best response to \(T\).}

Now suppose that, before the game begins, player 1 could commit to playing \(B\), and that player 2 can observe whether such a commitment has been made. The game proceeds as before if no commitment is made, and otherwise player 1 is locked into \(B\) and 2 is left to choose an action. Essentially, a commitment gives us a new game with a sequential structure in which player 1 moves first. This new structure is valuable for player 1. By committing to \(B\), 1 can ensure player 2 will choose a best response of \(L\), giving player 1 a payoff of 5. It is clear that player 1 would jump at the chance to commit.

The observation that commitments can be valuable has a long history, beginning with Stackelberg ([142], translated into English in Peacock [96]) and playing a prominent role in Schelling [124]. Early theories of bargaining, including Binmore [13] and Crawford and Varian [26] explore the power of commitment more formally, as does Frank [40]. While it is straightforward to see that it can be valuable to make commitments, it is less clear just how one does so.

Now let us think of a population of player 1s and another population of player 2s. Players from these populations are repeatedly matched to play the game given by (2). The indirect evolutionary approach assumes that the payoffs in (2) are “material payoffs” or “fitnesses.” These are the payoffs that are relevant in evolutionary terms. Evolution induces behavior from her agents by endowing them with preferences over the actions \(T\) and \(B\) (for player 1s) and \(L\) and \(R\) (for player 2s). These preferences need not match the fitnesses given in (2), but it is fitnesses and not preferences that govern the evolutionary process. Agents whose behavior leads to high fitnesses will reproduce relatively rapidly and the population will ultimately be dominated by such preferences. In particular, an agent may choose an action that performs wonderfully from the point of view of the agent’s preferences, all the while wasting away in the population because the action yields a low fitness. Evolution can thus mislead her agents, in the sense that preferences need
not match fitnesses, but cannot fool herself, in that high fitnesses remain the ticket to evolutionary success.

Is there any reason for preferences to be anything other than fitnesses in such a setting? The key here is the assumption that preferences are observable, in the sense that when two players meet, each player can observe the other’s preferences. The two matched players then play a complete-information version of the game given by (2), with their behavior governed by their preferences, and with the evolutionary implications of their behavior governed by the fitnesses given in (2). Suppose that player 2s have preferences that match fitnesses, as do some player 1s. However, the population also includes some player 1s whose preferences make $B$ a strictly dominant strategy, effectively committing themselves to $B$. In response to the former types of player 1, player 2 will choose $R$, giving 1 a payoff of 4. In response to the latter, player 2 will choose $L$, giving 1 a payoff of 5. As a result, the population will eventually be dominated by player 1s committed to playing $B$. There is thus evolutionary value in equipping agents with preferences that do not reflect their fitnesses.

Bolstered by results such as this, the indirect evolutionary approach has been interpreted as providing foundations for a collection of empirical, experimental, or introspective findings that appear inconsistent with material self interest, including the endowment effect, altruism, vengeance, punishment, and so on. These results are intriguing, but raise two questions. First, initial applications of the indirect evolutionary approach typically considered only a few possible preference specifications, often including preferences that match material fitnesses and one or more alternatives that are tailored to the game in question. In considering (2), for example, we considered the possibility that 1 might be committed to $B$, but there are many other possible preference specifications. What happens if they are present as well? Player 2, for example, would like to commit to $R$, for much the same reason. What if there are also player 2s who are so committed? What if the entire collection of preference specifications were allowed? Would we be confident that the commitment types emerging from simple models would also be selected from such a crowd?

More importantly, it was critical in the preceding argument that players could observe each other’s preferences. Being committed to $B$ is an advantage to player 1 only because it affects player 2’s behavior, inducing 2 to switch to $L$. Ok and Vega Redondo [94] and Ely and Yilankaya [37] confirm that if preferences are not observable, any limit of behavior under an indirect

\[13\]See Ostrum [95] for an introduction.
evolutionary model must constitute a Nash equilibrium in material fitnesses. The indirect approach in these cases gives us an alternative description of the evolutionary process, one that is perhaps less reminiscent of biological determinism, but leads to no new results.

Preferences are not typically high on the list of things taken to be observable in economic analysis. Is it reasonable to assume that preferences are observable? Frank [41] argues that we do often have good information about the preferences of others, and that there is a technological basis for that information. Our preferences are determined partly by emotions such as anger or embarrassment that are beyond our conscious control, expressed by involuntary changes in our facial expressions and body language. If one is prone to blushing when the center of attention, how much good does it do to remind oneself not to blush? Who can keep flashes of anger out of their eyes? At the same time, Guth [58] shows that preferences need not be perfectly observable. It suffices that player 2 sometimes be able to discern player 1’s preferences and react to them. As Guth notes, it is a seemingly quite strong assertion that this is never the case, arguably as unrealistic as the assumption that people can always observe one another’s preferences.

To evaluate these considerations, we must return to the evolutionary context. We think we can observe preferences because people give signals—a tightening of the lips or flash of the eyes—that provide clues as to their feelings. However, the emission of such signals and their correlation with the attendant emotions are themselves the product of evolution. A complete version of the indirect evolutionary approach would then incorporate within the model the evolution of preferences and the evolution of the attendant signals. In (2) for example, player 1 prefers \((T, L)\) to \((B, L)\). Evolution thus has an incentive to produce a version of player 1 whose signals match those emitted by player 1s committed to \(B\), inducing \(L\) from player 2, but who then plays \(T\). What prevents the appearance of such a mimic? We cannot simply assume that mimicry is impossible, as we have ample evidence of mimicry from the animal world, as well as experience with humans who make their way by misleading others as to their feelings, intentions and preferences.\(^{14}\)

14For introductions see Maynard Smith [82, pp. 85–87] and Harper [61].
new mimic appears, and on we go. It appears as if the result could well be a never-ending cycle, as in Robson [107].

In our view, the indirect evolutionary approach will remain incomplete until the evolution of preferences, the evolution of signals about preferences, and the evolution of reactions to these signals, are all analyzed within the model. Perhaps there are outcomes in which players can effectively make commitments by exhibiting the appropriate observable preferences, and there is some force barring the evolutionary pressure to produce mimics, giving us a stationary outcome featuring effective commitment. Perhaps instead the outcome is the sort of cyclical arms race envisioned by Robson [107], with our current situation being a point along this cycle in which some aspects of preferences are at least partially observable. The implications of these scenarios could well be quite different. Further work is required before we have a good idea of what these implications might be. Given the presence of mimics in the natural world, the topic is clearly important. But without more work along these lines, we have little idea what to make of the indirect evolutionary approach.

3 What Sort of Preferences?

A representation of preferences such as (1) combines a number of different features, including the choice of what to include as the arguments of the utility function, attitudes toward risk, and trade-offs between consumption at different times. We find it most convenient to address these features separately. We begin in this section by taking it for granted that we can reasonably think of preferences as being defined over a single homogeneous consumption good. We then break our investigation into two parts.

First, we strip away intertemporal considerations to focus on preferences over consumption within a single period. What form do we expect the function \( u(c) \) to take? What attitudes toward risk might have evolved? How might risk attitudes vary with one’s circumstances or characteristics?

Second, we examine preferences over intertemporal tradeoffs. How do we expect preferences to be aggregated over time? Should we expect preferences to be reasonably approximated by an additively separable utility function, as in (1)? If so, should we expect people to discount the future exponentially? At what rate? If not, how might we expect their discounting to depart from exponential? These questions are all the more pertinent in light of the recent explosion of interest in behavioral economics, much of which is built on the presumption that agents do not discount exponentially (cf.
3.1 Risk

3.1.1 Attitudes Toward Risk

The expected utility theorem has pride of place in the economic theory of behavior under risk. Whether one believes that expected utility maximization faithfully describes behavior or not, its salience in economic analysis is inescapable.

At first blush, it seems that evolution would surely induce preferences that can be characterized by expected utility maximization. Consider a large population made up of a number of different types of people, with each type characterized by a choice of economic lottery. All risk is independent across types and individuals, a case that we refer to as “idiosyncratic” (as opposed to “aggregate”) risk. For simplicity, we adopt the common assumption that all reproduction is asexual, or “parthenogenetic.”

Lotteries are defined over a set of allocations \( C \). Suppose any bundle \( c \in C \) produces the same expected offspring \( \Psi(c) \) for all types. Let \( q^i_k \) be the probability that the lottery chosen by type \( i \) produces the outcome \( c^i_k \). It follows that the expected number of offspring of type \( i \) is then

\[
\sum_k q^i_k \Psi(c^i_k).
\]

Since the population is large and all risk is idiosyncratic, this is also the growth rate of type \( i \). Thus the most successful type will be the type that maximizes this criterion. But this is simply the maximization of expected utility, where the role of the von Neumann-Morgenstern utility function \( u \) is played by the biological production function \( \Psi \).

This evolutionary foundation for expected utility maximization is critically dependent on all the risk being idiosyncratic, or independent across individuals. There seems no compelling reason why all risk should be idiosyncratic. Some of the risk in a hunter-gatherer society concerned the

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15See Ainslie [1], Loewenstein and Prelec [78], and Loewenstein and Thaler [79] for treatments of presently-biased preferences. See Rubinstein [118] for an alternative perspective. Early studies of present bias and self control by Pollak [100], Schelling [125], and Strotz [134] have engendered a large literature. For a few examples, see Elster [36], O’Donoghue and Rabin [92, 93], and Thaler and Shefrin [137].

16This section draws on Robson [109].

17We are not under the illusion that human reproduction is asexual, but doing justice to sexual reproduction leaves little analytic headroom to consider other issues.
weather, which clearly is a shared form of risk. In a modern setting, there continue to be important shared risks. One of these, the stock market, is particularly pertinent as these words are being written.

Idiosyncratic risk means essentially that a separate personal coin is flipped for each individual in each period, whereas aggregate risk is taken to be the opposite extreme in which a single public coin is flipped in each period—heads everyone wins, tails everyone loses. What difference would this make? Let’s warm up by considering a related puzzle. Suppose we have a deck of 52 cards, 26 red and 26 black. You must choose between two alternatives:

1. We will pay you $(3/2)^{52} \approx 1,400,000,000$;

2. We will pay you the expected value of the following lottery. You begin with a dollar. We go through the deck of cards, turning over each one. Each time a red card turns up, we double your total so far, while each time a black card comes up, there is no change in your running total.

What is your expected return from turning over the first card in the lottery? $3/2$. After that, things get more complex, because it depends now on whether the first draw was red or black. But surely it can’t be too bad to take the lottery? Surely the expected value of the lottery is something in the same ball park as $1,400,000,000$ if it isn’t this exactly?

The “lottery” is terrible, and in fact involved no uncertainty at all. The payoff is exactly $2^{26} = (\sqrt{2})^{52} \approx 67,000,000$, because there are 26 red cards and the doubling effect of each red card is independent of where it arises in the deck. The lottery is worse than the certain alternative because $\sqrt{2} < 3/2$.

What would happen if the deck were infinite, but we were concerned only with with the first 52 draws, or more generally with the first $T$ draws? Now the lottery really is a lottery. It no longer matters whether the first draw is red or black, since there is an infinite number of each color. It is not hard to show that the expected value of the lottery after $T$ draws is $(3/2)^T$. The two options are then precisely equivalent.

Remarkably, however, even with an infinite deck there is still a strong sense in which the lottery itself is much worse than the certain deal, involving the limit as $T \to \infty$. To see why, let us go back to using biological evolution as the background for the mathematics. There are two types. Type 1 has 2 offspring with probability 1/2, or 1 offspring also with probability 1/2. All the risk here is idiosyncratic, independent across all individuals and dates. Type 2 also has 2 offspring with probability 1/2, or 1 with probability 1/2,
but now the risk is aggregate. That is, either all the type 2 individuals alive at a particular date get a draw of 2, or they all get a draw of 1. An economist’s reaction here might well be that there should be no difference in the evolutionary success of the two types, since, from an individual’s point of view, there is no difference between the two lotteries. This turns out to be false.

Given a “large” population, the number of type 1s at date \( T \) is \( N(T) = (3/2)^T \) (assuming \( N(0) = 1 \)). That is, the number of type 1s grows by a factor of 3/2 in every period. The corresponding continuous growth rate is 
\[
\frac{\ln N(T)}{T} = \ln(3/2).
\]

The number of type 2s is inescapably random. It is not hard to show that for them, \( E(\tilde{N}(t)) = (3/2)^T \), matching the expression for type 1. However, the exact number of type 2s is \( \tilde{N}(T) = 2^{\tilde{n}(T)} \), where \( N(0) = 1 \) and \( \tilde{n}(T) \) is the random variable describing the number of heads in a sequence of \( T \) flips of a fair coin. There still exists a limiting continuous growth rate because now we have 
\[
\frac{\ln \tilde{N}(T)}{T} = \frac{\tilde{n}(T)}{T} \ln 2 \to \frac{1}{2} \ln 2 = \ln \sqrt{2},
\]
with probability one, as \( T \to \infty \) (by the strong law of large numbers). That is, in the original context, although a finite deck forces there to be exactly the same number of 1s as 2s, the law of large numbers has much the same effect when there is an infinite deck.

Of course, \( \sqrt{2} < 3/2 \) which implies that with probability one, the ratio of type-1 to type-2 agents goes to infinity. In a strong sense, then, the first type outdoes the second, despite the fact that the expected values of the two are exactly the same. Indeed, with probability one the mean number of type-2 agents grows faster than does the number of type-2 agents itself!

An early use of the word “martingale” was to describe the following betting strategy, which was presented by Casanova in his memoirs. Bet $1 on a fair coin (or 1 sequin in Casanova’s memoirs).\(^{18}\) If you win, quit, in the process having gained $1. If you lose, bet $2 on the next throw. If you win, quit, having gained $2 − $1 = $1. If you lose, bet $4 on the next throw. This strategy is claimed to ensure you will win $1.

Let us analyze this martingale betting strategy in more detail. Consider the possible outcomes after a maximum of \( T + 1 \) flips of the fair coin. One possibility is that you have lost every flip. That is, you might have lost 
\[
1 + 2 + \ldots + 2^T = 2^{T+1} − 1. \tag{19}
\]
The probability of this loss is the probability of

\(^{18}\)A sequin was a small gold coin used in Italy. Its value became debased over time, and the word entered English with its current meaning of a dress ornament.

\(^{19}\)Proof: The formula holds at \( T = 1 \). Suppose it holds at \( T \). Then 
\[
1 + 2 + \ldots + 2^{T+1} = 2^{T+2} − 1 = 2^{T+1} − 1.
\]
$T + 1$ heads, or $\left(\frac{1}{2}\right)^{T+1}$. The only other possibility is that you won, possibly stopping at some earlier time $S$. If you win, the amount won is always $1 = 2^S - (1 + ... + 2^{S-1})$. The probability of winning must be $1 - \left(\frac{1}{2}\right)^{T+1}$. The expected change in wealth is $-\left(\frac{1}{2}\right)^{T+1} \left(2^{T+1} - 1\right) + 1 - \left(\frac{1}{2}\right)^{T+1} = 0$, as should be obvious. That is, you can’t string together a finite series of finite fair bets, no matter how you do it, and expect to do any better than breaking even.

In the limit as $T \to \infty$, however, this is no longer true. The probability of losing tends to zero and that of winning tends to one. In the limiting distribution to which this process converges, you win \$1 for sure. Thus, the limit of the means, \$0, is not equal to the mean of the limiting distribution, \$1. How can this happen? The distribution after a finite number of flips puts a very small probability weight on a very large loss. This yields a non-vanishing contribution to the mean. In the limit, however, the probability of this loss converges to zero, giving us an upward jump in the mean “at the limit.”

In our simple biological example, the mean of the type 2 population is similarly held up by very small probabilities of very large populations. In the limit, these probabilities vanish, so the growth of the population is overestimated by the mean. Despite having the same mean, the population almost surely fares worse under aggregate than under individual uncertainty.

The implication of this difference is that individuals should be more averse to aggregate risk than to equivalent idiosyncratic risk. The example can be recast as an economic choice as follows. Suppose that bundles $c_1$ and $c_2$ induce the offspring levels 1 and 2 as above, so $\Psi(c_1) = 1$ and $\Psi(c_2) = 2$, where $\Psi$ is the common production function for expected offspring. Now individuals must choose between lottery 1 and lottery 2. Lottery 1 yields $c_1$ and $c_2$ each with probability 1/2, where all this risk is independent. Lottery 2 also yields $c_1$ and $c_2$ each with probability 1/2, but now all this risk is aggregate. From an expected utility point of view, these two lotteries should be equivalent. Indeed, even from the perspective of any decision theory that applies the apparently weak notion of “probabilistic sophistication,” these two lotteries should be equivalent. But it is not enough here to consider only one’s own payoffs and the associated probabilities; one must also consider how the uncertainty affects others. That is, preferences are interdependent. In an evolutionary environment, individuals should prefer lottery 1 to lottery 2.

The most general case that can easily be analyzed is as follows. Given an aggregate environment $z$, each type $i$ faces an idiosyncratic economic lottery
where \( q_{i,z}^{k} \) is the probability of receiving a commodity bundle \( c_{i,z}^{k} \). We let \( \Psi(c) \) be the expected offspring from bundle \( c \) for any state and any type, where any underlying risk here is also idiosyncratic. Hence \( \sum_k q_{i,z}^{k} \Psi(c_{i,z}^{k}) \) is the expected offspring of type \( i \) in state \( z \). If each state \( z \) has probability \( \rho_z \), then the long run limiting exponential growth rate of type \( i \) is

\[
\sum_z \rho_z \ln \left( \sum_k q_{i,z}^{k} \Psi(c_{i,z}^{k}) \right).
\]

Hence the type that maximizes this expression should be favored by natural selection. In particular, the preference between the idiosyncratic and aggregate lotteries mentioned above follows because

\[
\ln \left( (1/2) \Psi(c_1) + (1/2) \Psi(c_2) \right) > (1/2) \ln \Psi(c_1) + (1/2) \ln \Psi(c_2),
\]

by the strict concavity of the function \( \ln \).

The distinction between aggregate and idiosyncratic risk implies that people may strictly prefer to take an idiosyncratic lottery for reasons that are quite distinct from a conventional explanation in terms of the convexity of the von Neumann-Morgenstern utility. Perhaps the simplest example of this is due to Cooper and Kaplan [24]. Consider the evolutionary success of a parthenogenetic animal. Suppose the probability of a snowy winter is \( \rho \in (0, 1/2) \) and hence the probability of a clear winter is \( 1 - \rho \in (1/2, 1) \). These animals are hunted by predators whom they hope to escape by blending indistinguishably into their surroundings. As a result, animals that keep dark coats survive clear winters but die in snowy winters, while those that develop white coats survive snowy winters but die in clear ones. Clearly a type that always has a dark coat is doomed to extinction with the first white winter, and one that always has a white coat is doomed by the first clear winter. But consider a type whose members randomize—choosing a white coat with probability \( \pi \) and a dark coat with probability \( 1 - \pi \). That is, all individuals of this type are genetically identical, where this means merely that they choose their winter color from the same idiosyncratic lottery, but experience different ex post outcomes. The overall growth rate of this type is then

\[
r = \rho \ln \pi + (1 - \rho) \ln(1 - \pi),
\]

which is readily shown to be maximized by choosing \( \pi = \rho \). In particular, such “probability matching” allows this type to avoid extinction.

This argument is developed further by Bergstrom [11], who casts the story in terms of squirrels who might similarly adopt a mixed strategy in
saving food for a winter of variable length. Even if the long and harsh winters are extraordinarily rare, a pure type that stored enough food only for shorter and milder winters would be doomed to extinction. But a pure strategy of saving for the longest and harshest of winters is very wasteful, consuming resources and incurring risks to accumulate food that virtually always goes unused. The optimal response is a mixture in which only a small fraction of the population stockpiles sufficient food to ensure the worst of winters, allowing the population to avoid extinction while most members also avoid overwhelmingly wasteful accumulation.

