

An Evolutionary Approach Towards Time Preferences*

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Abstract

Genes are assumed to generate choice behavior in an environment where there are intertemporal tradeoffs. A gene survives the evolutionary process if it is not possible for a rare mutant gene to grow at a faster rate. Our goal is to represent the choice behavior of the surviving genes by a preference relation. We show that if choices affect the number of offspring but not the descendants' reproductive ability, this representation is time consistent, the discount factor is the inverse of the population growth factor, and the felicity functions are the products of the reproduction functions and the survival probabilities.

We also show that if newborn offspring are heterogeneous, for example due to transfers from parents, the preference representation is more subtle. The discount factor is still the inverse of the population growth factor, but the felicity function is essentially the sum of the expected discounted *reproductive values* of the individuals whom the parents' choices affect.

Key words: evolution, time preferences.

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1 Introduction

Most models in economics take preferences as given and derive the choices induced by these preferences. We do just the opposite. We characterize the choice behavior that would survive evolution and then represent this choice behavior with preferences. That is, we identify the preferences that induce evolutionarily stable choice behavior.

We identify each choice behavior with a gene. Hence, the choices an individual makes during her lifetime are determined by her genes, where these are inherited from her parents. In the simplest case, without sexual reproduction, populations can be defined as a group of individuals having the same genes. Populations with different genes may grow at different rates. Only those genes that induce the highest possible population growth rate given the physical environment survive evolution.

Our focus is on time preferences. Hence, individuals in our model face intertemporal trade-offs: Their current choices affect their lives in the future. In particular, current choices affect not only current reproduction but also reproduction in the future. We show that the behavior associated with the gene that survives evolution has a simple utility representation. The surviving gene has a time-consistent utility representation in which the discount factor is the inverse of the population growth factor and the instantaneous utility functions are the products of the reproduction functions and the survival probabilities. A simple example illustrates our approach and some of our results.

Example. Suppose that an individual survives for sure from age zero to age one, and survives with probability p from age one to age two, but then dies. She has one unit of endowment which she can split between the ages one and two. In each of these periods, if she is alive, she transforms her endowment into offspring according to a concave, increasing reproduction function f . That is, if an individual is alive and uses x of her endowment in a certain period, then she produces $f(x)$ expected offspring in that period. Assume that $f'(0) = \infty$. Each individual faces the same environment. A gene is a decision rule $x \in [0, 1]$, determining the use of the endowment in the first period. The endowment available in the second period is $1 - x$. Since offspring have the same gene as their parents, they use the same rule.

Fix a gene, x , and denote the number of individuals who are one year old at time t by y_t . The following equation recursively defines the law of motion of y_t :

$$y_{t+1} = f(x)y_t + pf(1-x)y_{t-1}.$$

Indeed, all one year old individuals at time t , y_t , allocate x to reproduction. Hence, the number of one year old individuals at time $t + 1$ who had one year old parents at birth is $f(x) y_t$. Similarly, $pf(1 - x) y_{t-1}$ is the number of one year old individuals at time $t + 1$ whose parents were two years old when they were born.

Dividing both sides by y_t yields

$$\frac{y_{t+1}}{y_t} = f(x) + pf(1 - x) \frac{y_{t-1}}{y_t}.$$

It can be shown that there exists a value of g such that $y_{t+1}/y_t = g$ asymptotically. That is, no matter what the initial proportions of one-year-old and two-year-old individuals in the population, the gene x generates a constant asymptotic growth factor g . Therefore, the previous equation can be rewritten as

$$g^2 = gf(x) + pf(1 - x).$$

Let $g(x)$ denote the positive solution of this equation for g . Then

$$g^2(x) - f(x)g(x) - pf(1 - x) \equiv 0 \text{ for all } x \in [0, 1].$$

After differentiating this identity,

$$2g(x)g'(x) - f(x)g'(x) - f'(x)g(x) + pf'(1 - x) = 0.$$

Let x^* denote the gene generating the largest possible growth rate and set $g^* = g(x^*)$. Since x^* maximizes g , it satisfies the first-order condition $g'(x^*) = 0$. The previous displayed equation for $x = x^*$ becomes

$$f'(x^*) = pf'(1 - x^*)/g^*.$$

This equation implies that the optimal decision x^* solves

$$\max_x f(x) + \frac{pf(1 - x)}{g^*}. \tag{1}$$

Equation (1) means that when an individual makes choices, she behaves as if she maximizes the expected discounted value of her offspring, with the discount factor equal to the inverse of the population growth factor.¹ The intuition behind this observation is the following. If the population is in steady state growth, with growth factor g , the value

¹In this example, the optimal choice is just one point. The representation in (1) cannot then be unique.

of an offspring today, measured by her relative contribution to the gene pool, is g times as high as that of an offspring tomorrow. Thus offspring born a period later should be discounted by g .

The paper substantially generalizes the result in the example. In particular, the reproduction function and the choice set of an individual are allowed to depend on previous decisions, the age of the individual, and random variables. We also sketch why, if the set of choice problems an individual might face during her lifetime is rich enough, the preferences are uniquely identified.

We generalize the argument by introducing a *carrying capacity constraint* into our basic model. The constraint means that per capita reproduction is a decreasing function of total population and converges to zero as the total population goes to infinity. Such a constraint forces the long-run growth factor to be one. Nonetheless, the choice behavior that survives evolution still maximizes the growth factor. With this constraint, our model still predicts that utility functions are identical to reproduction functions, but the discount rate is forced to be zero. Hence, impatience depends merely on variations in expected fertility.

Offspring in the example are homogeneous. An individual's decision affects only the number of her offspring, not their reproductive ability. We also consider a model where individuals' choices influence the reproductive abilities of their descendants and, as a result, offspring are heterogeneous. For example, a parent might donate some of her resources to her offspring. Offspring with *rich* parents are likely to reproduce more than offspring with *poor* parents. In the presence of such altruism, the surviving gene no longer maximizes the discounted present value of offspring, and the utility representation becomes more subtle. An individual's *reproductive value* must be generalized beyond just the discounted present value of the expected number of offspring. We show that the surviving gene still has a time-consistent expected utility representation. The discount factor is the inverse of the population growth factor. The utility function at age t is the weighted sum of the generalized reproductive values of all individuals affected by the choices an individual makes at age t .