Cooper and Kaplan [24] interestingly interpreted individuals who choose a white coat in their model after the flip of their coin as being “altruistic.” Why? The probability of such an individual dying in their model is higher than the probability of death for an individual with a dark coat simply because $1 - \rho > 1/2 > \rho$. The apparent altruism thus arises out of a choice that seems to decrease an agent’s probability of survival, while protecting the population from extinction. However, before we can interpret this choice as altruism, we must make sure of the correct notion of fitness (as a biologist would put it) or equivalently the correct utility function.

Grafen [55] offers a resolution of the altruism puzzle raised by Cooper and Kaplan. Consider a continuum of agents of size 1. Suppose $\pi$ of these agents choose white and $1 - \pi$ choose dark. Now consider the choice of a small mass of individuals of size $\varepsilon$. If they choose white, the expected fraction of the population they will constitute at the end of the winter is $\frac{\varepsilon \pi}{\rho}$, which equals $\varepsilon$ if $\rho = \pi$. If they choose dark, the expected fraction of the population they will constitute is $\frac{1 - \varepsilon}{1 - \pi}$, which again equals $\varepsilon$ if $\rho = \pi$. Each individual of the type that randomizes $(\rho, 1 - \rho)$ thus maximizes the expected fraction of the population it will comprise, and this expected fraction of the population is the appropriate notion of biological fitness. Death brings zero fitness no matter what the state of the population, but when you survive it matters how large you loom in the population.

To reinterpret this from an economic point of view, the result is that the usual selfish preferences are inadequate. It is instead important to consider how the likelihood of death and to consider how well you are doing when you do survive relative to others, and so the appropriate notion of utility must be interdependent (see Curry [27]).

3.1.2 Risk and Status

It is a common observation that people exhibit risk-aversion for some choices while also exhibiting risk-preference for others. People buy both insurance
and lottery tickets. The standard explanation for this behavior begins with Friedman and Savage [48], who suggested that the typical von Neumann-Morgenstern utility function is concave over low ranges of wealth but then becomes convex over a higher range. People with such utility functions would seek insurance protection against downside risk, while, at the same time buying tickets in a lottery that produces a small probability of a large increase in wealth. To account for the observation that actual lotteries have a nontrivial array of prizes rather than a single grand prize, there must also be a final range of wealth over which von Neumann-Morgenstern utility is again concave.

The Friedman-Savage explanation views utility as being defined over absolute wealth levels. The difficulty here is that absolute wealth levels have changed dramatically over a relatively short period of our recent history. If a Friedman-Savage utility function supported the simultaneous purchase of insurance and gambling in a particular country at a particular date, growth in wealth levels would cause difficulties in explaining the same behavior at a later date. The market for insurance should wither away, as the number of individuals in the requisite low range of wealth decreased. Lotteries should also have diminishing prizes over time, since a lower prize would attain the same target level of final wealth. Nothing in our current experience suggests that the demand for insurance has dissipated as our society has gotten wealthier, nor that lottery prizes are deteriorating.

Robson [108] (see also Robson [110]) shows that increased wealth can be reconciled with a persistent demand for both insurance and lottery tickets if people care not only about absolute wealth, but also about their position in the wealth distribution. Consider an individual with wealth \( w \) who also has a “status” \( S = F(w) \), where \( F \) is the continuous cumulative distribution function describing the wealth distribution in the relevant population. The population is represented by a continuum, normalized to have size 1. Hence status is the proportion of individuals that the individual outranks. The individual has von Neuman-Morgenstern utility that is concave in \( w \) but convex in \( S \):

\[
u(w, S) = \ln w + kS^\beta,\]

where \( k > 0 \) and \( \beta \geq 2 \). Suppose, for simplicity, that the wealth distribution

\[20\] A similar notion helps to account for patterns of consumption as a function of wealth or income, as was pointed long ago by Dusenberry [31]. See Rabin [103] and and Cox and Sadira [25] for another discussion of whether utility is usefully defined over absolute wealth levels.
is uniform, being given by

$$F(w) = \frac{w}{\gamma} \text{ for all } w \in [0, \gamma] \text{ and }$$

$$F(w) = 1 \text{ for all } w > \gamma.$$  

If \( v(w) = u(w, F(w)) \) it follows that

$$v''(w) < 0 \text{ for all } w \in (0, \tilde{w})$$

$$v''(\tilde{w}) = 0 \text{ where } \tilde{w} = \frac{\gamma}{(\beta(\beta - 1)k)^{1/\beta}}$$

$$v''(w) > 0 \text{ for all } w \in (\tilde{w}, \gamma) \text{ and }$$

$$v''(w) < 0 \text{ for all } w > \gamma,$$

where it is assumed that \( \beta(\beta - 1)k > 1 \) so that \( \tilde{w} < \gamma. \)

This example yields the concave-convex-concave utility described by Friedman and Savage. The convexity of \( u(w, S) \) in \( S \) is needed to obtain the intermediate range of wealth, \( (\tilde{w}, \gamma) \) over which \( v(w) \) is convex. The concavity of \( U(w, S) \) in \( w \) yields the concavity of \( v(w) \) over the initial and final ranges \((0, \tilde{w}) \) and \((\gamma, \infty) \). The latter range appears despite the status effect because \( f(w) = 0 \) on \((\gamma, \infty) \). Note that the first inflection point, \( \tilde{w} \), can fall anywhere in \((0, \gamma]\), depending on the values of the parameters.

This model allows not imply that the insurance industry will wither away with the growth of wealth over time. Suppose, for example, there is a uniform multiplicative shift in the wealth distribution, represented by an increase in \( \gamma \). The inflection point \( \tilde{w} \) is subject to the same multiplicative shift, so the same individual lies on the watershed between risk-aversion and risk preference. Similarly, this model is consistent with prizes in lotteries that grow over time in step with the growth of the wealth distribution. That is, the wealth level \( \gamma \) marking the transition from risk-preference to risk-aversion is subject to this same shift.\(^{21}\)

If the von Neumann-Morgenstern utility of wealth alone has a concave-convex-concave shape, as in Friedman and Savage, and individuals have access to a variety of fair bets, then individuals in an intermediate range will find it attractive to take gambles whose outcomes will put them either into a low initial range of wealth or a high terminal range (e.g., Friedman [47]). As a result, the middle class should disappear. However, Robson [108] shows that if the von Neumann-Morgenstern utility also depends on status, \(^{21}\)

\[^{21}\]This argument can be generalized to utility of the form \( u(w, S) = \ln w + v(S) \), where \( v \) is any increasing differentiable function and to an arbitrary continuous cumulative distribution function of wealth \( F \).
this redistribution of wealth will end before the middle class is completely depopulated. Robson [108] also discusses how a concern with status in this sense involves an externality. If I contemplate the effects of an increase in my wealth, I take into account the effect this has in increasing my status, but I neglect the effect it has in lowering other individuals’ status. There may well then be too much gambling. Less obviously, there may instead be too little—there are distributions of wealth that are stable, in the sense that no one wishes to take any fair bet, despite the existence of fair bets that induce a Pareto improvement.

How might the concern with status that lies at the heart of this model have evolved? Robson [110] considers how a concern for status and an attendant risk-preference might arise in a polygynous setting, where females choose males based on their wealth. We return to the possibility that status may play a role in preferences in Section 4.2

3.1.3 Implications

Where do we look for the implications of these evolutionary models, implications that Section 2.2 suggested should be the signature of the evolutionary approach? One obvious point stands out here. People should evaluate idiosyncratic and aggregate risks differently. A standard finding in psychological studies of risk attitudes is that a feeling of control is important if inducing people to be comfortable with risk.\(^{22}\) Risks arising out of situations in which people feel themselves unable to affect the outcome cause considerably more apprehension than risks arising out of circumstances people perceive themselves to control. People who fear flying think nothing about undertaking a much more dangerous drive home from the airport.\(^{23}\) The risk of a meteor strike that eliminates human life on Earth is considered more serious than many other risks with comparable individual death probabilities. Why might this be the case? The first task facing evolution in an attempt to induce different behavior in the face of idiosyncratic and aggregate risks is to give us a way of recognizing these risks. “Control” may be a convenient stand-in for an idiosyncratic risk. If so, then our seemingly irrational fear of uncontrolled risk may be a mechanism inducing an evolutionarily rational fear of aggregate risk.

\(^{22}\)See Slovic, Fischhoff and Lichtenstein [130] for an early contribution to this literature and Slovic [129] for a more recent introduction.

\(^{23}\)Indeed, Gigerenzer [52, pp. 31] suggests that direct death toll in the September 11, 2001 attack on New York’s World Trade Center may have been surpassed by the increased traffic deaths caused by subsequent substitution of driving for air travel.
3.2 Time

We now turn our attention from the within-period considerations captured by the function \( u(c) \) to the question of intertemporal trade-offs. In doing so, we strip away all considerations of the nature of \( u(c) \) by focussing on preferences over offspring. Hence, the agents in our model will do nothing other than be born, have offspring, and then die. In addition, no notion of the quality of offspring will enter our discussion. Agents will differ only in the number and timing of their offspring. In constructing this model, we seek as close a link as possible between the model and the criteria for evolutionary success. Whatever intermediate means evolution may have of pursuing these goals, her ultimate objective (in a world of homogeneous offspring) is for agents to have many offspring and to have them quickly. But how does she trade off many versus quickly? This becomes our central question.

Our basic notion is that of a “life history.” A life history specifies the number of offspring born to an agent at each of the agent’s ages. We assume that such life histories are heritable. The evolutionary approach proceeds by asking which life history will come to dominate a population in which a variety of life histories are initially present. In particular, we imagine mutations regularly inserting different life histories into a population. Some cause the group of agents characterized by such a life history to grow rapidly, some lead to slow rates of growth. The life history leading to the largest growth rate will eventually dominate the population. Having found such a life history, we will be especially interested in characterizing the implicit intertemporal trade-offs.

The question of why people discount is an old one. It seems intuitively obvious that future consumption is less valuable than current consumption, but why is this the case? A good place to start in one’s search for an answer is the work of Fisher [39, pp. 84–85], who pointed to one reason future reward might be discounted—an intervening death might prevent an agent from enjoying the reward. This gives us a link between mortality and discounting that has often reappeared (e.g., Yaari [149]), and that will again arise in our model. Hansson and Stuart [60] and Rogers [117] (see also Robson and Szentes [116]) point to a second factor affecting discounting. They construct models in which evolution selects in favor of people whose discounting reflects the growth rate of the population with whom they are competing. Our first order of business, in Section 3.2.1, is to put these ideas together in the simplest model possible, leading to the conclusion that evolution will induce people to discount exponentially at the sum of the
population growth rate and mortality rate. We then consider a sequence of variations on this model.

### 3.2.1 A Simple Beginning: Semelparous Life Histories

We begin by considering only *semelparous* life histories, in which an organism reproduces at a fixed, single age (if it survives that long) and then dies.\(^{24}\) We do not view this model as a realistic foundation for understanding discounting, but it does provide a revealing introduction to the relevant evolutionary forces.

A life history in this context is simply a pair \((x, \tau)\), where \(x\) is the agent’s expected number of offspring and \(\tau\) is the age at which these offspring are produced. The agents in this environment live a particularly simple life. They wait until age \(\tau\), possibly dying beforehand, and then have \(x\) offspring. At that point the parents may die or may live longer, but in the latter case do so without further reproduction. We need not choose between these alternatives because the possibility of such a continued but barren life is irrelevant from an evolutionary point of view. Agents who survive past their reproductive age may increase the size of the population at any given time, but will have no effect on the population growth rate. As a result, any mutation that sacrifices post-reproduction survival in order to increase the number of offspring \(x\) or decrease the age \(\tau\) at which they are produced will be evolutionarily favored, no matter what the terms of the trade-off.

We examine a group of agents whose members are all characterized by a particular life history \((x, \tau)\). We will speak throughout as if a life history is a deterministic relationship, with each age-\(\tau\) parent having precisely \(x\) offspring. The interpretation is that \(x\) is the *expected* number of offspring born to age-\(\tau\) parents. As long as the group size is sufficiently large and the random variables determining the number of offspring born to each parent are independent, then the average number of offspring will be very close to \(x\) and \(x\) will provide a very good approximation of the behavior of the evolution of the population.\(^{25}\) The life history \((x, \tau)\) is presumably the result of various choices on the part of the agent, such as where to seek food, what food to eat, when to mate, what sort of precautions to take against enemies, and so on, all of which have an important effect on reproduction, but which do not appear explicitly in our model.

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\(^{24}\)This section is based on Robson and Samuelson [115].

\(^{25}\) For typical limit theorems underlying this type of deterministic approximation, see Benaim and Weibull [9]. The case of a continuum of agents raises technical problems. See Al-Najjar [87] for a discussion.
An agent who delays reproduction increases the risk of dying before reaching reproductive age. In particular, an agent choosing \((x, \tau)\) survives for the length of time \(\tau\) required to reach reproductive age with probability \(e^{-\delta \tau}\), where \(\delta\) is the instantaneous death rate. If and only if the agent survives, the \(x\) offspring appear.

Consider a population characterized by strategy \((x, \tau)\), of initial size \(N_0\). How large will this population be at time time \(t > 0\)? Let us follow a dynasty, meaning a cohort of agents initially of age \(\tau'\), who have offspring when they reach age \(\tau\), with these offspring then having their offspring upon reaching age \(\tau\), and so on. From time 0 until time \(t\), there will have been approximately \(t/\tau\) intervals during which this dynasty will have first shrunk by factor \(e^{-\delta \tau}\), as the population is whittled away by death while awaiting its next opportunity to reproduce, and then multiplied itself by \(x\) as it reproduces. The population at time \(t\) is thus

\[
N_0 \left( e^{-\delta \tau} x \right)^{\frac{t}{\tau}}.
\]

The growth factor for this population is then \(e^{-\delta} \left( x \right)^{\frac{1}{\tau}}\).

If the population is characterized by a variety of life histories, then evolution will select for the value \((x, \tau)\) that maximizes \(e^{-\delta} \left( x \right)^{\frac{1}{\tau}}\) or, equivalently, that maximizes \(\ln x / \tau\).

Hence, evolution evaluates births according to the function \(\ln(\cdot)\) and discounts them hyperbolically. The equilibrium population will grow exponentially at the growth rate \(-\delta + \ln x / \tau\).

Have we just discovered an evolutionary foundation for the hyperbolic discounting that lies at the core of much of behavioral economics? Caution is in order on several counts. First, the phrase “hyperbolic discounting” is used to denote a variety of discounting patterns, many of which do not match (3). Perhaps the most common of these is the “\(\beta - \delta\)” formulation, in which payoffs in period \(t\) are discounted to the present (period 0) at rate \(\beta \delta^{t-1}\), with \(\beta > \delta\). As a result, the delay between the current and next periods is weighted especially heavily. In contrast, the preferences given by (3) represent hyperbolic discounting in the literal sense, in that period-\(t\) payoffs are discounted to the present by the factor \(1/t\). This discounting pattern is common in biological models of foraging (e.g., Houston and McNamara [67, chapter 4], Kacelnik [68], Bulmer [16, chapter 6]), but less common in economics. Second, hyperbolic discounting is especially intriguing to behavioral
economists for its ability to generate preference reversals. In contrast, no incentive for preference reversals arises in the present evolutionary context.

More importantly, we need to think more carefully about making the leap from (3) to behavior. The preferences captured by (3) are relevant for asking a number of questions about the comparative statics of evolution. For example, these preferences are the appropriate guide if we want to know which of two populations, characterized by different life histories, will grow faster, or which of two mutants will be most successful in invading a population. Suppose, however, that we are interested in using preferences to describe the choices we see in a particular population. Let \((x, \tau)\) be the equilibrium life history, giving rise to a population that grows exponentially at rate \(r = \ln \left( e^{-\delta} x^{\frac{1}{\tau}} \right) = -\delta + \frac{1}{\tau} \ln x \). Then consider the alternative strategy \((\tilde{x}, \tilde{\tau})\). Suppose this alternative strategy is feasible but not chosen (and hence gives a lower growth rate \(\tilde{r}\)). What preferences would we infer from this observation? We could assume that their preferences are given by (3). However, we could also assume that the agents evaluate births linearly and discount exponentially at rate \(-(\delta + r)\), so that \((x, \tau)\) is evaluated as \(e^{-(\delta+r)x}x\). In particular, to confirm that such preferences rationalize the choice of \((x, \tau)\), we need only note that:

\[
e^{-(\delta+r)x}x > e^{-(\delta+r)\tilde{x}}x \iff e^{-(\delta+r)x}x > e^{-r\tilde{x}}e^{-(\delta+r)\tilde{x}}x \iff r > \tilde{r}.
\]

Exponential discounting, at the sum of the death and optimal growth rates, thus characterizes the preferences with which evolution will endow her agents. This representation of preferences is intuitive. There are two costs of delaying reproduction. One of these is simply that death occurs at rate \(\delta\). The other is that a given number of offspring will comprise a smaller fraction of a population growing at rate \(r\). The sum of these two rates is the rate at which delaying births causes an agent to fall behind the population.

### 3.2.2 Extensions

With this basic result in hand, we consider six respects in which this analysis warrants generalization:

1. Once the optimal strategy has spread throughout the population, the population will grow exponentially at the resulting growth rate. In practice, we do not expect populations to grow without bound.

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26The second inference follows from the observation that \(e^{-(\delta+r)x}x = 1 = e^{-(\delta+r)\tilde{x}}\tilde{x}\).
2. We have allowed agents to reproduce only once, while we expect situations to be important in which agents can reproduce more than once.

3. Even if reproduction is the ultimate issue of concern to evolution, all of our experience as well as our economic literature suggests that we have preferences over many other things, commonly lumped together in economic models under the label of consumption.

4. The agents in our model are homogeneous, with every agent facing the same set of choices and making the same optimal choice. How do we incorporate heterogeneity into the model?

5. All of the uncertainty in the model is idiosyncratic, and hence washes out in the analysis of the population. What if there is aggregate uncertainty?

6. One motivation for studying evolutionary foundations for discounting is to glean insights into models of hyperbolic discounting, present bias, and preference reversal. We have found a hint of hyperbolic discounting in preferences that are relevant for evolutionary comparative statics, but none in the induced individual behavior. Does an evolutionary perspective lock us into exponential discounting?

The following sections examine each of these points in turn.

3.2.3 Environmental Capacity

The discount rate in our analysis is tied closely to the population growth rate. A more rapid population growth induces a higher discount rate, while a population that shrinks sufficiently rapidly will induce negative discounting (in which case reproduction is better deferred). If the population growth rate is zero, agents will discount at the death rate $\delta$.

The difficulty here is that we do not expect populations to grow without bound. If nothing else, an exponentially growing population will eventually produce a physical mass of agents too large to fit on the Earth, even neglecting any considerations of whether the planet can sustain them.\footnote{Pursuing this point into the more fanciful, the space occupied by an exponentially growing population will eventually contain a sphere whose radius expands at a rate exceeding the speed of light, ensuring that we cannot alleviate the problem by travel to other planets (at least under our current understanding of physics).} In some instances, resource constraints may not bind for a long time. One might then argue that an unconstrained model is a reasonable approximation of
our evolutionary past, even if not a good guide to our future. However, we must be wary of appealing to the latter type of short-run argument when interpreting a theory whose predictions consist of limiting results. Perhaps more to the point, it seems likely that environmental constraints constrained human growth rates to be near zero throughout much of our evolutionary past.

Nothing in our analysis changes if we modify the survival rate \( \delta \) to reflect environmental constraints on the population size. We can do so while retaining all of the analysis in Section 3.2.1, as long as we interpret the death rate appearing in our model as the steady-state rate that balances population growth and environmental constraints. In particular, notice that the discount rate in our exponential-discounting representation of preferences, given by

\[
\delta + r = \frac{1}{\tau} \ln x,
\]

is independent of the death rate. If an increasing population size uniformly increases the death rate, the growth rate will exhibit a corresponding decrease, leaving the discount rate unaffected. The discount rate is affected only by the life-history specification \((x, \tau)\).

### 3.2.4 Iteroparous Life Histories

We can easily generalize the analysis to \textit{iteroparous} life histories, in which an individual may have offspring at more than one age. It is convenient here to let time be measured discretely. Let each agent live for \( T \) periods, producing \( x_\tau \) offspring in each period \( \tau = 1, \ldots, T \). A life history is then a collection \((x_1, x_2, \ldots, x_T)\), where some of these entries may be zero.

Our basic tool for keeping track of the population is a \textit{Leslie} matrix (Leslie [73, 74]), given in this case by

\[
\begin{bmatrix}
  e^{-\delta}x_1 & e^{-\delta} & 0 & \ldots & 0 & 0 \\
  e^{-\delta}x_2 & 0 & e^{-\delta} & \ldots & 0 & 0 \\
  \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\
  e^{-\delta}x_{T-1} & 0 & 0 & \ldots & 0 & e^{-\delta} \\
  e^{-\delta}x_T & 0 & 0 & \ldots & 0 & 0
\end{bmatrix}
\]

Each row \( \tau = 1, \ldots, T \) in this matrix corresponds to the fate of agents of age \( \tau \) in the population in each period. The first entry in this row indicates that these agents have \( x_\tau \) offspring, which survive to become the next period’s 1-period-olds at rate \( e^{-\delta} \). The second term in the row indicates that at rate \( e^{-\delta} \), the agents of age \( \tau \) themselves survive to become one period older.
Letting $X$ be the Leslie matrix, the population at time $t$ is given by

$$N'(t) = N'(0)X^t,$$

where $N'(t)$ is a (transposed) vector $(N_1(t), \ldots, N_T(t))$ giving the number of agents in the population of each age $1, \ldots, T$ at time $t$. The fate of the population thus hinges on the properties of $X^t$. The Perron-Frobenius theorem (Seneta [126, Theorem 1.1]) implies that the Leslie matrix has a “dominant” eigenvalue $\phi$ that is real, positive, of multiplicity one, and that strictly exceeds the modulus of all other eigenvalues.\(^{28}\) This eigenvalue is the population growth factor, and its log is the corresponding growth rate, in the sense that (Seneta [126, Theorem 1.2])

$$\lim_{t \to \infty} \frac{X^t}{\phi^t} = vu',$$

where the vectors $u$ and $v$ are the strictly positive left ($u'X = \phi u'$) and right ($Xv = \phi v$) eigenvectors associated with $\phi$, normalized so that $u'v = 1$ and $\sum_{\tau=1}^T u_\tau = 1$.\(^{29}\)

Evolution must select for behavior that maximizes the eigenvalue $\phi$, or equivalently, that maximizes the long-run growth rate $\ln \phi$. This eigenvalue solves the characteristic equation

$$\begin{vmatrix} e^{-\delta}x_1 - \phi & e^{-\delta} & 0 & \cdots & 0 \\ e^{-\delta}x_2 & -\phi & S & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ e^{-\delta}x_{T-1} & 0 & 0 & \cdots & e^{-\delta} \\ e^{-\delta}x_T & 0 & 0 & \cdots & -\phi \end{vmatrix} = 0,$$

or, equivalently,

$$\Phi = x_1 + \frac{x_2}{\Phi} + \frac{x_3}{\Phi^2} + \ldots + \frac{x_T}{\Phi^{T-1}},$$

where

$$\Phi = \frac{\phi}{e^{-\delta}}.$$

Equation (5) gives us our basic description of preferences. Evolution will endow an agent with preferences (or more precisely, would endow an agent

\(^{28}\)We assume that the Leslie matrix $X$ is primitive, in that there exists some $k > 0$ for which $X^k$ is strictly positive. A sufficient condition for this is that there exist two relatively prime ages $\tau$ and $\tau'$ for which $x_\tau$ and $x_{\tau'}$ are both nonzero.

\(^{29}\)Regardless of the initial condition $N'(0)$, the proportion of the population of each age $\tau$ approaches $u_\tau$. The vector $v$ gives the “reproductive value” of an individual of each age, or the relative contribution that each such individual makes to the long run population.
with behavior consistent with such preferences) whose indifference curves are described by the right side of (5), with \( \Phi \) corresponding to the optimal growth rate. In particular, choices \((x_1, \ldots, x_T)\) that lead to a smaller value on the right side of (5) would leave to a lower growth rate and would be optimally rejected by the agent.

As with the case of semelparous life histories, we can draw two kinds of conclusions from these results. First, we can ask questions about “evolutionary comparative statics,” addressing the relative performance of alternative populations or alternative mutants within a population. Here, we once again recover hints of hyperbolic discounting, seen in the fact that the evolutionary criterion for evaluating alternative life histories, given by (5), contains our previous results for semelparous life histories as a special case. In particular, it is immediate from (5) that evolution is indifferent over two semelparous strategies \((x_1, \tau_1)\) and \((x_2, \tau_2)\) if and only if \(x_1^{\tau_1} = x_2^{\tau_2}\). This confirms that the semelparous analysis is a special case of this more general model. Preferences over the remaining iteroparous strategies are captured by connecting indifferent semelparous strategies with linear indifference surfaces. More generally, this population growth rate is a complex function of the fertility profile. If we let \( \Phi = \Phi(x_1, x_2, ...) \) be the function implicitly defined by (5), then the marginal rate of substitution between \(x_t\) and \(x_{t+1}\) is \( \Phi \) itself, which is a strictly increasing function of each \(x_\tau\) for \(\tau = 1, \ldots, T\). It is then immediate that there can be no additively separable representation of preferences.

Alternatively, we can ask about the behavior we would observe from agents. Agents can once again be induced to make optimal choices via exponentially discounting offspring at the sum of the death and optimal growth rates. Letting \((x_1, \ldots, x_T)\) be the optimal fertility profile and \( \Phi \) be implicitly defined by (5), we have

\[
1 = \frac{x_1}{\Phi} + \frac{x_2}{\Phi^2} + \ldots + \frac{x_T}{\Phi^T}.
\]

Now suppose an alternative fertility/utility profile \((x'_1, \ldots, x'_T)\) is feasible but is not chosen because it gives a smaller growth rate. Then

\[
\frac{x_1}{\Phi} + \frac{x_2}{\Phi^2} + \ldots + \frac{x_T}{\Phi^T} = 1 > \frac{x'_1}{\Phi} + \frac{x'_2}{\Phi^2} + \ldots + \frac{x'_T}{\Phi^T}.
\]

The agent’s behavior is thus consistent with exponentially discounted preferences.
3.2.5 Consumption

Economists are typically interested in preferences over consumption rather than births and mortality. Perhaps the simplest way to transform a model of preferences over fertility and mortality rates to a model of preferences over consumption is to assume that births are a function of consumption, so that preferences over consumption are those induced by the underlying preferences over births. Notice that in doing so, we are not assuming that every visit to a restaurant requires a quick calculation as to whether steak or fish is more likely to lead to more offspring. Instead, our presumption is that evolution simply gives the agent preferences over steak and fish, with evolution shaping these preferences to reflect the required calculation.

Consider for simplicity the case in which age-τ births depend only on age-τ consumption. Formally, let \( f_\tau(c_\tau) \) give age-τ births as a function of period-τ consumption \( c_\tau \). Suppose that all the \( f_\tau \) are strictly increasing and concave.

For any consumption vector \( c = (c_1, \ldots, c_T) \), an indifference curve is defined by (from (5),
\[
1 = \frac{f_1(c_1)}{\Phi} + \cdots + \frac{f_\tau(c_\tau)}{\Phi^\tau} + \cdots + \frac{f(T-1)(c_{T-1})}{\Phi^{T-1}} + \frac{f_T(c_T)}{\Phi^T},
\]
where \( \Phi \) is constant on a particular indifference surface. A higher value of \( \Phi \) corresponds to a higher indifference curve, so that consumption plan \((c_1', \ldots, c_T')\) is preferred to \((c_1, \ldots, c_T)\) if and only if
\[
1 = \frac{f_1(c_1)}{\Phi} + \cdots + \frac{f_T(c_T)}{\Phi^T} < \frac{f_1(c_1')}{\Phi} + \cdots + \frac{f_T(c_T')}{\Phi^T}.
\]

It follows readily that evolution’s indifference surfaces over consumption bundles \((c_1, \ldots, c_\Phi)\) have the usual shape, in the sense that evolution’s preferences can be described by a utility function \( U(c_1, \ldots, c_T) \) that is strictly increasing and quasi-concave.

This gives us the beginnings of an extension from models of reproduction to models of consumption. As long as period-τ reproduction is a function only of period-τ consumption, preferences over consumption will once again be described by an exponentially-discounted sum of utilities. In practice, of course, period-τ births will depend on the entire history of consumption. At the very least, one must have consumed enough to survive until period \( \tau \) in order to reproduce at that age. Period-τ births are thus implicitly a function

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30See Robson, Szentes and Ianchev [106] for more involved specifications.
of consumption at all preceding ages. This in turn opens the possibility
that the induced preferences over consumption may exhibit complicated
discounting patterns. There is much that remains to be done in terms of
exploring this connection between reproduction and consumption, including
especially the implications for discounting.

3.2.6 Heterogeneous Choices

We have hitherto implicitly assumed that all of our agents face the same
feasible set and choose the same alternative from that feasible set. How
do we incorporate some heterogeneity into the model? In addressing this
question, we keep things simple by retaining our basic framework of choice
of reproductive life histories.

Suppose that each agent entering our model is randomly and indepen-
dently (over time and agents) assigned one of \( N \) feasible sets, with \( p_n \) the
probability of being assigned to the \( n \)th feasible set, and with \( x_1(n), \ldots, x_T(n) \)
the life history chosen when faced with the \( n \)th feasible set. Some agents
may find themselves in the midst of plenty and face relatively rich feasible
sets, while others may face harder circumstances and more meager feasible
sets. The Leslie matrix associated with this population is given by

\[
\begin{bmatrix}
  e^{-\delta} \sum_{n=1}^{N} p(n) x_1(n) & e^{-\delta} 0 & \cdots & 0 \\
  e^{-\delta} \sum_{n=1}^{N} p(n) x_2(n) & 0 & e^{-\delta} & \cdots & 0 \\
  \vdots & \vdots & \vdots & \ddots & \vdots \\
  e^{-\delta} \sum_{n=1}^{N} p(n) x_{T-1}(n) & 0 & 0 & \cdots & e^{-\delta} \\
  e^{-\delta} \sum_{n=1}^{N} p(n) x_T(n) & 0 & 0 & \cdots & 0 \\
\end{bmatrix}
\]

The agent’s preferences can be derived from the corresponding characteristic
equation, or

\[
1 = \frac{\sum_{n=1}^{N} p(n) x_1(n)}{\Phi} + \frac{\sum_{n=1}^{N} p(n) x_2(n)}{\Phi^2} + \frac{\sum_{n=1}^{N} p(n) x_3(n)}{\Phi^3} + \cdots + \frac{\sum_{n=1}^{N} p(n) x_T(n)}{\Phi^T}
= p(1) \left( \frac{x_1(1)}{\Phi} + \frac{x_2(1)}{\Phi^2} + \cdots + \frac{x_T(1)}{\Phi^T} \right) + \cdots + p(N) \left( \frac{x_1(N)}{\Phi} + \frac{x_2(N)}{\Phi^2} + \cdots + \frac{x_T(N)}{\Phi^T} \right).
\]

In each of these choice situations, it follows that the optimal decision is con-
sistent with exponential discounting, where the discount rate now depends
on the overall population growth rate. Hence, those agents facing relatively
meager feasible sets will apply a discount factor seemingly higher than would
be warranted from consideration of that feasible set alone, while those facing a quite rich feasible set would apply a discount factor seemingly too low. Given the discount factor, however, we would observe a collection of choices that could together be rationalized as maximizing the same exponentially discounted utility function.\footnote{One can well imagine more complicated ways in which heterogeneity might be incorporated into the model, requiring a more sophisticated model. The tools for addressing such questions are provided by the theory of structured populations, as in Charlesworth [20].}

### 3.2.7 Nonexponential Discounting

The message to emerge from our analysis thus far is that we can expect to see agents evaluating intertemporal trades according to an exponentially discounted utility function. Depending on one’s point of view, this represents good news or bad news. On the one hand, it directs attention to the most common model of intertemporal choice in economics. At the same time, it provides little insight into departures from exponential discounting.

There are three obvious possibilities for exploring foundations of nonexponential discounting. Section 3.2.5 raises the first. Even if reproduction is discounted exponentially, the relationship between reproduction and consumption may be complicated and may induce nonexponential discounting of consumption. This possibility remains relatively unexplored.

Second, Sozou [133] and Dasgupta and Maskin [28] show that if the realization of a future consumption opportunity is subject to uncertainty, then the result can be a present bias in discounting. For example, Sozou supposes that there is a constant hazard rate that an opportunity to consume in the future may disappear before the proposed consumption date arrives. Someone else may consume the resource beforehand, or a predator may in the meantime block access to the resource. In the absence of any additional complications, this uncertainty has a straightforward effect on the agent’s behavior. Future payoffs are again exponentially discounted, with the relevant discount rate now being the sum of the death rate, population growth rate, and disappearance rate.

Sozou further assumes that the agent is uncertain about the hazard rate of consumption disappearance, updating her prior belief about this value as time passes. Suppose, for example, the agent initially compares one unit of consumption at time 0 with \( c \) units at time \( t > 0 \), and discounts (taking into account the likelihood that the latter will disappear before time \( t \) arrives) the latter at rate 10%. Now suppose that time \( t/2 \) has arrived, and the
agent must again compare a unit of current (i.e., time $t/2$) consumption with the same $c$ units of consumption at time $t$. If this choice is to be meaningful, it must be the case that over the interval $[0, \frac{t}{2}]$, the future consumption opportunity did not vanish. This is good news, leading the agent to conclude that the probability of disappearance is not as high as the agent’s prior distribution indicated.

More generally, let $c_\tau$ denote consumption at time $\tau$. The agents in Sozou’s model apply a higher discount factor when comparing $c_0$ and $c_1$ than when comparing $c_\tau$ and $c_{\tau+1}$: if the latter choice is still relevant at time $\tau$, then the agent will infer that the hazard rate at which consumption opportunities disappear is lower than originally suspected. However, this model will not generate preference reversals. In a typical preference reversal, an agent prefers $c_{\tau+1}$ from the choice $\{c_\tau, c_{\tau+1}\}$ when choosing at time 0, but then prefers $c_\tau$ when making the choice at time $\tau$. Invoking some stationarity, the standard route to constructing a preference reversal is to assume that the agent prefers $c_0$ from $\{c_0, c_1\}$ at time 0 as well as prefers $c_{\tau+1}$ from the choice $\{c_\tau, c_{\tau+1}\}$; coupled with an assumption that the agent makes the choice from $\{c_\tau, c_{\tau+1}\}$ at time $\tau$ precisely as she does the choice $\{c_0, c_1\}$ at time 0. It is this latter assumption that does not hold in Sozou’s model. If the choice from $\{c_\tau, c_{\tau+1}\}$ is relevant at time $\tau$, then the agent infers that the hazard rate at which consumption opportunities disappear is not as large as originally suspected. This only reinforces the patience that prompted the agent to originally prefer $c_{\tau+1}$ from the choice $\{c_\tau, c_{\tau+1}\}$.

Discount rates are thus not constant, but we would not observe the type of inconsistency in behavior that would induce the agent to take steps to restrict future choices.

In Dasgupta and Maskin [28], there is again the possibility that a consumption opportunity might disappear before it arrives, but the hazard rate at which this happens is constant and known. In the absence of any other considerations, we would then simply have constant discounting at this hazard rate (plus the relevant death and growth rates). On top of this, Dasgupta and Maskin add some additional uncertainty about when as well as whether the consumption will be realized. An opportunity to consume $c_\tau$ at time $\tau$ in fact gives the consumption at time $c_\tau$ with high probability, but with the remaining probability gives a consumption opportunity whose timing is distributed over the interval $[0, \tau]$ (all conditional on not having disappeared in the meantime). Fortuitous circumstances may bring the opportunity early. For example, consider two consumption opportunities, one promising consumption $c_\tau$ at time $\tau$ and one promising $c_{\tau'}$ at time $\tau' > \tau$. Suppose that at time 0, the agent prefers opportunity $(c_{\tau'}, \tau')$. If this is to be the
case, then we must have $c_{\tau'} > c_\tau$, since it would not be worth waiting longer for a lower reward. Now consider what happens as time passes. The dates $\tau$ and $\tau'$ at which the consumption opportunities will be realized draw nearer. This increases the value of each option, but this effect alone does not change the relative ranking of the two consumption prospects. The probability that either one is realized is scaled upward by a common factor reflecting that an interval has passed without the consumption disappearing. The other effect is that this same interval has passed without either consumption opportunity arriving early. This decreases the value of each option, but especially decreases the value of option $(c_{\tau'}, \tau')$, since it involves the larger quantity of consumption and hence its early arrival is a relatively lucrative outcome. Hence, as time passes, the relative ranking shifts toward $(c_\tau, \tau)$. If the two bundles are sufficiently closely ranked to begin with, and if the prospect of early arrival is sufficiently important, preferences will reverse to bring $(c_\tau, \tau)$ into favor as time passes.

Dasgupta and Maskin’s analysis thus provides us with an evolutionary account of preference reversals. At the same time, it does not give rise to the sorts of inconsistency and commitment issues that appear in behavioral models. The preference reversal as time $\tau$ draws near reflects an optimal response to the changing time-profile of the consumption opportunities. As a result, an agent would never have an incentive to preclude such reversals.

Dasgupta and Maskin sketch an extension of their model that gives rise to commitment issues. Very roughly speaking, they suppose that evolution has endowed people with preferences that are appropriate for the distributions of early consumption arrivals that were common over the course of our evolutionary history. Then they consider an agent facing a choice that the agent knows to involve distributions atypical of this history. The agent’s preferences may call for a preference reversal that the agent would rationally strive to prevent, giving rise to incentives for commitment.

The preferences emerging from the models of Sozou [133] and Dasgupta and Maskin [28] give rise to a delicate issue of interpretation. An essential feature of both models is that consumption opportunities are subject to uncertainty. In addition, both models begin with the assumption that the evolutionary objective is to maximize total consumption, with discounting reflecting the uncertainty inherent in pursuing a consumption opportunity. The analysis of Sections 3.2.1–3.2.4 suggests that even in the absence of uncertainty, we can expect discounting, so that maximizing total consumption is not an obvious point of departure. Fortunately, building the type of considerations uncovered in Sections 3.2.1–3.2.4 into the models of Sozou or Dasgupta and Maskin appears to be straightforward. Second, our underly-
ing view is that evolution shapes our behavior, with preferences being an analytical tool we choose to represent this behavior. The standard approach in constructing this representation is to use preferences and feasible sets to capture different aspects of an agent’s choice problem, with the feasible set describing the alternatives and constraints on the choice. In particular, the standard approach would view consumption opportunities subject to uncertainty and consumption opportunities without uncertainty as different objects, with preferences first defined in the absence of uncertainty and then extended to uncertain outcomes via an expected utility calculation. In using discounting to capture the effects of uncertainty about consumption, the models of Sozou and Dasgupta and Maskin blur the distinction between the feasible set and preferences.

In some cases, this blurring may be precisely what is required. In particular, suppose our evolutionary model of behavior incorporates the mismatch possibility that preferences evolved in one environment but may be applied in another. If this is the case, then we must know not only the choices induced by evolution, but also the process by which these choices are induced. We thus have no alternative but to model the mechanics of the agents’ decision making. It may well be that evolution has responded to some of the uncertainty in our environment by altering our discounting rather than our representation of the feasible set. Notice, however, that establishing the process by which choices are implemented is a taller order than describing the choices themselves.

A third possibility under which preferences may no longer exhibit exponential discounting is explored by Robson and Samuelson [113]. We have assumed in Sections 3.2.1–3.2.6 that the uncertainty faced by the agents is idiosyncratic, in the sense that there is no aggregate uncertainty. In contrast, aggregate uncertainty may well have been an important feature of our evolutionary environment. Periods in which the weather was harsh, food scarce, disease rampant, or predators prevalent may have a common impact on a population. What effect does this have on our analysis of time preference?