As a final key step towards greater realism, we introduce sexual reproduction into our model. This has substantial implications for which gene survives. To see this, suppose that parents can transfer resources to their offspring, and the reproductive value of offspring depend on these transfers. Further assume that an offspring inherits the gene of one of her parents, with equal probabilities for that of each parent. A parent cannot recognize the gene of the offspring. The surviving gene tends to make a smaller transfer to her offspring

because this offspring may not share this gene with the parent. The parent would rather use the resources released to improve her own reproductive value.

In this case, the surviving choice behavior maximizes its growth rate *as if its frequency was zero in the population*. The reason is the following. Take a population with a given gene. Under what conditions is it impossible for this population to be invaded by a mutant? Suppose then that an arbitrarily small proportion of the population is replaced by mutants. Mutants grow fastest initially if they maximize their growth rate taking into account that their frequency in the population is zero. Also notice that mutants can grow as fast as the original population just by following the same choice behavior. Hence, the only way to ensure that the mutants cannot grow strictly faster than the original population is for the choice behavior of the original population to maximize the growth rate of the associated gene as if its frequency was zero.

This implies that individuals still maximize the discounted present value of the sum of the expected reproductive values of all individuals affected by the choices, but they discount their offspring by an additional factor of two, their grandchildren by four, etc. This is because, if a gene's frequency is zero in a population, then the probability of the other parent having the same gene is zero, and hence, the probability that the offspring has the same gene is one half. This argument provides a rationale for why individuals discount their grandchildren twice as much as their children. This discounting arises even though, in the evolutionary equilibrium, all individuals have the same gene.²

Literature Review

Numerous papers contain the idea that evolution can at least partially explain preferences. The first is probably Becker (1976), who uses an evolutionary argument to explain altruism. Most papers on the evolution of preferences focus on attitudes towards risk and altruism. Overviews of the theories on the relationship between biology and economic behavior can be found in Robson (2001 and 2002). Here we review only some papers concerned with the evolution of time preferences.

The paper most closely related to ours is Rogers (1994). The author has exactly the same goal as we do: to explain time preferences by natural selection. Unfortunately, there are several problems with Rogers' model and analysis. Most importantly, perhaps,

²Bergstrom (1995) analyzes games played by siblings. He concludes that the strategy that cannot be invaded by a mutant chooses an action as if the opponent mimics this action with probability half. This is the same principle as here. That is, although, in equilibrium, siblings have the same genes and take the same actions, they behave as if this probability was only a half.

the preferences pinned down by Rogers do not generate evolutionarily optimal choice behavior, because his analysis applies the wrong notion of reproductive value. We discuss these issues in detail in Section 4.3. Robson and Szentes (2007) analyzes an example that fits to the framework of Rogers and provides a detailed discussion about the problems associated with Rogers (1994).

Hansson and Stuart (1990) consider a neoclassical growth model in which clans compete for shares of resources. A clan's production depends on the stock of clan-specific capital and on the total population of all clans. The clans face a carrying capacity constraint, meaning that per capita production decreases as total population rises. An individual is active for only one period, and a clan's behavior is described by a consumption-saving decision. Higher consumption results in higher immediate population growth but a smaller capital stock, and hence smaller output, for the next generation. The carrying capacity constraint means that the clans' size must be constant in the long-run equilibrium. As a result, evolution selects clans with a zero rate of time preference. Agents maximize the per capita steady state consumption of current and future generations.

Robson and Wooders (1997) also derive a zero rate of time preference in a growth model where total output depends on capital and labor. Both labor and capital in the model can be of many types. The per capita income of each type of labor determines its growth rate. The authors show that when the balanced growth rate is maximized, income must be distributed across individuals in accordance with marginal product pricing.

Both Hansson and Stuart (1990) and Robson and Wooders (1997) contribute to understanding the discounting of future generations. However, the choice problems that these papers investigate are not sufficient to characterize individual preferences and to establish a tight relationship between utility functions and fertility. In particular, the conclusion regarding the zero rate of time preference is an artifact of the simplicity of the choice problems.

Two recent papers conclude that evolution might produce time-inconsistent preferences. Samuelson and Swinkels (2005) assume that agents cannot process information perfectly. Agents make decisions based on incorrect priors. As a result, time-inconsistent preferences can survive evolution because they compensate for faulty information processing.

Dasgupta and Maskin (2005) argue that, during the evolutionary process, individuals could have faced the following type of typical choice problem. There are two random options, A and B . At time zero, option A is more attractive than option B . However, if A

has not yielded fruit after some time, option B becomes more attractive. As a result, an individual rationally chooses option A at time zero and switches to option B after some time. The authors argue that in modern times, individuals face atypical situations, which they did not face during the evolutionary process. They associate each modern option with an option more typically available before, perhaps A or B , for example. This may generate actual time inconsistency. In other words, Maskin and Dasgupta (2005) take the view that although evolution optimally shaped behavior, individuals behave suboptimally in civilized society. Unlike Samuelson and Swinkels (2005) and Maskin and Dasgupta (2005), we assume that neither the information structure nor individuals' choice problems change over time.

2 The Basic Environment

2.1 The Model

Time is discrete, and an individual lives for at most T periods. In every period, the individual has to make a choice from a certain set. These choices affect three objects related to the life of this individual: her choice sets in the future, her probabilities of survival, and the expected number of her offspring.

The Choice Sets.— The choice set at age t is a subset of Ω and is determined by the history of previous decisions and a stochastic variable. Let c_t denote the choice of an individual at age t , and c^t the history of choices up to age t , (c_1, \dots, c_t) . Let s^t be the realizations of a random variable that affects the choice set of the individual at age t . The random variables, $\{s^t\}_1^T$, can be autocorrelated and can be influenced by previous choices. Let β_t denote (c^{t-1}, s^t) and let B_t denote the set of all possible realizations of β_t . Finally, $b_t(\beta_t) \subset \Omega$ denotes the set from which an individual chooses at age t .