To capture the possibility of aggregate uncertainty, we assume that in each period \( t \), a Leslie matrix \( X(t) \) is drawn from a distribution over such matrices, with \( X(t) \) then describing the fate of the population, in terms of both reproduction and death, during that period. A period of particularly harsh weather may be characterized by a Leslie matrix with high death rates, while a period in which food is quite plentiful may be characterized by favorable survival rates. The matrix \( X(t) \) may itself contain values that are the averages of idiosyncratic uncertainty, but as before this will have no
effect on the analysis.

Given an initial population \( N'(0) = (N_1(0), \ldots, N_T(0)) \) with \( N_\tau(0) \) of agents of age \( \tau \), the population at time \( t \) is then given by (cf. (4))

\[
N'(t) = N'(0) \tilde{X}(1) \tilde{X}(2) \cdots \tilde{X}(t),
\]

where \( \tilde{X}(t) \) is the random Leslie matrix in time \( t \). We thus have a product of random matrices, a much less tractable object than the product of the fixed Leslie matrices arising in (4). It is not even immediately obvious that such a product has an appropriate limit. Fortunately, there are quite general theorems establishing the limiting growth rates of such products (e.g., Furstenberg and Kesten [50, Theorem 2] and Tanny [135, Theorem 7.1]), but the model is still considerably less tractable than the case of idiosyncratic uncertainty.

Aggregate uncertainty opens up all sorts of new possibilities for discounting patterns. We present here a simple example to illustrate some of these possibilities, leaving a more systematic analysis to Robson and Samuelson [113]. Suppose that there are \( T \) possible Leslie matrices, \( X_1, \ldots, X_T \). Under Leslie matrix \( X_\tau \), only offspring born to parents of age \( \tau \) survive, with expected offspring per parent denoted by \( x_\tau \). The Leslie matrices are drawn independently across periods and are equally likely in any given period. In each period and under every Leslie matrix, all existing agents face an idiosyncratic death risk, with death rate \( \delta \).

We thus have a rather extreme form of aggregate uncertainty, but one that significantly simplifies the resulting calculations, while driving home the point that aggregate uncertainty can lead to new results. Section 6.1 proves the following.

**Proposition 1** Almost surely,

\[
\lim_{t \to \infty} \frac{1}{t} \ln u' \tilde{X}(1) \cdots \tilde{X}(t)v = \ln S + \frac{\sum_{\tau=1}^{T} \ln x_\tau}{\sum_{\tau=1}^{T} \tau}.
\]  

(7)

Preferences are thus represented by the undiscouted sum of the logs of the offspring in each state. In contrast to our previous findings, there is no impatience here, no matter what the population growth rate (given by (7)) and death rate. A reduction in fertility at age \( \tau \) reduces the growth rate via its effect on the term \( \sum_{\tau=1}^{T} \ln x_{\tau} u_{\tau} \), the extent of this reduction does not depend upon the age in question.

We can push this example somewhat further. Suppose \( T = 2 \), to keep the calculations simple, and that instead of being independent across periods,
the environment is drawn from a symmetric Markov process with persistence \( \alpha \), i.e., with probability \( \alpha \) the environment in period \( t \) is the same as in period \( t - 1 \), and with probability \( 1 - \alpha \) the environment changes from period \( t - 1 \) to period \( t \). Section 6.1 proves

**Proposition 2** *Almost surely,*

\[
\lim_{t \to \infty} \frac{1}{t} \ln u' \tilde{X}(1) \ldots \tilde{X}(t) v = \frac{2\alpha \ln x_1 + \ln x_2}{2 + 2\alpha}.
\]

For the case of \( \alpha = 1/2 \), or no persistence, we have Proposition 1’s result that there is no discounting. Assuming \( \alpha > 1/2 \) generates impatience, while assuming \( \alpha < 1/2 \), so that environments are negatively correlated, generates negative discounting—the future is weighted more heavily that the present.

What lies behind these results? The key factor behind Proposition 1 is that only one age class reproduces in any period. In the steady state, each cohort thus has a uniform distribution of parental ages. That is, \( 1/T \) of that cohort’s parents were of each age.\(^{32}\) Repeating this argument, it follows that the number of such agents is proportional to a power of \( x_1 x_2 \ldots x_T \). In light of this, evolution will seek to maximize \( \ln x_1 x_2 \ldots x_T \), leading to the no-discounting result. If expected offspring are equal across ages, then evolution is indifferent as to where an increment to expected offspring appears.

It is clearly an extreme assumption that only one age of parent has offspring in any given state of the environment. We present this result not for its realism, or because we would like to suggest that evolutionary models should lead us to expect that people do not discount, but to illustrate how aggregate uncertainty can lead to new and counterintuitive results. In Robson and Samuelson \([113]\) we first show that if aggregate uncertainty bears equally on all survival rates, then we have a wedge between the rate of discounting and the sum of the growth and mortality rates. We then consider cases in which the extent of aggregate uncertainty in the environment is relatively small, unlike the models we have just presented. This reflects a belief that results emerging from models with relatively modest doses of aggregate uncertainty are a better point of departure for our analysis than models with drastic specifications of uncertainty. We present plausible, but by no means universal, conditions for aggregate uncertainty to lead to a present bias in discounting. Once again, however, this present bias leads to neither preference reversals nor a desire for commitment. The search for

\(^{32}\text{It is this property that fails, vitiating the argument leading to Proposition 1, when births are not so perfectly synchronized.}\)
evolutionary foundations of preference reversals and commitment remains an important area of research.

3.2.8 Implications

Our search again turns to implications. We can start with the observation that discounting in general has nothing to do with death rates. An increase in the death rate simply induces a corresponding decrease in the growth rate (for fixed fertilities \(x_1, \ldots, x_T\)), leaving discounting unchanged. Higher fertility should thus correspond to higher discounting, holding the death rate constant, but higher death rates (holding fertility constant) should not.

Looking a bit beyond our model, the remarks of the previous paragraph correspond to cross-population comparisons of discounting, in the sense that we would need to compare different populations whose discount factors have been adapted by evolution to their various circumstances. Suppose in contrast that we examine different types within a population. Here, the relevant terms in the discount factor are the average growth rate of the population and the death rate of the particular type in question. As a result, agents with higher death rates within a population should exhibit higher discount rates. Daly and Wilson [145] find just such a relationship.

Finally, the models suggest that evolution may more readily lead to non-exponential discounting, often in the form of a present bias, than to generate preference reversals. This suggests that experimental or empirical evidence may accordingly more readily exhibit declining discount factors than preference reversals. It is then perhaps unsurprising that some investigations do not find a great willingness to pay for the ability not to reverse preferences (e.g., Fernandex-Villaverde and Mukherji [38]).

4 Preferences over What?

Our next selection of topics takes us somewhat deeper into preferences, asking what we should expect to find as the arguments of the function \(u\). The standard assumption throughout much of economics is that \(u\) depends only on an agent’s own consumption, as in (1). At the same time, there is considerable suspicion that other factors also enter our preferences. As we have explained above, the goal is to incorporate such possibilities while still retaining some discipline in our work. This section examines three dimensions along which an evolutionary analysis is helpful.

Our guiding principle is that to understand our utility function, we must think through the constraints on what evolution can do in designing us to
make good decisions. In each case, in the absence of such constraints, we would come back to a standard utility function defined only over an individual’s own consumption. However, if something prevents the construction of such a perfect utility function, then evolution may optimally compensate by building other seemingly anomalous features into our utility function. Intuitively, we have an evolutionary version of the theory of the second best.33

Under this approach, the analysis will be no more convincing than the case that can be made for the constraints. In this sense, Gould and Lewontin’s [53] critique of evolutionary psychology recurs with some force, since one suspects that a judiciously chosen constraint will allow anything to be rationalized.

Before even departing on this line of research, we should be willing to respond to this argument by arguing that it is prohibitively costly for evolution to enhance significantly our cognitive powers. Otherwise, we would expect evolution to simply have done away with whatever constraints might appear in our decision-making. Evolutionary psychologists routinely appeal to limits on our cognitive capabilities, finding evidence for these limits in the relatively large amount of energy required to maintain the human brain (Milton (1988)), the high risk of maternal death in childbirth posed by infants’ large heads (Leutenegger (1982)), and the lengthy period of human postnatal development (Harvey, Martin and Brock (1986)).

Notice that there is no question of evolution’s designing us to solve some problems of inordinate complexity. The human eye and the attendant information processing is an often-cited triumph of biological engineering. Our argument requires only that evolution cannot ensure that we can solve every complex problem we encounter, and that she will accordingly adopt information-processing shortcuts whenever she can. “In general, evolved creatures will neither store nor process information in costly ways when they can use the structure of the environment and their operations upon it as a convenient stand-in for the information-processing operations concerned.” (Clark (1993, pl. 64)).34

33Beginning with Lipsey and Lancaster [76], the theory of second best has become a pillar of welfare economics, noting that if some of the conditions for an optimal outcome fail, then moving closer to satisfying the remaining conditions may not improve welfare. In our context, we can first imagine a first-best or unconstrained design that would lead to evolutionary success for an agent. The idea is then that if feasibility constraints preclude implementing some features of this design, it may not be optimal to insist on all of the remaining features.

34LeDoux (1996) discusses the incentives for evolution to arm us with a mix of “hard-wired” and cognitive responses to our environment, arguing that many of our seemingly hard-wired reactions are engineered to economize on information processing.
We should also expect to see evidence that humans often make mistakes in processing complicated information. Psychologists have conducted a wealth of experimental studies suggesting that people are poor Bayesians (e.g., Kahneman and Tversky (1982)).

4.1 Context

This section, borrowing from Samuelson and Swinkels [122], examines one respect in which our utility seemingly depends upon more than simply what we consume. We consider the possibility that utility also depends upon what we do not consume: the utility of a choice can depend importantly on the set of salient alternative choices. A salad may be less attractive when presented within the sight and smell of a grilling steak, while toiling away at work on a gorgeous spring day may be less difficult in a windowless office that one with a panoramic view.\(^{35}\)

It is no surprise, of course, that choices typically depend on the set of alternatives. Who would doubt that it is more tempting to skip work on a warm, sunny day than on a cold bitter one? Our interest is in the fact that the salience of the alternatives appears to affect our choices and hence our preferences. Knowing that one can order dessert is different than having the dessert cart at one’s table. Knowing that it’s nice outside is different than being able to see the sun and feel the warm breeze.\(^{36}\)

As we have suggested, our evolutionary model will revolve around a constraint on evolution’s ability to design agents. We assume in this case that evolution cannot equip her agents with a perfect prior understanding of the causal and statistical structure of the world. Our belief here is that the com-

\(^{35}\)Gardner and Lowinson [51], Loewenstein [77], Mischel, Shoda and Rodriguez [86], and Siegel [128] examine the importance of salient alternatives. The possibility that preferences over objects may depend on the set from which they are chosen has attracted theoretical and experimental attention from psychologists (e.g., Tversky and Simonson [138] and Shafir, Simonson and Tversky [127]). Gul and Pesendorfer [56] present a model of such preferences centered on the assumption that resisting tempting alternatives is costly. Laibson [71] examines a model in which instantaneous utilities adjust in response to external cues. Our interest here is not so much the mechanism by which this interaction between the set of alternatives and the utility of particular alternatives is generated, but rather the question of why evolution might have endowed us with such preferences in the first place.

\(^{36}\)In a similar vein, psychologists have suggested that our behavior is driven partly by a collection of utility-altering visceral urges (Loewenstein [77]). It is again straightforward to appreciate why we have urges reflecting direct evolutionary consequences such as hunger, thirst, or fatigue (Pluchik [99]). The subject of this inquiry is the less obvious question of why the strength of these urges can depend on the set of unchosen consequences.
plexity of a perfect prior is simply out of reach of a trial-and-error mutation process.\textsuperscript{37} Nor can the agents themselves be trusted to infer this information from our environment. An agent cannot learn the relationship between specific nutrients and healthy births by trial and error quickly enough to be useful, and we certainly cannot learn quickly enough that even many generations of ample food might still be followed by famine in the next year.\textsuperscript{38}

4.1.1 A Model

An agent in this model enters the environment and must either accept or reject an option. Accepting the option leads to a lottery whose outcome is a success with probability $p$ and a failure with probability $1-p$. Rejecting the option leads to a success with probability $q$ and a failure with probability $1-q$. This is the only decision the agent makes. We might think of the option as an opportunity to consume and success as reproducing. The parameters $p$ and $q$ are random variables, reflecting the benefits of eating and the risks required to do so in any given setting. The probability of success may be either increased ($p > q$) or decreased ($p < q$) by accepting the option.

The agent is likely to have some information about the likely values of $p$ and $q$. For example, the agent may know whether game is plentiful, whether food is nearby but guarded by a jealous rival, or whether a drought makes it particularly dangerous to pass up this opportunity. However, the agent is unlikely to know these probabilities precisely. We model this by assuming that the agent observes a pair of scalar signals $s_p$ about $p$ and $s_q$ about $q$. The probabilities $p$ and $q$ are independent, $p$ is a sufficient statistic for $s_p$, and $q$ is a sufficient statistic for $s_q$. The joint distribution of $p$, $q$, $s_p$, and $s_q$ is given by $F$. We assume that $s_p$ and $s_q$ satisfy the monotone likelihood ratio property with respect to $p$ and $q$ respectively, so that (for example) $E\{p|s_p\}$ is increasing in $s_p$.

As a result of an evolutionary process, the agent is equipped with a rule $\phi$ for transforming signals into estimates of the probability of success. We assume that $\phi$ is continuous and strictly increasing. The crucial restriction

\textsuperscript{37}For example, it is difficult to randomly create an agent who knows not only that the probability of a successful birth from a random sexual encounter is about 2\% (Einon, [32]), but also how this probability varies systematically with health, age, and other observable features of the mate.

\textsuperscript{38}This constraint is well-accepted in other areas of study. Focusing on reactions to danger, LeDoux [72, pp. 174–178] notes that evolution deliberately removes some responses from our cognitive control precisely because her prior belief is strong. “Automatic responses like freezing have the advantage of having been test-piloted through the ages; reasoned responses do not come with this kind of fine-tuning.”
in our model is that the agent must use the same rule \( \phi \) for evaluating all signals. If, for example, \( p \) and \( q \) come from different processes and with information of varying reliability, proper Bayesian updating requires that different updating rules be applied to \( s_p \) and \( s_q \). Our assumption is that evolution cannot build this information about the prior or signal-generation process into the agent’s beliefs. This constraint that belief formation cannot be tailored to every situation (captured simply in this setting by assuming a single \( \phi \)) is critical.\(^{39}\)

Utility may be derived both from the outcome of the agent’s action and from the action itself. A success leads to an outcome (e.g., successful reproduction) that yields a utility of \( x \). A failure gives the agent a utility that we can normalize to zero. The act of accepting the option (e.g., eating the food) yields a utility of \( y \).\(^{40}\)

### 4.1.2 Utility

We view evolution as choosing values \( x \) and \( y \) that maximize an agent’s probability of success. No generality is lost by taking \( x = 1 \). The question is the choice of \( y \). If \( y = 0 \), then utilities are attached only to outcomes and not to actions. In this case, we would be motivated to eat not because we enjoy food, but because we understand that eating is helpful in surviving and reproducing. If \( y \) is nonzero, then actions as well as outcomes induce utility.

The optimal decision rule from an evolutionary perspective is then

\[
\text{accept } \text{if } f(p - q) > 0, \tag{8}
\]

while the agent’s utility-maximizing decision is

\[
\text{accept } \text{if } f(y + \phi(s_p) - \phi(s_q)) > 0. \tag{9}
\]

Consider

\[
E\{p - q|\phi(s_p) - \phi(s_q) = t\}.
\]

This is the expected success-probability difference \( p - q \) conditional on the agent having received signals that lead him to assess this difference at \( t \). To

\(^{39}\)Without this restriction, the solution to the problem is again trivial. Evolution need only attach a larger utility to a success than to a failure, while designing the agent to use Bayes’ rule when transforming the signals he faces into posterior probabilities, to ensure that the agent’s choices maximize the probability of success.

\(^{40}\)Attaching another utility to the act of rejecting the option opens no new degrees of freedom at this stage.
make our results easier to interpret, we assume throughout that
\[ dE\{p - q|\phi(s_p) - \phi(s_q) = t\} \geq 0, \]
so the expected difference in success probabilities \( p - q \) is weakly increasing in the agent’s assessment of this difference.\(^{41}\)

We then have the following characterization of the optimal utility function:

**Proposition 3** The fitness-maximizing \( y \) satisfies
\[ E\{p - q|\phi(s_p) - \phi(s_q) = -y\} = 0. \]
In particular, the agent’s fitness is maximized by setting \( y = 0 \) if and only if
\[ E\{p - q|\phi(s_p) - \phi(s_q) = 0\} = 0. \]

**Proof.** When Conditions (10) and (12) hold, setting \( y = 0 \) ensures that the agent’s choice rule (9) coincides with the (constrained) optimal choice rule (8). There is then no way to improve on the agent’s choices. More generally, let \( E\{p - q|\phi(s_p) - \phi(s_q) = -y\} > (<) 0. \) Then the expected probability of success can be increased by increasing (decreasing) \( y. \)

From (12), if the agent interprets his signals correctly, then there is no evolutionary value in attaching utilities to actions. The agent will make appropriate choices motivated by the utility of the consequences of his actions. The agent will still sometimes make mistakes, but without better information there is no way to eliminate these mistakes or improve on the expected outcome.

From (11), if the agent does not interpret his signals correctly, then evolution will attach utilities to his actions in order to correct his inferences at the marginal signal, i.e., at the signal at which the expected success probabilities are equal. The agent must be indifferent \( (y + \phi(s_p) - \phi(s_q) = 0) \) when his signal would lead a perfect Bayesian to be indifferent \( (E\{p - q|\phi(s_p) - \phi(s_q) = -y\} = 0). \)

An implication of Proposition 3 is that we should not expect utilities to reflect the average value of various actions to which they are attached. First, we can expect utilities to be attached to actions only to the extent that

\(^{41}\)This is an intuitive assumption and is true in many simple examples, it is not a general implication of our monotone likelihood ratio property assumption.
agents sometimes misunderstand the likelihoods of the attendant outcomes. If the outcomes are correctly assessed, then actions, no matter how valuable, need receive no utility. Optimal utilities thus reflect not the evolutionary value of an action, but the error the agent makes in assessing that evolutionary value. Second, one might think that fitness would be maximized by a utility function that corrected this error on average. As (11) makes clear, what counts is the error the agent makes in the marginal cases where he is indifferent between two actions.

We illustrate by constructing an example in which the agent on average overestimates the value of accepting the option, but evolutionary fitness is nonetheless improved by setting $y > 0$, pushing him to accept the option more than he otherwise would. Let

$$E\{p - q|\phi(s_p) - \phi(s_q) = t\} = a + bt,$$

with $a > 0$ and $b > 0$. Solving (11), the optimal utility is

$$y = \frac{a}{b}. \quad (13)$$

Assume that $\phi(s_p) - \phi(s_q)$ is large on average and that $b < 1$. Because $\phi(s_p) - \phi(s_q)$ is on average large and $b < 1$, the agent on average overestimates the value of the option. However, since $y = \frac{a}{b} > 0$, the agent’s fitness is maximized by pushing the agent even more toward acceptance. We see here the importance of the agent’s marginal beliefs: When $\phi(s_p) - \phi(s_q) = -\frac{a}{b}$ (so that $E\{p - q|\phi(s_p) - \phi(s_q)\} = 0$), the agent underestimates the relative value of the option (thinking it to be negative), even though he overestimates it on average.