Fertility and Survival Probabilities.— An individual's choices and other random variables determine her survival probabilities and the expected number of her offspring. Assume that a newborn survives to age one with probability p_0 . The survival probability from age t to age $t + 1$ is $p_t(c_t, \alpha_t)$, where $\alpha_t = (c^{t-1}, \bar{s}^t)$, and \bar{s}^t is a realization of a random variable age t . The expected number of offspring at age t , conditional on being alive, is denoted by $f_t(c_t, \alpha_t)$. We refer to f_t as the age- t reproduction function. The random variables, $\{\bar{s}^t\}_1^T$, can again be autocorrelated and influenced by previous decisions. We also allow s^t and \bar{s}^t to be correlated. Let A_t denote the set of possible realizations of α_t .

The Genes. — Let C_t denote $A_t \times B_t$, and $\gamma_t = (\alpha_t, \beta_t)$. Let $\mu_t(\cdot : \gamma_{t-1}, c_{t-1})$ denote the probability measure over C_t conditional on (γ_{t-1}, c_{t-1}) .³ We define a gene as a collection of choice functions, $\{c_t\}_{t=1}^T$, where $c_t : C_t \rightarrow \Omega_t$, such that $c_t(\alpha_t, \beta_t) \in b_t(\beta_t)$ for all $\beta_t \in B_t$. That is, if an individual with a gene $\{c_t\}_{t=1}^T$ faces a choice set b at age t , and $\gamma_t = (\alpha, \beta)$, she chooses $c_t(\alpha, \beta) \in b$. Since offspring have the same genes as their predecessors, they make the same choices.

We have set up an abstract model to illustrate the generality of the results in this section. The following examples might illuminate the set-up here.

Example 1. Suppose that $T = 2$ and there is a single consumption good that can be transformed into offspring. The individual receives endowments according to a random process. Let I_i denote the endowment at age i ($i = 1, 2$). She can save at an interest factor $R (\geq 0)$. The individual survives until the age of two for sure, that is, $p_0 = p_1 \equiv 1$. The number of offspring at age one is $(h_1 c_1)^\theta$ where c_1 is the consumption in the first period, $h_1 (\in \mathbb{R})$ is a realization of a random variable determining the health of the individual at age one, and θ is a constant. The number of offspring at age 2 is $(\vartheta c_1 + c_2)^\theta$, where c_2 is the consumption at age two and ϑ is a constant.

The choice set of the individual at age one is determined by I_1 , that is, $s_1 = \beta_1 = I_1$. She can choose to consume anything in $[0, I_1]$, therefore $b_1(\beta_1) = [0, I_1]$. Her second period choice set depends on her endowments, I_1 and I_2 , and also on her consumption in the first period, c_1 , that is, $\beta_2 = (c_1, I_1, I_2)$ and $b_2(\beta_2) = R(I_1 - c_1) + I_2$. The fertility of the individual at age one is determined by h_1 and, at age two, it is influenced only by c_1 . Therefore, $\alpha_1 = \bar{s}_1 = h_1$ and $\alpha_2 = c_1$. ■

The next example shows that our model is general enough to accommodate the following trade-off of central biological interest. If an individual allocates more of her resources to reproduction her probability of survival decreases.

Example 2. Suppose that $T = 2$, and the individual receives random resources at ages one and two. Let y_1 and y_2 denote the amounts of these resources, and assume that $y_1, y_2 \in (0, 1)$. These resources represent the energy the individual has to allocate among different activities. The individual survives from age zero to age one with fixed probability p_0 . At age one, the individual allocates energy $e_1 \leq y_1$ to self-preservation, so surviving

³This notation allows events more than one period before age t to influence the distribution of γ_t , because γ_{t-1} can summarize those events. We do not need any Markovian restriction on the distributions of random variables.

from age one to age two with probability e_1 . The individual at age one also allocates energy $r_1 \leq y_1 - e_1$ to reproduction, so her expected number of offspring at age one is $A(r_1)^\theta$, where $A, \theta > 0$. The expected number of offspring of the individual at age two conditional on being alive is simply $A(y_2)^\theta$. Thus, the only choice the individual has is to allocate y_1 between e_1 and r_1 .

The choice set of the individual at age one is determined by y_1 , that is, $s_1 = \beta_1 = y_1$. She can choose any $(e_1, r_1) \in \mathbb{R}_+^2$ as long as $e_1 + r_1 \leq y_1$, therefore $c_1 = (e_1, r_1)$ and $b_1(\beta_1) = \{(e_1, r_1) \in \mathbb{R}_+ : e_1 + r_1 \leq y_1\}$. The fertility of the individual at age one is determined by r_1 alone, so $\alpha_1 = \bar{s}_1 = \emptyset$. At age two, the fertility is influenced only by y_2 , so $\alpha_2 = y_2$. ■

Our objective is to analyze the genes that induce the highest population growth rate. We assume that at time zero there is a measure $\lambda_t (\in (0, 1))$ of individuals of age t , all having the same gene. To apply the law of large numbers, we assume that the random variables described above are independent across individuals. Thus, although individuals face uncertainty, there are no aggregate shocks. We shall argue that the population growth rate corresponding to a gene is asymptotically constant and does not depend on the initial conditions, $\{\lambda_t\}_{t=1}^T$.

Population growth. — Fix a gene $c = \{c_t\}_1^T$. Let $a_t(c)$ denote the expected number of offspring of a t -year-old individual having gene c , where the expectation is formed at age zero.⁴ Let y_τ denote the measure of newborns at time τ . The law of motion of y_τ is:

$$y_\tau = \sum_{i=1}^T y_{\tau-i} a_i(c). \quad (2)$$

Pollard (1973), in Chapter 4.6, shows that if an equation like (2) describes the evolution of generations, then the population asymptotically grows at a fixed rate, so $y_\tau/y_{\tau-1} \equiv g(c)$ asymptotically. Hence (2) can be rewritten as

$$g(c) = \frac{y_\tau}{y_{\tau-1}} = \sum_{i=1}^T \frac{y_{\tau-i}}{y_{\tau-1}} a_i(c) = \sum_{i=1}^T \prod_{j=0}^{i-2} \frac{y_{\tau+j}}{y_{\tau+j+1}} a_i(c) = \sum_{i=1}^T \frac{a_i(c)}{g(c)^{i-1}}. \quad (3)$$

Given a gene c , the polynomial defined by (3) has T complex roots. The population growth factor is the largest modulus of any of these roots. Indeed, the root with the largest

⁴Formally,

$$a_t(c) = \int \cdots \int p_0 \prod_{i=1}^{t-1} p_i(c_i(\gamma_i), \alpha_i) f_t(c_t(\gamma_t), \alpha_t) \mu_t(\gamma_t : \gamma_{t-1}, c_{t-1}(\gamma_{t-1})) \cdots \mu_1(\gamma_1).$$

modulus is itself a positive real number (Pollard (1973) Chapter 4.6). Given equation (3), we can restate our objective formally: We seek to identify the gene, c , that maximizes $g(c)$ defined by (3).

In order to guarantee that the integrals defining $\{a_t(c)\}_{t=1}^T$ exist and that there exists a gene that maximizes the growth rate we need additional assumptions on the primitives of our model. It is clearly sufficient to assume that Ω and C_t are compact and p_t, f_t are continuous for $t = 1, \dots, T$.⁵

2.2 Results

Our goal in this section is to find a utility representation for the choices of the surviving genes. That is, we want to find a function, mapping from choices to real numbers, that is maximized by the surviving gene.

Recursive utility representation. — The collection of utility functions $\{U_t\}$ represents the collection of choices $\{c_t\}_{t=1}^T$ if

$$c_T(\gamma_T) = \arg \max_{c \in b_T(\beta_T)} U_T(c, \alpha_T) \quad \forall \gamma_T \in C_T \quad (4)$$

and, for all $t < T$ and $\gamma_t \in C_t$,

$$c_t(\gamma_t) = \arg \max_{c \in b_t(\beta_t)} U_t(c, \alpha_t) + E_t \left(\sum_{i=t+1}^T U_i(c_i, \alpha_i) \mid \gamma_t, c \right). \quad (5)$$

A recursive utility representation automatically implies a certain form of time consistency. The solution to an individual's maximization problem at age t involves her expectations about her decisions at ages $t + 1, \dots, T$. These expectations must be correct. Since the vector β_t directly influences only the choice sets, we do not allow the instantaneous utility to directly depend on this vector.⁶

Theorem 1 *The surviving gene has this utility representation:*

$$U_t(c_t, \beta_t) = \frac{p_0 \prod_{i=1}^{t-1} p_i(c_i, \alpha_i) f_t(c_t, \alpha_t)}{(g^*)^t}, \quad (6)$$

where g^* is the largest growth factor satisfying (3).

⁵Alternatively, one can assume that Ω and C_t are finite sets for $t = 1, \dots, T$.

⁶Allowing β_t to influence f_t would be similar to letting prices enter preferences in standard consumer theory.

Theorem 1 implies that an individual who has the surviving gene behaves as an expected utility maximizer with geometric discounting. The age- t instantaneous utility function is the age- t reproduction function multiplied by the survival probability to age t . The discount factor is the inverse of the population growth factor.⁷

Note that an age- t individual then maximizes

$$E \sum_{i=t}^T \frac{\prod_{j=t}^{i-1} p_j(c_j, \alpha_j) f_i(c_i, \alpha_i)}{(g^*)^{i-t}}. \quad (7)$$

This expression is the discounted present value of the expected number of offspring, conditional on being alive at age t . Fisher (1958) refers to (7) as the reproductive value of an individual.

Proof. Let \underline{C} denote the set of genes that have recursive utility representation defined by (6). Let \overline{C} denote the set of those genes that maximize the growth factor, g , characterized by (3). It is obviously enough to show that $\underline{C} = \overline{C}$.

The definition of recursive utility representation yields that $\{U_t\}_{t=1}^T$ represents the gene $c = \{c_t\}_{t=1}^T$ if and only if c is a solution for a T -period stochastic dynamic programming problem where the *return function* at time t is U_t and there is no discounting. It is well-known that c is a solution for this problem if and only if c maximizes

$$E_0 \left(\sum_{i=1}^T U_i(c_i, \alpha_i) \right),$$

when subject to the same constraints that appear in (4) and (5). Therefore, $c = \{c_i\}_{i=1}^T \in \underline{C}$ if and only if c maximizes the discounted age-one value of offspring, where the discounting is done according to g^* , and the expectations are formed at age zero. The discounted age-one value of the expected number of offspring of an individual is the right-hand-side of (3), $\sum_{i=1}^T a_i(c) / (g^*)^{i-1}$.

Suppose that $\bar{c} = \{\bar{c}_i\}_{i=1}^T \in \overline{C}$ and $\underline{c} = \{\underline{c}_i\}_{i=1}^T \in \underline{C}$. We show that $\bar{c} \in \underline{C}$ and $\underline{c} \in \overline{C}$. Let $g(\tilde{c})$ denote the growth factor induced by \tilde{c} . Then

$$g^* = \sum_{i=1}^T \frac{a_i(\bar{c})}{(g^*)^{i-1}} \leq \sum_{i=1}^T \frac{a_i(\underline{c})}{(g^*)^{i-1}} \leq \sum_{i=1}^T \frac{a_i(\underline{c})}{g(\underline{c})^{i-1}} = g(\underline{c}).$$

⁷This discount factor is not the familiar discount factor in economics associated with the pure rate of time preference. This is a convenient way to proceed here with no substantive implications. For one thing, the pure rate of time preference is often taken to incorporate mortality. But it is convenient that the present discount factor does not vary with age, despite mortality rates and reproduction functions that may well do so. Indeed, this age dependence implies it is not possible to even define a pure rate of time preference here in a straightforward way.