It follows from (13) that, as one might expect, a choice with a large expected value (large $a$) will tend to have a large utility. It is thus no surprise that we have a powerful urge to flee dangerous animals or eat certain foods. However, there is also a second effect. The smaller is $b$, the larger is $y$. The point is that the less informative is the agent’s information, holding fixed his average assessment, the more negative is the relevant marginal signal. When $b$ is near zero, evolution effectively insists on the preferred action. While blinking is partly under conscious control, our utility functions do not allow us to go without blinking for more than a few seconds. It would seem that we are unlikely to have reliable information suggesting that this is a good idea. The experience of trying not to cough after mis-swallowing a sip of water at a dinner party has much the same aspect.
4.1.3 Choice-Set Dependence

In this section, we show how a setting where the agent makes different mistakes in different contexts creates evolutionary value for a utility function that depends on things that have no direct impact on evolutionary success. Rather, their role is to tailor utility more closely to the specific informational context at hand. How any given feature optimally affects utility thus depends both on its direct evolutionary impact and how it correlates with errors in information processing.

Suppose that the environment may place the agent in one of two situations. The success probability when rejecting the option is $q$ in either case, with success probability $p_1$ and $p_2$ when accepting the option in situations 1 and 2. The corresponding signals are $s_q$, $s_{p_1}$ and $s_{p_2}$. We initially assume that, as before, the agent derives a utility of 1 from a success, 0 from a failure, and utility $y$, the same value in both situations, from the act of accepting the option.

For example, suppose that in situation 2, accepting the option entails an opportunity to eat a steak. As we have shown, evolution optimally attaches a utility $y$ to steak satisfying

$$E(p - q|\phi(s_p) - \phi(s_q) = -y) = 0.$$ 

Now suppose that in situation 1, accepting the option entails eating a steak at the end of a hunting trip. The agent is likely to have quite different sources of information about these two situations and thus to make quite different errors in processing this information. In particular, the hunter may have an idea of what hazards he will face on the hunting trip before achieving consumption and how these will affect the probability $p_1$. Only coincidentally will it then be the case that $E(p - q|\phi(s_p) - \phi(s_q) = -y, \text{steak on hand})$ equals $E(p - q|\phi(s_p) - \phi(s_q) = -y, \text{steak to be hunted})$. But if these two are not equal, the agent’s expected fitness can be increased by attaching different utilities to accepting the option in the two situations.

How can evolution accomplish this? One possibility is to attach utilities to more actions. The agent can be given a taste for meat, a disutility for the physical exertion of hunting, and a fear of the predators he might encounter. However, there are limits to evolution’s ability to differentiate actions and attach different utilities to them—what it means to procure food may change too quickly for evolution to keep pace—and the set of things from which we derive utility is small compared to the richness of the settings we face. As a result, evolution inevitably faces cases in which the same utility is relevant to effectively different actions. This is captured in our simple model with
the extreme assumption that $y$ must be the same in the two situations. The critical insight is then that the agent’s overall probability of success can be boosted if utility can be conditioned on some other reliable information that is correlated with differences in the actions.

Assume that in situation 2, a utility of $z$ can be attached to the act of foregoing the option. We say that an option with this property is salient. In practice, an option is salient if its presence stimulates our senses sufficiently reliably that evolution can tie a utility to this stimulus, independently of our signal-processing.\footnote{The importance of salient alternatives is well studied by psychologists (Gardner and Lowinson [51], Mischel, Shoda and Rodriguez [86], Siegel [128]) and is familiar more generally—why else does the cookie store take pains to waft the aroma of freshly-baked cookies throughout the mall?} In our example, the presence of the steak makes it salient in situation 2. The question now concerns the value of $z$. If fitness is maximized by setting $z \neq 0$, then there is evolutionary advantage to tailoring the utility gradient between accepting and rejecting the option to the two situations, and we have “choice-set dependence.” Only if $z = 0$ do we have a classical utility function.

**Proposition 4** The optimal utility function $(x, y, z)$ does not exhibit choice-set dependence (sets $z = 0$) if and only if there exists $t^*$ such that

$$E\{p_1 - q|\phi(s_{p_1}) - \phi(s_q) = t^*\} = E\{p_2 - q|\phi(s_{p_2}) - \phi(s_q) = t^*\} = 0. \quad (14)$$

**Proof.** Given (14), the agent’s estimates of the success probabilities in Situations 1 and 2 are equally informative at the relevant margin. Setting $z = 0$ and $y = -t^*$ ensures that (11) holds in both situations, and there is thus no gain from choice-set dependence. Conversely, suppose that the agent’s beliefs are differentially informative in the two situations (i.e., (14) fails). Then fitness can be enhanced by attaching different utility subsidies in the two situations. This can be accomplished by choosing $y$ to induce optimal decisions in situation 1 and $y - z$ (and hence $z \neq 0$) to induce optimal decisions in situation 2.

For example, using choice-set dependence to boost the relative attractiveness of steak when it is available ($z < 0$), in contrast to simply increasing the utility of steak across the board (increasing $y$), might reflect a situation in which evolution finds it beneficial to grant substantial influence to the agent’s beliefs about the consequences of production, while allowing less influence to his beliefs about consumption.
4.1.4 Implications

Our model of the evolution of choice in the face of coarse priors tells us that evolution will generally find it useful to exploit choice set dependence. Anyone who has ever said, “Let’s put these cashews away before we spoil our dinner,” has practical experience with choice-set dependence. Best of all is to be without the temptation of their presence. Once they are there, eating is the preferred choice. Worst of all is looking at the cashews without indulging.\textsuperscript{43}

Which alternatives are salient in any given context is again the result of evolution. As it turns out, a sizzling steak is salient while a steak in the grocer’s freezer is not. Cashews on the table are salient; those in the pantry are less so. What is salient reflects both the technological constraints faced by evolution and the incremental value of tailoring utility to specific contexts.

Choice-set dependence gives rise to internal conflict and self-control and problems of self control. For example, suppose the agent begins by choosing between an unhealthy but gratifying meal and a diet meal. Situation 1 corresponds to a lonely meal at home, with a refrigerator full of diet dinners and a steak in the freezer. Situation 2 corresponds to a steakhouse with a supplementary dieter’s menu. Suppose that evolution has designed our preferences so that steak is subsidized when it is salient. Then the agent may prefer situation 1 even if there is some cost in choosing situation 1, in order to ensure that he rejects the steak.

Choice-set dependence has implications for self control beyond those of present bias. First, difficulties with self control can arise without intertemporal choice. One can strictly prefer junk food that is hidden to that which is exposed, knowing that one will find it painful to resist the latter, all within a span of time too short for nonstandard discounting to lie behind the results. More importantly, because our utility for one choice can be reduced by the salient presence of another, it may be valuable to preclude temptations that one knows one will resist. Someone who is certain she will stick to a diet may still go to some lengths not to be tempted by rich food.

When gut instincts and dispassionate deliberations disagree, the “rational” prescription is to follow the head rather than the heart. In our model, a strong utility push in favor of an action indicates either that the action has been a very good idea in our evolutionary past or that this is a setting in which our information has typically been unreliable. There is thus infor-

\textsuperscript{43}Thaler [136, p. xv] reports a similar incident, explaining it with much the same preferences.
mation in these preferences. The truly rational response is to ask how much weight to place on the advice they give.

4.2 Status

We now return to the consideration of status, on which we touched briefly in Section 3.1.2. People’s preferences often appear to depend not only on their own consumption, but also on the consumption of others, so much so that “keeping up with the Jones’ ” is a familiar phrase. Frank [42], Frey and Stutzer [45, 46], and Neumark and Postlewaite [90] highlight the importance of such effects, while the suggestion of a link between desired consumption and one’s past consumption or the consumption of others is an old one, going back to Veblen [140] and Dusenberry [31].

There are two basic approaches to explaining such relative consumption effects. One retains the classical specification of preferences, building a model on the presumption that people care directly only about their own consumption. However, it is posited that some resources in the economy are allocated not via prices and markets but according to status. In addition, it is supposed that one attains status by consuming more than do others, perhaps because the ability to do so is correlated with other characteristics that are important for status. A flashy sports car may then be valued not only for its acceleration, but also for its vivid demonstration that the driver has spent a great deal of money. Tuna may taste better than caviar, but fails to send the same signal. The resulting behavior will be readily rationalized by preferences in which people care about their consumption and about how their consumption relates to that of others. For example, Cole, Mailath and Postlewaite (1992) construct a model in which competition for mates induces a concern for status, around which a subsequent literature has grown.

The second alternative explanation is that evolution has directly embedded a concern for status into our preferences. As usual, our models of this possibility evolve around some constraint on evolution’s ability to shape behavior. We consider two possible sources of relative consumption effects, arising out of two such constraints.

4.2.1 Information and Relative Consumption

Relative consumption effects may have been built into our preferences as a means of extracting information from the behavior of others. We present a simple model of this possibility here, expanded and examined more thoroughly in Samuelson [121] and Nöldeke and Samuelson [91].
The idea that one can extract information from the actions of others is familiar, as in the herding models of Banerjee (1992) and Bikhchandani, Hirshleifer and Welch (1992). In our case, agents observe their predecessors through the filter of natural selection, biasing the mix of observations in favor of those who have chosen strategies well-suited to their environment. An agent’s observed behavior thus mixes clues about the agent’s information with clues about his evolutionary experience, both of which enter the observer’s inference problem. The problem then resembles that of Banerjee and Fudenberg (1995) and Ellison and Fudenberg (1993, 1995) more than pure herding models.

At the beginning of each period \( t = 0, 1, \ldots \), the environment is characterized by a variable \( \theta_t \in \{\theta, \overline{\theta}\} \). The events within a period proceed as follows:

1. Each member of a continuum of surviving agents gives birth, to the same, exogenously fixed number of offspring. Each offspring is characterized by a parameter \( \epsilon \). We interpret each offspring as (not necessarily independently) drawing \( \epsilon \) from a uniform distribution, while assuming the realized values of \( \epsilon \) are uniformly distributed on \([0, 1]\).

2. Each newborn observes \( n \) randomly selected surviving agents from the previous generation, discerning whether each chose action \( z \) or \( \overline{z} \).

3. All parents then die. Each member of the new generation chooses an action \( z \in \{z, \overline{z}\} \).

4. Nature then conducts survival lotteries, where \( h : \{z, \overline{z}\} \times [0, 1] \times \{\theta, \overline{\theta}\} \rightarrow [0, 1] \) gives the probability that an agent with strategy \( z \) and characteristic \( \epsilon \) survives when the state of the environment is \( \theta \). Again, we assume no aggregate uncertainty.

5. Nature draws a value \( \theta_{t+1} \in \{\theta, \overline{\theta}\} \).

We interpret the actions \( z \) and \( \overline{z} \) as denoting low-consumption and high-consumption lifestyles. The survival implications of these actions depend upon individual characteristics and the state of the environment. Some agents may be better-endowed with the skills that reduce the risk of procuring consumption than others. Some environments may feature more plentiful and less risky consumption opportunities than others. These effects appear
in the specification of the survival probabilities \( h(z, \epsilon, \theta) \), given by

\[
\begin{align*}
    h(\bar{z}, \epsilon, \theta) &= \frac{1}{2} \\
    h(\bar{z}, \epsilon, \overline{\theta}) &= \frac{1}{2} + b(\epsilon - q) \tag{15} \\
    h(\bar{z}, \epsilon, \theta) &= \frac{1}{2} + b(\epsilon - (1 - q)), \tag{16}
\end{align*}
\]

where \( 0 < q < 1/2 \) and, to ensure well-defined probabilities, \( 0 < b < 1/(2(1 - q)) \). The low-consumption action \( \bar{z} \) yields a survival probability of \( \frac{1}{2} \), regardless of the agent’s characteristic or state of the environment. The high-consumption action \( \overline{\theta} \) yields a higher survival probability for agents with higher values of \( \epsilon \) and yields a higher survival probability when the state is \( \overline{\theta} \).

The environmental parameter \( \theta \) follows a Markov process, retaining its current identity with probability \( 1 - \tau \) and switching to its opposite with probability \( \tau \). An agent’s strategy identifies an action as a function of the agent’s characteristic \( \epsilon \) and information. Strategies (but not characteristics or actions) are heritable and are thus shaped by natural selection.

Our interest concerns cases in which fluctuations in the state \( \theta \) are not perfectly observed by the agents and are sufficiently transitory that Nature cannot observe them.\(^{44}\) It follows from the monotonicity of (15)–(16) that an optimal strategy must take the form of a cutoff \( \epsilon^*(\cdot) \), conditioned on the agent’s information, such that action \( \overline{\theta} \) is chosen if and only if \( \epsilon > \epsilon^*(\cdot) \).

Let \( \psi_t \) be the proportion of strategy \( \overline{\theta} \) among those agents who survived period \( t - 1 \). Then a period-\( t \) new-born observes \( \overline{\theta} \) on each survivor draw with probability \( \psi_t \) and observes \( \bar{z} \) with probability \( 1 - \psi_t \). Let \( \Psi(E, \theta_t) \) be the proportion of surviving period-\( t \) agents who chose \( \overline{\theta} \), given that (i) these agents, as new-borns, drew observations from the distribution described by \( \psi_t \), (ii) the period-\( t \) state of the environment relevant for Nature’s survival lotteries is \( \theta_t \), and (iii) every agent’s decision rule is given by the decision \( E = \{\epsilon^*(n), \ldots, \epsilon^*(0)\} \). We can describe our system as a Markov process \( (\psi_t, \theta_t) \) defined on the state space \([0, 1] \times \{\theta, \overline{\theta}\}\). Letting \( \Theta \) denote the transition rule governing the state \( \theta_t \), \( (\Psi_E, \Theta) \) denotes the transition rule for

\(^{44}\)If the state \( \theta \) can be observed, then evolution faces no constraints in designing strategies to maximize the survival probabilities given by (15)–(16), and observations of the previous generation are irrelevant for behavior.
the process \((\psi_t, \theta_t)\), where:

\[
\begin{align*}
\psi_{t+1} &= \Psi_E(\psi_t, \theta_t) \\
\theta_{t+1} &= \Theta(\theta_t).
\end{align*}
\]

The optimal strategy \(\epsilon^*(\cdot)\) maximizes

\[
\int_{\Theta \times \Psi} \rho(\theta, \psi) \ln \left( \int_K f(k|\theta, \psi)p(\epsilon^*(k), \theta)dk \right) d\theta d\psi,
\]

where \(\rho\) is the stationary distribution over states \((\theta, \psi) \in [0, 1] \times \{\theta, \overline{\theta}\}\), \(f\) is the distribution over number \((k)\) of \(\bar{z}\) agents observed when sampling the previous generation (given the state \((\theta, \psi))\), and \(p\) is the probability that an agent characterized by decision rule \(\epsilon^*\) (i.e., chooses \(\bar{z}\) if and only if \(\epsilon > \epsilon^*)\) survives in state \(\theta\).

The key question in characterizing an optimal strategy is now the following: if the agent observes a relatively large value of \(k\), is the environment more likely to be characterized by \(\theta\) or \(\overline{\theta}\)? Let \(\rho(\overline{\theta}|k)\) be the posterior probability of state \(\overline{\theta}\) given that an agent has observed \(k\) agents from the previous generation choosing \(\bar{z}\). These updating rules are an equilibrium phenomenon. The expectation is that an agent observing more instances of high consumption will think it more likely that the state is \(\overline{\theta}\) and hence be more willing to choose high consumption, i.e., that \(\epsilon^*(k)\) should be decreasing in \(k\). We say that a strategy \(\{\epsilon^*(n), \ldots, \epsilon^*(0)\}\) is admissible if it exhibits this property.

Let the function \(\rho_{E}(\bar{\theta}|k, t)\) give the probability that the state in time \(t\) is \(\bar{\theta}\), given a time-\(t\) observation of \(k\) values of \(\bar{\theta}\). The role of \(k\) in this probability balances two considerations—the extent to which an observation of a large \(k\) indicates that the previous-period state was relatively favorable for strategy \(\bar{z}\) (i.e., was \(\overline{\theta}\)), and the probability that the state may have changed since the previous period. Samuelson [121] proves:

**Lemma 5** There exists a value \(q^* \in (0, \frac{1}{2})\) such that for any \(q \in (q^*, \frac{1}{2})\) and any admissible \(E\), there exist probabilities \(\rho_{E}(\bar{\theta}|k)\) \((k = 0, \ldots, n)\) satisfying, for all initial conditions,

\[
\lim_{t \to \infty} \rho_{E}(\bar{\theta}|k, t) = \rho_{E}(\bar{\theta}|k).
\]

The \(\rho_{E}(\bar{\theta}|k)\) satisfy \(\rho_{E}(\bar{\theta}|k + 1) > \rho_{E}(\bar{\theta}|k)\).

The restriction that \(q > q^*\) ensures that the population can never get too heavily concentrated on a single action, either \(\bar{z}\) or \(\bar{z}\). This in turn ensures
that changes in the environmental state are reflected relatively quickly in the observed distribution of actions, and hence that the latter is informative.\footnote{To see how this could fail, consider the extreme case of $q = 0$. In this case, it is possible that virtually the entire population chooses $z$. A change from state $\bar{\theta}$ to $\bar{\theta}$ will then not produce a noticeable change in the distribution of actions for an extraordinarily long time, causing this distribution to be relatively uninformative.}

The inequality $\rho_E(\theta|k+1) > \rho_E(\theta|k)$ indicates that observations of high consumption enhance the posterior probability that the state of the environment is $\bar{\theta}$. This is the foundation of relative consumption effects.

An equilibrium is a specification of $E$ that is optimal in the induced stationary state. Hence, in defining an equilibrium, we use the limiting probabilities $\rho_E(\theta|k)$ to evaluate the payoff of a strategy. This reflects an assumption that the process governing the state of the environment persists for a sufficiently long time that (i) evolution can adapt her agents to this process, and (ii) the limiting probabilities $\rho_E(\theta|k)$ are useful approximations for evolution of the information-updating problem facing the agents. Nöldeke and Samuelson \[91\] show that:

**Proposition 6** There exists $q^* \in \left(0, \frac{1}{2}\right)$ and $\tau^* > 0$ such that for any $q \in (q^*, \frac{1}{2})$ and $\tau \in (0, \tau^*)$, an equilibrium with an admissible strategy $\{\epsilon^*(n), \ldots, \epsilon^*(0)\}$ exists. In any such equilibrium, $\epsilon^*(k+1) < \epsilon^*(k)$.

Agents are more likely to choose high consumption, i.e., choose $z$ for a wider range of $\epsilon$, when $k$ is large. Observations of high consumption, by increasing the expectation that the environment is in a state favorable to high consumption, increase an agent’s propensity to choose high consumption. A revealed preference analysis of behavior would thus uncover relative consumption effects, in which agents optimally exploit information by conditioning their consumption on observations of others’ consumption.

It is important to note that an agent’s survival in this model depends only on the agent’s own consumption. The route to genetic success is to choose optimal consumption levels, regardless of others’ choices. The consumption levels of others are relevant only because they serve as valuable indicators of environmental information that neither the agents nor Nature can observe.

There are many ways Nature could induce the optimal behavior characterized by Proposition 6, from hard-wired stimulus-response machines to calculating agents who understand Bayes’ rule and their environment and who make their decisions so as to maximize the expected value of a utility function defined in terms of only their own consumption. Our argument thus far accordingly provides no reason to believe that relative consumption
effects are built directly into preferences, and no reason why we should care about which of the many observationally-equivalent methods Nature might have chosen to implement such behavior.