The first inequality follows from $\underline{c} \in \underline{\mathcal{C}}$, that is, \underline{c} maximizes the discounted age-one value of offspring at age zero. The second inequality follows from the observations that the right-hand side of (3) is weakly decreasing in g and $g^* \geq g(c)$. The equalities are (3) for $c = \bar{c}$ and $c = \underline{c}$ respectively. Since g^* is the maximum growth factor, it follows that $g^* \geq g(\underline{c})$, and hence, both inequalities must hold with equality. But

$$\sum_{i=1}^T \frac{a_i(\bar{c})}{(g^*)^{i-1}} = \sum_{i=1}^T \frac{a_i(\underline{c})}{(g^*)^{i-1}}$$

implies that $\bar{c} \in \underline{\mathcal{C}}$. Finally, $g^* = g(\underline{c})$ implies that $\underline{c} \in \bar{\mathcal{C}}$. ■

Identification of preferences. — A natural question is: Under what circumstances is the utility representation unique? Recall from standard consumer theory that the preferences of a consumer can be deduced from her behavior only if she faces enough choice problems. That is, to identify a consumer's preferences, one must observe the choices she makes from various budget sets. Similarly, our utility representation of the surviving gene is unique if and only if there is enough variation in the resource constraints. Instead of developing a general uniqueness theorem, we show by example that the representation is unique if there is enough variation in the resources an individual potentially has.

If $\{U_t\}_{t=1}^T$ is a utility representation of the surviving gene and $V_t = \theta U_t + \theta_t$, where $\theta, \theta_1, \dots, \theta_T \in \mathbb{R}_+$, then $\{V_t\}_{t=1}^T$ is also a utility representation of the gene. Hence we show uniqueness only up to these linear transformations.

Example 3. We modify the example described in the introduction as follows. An individual still lives for two periods and has the reproduction function f and survival probability $p (> 0)$. However, a newborn individual has endowment $b \in (0, \infty)$ to allocate between the two periods and faces a saving technology characterized by $R \in (0, \infty)$. The numbers b and R are realizations of independent random variables with full support on \mathbb{R}_+ , and are independent across individuals. If an individual saves $b - x$ of her resources, she receives $R(b - x)$ one period later. In this example, a gene is a function $c: (0, \infty)^2 \rightarrow [0, 1]$. That is, if an individual has endowment b and can save at interest factor R , she uses $c(b, R)$ of her endowment in the first period and $R(b - c(R))$ in the second period.

An argument identical to the one used in the example in the introduction yields that the following first-order condition uniquely identifies the surviving gene:

$$f'(c(b, R)) = \frac{Rp f'(R(b - c(b, R)))}{g^*} \quad \text{for all } (b, R) \in (0, \infty)^2, \quad (8)$$

where g^* is the largest possible growth factor.

For all $x, y \in (0, \infty)$, there exist $R, b \in (0, \infty)$ such that $c(b, R) = x$ and $R(b - c(b, R)) = y$.⁸ Let $R(x, y)$ denote the interest factor corresponding to x and y . The first-order condition, (8), can be rewritten as

$$f'(x) = \frac{R(x, y) p f'(y)}{g^*} \quad \text{for all } x, y \in (0, \infty).$$

Now suppose that $\{U_1, U_2\}$ are the instantaneous utilities in the preference representation. Then, by (8), $\{U_1, U_2\}$ must satisfy the following first-order condition for all $x, y \in (0, \infty)$:

$$U_1'(x) = \frac{R(x, y) U_2'(y)}{g^*}. \quad (9)$$

Fix $x_0 \in (0, \infty)$. Since the utilities can be determined only up to a linear transformation, normalize $U_1'(x_0)$ to be $f'(x_0)$. To establish uniqueness up to linear transformations, we now show that $U_1' = U_2' = f'$. Indeed, for all $y \in (0, \infty)$,

$$U_2'(y) = \frac{g^* U_1'(x_0)}{R(x_0, y)} = \frac{g^* f'(x_0)}{R(x_0, y)} = p f'(y),$$

where the first equality follows from (9), the second one from the normalization of $U_1'(x_0)$, and the third one from (8). Then from (9), for all $x \in (0, \infty)$,

$$U_1'(x) = \frac{g^* U_2'(y)}{R(x, y)} = \frac{g^* p f'(y)}{R(x, y)} = f'(x).$$

■

Commonly used preferences. — Next, we investigate the conditions under which Theorem 1 implies various restrictions on preferences that are often used by economists. A desired and often required property of preferences in dynamic models is time separability.

Remark 1 *The utility representation of the surviving gene is time separable if and only if the reproduction functions and survival functions do not depend on previous choices.*

Although, in general, utilities do depend on past choices, they never depend on future choices because future choices do not influence an individual's reproductive output. Therefore, our theory rejects those behavioral preferences in which the anticipation of future events directly enters into the felicities.

In addition to time separability, most models assume that an agent's utility function is age invariant.

⁸To see this, note that, if $R = f'(x) / [g^* p f'(y)]$ and $b = x + y/R$, the first-order condition in (8) is satisfied.

Remark 2 *The utility representation of the surviving gene is time separable and the instantaneous utility function is the same at all ages if and only if the reproduction functions and survival functions depend on neither previous decisions nor age.*

Most economic models also assume that the realization of states of the world has no impact on utility. Our model predicts that this is true only as long as the state of the world has no impact on fertility.

Remark 3 *The instantaneous utilities in the preference representation of the surviving gene are state independent if and only if the reproduction function and survival function do not depend on these states.*

A carrying capacity constraint. — A simple way to model a carrying capacity constraint is as follows.⁹ Assume that the reproduction function depends on total population, N , so the expected number of offspring at age t is $f_t(c_t, \alpha_t, N)$, where $\partial f_t / \partial N < 0$ and $\lim_{N \rightarrow \infty} \sup_{c_t, \alpha_t} f_t = 0$.