The next step in the argument returns us to the observation that Nature faces a variety of obstacles in inducing behavior that will maximize expected utility. Suppose that in addition to the number $k$ of preceding agents observing high consumption, the agent also observes a signal $\xi$ that is more likely to take on high values when the environment is $\theta$. Suppose also that the agent does not process this signal perfectly. In Samuelson [121], this imperfect-information processing assumption is made operational by assuming that the agent observes an informative signal $\xi$, as well as an uninformative signal $\zeta$, but does not recognize this distinction, instead simply processing all signals as if they were informative. Recognizing that both $\xi$ and $\zeta$ play a role in the agent’s information, evolution finds the agent’s information less informative than does the agent. She thus reduces the sensitivity of the agent’s actions to his information. This reduced sensitivity can be accomplished by a utility function that discourages the agent from straying too far from a target action $\hat{\epsilon}(k)$ that depends upon the agent’s observation of others’ consumption. In particular, evolution can make the agent’s utility depend upon his value of $\epsilon$, his action ($z$ or $\overline{z}$), and the number $k$ of high-consumption agents observed in the previous period (the relative consumption effect). Consider a value $\epsilon^*$ and the posterior belief $\hat{\rho}_E(\theta|k, \xi, \zeta)$ that would make the cutoff $\epsilon^*$ optimal given perfect information processing. Given that the agent is sometimes responding to an uninformative signal, evolution now has an incentive to boost the agent’s marginal utility at $\epsilon^*$ above zero (i.e., $\epsilon^* < \epsilon(k)$) if the agent has received a large signal convincing him that $\theta$ is quite likely; or depressed below zero (i.e., $\epsilon^* > \epsilon(k)$), if the agent has received a small signal. Evolution thus requires that the agent observe more persuasive information than would be the case with errorless information processing before straying too far from a consumption strategy that makes high consumption more likely when more instances of high consumption have been observed. Evolution accomplishes this by not only inducing the agent’s behavior to respond to the behavior of others, but by using the ability to make the agent’s utility respond to the behavior of others.

We now have relative consumption effects built directly into preferences, in order to induce relative consumption effects in behavior. Notice that the case for the preference effect is somewhat more tenuous than for the behavioral effect. We can expect relative consumption effects in behavior whenever agents face environmental uncertainty. Relative consumption ef-
fects in preferences are one solution to a particular constraint in Nature’s design problem. However, the general principle remains that if Nature cannot ensure the agent processes information perfectly, then she will find it advantageous to compensate by manipulating other features of the agent’s decision-making apparatus, with relative consumption effects in preferences being one possible result.

4.2.2 Adaptive Utility

Robson [111, pp. 17–19] suggests a related but alternative motivation for relative consumption effects, one that brings back an old question in economics—is utility reasonably viewed as a cardinal or ordinal concept? The concept of cardinal utility traces back to the English philosopher and lawyer Jeremy Bentham [10]. Bentham believed that utility derived from pleasure or pain, and proposed to make judgments about policy by summing these utilities across the individuals involved. The result was his maxim “he greatest good for the greatest number,” which, as Paul Samuelson is said to have remarked, has too many greatests in it to be implementable.

The view that utility is a cardinal notion, perhaps based on some measurable concept of pleasure, raises a number of awkward questions. A key thread in economic thought after Bentham pared back the notion of utility to take refuge in an ordinal interpretation. In the context of consumer theory, it was realized that utility simply did not need to be cardinal—one needed only indifference curves and an appropriate set of labels. That such stripping down was philosophically a good idea was justified by an appeal to “Occam’s Razor.” Although matters are less cut-and-dried in the original context of welfare theory, most economists also became skeptical of interpersonal comparisons based on cardinal utility, often settling finally for a weak welfare criterion that is independent of them—Pareto efficiency.

Even if we set aside welfare comparisons, at least for a start, there remain awkward questions for the theory of individual choice. For example, psychologists (see Frederick and Loewenstein [43]) discuss how a burst of intense pleasure stems from winning the lottery, but this pleasure subsides fairly quickly, with the winner ending up feeling only slightly better than before winning. Analogously, the intense sadness that arises from becoming the victim of a crippling accident fades, so that one ends up only a little sadder than before the accident. In both cases, the dominant effect is that if you were happy before, you will be happy now; if you were miserable before, you will be miserable now. These findings seem to suggest that people should not particularly running the risk of a catastrophic accident or should
not buy lottery tickets. Why take precautions to avoid only a slight loss, or incur costs in search of a slight gain? But people do try to avoid being maimed and do buy lottery tickets.

The general issue here is that identifying utility with pleasure forces us to address the adaptive nature of pleasure. Whether an experience makes you happy or sad depends on what you were expecting, on what you had before, on what those around you are receiving. Fortunately, this issue of adaptation is not so awkward upon closer examination. More than that, adaptation of utility is precisely what you would expect as biologically optimal. Furthermore, the behavior that it generates need not be very different from what the conventional model generates.

The issue is perhaps analogous to an old-fashioned voltmeter, one with a needle. To get an accurate reading from a voltmeter, one must first estimate the range into which the unknown voltage falls. If the range is set too high, there is no usable reading, since the needle hardly budges; if the range is set too low, your meter may self-destruct. Only if the range is set right can you obtain useful information. The problem is that the voltmeter, like all real measuring devices, have limited sensitivity. Similarly, biological organisms have limited perceptual discrimination.

Consider the following example. An individual organism must choose between two lotteries. Each lottery is an independent draw from the same known continuous cumulative distribution function $F$. The individual must choose a lottery after the draws are made, but can only perceive whether each realization is above or below some threshold $c$. These two perceptual possibilities are experienced as hedonic utility, which is then either high or low. If the outcomes of both lotteries lie above or both lie below $c$, choice is made randomly, so that mistakes arise, with probability $1/2$.

What value of $c$ minimizes the probability of error? This probability of error is

$$PE(1) = \frac{1}{2} \Pr\{x_1, x_2 < c\} + \frac{1}{2} \Pr\{x_1, x_2 > c\}$$

$$= \frac{1}{2}(F(c))^2 + \frac{1}{2}(1 - F(c))^2$$

$$= \frac{1}{2}y^2 + \frac{1}{2}(1 - y^2),$$

where $x_1$ and $x_2$ are the outcomes of the two lotteries and $y = F(c)$. This is a convex function. The first-order condition for this minimization problem is

$$\frac{dPE(1)}{dy} = y - (1 - y) = 0,$$
so that one should choose \( c \) so that \( y = F(c) = \frac{1}{2} \). Hence, it is optimal to choose \( c \) to be the median of the distribution described by \( F \). In particular, it is optimal to set a threshold that adapts to the circumstances in which hit is to be used, as captured by \( F \).

The probability of error is not the most convincing objective here. After all, some errors involve a very big gap between the \( x \) you chose and the \( x \) you could have had, and some involve a very small gap. A more plausible objective would be to maximize the expected value of the \( x \) you receive. Thus, fitness is identified with \( x \).\(^{46}\) Now the value of the threshold \( c \) should be set at the mean of the distribution rather than the median.

Netzer [89] examines the problem of maximizing the expected payoff further, considering a more general model in which the individual can perceive an arbitrary number of thresholds. We will continue here with illustrative and more tractable problem of minimizing the probability of error. Consider the more general case where the individual has \( N \) threshold values \( c_1 < c_2 < ... < c_N \).

The probability of error is now

\[
PE(N) = \frac{1}{2}(y_1)^2 + ... + \frac{1}{2}(y_{n+1} - y_n)^2 + ... + \frac{1}{2}(1 - y_N)^2,
\]

where \( y_n = F(c_n) \) for \( n = 1, ..., N \). This is again a convex function of \((y_1, ..., y_N)\) so that satisfying the first-order conditions is still necessary and sufficient for a global minimum. These first-order conditions are

\[
\frac{\partial PE(N)}{\partial y_1} = 0 \quad \text{so} \quad y_2 - y_1 = y_1 - 0
\]

\[
\frac{\partial PE(N)}{\partial y_n} = 0 \quad \text{so} \quad y_{n+1} - y_n = y_n - y_{n-1}, \quad \text{for} \quad n = 2, ..., N - 1
\]

\[
\frac{\partial PE(N)}{\partial y_N} = 0 \quad \text{so} \quad 1 - y_N = y_N - y_{N-1}.
\]

Hence, the solution is

\[
y_1 - 0 = k, \quad y_{n+1} - y_n = k, \quad \text{for} \quad n = 2, ..., N - 1 \quad \text{and} \quad 1 - y_N = k.
\]

\(^{46}\)This assumption is relatively innocuous, in the sense that, if fitness were a monotonically increasing function of \( x \), we could easily find the cumulative distribution function over fitness that is implied by the given distribution over \( x \). The resulting mathematics is a bit harder, but it does not make a significant qualitative difference.
It must then be that $k = 1/(N + 1)$, so that

$$y_n = F(y_n) = n/(N + 1), \text{ for } n = 1, \ldots, N.$$  

For example, if $N = 9$, the thresholds should be at the deciles of the distribution.

What is the probability of error $PE(N)$ when the thresholds are chosen optimally like this? We have

$$PE(N) = \frac{1}{2(N + 1)^2} + \ldots + \frac{1}{2(N + 1)^2} = \frac{1}{2(N + 1)} \to 0, \text{ as } N \to \infty.$$  

It is thus clearly advantageous to have as many thresholds as possible, i.e., to be able to perceive the world as finely as possible. Unfortunately, the ability to measure the world more precisely is biologically costly. Suppose the individual incurs a cost that is proportional to the probability of error as well as a cost $c(n)$ that depends directly on $N$, so that more thresholds are more costly. The total cost is then

$$PE(N) + c(N),$$  

which should be minimized over the choice of $N$. If $c(N) \to 0$, in an appropriate uniform sense, it follows readily that $N \to \infty$, and that $PE(N) + c(N) \to 0$. As costs decline, the resulting choice behavior is exactly as conventionally predicted, though utility remains adaptive, even in this limit, the the choice of threshold values. If perception or computation is costly, then utility will again be adaptive and we will see behavior not easily captured by a conventional model.

### 4.2.3 Adaptive Utility and Relative Consumption

Rayo and Becker [104] explore the implications of adaptive utility. They are especially interested in the question of how the specification of the utility function is calibrated to its environment. The adaptation they consider has two aspects, namely

1. habituation—utility adjusts so that people get used to a permanent shift, positive or negative, in their circumstances, and
2. peer comparisons—people are concerned with relative income or wealth.
What these have in common is a description in terms of a reference point that is determined by your own past outcomes, or by the past and present outcomes of peers, respectively.

Rayo and Becker [104] again view utility as hedonic, as a biological device that induces appropriate actions by an individual. In particular, evolution chooses the mapping from material outcomes into pleasure in the most effective way possible. In the present context, this most effective way involves the construction of a reference point that reflects the individual’s expectations of the world.

As in Robson [112], there is a metaphorical principal-agent problem here, with evolution as the principal and the individual as the agent. Evolution “wishes” the individual to be maximally fit, and she has the extraordinary ability to choose the utility function of the agent to her best advantage.

The key ingredients of the model are a limited range of utility levels that are possible, and a limited ability to make fine distinctions. Consider an agent undertaking a one shot project. She first observes a state $s$ specifying the physical state of the world—the availability of game animals, the presence of sabre-toothed tigers, and so on. Next, she adopts a strategy $x \in X$—this strategy might be a method of hunting, for example. Let $f(y | x, s)$ be the probability density of output $y \in \mathbb{R}$ given $x$ and $s$. This density is known to the agent. Note that $y$ need not, in principle, be the final good here. From a biological point of view, that role should be reserved for offspring. Rather $y$ may represent directly observable intermediate goods such as money or food. Evolution attaches utilities to values of $y$ to induce choices that in turn have the desired effects in terms of offspring. We omit this latter step and simply concentrate on the production of $y$. The agent is guided by the coupling of emotional rewards to this observed output. The agent then chooses $x$ so as to maximize her expected emotional payoff.

Why might it be advantageous for evolution to do this rather than to simply prescribe the agent’s choice as a function of $s$? Perhaps evolution is daunted by the sheer complexity of the second option. More importantly, perhaps there are novel $s$’s and novel $f$’s, precluding evolution from simply giving the agent fixed instructions, but allowing evolution to rely on the agent’s ability to estimate the expected emotional reward and act to maximize it.

Let $V(y)$ be the hedonic utility of income $y$, with $V'(y) > 0$. The the bottom line for the agent is then to maximize

$$E[V | x, s] = \int V(y)f(y | x, s)\,dy$$
over the choice of $x \in X$.

Evolution has the ability to choose $V$ optimally. We assume that evolution wants to maximize $E(y)$. A key element of the model is that there are bounds on $V$ so that

$$V \in [\underline{V}, \bar{V}],$$

which we can then normalize so that $V \in [0, 1]$. The constraints might ultimately reflect the fact that there are a finite number of neurons in the brain, and hence limits on the positive and negative sensations evolution can engineer the agent to produce. These upper and lower constraints on $V$ will typically be be binding, in that evolution would benefit from a wider range of emotional responses. It is expensive, however, to enlarge the range, and so this range must be finite and evolution must use utilize this range optimally.

A second key element in the model is limited discrimination. This takes the precise form that, if

$$|E[V \mid x_1, s] - E[V \mid x_2, s]| \leq \varepsilon,$$

then the individual cannot rank $x_1$ and $x_2$. Hence all choices within $\varepsilon$ of $\max_{x \in X} E[V \mid x, s]$ are "optimal." It is assumed that the agent randomizes uniformly, or at least uses a continuous distribution with full support, over this satisficing set. Of course evolution would also prefer a smaller value of $\varepsilon$, but this is again expensive, and she will have to optimize given the optimal $\varepsilon > 0$.

Output is given by

$$\tilde{y} = m(x, s) + \tilde{z},$$

where $\tilde{z}$ has a continuous unimodal distribution with $E(\tilde{z}) = 0$ and hence

$$E\tilde{y} = m(x, s).$$

That is, the effect of changes in $x$ or $s$ is to shift the entire distribution of output up or down without changing its shape. A choice of $x$ that increases $m(x, s)$ entails a new distribution that first-order stochastically dominates the old one.

The following trick simplifies the notation. Define

$$\varphi(x, s) = \frac{E[y \mid x, s] - \min_x E[y \mid x, s]}{\max_x E[y \mid x, s] - \min_x E[y \mid x, s]} \in [0, 1].$$

This index captures the relative efficiency of choice $x$ in state $s$. This permits the problem to be simplified by being formulated in terms of $\varphi$ rather than
x. Expected output can then be rewritten as
\[ E[y \mid x, s] = \varphi \max_x E[y \mid x, s] + (1 - \varphi) \min_x E[y \mid x, s] \equiv E[y \mid \varphi, s] \]
where \( E[y \mid \cdot, s] \) is monotone increasing. Output can be expressed as \( \tilde{y} = m(\varphi, s) + \tilde{z} \), so that the probability distribution of \( y \) is now \( f(y \mid \varphi, s) \).

Consider first the simplest case that the state does not matter so
\[ E[y \mid \varphi, s] = E[y \mid \varphi] \]
and
\[ E[V \mid \varphi] = \int V(y)f(y \mid \varphi)dy. \]
The satisficing set is now
\[ \{ \varphi \mid E[V \mid \varphi] \geq \max_{\varphi} E[V \mid \varphi] - \varepsilon \} = [\varphi_{\text{min}}(V, \varepsilon), 1], \]
where
\[ E[V \mid \varphi_{\text{min}}(V, \varepsilon)] = E[V \mid 1] - \varepsilon. \]
Evolution’s problem becomes
\[ \max_{\varphi \in [0, 1]} \varphi_{\text{min}}(V, \varepsilon) \equiv \varphi^*. \tag{18} \]

**Lemma 7** If \( V^* \) solves (18) then \( V^* \) solves
\[ \max_{\varphi \in [0, 1]} E[V \mid 1] - E[V \mid \varphi^*]. \tag{19} \]

**Proof.** Suppose not. Then \( \exists V \neq V^* \) such that
\[ E[V \mid 1] - E[V \mid \varphi^*] > E[V^* \mid 1] - E[V^* \mid \varphi^*] = \varepsilon, \]
since \( \varphi^* = \varphi_{\text{min}}(V^*, \varepsilon) \). But this implies that \( \varphi_{\text{min}}(V, \varepsilon) > \varphi^* \), a contradiction. \( \blacksquare \)

**Proposition 8** Problem (18) has as its essentially unique solution
\[ V^*(y) = \begin{cases} 1 & y \geq \hat{y} \\ 0 & y < \hat{y} \end{cases} \]
where \( \hat{y} \) solves
\[ f(\hat{y} \mid 1) = f(\hat{y} \mid \varphi^*). \]
Proof. (18) has a solution and it must also solve (19). That is:

$$\max_{V \in [0,1]} \int V(y)[f(y \mid 1) - f(\hat{y} \mid \varphi^*)] dy.$$ 

Hence

$$V^*(y) = \begin{cases} 
1 & f(y \mid 1) \geq f(\hat{y} \mid \varphi^*) \\
0 & f(y \mid 1) < f(\hat{y} \mid \varphi^*) 
\end{cases}.$$ 

The claimed solution follows from the single crossing property of the densities. This solution is essentially unique, and so must solve (18) also. 

Evolution thus designs the agent with a “bang-bang” utility function, choosing a cutoff $\hat{y}$ such that outcomes above this cutoff induce the maximum possible utility, while those below minimize utility. As $\varepsilon \to 0$, we have $\varphi^* \to 1$ and $\hat{y} \in [E(y \mid \varphi^*) - E(y \mid 1)] \to E(y \mid 1)$. The resulting function $V$ penalizes the agent at the maximal rate for choosing suboptimal $x$.

In general, one might expect an $S$-shaped utility function to be more realistic than the cliff shape or bang-bang utility function we have derived. Rayo and Becker [104] show that an $S$ shape would arise if deviations from a given reference level $V_0$ were costly. Alternatively, it might be that the agent knows more about the output technology than does evolution. Now evolution might not be able to target $E(y \mid 1)$, instead having to smooth out $V$ to provide strong incentives over a range of possible $E(y \mid 1)$’s.

Where do we see relative considerations in this model? Let us introduce time, thereby allowing for both individual habit formation and peer comparisons, both valuable for the information they provide evolution about the size of an aggregate shock that is relevant to how she calibrates utility. Suppose that

$$\tilde{y}_t = m(x_t, s_t) + \bar{z}_t$$

so that, as before

$$\hat{y}_t = m(\varphi_t, s_t) + \bar{z}_t.$$ 

We now assume that $\max_{x_t} E[y_t \mid x_t, s_t]$ and $\min_{x_t} E[y_t \mid x_t, s_t]$ may vary with $s_t$. It follows that $m(\varphi_t, s_t)$ may then also vary with $s_t$. In particular, it is assumed that the extreme values may depend on which element, $\Omega_t$, say, of a partition of $S$ is attained. Accordingly, output becomes

$$\tilde{y}_t = m(\varphi_t, \Omega_t) + \bar{z}_t.$$
The variable $\Omega_t$ might be the weather, for example. It is assumed that evolution knows $\Omega_t$ so that $\Omega_t$ can be built in $V_t$. The agent still has the objective $\max_x V_t$.

This dynamic problem is assumed to reduce to a sequence of one shot problems that will be connected only via the construction of the reference point. The optimal limiting utility function is
\[
V(y) = \begin{cases} 
1 & y \geq \hat{y} = E[y \mid 1, \Omega_t] \\
0 & y < \hat{y}.
\end{cases}
\]

Suppose now that $\tilde{y}_t = \varphi_t + \tilde{\theta}_t$, where $\tilde{\theta}_t = \theta_{t-1} + \tilde{z}_t$ is Markovian, so that $E(\tilde{z}_t) = 0$. Then
\[
y_t = \varphi_t + \tilde{\theta}_{t-1} + \tilde{z}_t = \varphi_t + y_{t-1} - \varphi_{t-1} + \tilde{z}_t.
\]

In the limiting equilibrium, $\varphi_t = \varphi_{t-1} = 1$, so that
\[
y_t = y_{t-1} + \tilde{z}_t,
\]
and $\dot{y}_t = y_{t-1}$. Hence the individual is happy if and only if current output exceeds last period’s output.

If the agent did not adapt like this, all decisions would eventually look good or bad, as the process drifted up or down, and the individual’s incentives would disappear. In equilibrium, the agent is punished as severely for bad luck as she would be for a bad decision. That is, in equilibrium, the decisions are optimal and happiness is purely a matter of luck.