If, for a fixed N , a choice behavior induces a growth factor larger than one, the total population increases, which slows reproduction. Hence the population's growth rate declines and eventually is forced to be zero. Therefore, in a steady state, the total population must be constant, say at N^* . The choice behavior that survives evolution still maximizes g subject to (3). There is an additional constraint, however— N^* must be such that the g defined by (3) is equal to one.

The recursive utility representation with a carrying capacity constraint is identical to the representation described in Theorem 1, with $g^* = 1$. Any impatience is due to the age dependence of expected fertility. For example, individuals might prefer immediate rewards if fertility declines with age, so they can transform resources into offspring more efficiently today than tomorrow.

3 Altruism and Sex

This section develops the basic model further to provide a richer theory of intertemporal choices. So far, we have assumed that an individual's choices affect only the number of her offspring. In the first place, then, we consider a model in which an individual can transfer some of her endowment to her offspring, which increases their reproductive ability at the

⁹Hansson and Stuart (1990), for example, also introduce such a constraint.

cost of reducing her own. Such transfers derive from a parental endowment that may vary with parental age. Second, we explore the consequences of sexual reproduction. This reduces the level of parental concern for offspring. Both of these extensions have serious implications for the preferences representing the evolutionary optimal behavior.

3.1 Altruism

The utility representations in this section differ from those above because newborn individuals are no longer identical. As a consequence of the ability to transfer resources to future generations, individuals with wealthy parents are likely to receive more transfers and reproduce more. We shall show that the surviving gene therefore does not behave as if it maximizes the discounted present value of the expected number of descendants. Two offspring produced by a given individual at different ages may have different reproductive abilities and make different asymptotic contributions to the gene pool, so their *value* is different.

Suppose that an individual lives for at most T periods. In each period, the individual produces (asexually) exactly one offspring if she is still alive. Furthermore, at age t , an individual receives endowment I_t . The endowment I_t is a random variable distributed on \mathbb{R}_+ according to a c.d.f. G_t . An individual of age t survives until the next period with probability $p_t(c_t)$, where c_t is the individual's consumption at age t , and p_t is increasing. A newborn offspring surely survives until age one. A parent can transfer part of the endowment to her newborn offspring, who will certainly save it to age one, given that survival to age one is automatic. Let $s_t(I_t)$ denote the parental transfer to an offspring produced at age t if the parental endowment is I_t . The parent consumes whatever she does not transfer. One period later, the now one year old offspring receives $Rs(I_t)$, where $R \in \mathbb{R}_+$. For simplicity, when a one-year-old individual determines her transfer to her current newborn, she observes neither the income derived from her parent nor her parent's age. This one year old then consumes all of her remaining income and the transfer from her parent. A gene is a profile of saving decisions, $\{s_t\}_1^{T-1}$, where $s_t : \mathbb{R}_+ \rightarrow \mathbb{R}_+$.

Each individual in this model faces a trade-off: Consuming more increases the individual's own survival probability but decreases the probability that her newborn child will survive from age one to age two.

From the evolutionary perspective, it is often plausible that parents can only make transfers to their newborns but not to their older offspring. Indeed, parents in most

species are only in contact with their children at very early ages. Note also that one could interpret saving, in general, as body fat accumulation.

We could have specified a more complicated model in which individuals might have more than one offspring in each period, save for their own future, transfer resources to offspring older than one, or where consumption affects not only survival probabilities but also fertilities. However, the simple model is enough to demonstrate some of the subtleties associated with choices that have effects on the reproductive abilities of offspring.

Population growth and the surviving gene. — Fix a gene $\{s_i\}_1^{T-1}$. Introduce the following notation:

$$p^1(s) = \int_{\mathbb{R}_+} p_1(I_1 - s_1(I_1) + Rs) dG_1(I_1).$$

That is, $p^1(s)$ denotes the ex-ante probability that a newborn offspring survives until age two, given that her parent transferred s to her. Further, let

$$P_1^j = \int_{\mathbb{R}_+} p^1(s_j(I_j)) dG_j(I_j), \quad j = 1, \dots, T$$

then denote the ex-ante probability that a newborn offspring survives until age two, given she had a parent of age j .¹⁰ Let μ_j denote the steady state probability that an individual's parent is of age j . Then the unconditional probability of surviving until age two is

$$P_1 = \sum_{j=1}^T \mu_j P_1^j.$$

Furthermore, let

$$P_j = \int_{\mathbb{R}_+} p_j(I_j - s_j(I_j)) dG_j(I_j), \quad j = 2, \dots, T-1,$$

be the probability that an individual of age j ($j \geq 2$) survives until age $j+1$. Let y_τ denote the number of newborn offspring at time τ . The following equation defines the motion of y_τ :

$$y_\tau = y_{\tau-1} + y_{\tau-2}P_1 + y_{\tau-3}P_1P_2 + \dots + y_{\tau-T}P_1 \dots P_{T-1}. \quad (10)$$

We show in the Appendix that the growth factor of the population in steady state is

¹⁰Recall, an offspring certainly survives until age one.

implicitly defined by the following equation¹¹

$$g = P_1^1 \left(\frac{1}{g(g-1)} + \sum_{j=3}^T \frac{\prod_{k=2}^{j-1} P_k}{g^{j-1}(g-1)} \right) + \sum_{j=2}^T \frac{P_1^j}{g^{j-1}} \prod_{k=2}^{j-1} P_k. \quad (11)$$

Recall that, in the case of homogenous offspring, the right-hand side of the growth equation, (3), could be interpreted as the reproductive value of a newborn. We now show that the right-hand side of (11) has a similar natural interpretation.

Intuition and reproductive values. — It is less clear how one should define an individual's reproductive value in this model. A newborn individual with a wealthy parent receives a high transfer and is more likely to survive from age one to age two. How, then, can one compare the reproductive values of two newborns? Notice that at age two, before the realization of I_2 , all individuals are identical. Hence, a candidate for measuring the reproductive value of an individual is the discounted present value of the expected number of all two-year-old descendants, where the discounting factor is again the growth factor.