### 4.2.4 Implications

Why do we care about relative consumption effects, and why do we care whether they might enter preferences directly? Our current world is much different from the ancestral environment in which our preferences evolved. If we were concerned only with the ancestral environment, then our interest would not extend beyond the behavior that maximizes fitness. We would be interested in whether behavior exhibited relative consumption effects, but we could ignore imperfections such as the agent’s noisy information processing that have only a minor impact (or, in the case of our simple model, no impact) on the constrained-optimal behavior implemented by evolution. If we are concerned with our current world, however, then we must recognize that these imperfections can have a important impact on the mechanism.
by which evolution induces her optimal behavior, and that the implement-
ing mechanism can in turn have an important impact on the behavior that
appears once the agents are transplanted from the ancestral environment
to our much different modern environment. For example, perfect Bayesians
will never erroneously imitate uninformative consumption decisions. Relative
consumption effects that are embedded in preferences may cause agents
in a modern environment to condition their behavior on a variety of unin-
formative or misleading signals, regardless of the uncertainty they face.

What would we expect to see in a world of relative consumption ef-
effects? First, we should see evidence that evolution designs agents to either
consciously or unconsciously make use of environmental cues in shaping con-
sumption decisions. Experiments have shown that some animals condition
their fat accumulation on day length, a source of information that is reason-
ably reliable in natural environments but that can be used to manipulate
feeding behavior in laboratory settings (Mercer, Adam and Morgan (2000)).
A variety of young animals, including humans, have been shown to be more
likely to consume foods that they have observed others consuming (Smith
(2002, Section 2.1)). More striking is recent evidence that a low birth weight
puts one relatively at risk for subsequent obesity. The conventional inter-
pretation is that poor maternal nutrition is a prime contributor to a low
birth weight as well as a prime indicator of a meager environment, so that
a low birth weight provides information to which the optimal reaction is a
tendency to store more bodily food reserves (Petry and Hales (2000)).

In addition, we should observe an inclination to conform to the behav-
ior of others that will sometimes appear to be unjustified on informational
grounds. Psychologists again commonly report a taste for conformity (Aron-
son (1995, chapter 2), Cialdini (1988, chapter 4)), even in situations in which
one would be extremely hard-pressed to identify an objective information-
based reason for doing so.\footnote{The work of Asch (1956) is classic, in which an apparent desire to conform prompted experimental subjects to make obviously incorrect choices when matching the lengths of lines, while denying that they were influenced by the choices of others.}

Our model of relative consumption effects directs attention to conformity
effects that initially appear somewhat counterintuitive. The model suggests
that relatively low-productivity agents will strive to increase consumption,
while high productivity agents will attenuate their consumption, both in or-
der to not be too conspicuously different. The latter finding contrasts with
the popular view of relative consumption effects as creating incessant incen-
tives to consume more in order to “keep up with the Joneses.” Do we expect

47 The work of Asch (1956) is classic, in which an apparent desire to conform prompted experimental subjects to make obviously incorrect choices when matching the lengths of lines, while denying that they were influenced by the choices of others.
internet billionaires to lie awake at night, desperately searching for ways to
dispose of their wealth so as to look more like ordinary people? Notice first
that information-based relative consumption effects are consistent with out-
comes in which some people happily, even gloatingly, consume more than
others, perhaps much more. Higher-productivity agents optimally consume
more than lower-productivity agents, both in the model and in the world.
The billionaire need not lie awake at night.

More importantly, the behavior predicted by the model is that agents
who observe others consuming more should themselves consume more. But
this is typically what one means by “keeping up with the Joneses.” Information-
based relative consumption effects imply not that we must observe people
endeavoring to reduce their consumption, but rather that people whose char-
acteristics lead to high consumption levels should strive less vigorously to
keep ahead of the Joneses than they would to catch up if the Joneses were
ahead.

Preferences incorporating relative consumption effects give rise to the
risk that agents will react to others’ consumption in ways that do not re-
fect the informational content of their surroundings, leading to outcomes
that are inefficient (conditional on the environment). Evolution may have
optimally incorporated these risks in the ancestral environment in which
our preferences evolved, but new problems appear as agents apply their be-
havioral rules to a modern industrial society for which they are likely to be
a poor match.\textsuperscript{48} In addition, to the extent that evolution has responded
to this risk, she has done so to maximize the fitness of her agents. From
our point of view, it is utility and not fitness that counts. Studying evolu-
tionary foundations allows us to gain insight into the difference between
evolution’s preferences in the ancestral environment and our preferences in
our current world, in turn helping us assess modern social developments or
policy interventions.

For example, it is likely that the observations which motivate information-
based relative consumption effects are stratified, with evolution finding it
optimal for her agents to react more strongly to the generally more relevant
consumption of others who appear to be “like them” than to people whose
circumstances are quite different. Hence, we may be unfazed by compar-
isons with internet billionaires, but may be much more conscious of how our
consumption compares with that of our colleagues. However, the concept of
likeness on which such stratification is based is likely to be both endogenous

\textsuperscript{48}For example, Frank (1999) argues that relative consumption effects lead Americans
to undersave, overconsume luxury goods, and underconsume leisure and public goods.
and liable to manipulation. The development of modern advertising and mass communications may accentuate the visibility of high consumption levels and hence the inefficiencies caused by relative consumption effects. Information and communication technologies may thus bear a hidden cost.

Suppose next that we consider an inequality policy designed to decrease the variation in individual productivities, perhaps by enhancing the productivity of those at the bottom of the income and consumption scale. This will tend to compress the distribution of consumption levels. Consumers will thus observe others who look more like themselves, attenuating the distortions caused by information-based relative income effects. In contrast, if agents seek status that is tied to conspicuous consumption, then compressing the distribution of consumption increases the returns to investing in status, since a given increase in consumption now allows one to “jump over” more of one’s contemporaries. The result can be a ruinous race to invest in status, possibly making everyone worse off (Hopkins and Kornienko (2002)). Policy prescriptions can thus depend critically on whether relative consumption effects arise out of information or status concerns.

4.3 Group Selection

It is uncanny how close Darwin came to the modern view of biological evolution, given that a detailed understanding of the mechanics of genetic inheritance lay far in the future. In particular, he emphasized that a certain variation would spread if this variation led to greater reproductive success for individuals and was genetically transmitted to their descendants. However, Darwin also wandered occasionally into what would now be called “group selection.” Thus, he thought an individual human might engage in behavior that is beneficial to the survival of a group, even if this behavior had a fitness cost to the individual.49

There is a “folk wisdom” appeal to group selection in biology, and this mechanism was once routinely invoked in popular accounts of natural selection. For example, the idea that a predator species is doing a prey species a favor by eliminating its weakest members involves an especially silly form of group selection. More scientifically, the English experimental biologist Wynne-Edwards [147, 148] provided an clear and explicit manifesto on group selection, in the process becoming a favorite target for those wishing to argue against it. For example, he argued that birds limit the size of their clutches of eggs to ensure that the size of the population does not exceed

49This section is based on Robson [114].
the comfortable carrying capacity of the environment. That is, individuals act in the best interest of the species.

These particular group selection arguments were effectively devastated by Williams [144]. If a new type of individual does not so obligingly limit her clutch, for example, why would this more fertile type not take over the population, and in the process damn the standard of living? This challenge to the logic of group selection was complemented by aspirations as to its usefulness. For example, one can find compelling arguments as to why it is in the interests of an individual to limit her clutch size. For example, it might be that, beyond a certain point, an increase in the number of eggs reduces the expected number of offspring surviving to maturity, because each egg then commands a reduced share in parental resources. A finite optimum for clutch size is then to be expected. Thus, observations suggesting that clutch sizes are limited do not compel a group selection interpretation.

Dawkins [29] has been even more insistent than Williams in rejecting group selection, in the process going further in arguing for the primacy of the gene rather than individual as a still more basic unit of selection. Subsequent work suggests that there certainly are phenomena best understood at the level of the gene.

Consider, for example, meiotic drive, also known as segregation distortion. This refers to any process which causes one gametic type to be over- or under-represented in the gametes formed during meiosis, and hence in the next generation. A classic example of meiotic drive concerns the T locus in mice. This locus controls tail length, but also the viability of the mouse. The following facts apply—TT homozygotes have normal long tails, Tt heterozygotes have short tails, which is presumably somewhat disadvantageous, and tt homozygotes are sterile. If this were the whole story, there would be unambiguous selection against the t allele. However, the wrinkle is that the Tt heterozygotes transmit the t allele with about probability 90% to their sperm, rather than the usual Mendelian 50%. Hence when the t allele is rare, this strong meiotic drive will overcome the slight fitness disadvantage of short tails and the frequency of the t allele will increase. Eventually, the tt homozygotes will occur with appreciable frequency, and there will be an equilibrium mixture of the two alleles. This exhibits two levels of selection: positive selection for t haplotypes at the level of the gene, but negative selection for tt individuals at the level of the organism.

We want to be clear in recognizing the primacy of the gene as the unit of evolutionary selection. At the same time, there are many cases where the interests of the gene and the individual do not conflict. In addition, it is often difficult to give concrete form to the notion of the gene as the unit of
selection, given our ignorance of the details of the transformation of genes into individual traits, particularly for complex behavioral characteristics. (Grafen [54] advocates finessing such detailed questions on the genetic basis of individual variation, an argument refereed to as his “phenotypic gambit.”) Hence, despite the theoretical primacy of the gene, we restrict attention here to the comparison between individual level and the group level of selection.

4.3.1 The Haystack Model

In order to fix ideas, we consider the classic haystack model, offered by Maynard Smith [81] to study the issue of individual selection versus group selection. Our account simplifies the standard model in several ways. Perhaps most importantly, reproduction here is assumed here to be asexual.

There are a number of haystacks in a farmer’s field, where each haystack is home to two mice. Each pair of mice plays the prisoner’s dilemma, with the usual two choices—cooperate or defect. Payoffs for each individual take the concrete form of the number of offspring. Offspring inherit their mother’s choice of strategy. There are a number of subsequent stages of play, where the mice in each haystack are paired at random. The number of individuals within the haystack choosing each strategy then grows in an endogenous fashion, as does the overall size of the group. Every so often, once a year, say, the haystacks are removed, and the mice are pooled into a single large population. Now pairs of mice are selected at random from the overall population to recolonize the next set of haystacks, and excess mice die.

To give an example, consider the following version of the prisoner’s dilemma:

\[
\begin{array}{c|cc}
&C & D \\
\hline
C & 2, 2 & 0, 4 \\
D & 4, 0 & 1, 1 \\
\end{array}
\]

As a further simplification, suppose that there are a large number of haystacks and therefore individuals, although this convention facilitates group selection and hence is not innocent. Suppose that the initial fraction of C’s in the population is \( f \in [0, 1] \). Hence the fraction of haystacks that are colonized by 2 C’s is \( f^2 \); the fraction that are colonized by 2 D’s is \( (1 - f)^2 \); and the fraction that have one of each is \( 2f(1 - f) \). There are \( T \) rounds of play within each haystack. It follows that each pair of C’s gives rise to \( 2^{T+1} \) descendants, who are also C’s. Each pair of D’s gives rise to just 2 D’s. Each pair of one C and one D gives rise to 4 D’s.

At the end of the \( T \) periods of play, the new fraction of C’s in the
population is,
\[ f' = \frac{2^{T+1} f^2}{2^{T+1} f^2 + 8 f (1-f) + 2 (1-f)^2} \]

Let us check first what happens if \( T = 1 \). In this case, \( f' < f \) if and only if
\[
4 f < 4 f^2 + 2 (1 - f) (3 f + 1) = 2 + 4 f - 2 f^2 \iff f < 1.
\]

That is, in this case, the \( D \)'s will increase, and \( f \to 0 \). This is not surprising, since with \( T = 1 \), we simply have an elaborate description of the usual prisoner’s dilemma—the extra generality available in the structure of the haystack model is not used. Pairs are broken up immediately so that there is no opportunity to exploit the total payoffs for the haystack/group that arise from two initial \( C \)'s.

These total payoffs may quickly outstrip those from any other possible starting combination of mice. Consider then \( T > 2 \), in which case we have \( f' > f \) as long as \( f \) is close enough to 1. Indeed, this is true if and only if
\[
2^{T+1} f > 2^{T+1} f^2 + 8 f (1-f) + 2 (1-f)^2 = 2^{T+1} f^2 + 2 (1-f) (3 f + 1)
\]
which in turn holds if and only if
\[ T(f) = 2^{T+1} f^2 + 2 (1-f) (3 f + 1) - 2^{T+1} f < 0. \]

Moreover, this follows for all \( T > 2 \), since
\[
T(1) = 0, \text{ and } T'(1) = 2^{T+2} - 8 - 2^{T+1} = 2^{T+1} - 8 > 0.
\]

The differential growth rate of groups founded by cooperators is thus sufficiently strong as to allow cooperation to dominate a population whose initial proportion of cooperators is sufficiently large. Cooperation is rescued in the prisoners’ dilemma by group selection.

Maynard Smith’s intention here was to give the devil his due by building a model in which group selection might well have an effect. At the same time, he wished to show that the assumptions needed to make group selection comparable in strength to individual selection would be unpalatable. First, in order for group selection to be effective in the haystack model, there must be a large number of groups. Otherwise, with only a small number of groups, there is a chance of losing all the \( C \)s due to sampling, even if there are many \( C \)s to start with. The same could be said about the \( D \)s, of course, but the situation is asymmetrical, since to generate no \( D \)s requires forming all groups with only \( C \)s, while all of the \( C \)s will be lost even if there are many groups with a single \( C \).
Second, there must be a mechanism that insulates the groups from one another. Only then can a cooperative group be immune to infection by a defecting individual, and maintain its greater growth rate. Groups must thus be isolated from the appearance of migrating $D$s as well as $D$ mutants. Third, even with the temporary insulation of each haystack in this model, cooperation will only evolve if there are sufficient rounds of play within each haystack, so that cooperation amasses a sufficient advantage as to survive the next sampling.

A widespread view within biology is that group selection is logically coherent, but that the requirements of a large number of groups, sufficient isolation of groups, barriers to migration and mutation, and differential group success rates, all combine to limit the applicability of group selection. Intuitively, a loose description of the problem with group selection is that it relies too heavily upon a group becoming extinct as a likely consequence of a choice that is bad for the group. There is clearly scope in reality for individual selection, since individuals die frequently. Group selection strikes many as less plausible.

### 4.3.2 Selection Among Equilibria

When does group selection matter in biology? Most of the attention has been devoted to the possibility of group selection leading to different results than would individual selection, as in the prisoner’s dilemma. However, there is a compelling alternative scenario in which group selection may well operate robustly, in any species. This is as a mechanism to select among equilibria (Boyd and Richerson [15, 14]).

Consider a population that is divided into various subpopulations, largely segregated from one another, so that migration between subpopulations is limited. The members of each subpopulation are randomly matched to play the same symmetric game, which has several symmetric equilibria. For example, suppose the game is the simplest $2 \times 2$ coordination game:

\[
\begin{array}{cc}
A & B \\
A & 2, 2 & 0, 0 \\
B & 0, 0 & 1, 1 \\
\end{array}
\]

Individual selection ensures that some equilibrium is attained within each subpopulation. In general, some subpopulations would play the $A$ equilibrium, and some would play the $B$ equilibrium. Each of these configurations is internally robust. That is, if there were the occasional $B$ arising by mutation in an $A$ subpopulation, it would find itself at a disadvantage and would
die out. Similarly an $A$ mutant in a $B$ population would die out, despite the ultimate advantage of getting to the all-$A$ configuration. Alternatively, a small group of individuals may occasionally migrate from one subpopulation to another. If the newcomers did not match the prevailing action in their new subpopulation, the newcomers will die out.

But think about the competition between subpopulations. The $A$ subpopulations grow faster than do the $B$ ones. Eventually, then, it is reasonable to suppose the $B$ ones eventually die out completely. That is, group selection is free to operate in a leisurely fashion to select the Pareto superior equilibrium. There is no tension here between the two levels of selection, and hence no calculations that need to be made about the number of groups or rates of mutation and migration. Indeed, given enough time, virtually any group structure will lead to a population dominated by the Pareto superior equilibrium. The implication, in Boyd and Richerson’s [15, 14] view, is that group selection theories have missed the boat by concentrating on the prisoners’ dilemma. The true strength of group selection may be not to motivate behavior at odds with individual selection, but as a force mitigating between various contenders for the outcome of individual selection.

### 4.3.3 Group Selection and Economics

Why does group selection matter in economics? Group selection is the most obvious mechanism for generating preferences in humans to behave in the social interest rather than that of the individual. At stake then is nothing less than the basic nature of human beings.

As an economist, one should be skeptical of the need to suppose that individuals are motivated by the common good. Economic theory has done well in explaining a wide range of phenomena on the basis of selfish preferences, and so the view of the individual as the unit of selection is highly congenial to economists. Furthermore, to the extent that armchair empiricism suggests that non-selfish motivations are sometimes present, these seem as likely to involve malice as to involve altruism. For example, humans seem sometimes motivated by relative economic outcomes, which involve apparently involves a negative concern for others. Group selection is a blunt instrument that might easily “explain” more than is true.

There are, nevertheless, some aspects of human economic behavior that one is tempted to explain by group selection. For example, human beings are often willing to trade with strangers they will likely never see again, as might be analogous to cooperating in the one-shot prisoner’s dilemma. There is no shortage of reliable data showing that human beings are capable
of such apparently irrationally cooperative behavior, in appropriate circumstances. Whatever the underlying reasons for this, it is a significant factor in supporting our modern economic and social structure.

It is sometimes argued that the structure of hunter-gatherer societies helps account for such cooperative behavior. Hunter-gatherer societies were composed of a large number of relatively small groups, and individuals within each group were often genetically related. Perhaps, so the argument goes, we acquired an inherited psychological inclination towards conditional cooperation in such a setting, partly perhaps as a result of group selection. These inclinations then carried over into modern societies, despite genetic relatedness now being essentially zero on average.

It is hard to believe, however, that hunter-gatherers never encountered strangers. If there were good reasons to condition on this distinction, why would corresponding different strategies not have evolved? Why wouldn’t we now use the “defect against strangers” response nearly always? Even if we did somehow acquire a genetic inclination to cooperate in archaic societies, shouldn’t we now be in the process of losing this inclination in modern large and anonymous societies?

Sober and Wilson [132] push energetically for a rehabilitation of group selection within biology. They argue that kin selection—the widely accepted notion that individuals are selected to favor their relatives—should be regarded as a special case of group selection. Sober and Wilson certainly make the case that these phenomena can be viewed in an integrated fashion. Indeed, what matters most fundamentally is the likelihood that altruistic individuals will be preferentially matched with other altruistic individuals. However, the mechanisms for achieving this are quite different for kin selection and group selection, so, despite the formal similarities that exist, acceptance of the former does not require acceptance of the latter. In the end, a skeptical but not dogmatic view of the importance of group selection to human economic behavior seems warranted.

4.3.4 Implications

Of all the topics considered in this essay, group selection has perhaps the widest range of potential applications. With the appropriate model, group selection allows us to rationalize almost any behavior. This may explain why biologists, though readily conceding the logical coherence of group selection arguments, typically exhaust all other avenues before turning to group se-
lection as an explanation.⁵⁰ We view finding ways to assess group selection arguments, and to separate those circumstances in which group selection is an essential element of an explanation from those in which it provides a convenient alternative story, as one of the foremost challenges facing those working on the evolutionary foundations of economic behavior.

5 Concluding Remark

This essay has addressed a broad subject area, and has all too predictably touched only a fraction of it, despite consuming many pages. We believe there is much to be learned, and much yet to be done, in studying the evolutionary foundations of discounting, and of economic behavior more broadly. Pursuing these topics should bring economists increasingly into contact with work in biology and psychology, both of which have much to offer. We have no doubt that we can continue to produce elegant evolutionary models. Will they remain simply nice models, or will they serve as the basis for the type of applied work that motivates our interest in them? This remains to be seen.