Fix a gene $\mathbf{s} = \{s_t\}_1^{T-1}$. Let $V_t(g, \mathbf{s})$ denote the reproductive value of an individual at age t , the discounted value of the expected number of two-year-old descendants, discounted by the factor g . At age T , an individual has one offspring who will survive until age two with probability P_1^T . Since the offspring will turn two years old in two years, she must be discounted by g^2 . At age one, the offspring also produces its own offspring, who survives until age two with probability P_1^1 . Further, each of these offspring produces one offspring at age one, and each such offspring survives with probability P_1^1 . Altogether,

$$V_T(g, \mathbf{s}) = \frac{P_1^T}{g^2} + P_1^1 \sum_{i=3}^{\infty} g^{-i} = \frac{P_1^T}{g^2} + \frac{P_1^1}{g^3} \frac{g}{g-1}. \quad (12)$$

Now consider the value of an individual at age $t < T$:

$$V_t(g, \mathbf{s}) = \left[\frac{P_1^t}{g^2} + \frac{P_1^1}{g^3} \frac{g}{g-1} \right] + \frac{P_t}{g} V_{t+1}. \quad (13)$$

The first and second terms correspond to the discounted present value of the two-year-old descendants of the individual's newborn offspring as in (12). The last term is the individual's own expected, discounted reproductive value. Equations (12) and (13) imply

¹¹In what follows, we adopt the following convention: $\prod_{i=a}^b x_i = 1$ if $a > b$.

that

$$V_t(g, \mathbf{s}) = \sum_{j=t}^T \frac{\prod_{k=t}^{j-1} P_k}{g^{j-t}} \left(\frac{P_1^1}{g^3} \frac{g}{g-1} + \frac{P_1^j}{g^2} \right). \quad (14)$$

Suppose that an individual at age t has endowment I_t . Intuitively, when making choices, she should maximize the properly discounted reproductive value of the individuals whom her choices affect. That is, she should solve the following maximization problem:

$$\max_{s \in [0, I_t]} p_t(I_t - s) \frac{V_{t+1}(g, \mathbf{s})}{g} + p^1(s) \frac{V_2(g, \mathbf{s})}{g^2}. \quad (15)$$

The first term in the maximization problem is the individual's own survival probability times her discounted reproductive value. The second term is the survival probability of her newborn until the age of two times the discounted reproductive value of this offspring.

Let g^* denote the largest possible growth factor and \underline{S} denote the set of genes that solves (15) with $g = g^*$ for all t and I_t . Let \bar{S} denote the set of those genes that maximize g subject to (11).

Lemma 1 $\underline{S} = \bar{S}$.

Proof. According to (14), the reproductive value of a two-year old individual is

$$\begin{aligned} V_2(g, \mathbf{s}) &= \frac{P_1^1}{g^2(g-1)} + \frac{P_1^2}{(g)^2} + P_1^1 \sum_{j=3}^T \frac{\prod_{k=3}^{j-1} P_k}{(g)^j(g-1)} + \sum_{j=3}^T P_1^j \frac{\prod_{k=2}^{j-1} P_k}{g^{j-2}} \\ &= P_1^1 \left(\frac{1}{g^2(g-1)} + \sum_{j=3}^T \frac{\prod_{k=2}^{j-1} P_k}{g^j(g-1)} \right) + \sum_{j=2}^T \frac{P_1^j}{g^j} \prod_{k=2}^{j-1} P_k. \end{aligned}$$

Hence, the growth equation (11) can be rewritten as

$$g(\mathbf{s}) = g(\mathbf{s}) V_2(g(\mathbf{s}), \mathbf{s}). \quad (16)$$

Suppose now that $\underline{\mathbf{s}} = \{\underline{s}_i\}_1^{T-1} \in \underline{S}$ and $\bar{\mathbf{s}} = \{\bar{s}_i\}_1^{T-1} \in \bar{S}$. Then

$$g^* = g^* V_2(g^*, \bar{\mathbf{s}}) \leq g^* V_2(g^*, \underline{\mathbf{s}}) \leq g(\underline{\mathbf{s}}) V_2(g(\underline{\mathbf{s}}), \underline{\mathbf{s}}) = g(\underline{\mathbf{s}}).$$

The equalities are just (16) for $\bar{\mathbf{s}}$ and $\underline{\mathbf{s}}$ respectively. The first inequality follows from $\underline{\mathbf{s}} \in \underline{\mathcal{S}}$, that is, $\underline{\mathbf{s}}$ maximizes $V_2(g^*, \cdot)$. The second inequality follows from $gV(g, \mathbf{s})$ being decreasing in g . Since $g^* \geq g(\underline{\mathbf{s}})$ both inequalities must hold with equality. From

$$g^*V_2(g^*, \bar{\mathbf{s}}) = g^*V_2(g^*, \underline{\mathbf{s}})$$

it follows that $\bar{\mathbf{s}} \in \underline{\mathcal{S}}$. Since $g^* = g(\underline{\mathbf{s}})$ it follows that $\underline{\mathbf{s}} \in \bar{\mathcal{S}}$. ■

Recursive utility representation. — We again can find a utility representation for the surviving gene, that is, for the behavior defined by the maximization problems in (15). It is useful to compute the reproductive value, $V_0(s)$, of a newborn whose parent transferred s to her. Notice that

$$V_0(s) = \frac{P_1^1}{g^{*3}} \frac{g^*}{g^* - 1} + \frac{p^1(s)}{g^{*2}}.$$

The reason is the following. First, $V_2(g, s) = 1$ by (16). At age one, each individual produces one offspring, who survives until age two with probability P_1^1 . In addition, each of the newborn offspring also produces one of her own offspring at age one, and each such offspring survives with probability P_1^1 . This explains the first term. Furthermore, the individual survives until the age of two with probability $p^1(s)$, when her reproductive value is one.