6 Proofs

6.1 Proof of Proposition 1

We provide the proof for the case in which \( N(0) = \left( \frac{1}{T}, \ldots, \frac{1}{T} \right) \). Relaxing this assumption requires only more tedious notation.

Fix a time \( t \). Let \( \tau_t \) identify the event that the period-\( t \) Leslie matrix features \( x_{\tau_t} \neq 0 \) (and all other \( x_{\tau_{t'}} = 0 \)). We say in this case that environment \( \tau_t \) has been drawn in period \( t \). Then only parents of age \( \tau_t \) reproduce in period \( t \), having \( x_{\tau_t} \) offspring. There are \( S^t \tau_t N_0(t - \tau_t) \) such parents, so that we have

\[
N_0(t) = S^t \tau_t x_{\tau_t} N_0(t - \tau_t).
\]

We can perform this operation again. Let \( \tau_{t - \tau_t} \) be the environment drawn at time \( t - \tau_t \). Then we have

\[
N_0(t) = S^{\tau_t} x_{\tau_t} S^{\tau_{t - \tau_t}} x_{\tau_{t - \tau_t}} N_0(t - \tau_t - \tau_{t - \tau_t}).
\]

⁵⁰One is reminded in this respect of Wilson’s [146] caution to economists that reputation models may well make things too easy to explain.
Continuing in this fashion, we have
\[ N_0(t) = S^t x_{\tau_1} x_{\tau_1-\tau_1} x_{\tau_1-\tau_1-\tau_1} x_{\tau_1-\tau_1-\tau_1-\tau_1} \cdots \frac{1}{T} \]
for a sequence \( \tau_t, \tau_{t-\tau_1}, \tau_{t-\tau_1-\tau_1}, \tau_{t-\tau_1-\tau_1-\tau_1}, \ldots \) with the property that \( \tau_t \) is the environment drawn in period \( t \), \( \tau_{t-\tau_1} \) is the environment drawn in period \( t-\tau_t \), \( \tau_{t-\tau_1-\tau_1} \) is the environment drawn in period \( t-\tau_t-\tau_1 \), and \( \tau_{t-\tau_1-\tau_1-\tau_1} \) is the environment drawn in period \( t-\tau_t-\tau_1-\tau_1 \), and so on. The \( 1/T \) represents the initial mass of parents of the appropriate age, and the sequence \( \tau_t, \tau_{t-\tau_1}, \ldots, \tau_{t'}, \tau_{t''} \) has the properties
\[
\tau_t + \tau_{t-\tau_1} + \ldots + \tau_{t'} < t \quad \text{ (20)}
\]
\[
\tau_t + \tau_{t-\tau_1} + \ldots + \tau_{t'} + \tau_{t''} \geq t. \quad \text{ (21)}
\]
Hence, the final environment in this sequence, \( \tau_{t''} \), causes offspring to survive who are born to a generation of parents that were alive at time 0. The age of these parents at time 0 depends upon the period in which \( \tau_{t''} \) is drawn and the realization of \( \tau_{t''} \), and may be any of the generations alive at time 0. Since there are \( 1/T \) of each age at time 0, the final \( 1/T \) is applicable regardless of which time-0 age is relevant.

We can then write
\[
N_0(t) = \frac{1}{T} S^t \prod_{\tau=1}^{T} x_{\tau}^{r_{\tau}(t)}
\]
and hence, taking logs and then dividing by \( t \),
\[
\frac{1}{t} \ln N_0(t) = \ln S + \sum_{\tau=1}^{T} \frac{r_{\tau}(t)}{t} \ln x_{\tau} - \frac{\ln T}{t}, \quad \text{ (22)}
\]
where \( r_{\tau}(t) \) is the number of times environment \( \tau \) is drawn in the sequence \( \tau_t, \tau_{t-\tau_1}, \tau_{t-\tau_1-\tau_1}, \tau_{t-\tau_1-\tau_1-\tau_1}, \ldots, \tau_{t''} \). Our analysis then rests on examining the numbers \( r_1(t), \ldots, r_T(t) \). Notice that so far, we have made no use of independence assumptions, having only rearranged definitions. Independence plays a role in examining the \( r_{\tau}(t) \).

The argument now proceeds along the following lines:

- As \( t \) gets large, each of the \( r_{\tau}(t) \) converges to \( R_{\tau}/T \), where \( R_{\tau} \) is the total number of draws in the sequence, since each environment is equally
likely and environments are drawn independently each time one is
drawn. This gives
\[
\lim_{t \to \infty} \sum_{\tau = 1}^{T} \frac{r_\tau(t)}{t} \ln x_\tau = \lim_{t \to \infty} \sum_{\tau = 1}^{T} \frac{R_\tau}{T \tau} \ln x_\tau.
\]

- From (20)–(21), the total number of draws \( R_t \) is determined approximately (with the approximation arising out of the fact that the parents of those offspring who survive as a result of draw \( \tau_{\nu} \) may be older than 1 at the beginning of the process, and with the approximation thus becoming arbitrarily precise as the number of draws increases) by
\[
\sum_{\tau = 1}^{T} \frac{R_\tau}{T} = \sum_{\tau = 1}^{T} \frac{t}{T} = t.
\]

- This is the statement that the total of the reproductive lengths drawn in the course of the sequence \( \tau_1, \tau_{t-\tau_1}, \tau_{t-\tau_1-\tau_{t-\tau_1}}, \tau_{t-\tau_1-\tau_{t-\tau_1-\tau_{t-\tau_1}}}, \ldots, \tau_{t_{\nu}} \) must equal \( t \). This gives
\[
\lim_{t \to \infty} \sum_{\tau = 1}^{T} \frac{r_\tau(t)}{t} \ln x_\tau = \frac{\sum_{\tau = 1}^{T} \ln x_\tau}{\sum_{\tau = 0}^{T} \tau}.
\]

Inserting this in (22) gives (7), the desired result.

Our first step in making this argument precise is to confirm that the random draws determining the environments in the sequence \( \tau_1, \tau_{t-\tau_1}, \tau_{t-\tau_1-\tau_{t-\tau_1}}, \tau_{t-\tau_1-\tau_{t-\tau_1-\tau_{t-\tau_1}}}, \ldots, \tau_{t_{\nu}} \) are independent. This is not completely obvious. While the environment is determined independently in each period, the identities of the periods at which the draws are taken in this sequence are endogenously (and hence randomly) determined, potentially vitiating independence.

To examine this question, we construct a model of the stochastic process determining the environment. Consider the measure space \((0, 1], \mathcal{B}, \lambda)\), where \( \lambda \) is Lebesgue measure and \( \mathcal{B} \) is the Borel \( \sigma \)-algebra. We now model the process determining the environment by letting \( \xi(1) \) be a random variable defined by
\[
\omega \in \left( \frac{\tau - 1}{T}, \frac{\tau}{T} \right) \Rightarrow \xi(1)(\omega) = \tau, \quad \tau = 1, \ldots, T.
\]
We then define $\xi(2)$ by

$$\omega \in \left\{ \left( h + \frac{\tau - 1}{T^2}, h + \frac{\tau}{T^2} \right) \text{ for some } h \in \{0, 1, \ldots, T\} \right\} \Rightarrow \xi(2)(\omega) = \tau, \quad \tau = 1, \ldots, T.$$  

Continuing in this fashion gives a countable sequence of random variables that are independent and that each are equally likely to take each of the values $1, 2, \ldots, T$. We interpret $\xi(t)$ as determining the environment at time $t$. But it is now a straightforward calculation that

$$\Pr\{\xi(t) = \tau, \xi(t - i) = \tau'\} = \frac{1}{T^2}$$

for any $\tau$ and $\tau'$, and hence that $\xi(t)$ and $\xi(t - t_t)$ are independent. This in turn ensures that the sequence $\tau_t, \tau_{t-t_t}, \tau_{t-t-t_t-t_t}, \tau_{t-t-t-t_t-t_t-t_t-t_t}, \ldots, \tau_{t''}$ is independent.

Let

$$K \equiv \sum_{\tau=1}^{T} \tau.$$  

Our goal is to show that with probability one,

$$\lim_{t \to \infty} \frac{r_{\tau}(t)}{t} = \frac{1}{K}, \quad (A5)$$

which combines with (26) to imply (15), giving the desired result.

We now construct a model of the process determining the frequencies $r_{\tau}(t)$. To do this, consider the measure space $([0, 1], \mathcal{B}, \lambda)$, where $\lambda$ is Lebesgue measure and $\mathcal{B}$ is the Borel $\sigma$-algebra. Let $\zeta(1)$ be a random variable defined by

$$\omega \in \left( \frac{\tau - 1}{T}, \frac{\tau}{T} \right) \Rightarrow \zeta(1)(\omega) = \tau, \quad \tau = 1, \ldots, T.$$  

We then define $\zeta(2)$ by

$$\omega \in \left\{ \left( h + \frac{\tau - 1}{T^2}, h + \frac{\tau}{T^2} \right) \text{ for some } h \in \{0, 1, \ldots, T\} \right\} \Rightarrow \zeta(2)(\omega) = \tau, \quad \tau = 1, \ldots, T.$$  

Continuing in this fashion again gives a countable sequence of random variables that are independent and that each are equally likely to take each of the values $1, 2, \ldots, T$. In particular, having fixed $t$, we think of $\zeta(1)$ as describing the draw of the environment at time $t$. Then, noting that $\zeta(2)$ is independent of $\zeta(1)$ and has the same distribution as $\xi(t - t_t)$ regardless
of the value of \( \tau_t \), we think of \( \zeta_2 \) as describing the draw of the environment at time \( t - \tau_t \). Similarly, \( \zeta(3) \) describes the draw at time \( t - \tau_t - \tau_{t-\tau_t} \), and so on. The frequencies \( r_\tau(t) \) thus are determined by the draws from the collection \( \zeta(1), \ldots, \zeta(\hat{t}(t)) \) for some number \( \hat{t}(t) \). The time \( \hat{t}(t) \) is randomly determined and is given by

\[
\hat{t}(t) = \max\{t : \sum_{s=0}^{t-1} \tau_s < t\}. \tag{A6}
\]

Then \( r_\tau(t) \) is the number of times environment \( \tau \) is drawn by the random variables \( \zeta(1), \ldots, \zeta(\hat{t}(t)) \).

Fix \( \epsilon > 0 \) and define \( t'(t) \) (hereafter typically written simply as \( t' \)) to satisfy

\[
t'(t) \left( \left( \frac{1}{T} - \epsilon \right) K + T^2 \epsilon \right) = t. \tag{A7}\]

Notice that \( t > t'(t) \) (this is equivalent to \( T^2 > K \)) and that \( t' \) is linear and increasing in \( t \). Intuitively, \( t'(t) \) will be useful because (as we will see) with high probability \( t'(t) < \hat{t}(t) \), i.e., with high probability, the random stopping time has not yet been encountered by time \( t'(t) \).

Let \( p_i(t') \) be the number of times environment \( i \) is drawn by the random variables \( \zeta(1), \ldots, \zeta(t') \). Then choose \( t \) and hence \( t'(t) \) sufficiently large that, with probability at least \( 1 - \epsilon \), we have

\[
\frac{1}{T} - \epsilon < \frac{p_\tau(t')}{t'} < \frac{1}{T} + \epsilon \tag{A8}
\]

for \( \tau = 1, \ldots, T \). The strong law of large numbers ensures the existence of such \( t \). Let \( \Sigma \subset [0,1] \) be the event that these inequalities hold (and note that \( \lambda(\Sigma) \geq 1 - \epsilon \)). For our purposes, the key characteristic of \( \Sigma \) is that on \( \Sigma \),

\[
t' \left( \left( \frac{1}{T} - \epsilon \right) K + T \epsilon \right) \leq \sum_{s=1}^{t'} \zeta(s) \leq t' \left( \left( \frac{1}{T} - \epsilon \right) K + T^2 \epsilon \right) = t. \tag{A9}
\]

The term \( \sum_{s=1}^{t'} \zeta(s) \) is the sum of the realizations of the \( t' \) random variables \( \zeta(1), \ldots, \zeta(t') \). The left term is the smallest value this sum can take on \( \Sigma \), which is obtained by first assuming that every value \( i \in \{1, \ldots, T\} \) appears just often enough to attain the minimum frequency \( \frac{1}{T} - \epsilon \) (giving the term \( \left( \frac{1}{T} - \epsilon \right) K \)), and then that all additional draws \( (t'(1 - (\frac{1}{T} - \epsilon)T) = t'T \epsilon \) of them) all give environment 1. The third term is the largest value this
sum can take on $\Sigma$, which is obtained by first assuming that every value $i \in \{1, \ldots, T\}$ appears just often enough to attain the minimum frequency $\frac{1}{T} - \epsilon$ (giving the term $\left(\frac{1}{T} - \epsilon\right) K$), and then that all additional draws ($t'(1 - \left(\frac{1}{T} - \epsilon\right)T) = t'T\epsilon$ of them) all give environment $T$. Comparing with (A6), (A9) is the statement that on $\Sigma$, $t'(t) < \hat{t}(t)$, and hence on $\Sigma$, all of the random variables $\zeta(1), \ldots, \zeta(t')$ are relevant.

We now put bounds on $r_\tau(t)/t$. First, note that (using (A7) for the first equality)

$$t - t' \left(\left(\frac{1}{T} - \epsilon\right) K + T\epsilon\right) = t' \left(\left(\frac{1}{T} - \epsilon\right) K + T\epsilon\right) - t' \left(\left(\frac{1}{T} - \epsilon\right) K + T\epsilon\right) = t'(T^2 - T)\epsilon.$$ 

Then, on $\Sigma$, we have

$$\frac{\rho_\tau(t')}{t} \leq \frac{r_\tau(t)}{t} \leq \frac{\rho_\tau(t') + t'(T^2 - T)\epsilon}{t}.$$ 

In particular, a lower bound on $r_\tau(t)$ is given by assuming that no further draws of environment $\tau$ occur past time $t'$, giving $r_\tau(t) = r_\tau(t')$. An upper bound is given by assuming that every subsequent draw is environment $\tau$, and that there are $t - t' \left(\left(\frac{1}{T} - \epsilon\right) K + T\epsilon\right) = t'(T^2 - T)\epsilon$ such draws.

Inserting lower and upper bounds for $\rho_\tau(t')$ (given that we are in $\Sigma$) in the appropriate places, this is (cf. (A8))

$$\frac{t' \left(\frac{1}{T} - \epsilon\right)}{t} \leq \frac{r_\tau(t)}{t} \leq \frac{t' \left(\frac{1}{T} - \epsilon\right) + (T^2 - T)\epsilon}{t}.$$ 

and, using (A7),

$$\frac{1}{T} - \epsilon \leq \frac{r_\tau(t)}{t} \leq \frac{1}{T} - \epsilon + (T^2 - T)\epsilon.$$ 

There thus exist constants $0 < c < \overline{c}$ such that, for any sufficiently small $\epsilon$ and for all sufficiently large $T$,

$$\Pr \left\{ \frac{1}{K} - c\epsilon < \frac{r_\tau(t)}{t} < \frac{1}{K} + \overline{c}\epsilon \right\} \geq 1 - \epsilon$$ 

which implies (A5).
6.2 Proof of Proposition 2

The Leslie matrices identifying the two environments are:

\[
A = \begin{bmatrix}
Dx_1 & D \\
0 & 0
\end{bmatrix}
\]

\[
B = \begin{bmatrix}
0 & D \\
Dx_2 & 0
\end{bmatrix}.
\]

The transition matrix between environments, \(M\), is given by

\[
M = \begin{bmatrix}
\alpha & 1 - \alpha \\
1 - \alpha & \alpha
\end{bmatrix}.
\]

We then note that the stationary distribution of the matrix \(M\) attaches probability 1/2 to each environment. We consider the case in which the initial environment is drawn from this stationary distribution, so that the prior expectation for any period is also this distribution. (If the initial environment is drawn from some other distribution, we need only let the process run sufficiently long that it is almost always near the stationary distribution.) Note that

\[
M^2 = \begin{bmatrix}
\alpha^2 + (1 - \alpha)^2 & 2(1 - \alpha)\alpha \\
2(1 - \alpha)\alpha & \alpha^2 + (1 - \alpha)^2
\end{bmatrix} = \begin{bmatrix}
1 - 2(1 - \alpha)\alpha & 2(1 - \alpha)\alpha \\
2(1 - \alpha)\alpha & 1 - 2(1 - \alpha)\alpha
\end{bmatrix}.
\]

We now construct a backward chain. Note first

\[
\Pr(s_{t-1} = A|s_t = A) = \frac{\Pr(s_t = A|s_{t-1} = A)\Pr(s_{t-1} = A)}{\Pr(s_t = A|s_{t-1} = A)\Pr(s_{t-1} = A) + \Pr(s_t = A|s_{t-1} = B)\Pr(s_{t-1} = B)} = \frac{\alpha\frac{1}{2}}{\alpha\frac{1}{2} + (1 - \alpha)\frac{1}{2}} = \alpha.
\]

Similarly,

\[
\Pr(s_{t-2} = A|s_t = B) = \frac{\Pr(s_t = B|s_{t-2} = A)\Pr(s_{t-2} = A)}{\Pr(s_t = B|s_{t-2} = A)\Pr(s_{t-2} = A) + \Pr(s_t = B|s_{t-2} = B)\Pr(s_{t-2} = B)} = \frac{2(1 - \alpha)\alpha\frac{1}{2}}{2(1 - \alpha)\alpha\frac{1}{2} + (1 - 2(1 - \alpha)\alpha)^\frac{1}{2}} = 2(1 - \alpha)\alpha.
\]
The backward chain, giving the state in either period $t-1$ or $t-2$ as a function of the current state (the former if the current state is $A$, the latter if $B$), is then given by
\[
\begin{pmatrix}
\alpha & 1 - \alpha \\
2(1 - \alpha)\alpha & 1 - 2(1 - \alpha)\alpha
\end{pmatrix}.
\]
We now reverse our view of the process, starting our numbering at the end, and think of this as a forward chain, giving the state in period $t+1$ as a function of the state in period $t$. The stationary distribution of this chain solves
\[
[p, 1-p] \begin{pmatrix}
\alpha & 1 - \alpha \\
2(1 - \alpha)\alpha & 1 - 2(1 - \alpha)\alpha
\end{pmatrix} = \begin{pmatrix} p \\ 1 - p \end{pmatrix},
\]
giving
\[
\begin{align*}
p\alpha + 2(1 - \alpha)\alpha(1 - p) &= p \\
2(1 - \alpha)\alpha(1 - p) &= p(1 - \alpha) \\
2\alpha(1 - p) &= p \\
2\alpha - 2\alpha p &= p
\end{align*}
\]
\[
\begin{align*}
p &= \frac{2\alpha}{1 + 2\alpha} \\
1 - p &= \frac{1}{1 + 2\alpha}.
\end{align*}
\]
Now we fix a time $T$ and calculate how many draws $t$ will be taken from the forward chain by time $T$, which is given by
\[
\left[ \frac{2\alpha}{1 + 2\alpha} + \frac{1}{1 + 2\alpha} \right] t = T.
\]
Our expression for the population at time $T$ is then given by
\[
N_T = \left( x_1^p x_2^{1-p} \right)^T = \left( x_1^{\frac{2\alpha}{1 + 2\alpha}} x_2^{\frac{1}{1 + 2\alpha}} \right)^T \frac{T}{2\alpha + 1} + \frac{2}{1 + 2\alpha}
\]
and hence
\[
\frac{1}{T} \ln N_T = \ln \left( x_1^{\frac{2\alpha}{1 + 2\alpha}} x_2^{\frac{1}{1 + 2\alpha}} \right)^\frac{T}{2\alpha + 1} + \frac{2}{1 + 2\alpha} = \ln \left( x_1^{\frac{2\alpha}{1 + 2\alpha}} x_2^{\frac{1}{1 + 2\alpha}} \right) + 2\alpha \ln x_1 + \ln x_2 = \frac{2\alpha \ln x_1 + \ln x_2}{2 + 2\alpha}.
\]
References