Proposition 1 *The surviving gene has this utility representation:*

$$U_t(s_t, s_1, \dots, s_{t-1}) = \frac{p_1(s_1) \cdots p_{t-1}(s_{t-1})}{g^{*t}} V_0(s_t). \quad (17)$$

Proof. See the Appendix. ■

This representation implies that at age t , an individual with income I_t maximizes

$$V_0(s_t) + p_t(I_t - s_t) E \left[\frac{V_0(s_{t+1})}{g^*} + \sum_{i=t+1}^T \frac{p_{t+1} \cdots p_i}{(g^*)^{i-t+1}} V_0(s_{i+1}) \right]. \quad (18)$$

It is worth comparing the utility functions in (7) and (17). In the former case, the utility at age t is the number of offspring produced at age t . Since offspring are identical, their reproductive values are the same and can be normalized to be one. Hence, the discounted sum of expected offspring is also the discounted sum of the expected reproductive values of offspring. That is, the utility at age t is the discounted sum of the expected reproductive values of those descendants directly affected by the individual's age- t choices.

It follows that (17) can be viewed as a generalization of (7). The expression $V_0(s_t)$ is exactly the reproductive value of the offspring of an individual who gave birth to the offspring at age t and transferred s_t to this offspring. In the maximization problem (17), this term is multiplied by $p_1 \cdots p_{t-1}$, the probability that this offspring will actually be born. Hence, the age- t utility of an individual is again the discounted sum of the expected reproductive values of all descendants directly affected by the individual's choices at age t .¹²

Measuring reproductive value. — In the model of this section, all two-year-old individuals are identical. That is why a natural measure of reproductive value is the discounted present value of the expected number of two-year-old descendants. Of course, in a more general setting, individuals are heterogeneous. In general, the reproductive values should be defined as the relative shares attained in the population, in the limit as the time into the future tends to infinity. For a discussion on generalized reproductive values, see Robson and Szentes (2007).

3.2 Sex

Consider the following modification of the model of this section. Suppose that, in each period, individuals of the same age are matched, and each match produces two offspring. An offspring inherits the gene of one of her parents, with equal probabilities for that of each parent. Each parent is randomly assigned to one of the newborn offspring.¹³ The offspring receives a transfer from the parent who is assigned to her.¹⁴ When the parent decides how much to save for her newborn child, she does not know whether the child inherited her gene or that from the other parent.

The goal in this section is to characterize the gene that cannot be invaded by any *mutation*. Consider a population with a gene \bar{s} . A *small* proportion of the population is then replaced by a mutant gene s . The question becomes: For what gene \bar{s} is it true that no matter what s is, the mutant gene s grows no faster than the original gene \bar{s} ?

An intuitive description of the surviving gene. — We claim that the gene that survives

¹²In the model of this section, the choice on an individual at a certain age directly affects only her newborn offspring. Had the choices affected many offspring, the utility would be the sum of the reproductive value of all these offspring.

¹³This assignment is independent of the gene of the offspring.

¹⁴Thus, this model becomes comparable to the one analyzed in the previous section. We could have also assumed that the transfer from each parent is shared equally between each of the two offspring.

evolution maximizes the growth factor of its population as if its frequency in the population was zero. In other words, although each individual may have the same gene in equilibrium, this gene maximizes its growth factor as if it was rare.

We now explain why this is so. Consider an arbitrary homogenous population. Color an infinitesimal fraction of the population green, where offspring inherit this color with probability half. Since the choice behavior of the green individuals has not changed, the green fraction of the population grows exactly at the same rate as the rest of the population.

Now, let us instead color an infinitesimal fraction of the population yellow. This color is tied to a possibly different choice of savings and the combination is inherited as described above. Consider the initial growth rate induced by the various possible choices made by the yellow population, given it remains a small fraction of the original population. Consider now the choice behavior that maximizes this growth rate. Clearly, this choice behavior maximizes the growth rate of the yellow population when we take into account its zero frequency in the total population. If this optimal behavior is different from that made by the original population, it must be that the yellow population outgrows the original population. This follows since one option is always to mimic the green population, which does exactly as well as the original population. If this optimal behavior is the same, on the other hand, then any yellow mutant that makes a different choice will be strictly outdone. Therefore, the original population cannot be invaded if and only if it behaves exactly as does the yellow gene.

The formal characterization of the surviving gene. — Consider a population described by the gene $\bar{\mathbf{s}}$. Suppose that this population is invaded by a small proportion of mutants. The behavior of the mutants is governed by the gene \mathbf{s} . We characterize the gene \mathbf{s} that grows fastest in the original population. Define

$$\bar{P}_1^j = \int_{\mathbb{R}_+} \int_{\mathbb{R}_+} p_1(I_1 - s_1(I_1) + R\bar{s}_j(I_j)) dG_1(I_1) dG_j(I_j).$$

That is, \bar{P}_1^j denotes the ex-ante probability that a newborn mutant survives until age two, if she had a parent of age j , and received a transfer from her non-mutant parent. We can again use the growth equation to characterize the optimal behavior of the mutant gene. The motion of the mutant population can be described by the equation

$$y_\tau = y_{\tau-1} + y_{\tau-2}\tilde{P}_1 + y_{\tau-3}\tilde{P}_1P_2 + \cdots + y_{\tau-T}\tilde{P}_1 \cdots P_{T-1}, \quad (19)$$

where $\tilde{P}_1 = \sum_{t=1}^T \mu_t (P_1^t + \bar{P}_1^t) / 2$. Here, μ_t is the proportion of i -year-olds in the mutant gene pool, ignoring newborns. (These proportions need not match those in the general population.) The only difference between (10) and (19) is that \tilde{P}_1 replaces P_1 throughout. The reason is that a mutant offspring receives transfer from her mutant parent only with probability one half. With probability one half the offspring receives the transfer from the other parent. The growth equation of the mutant population is

$$g = \frac{P_1^1 + \bar{P}_1^1}{2} \left(\frac{1}{g(g-1)} + \sum_{j=3}^T \frac{\prod_{k=2}^{j-1} P_k}{g^{j-1}(g-1)} \right) + \sum_{j=2}^T \frac{P_1^j + \bar{P}_1^j}{2g^{j-1}} \prod_{k=2}^{j-1} P_k. \quad (20)$$

The growth rate of the mutant population is maximized if and only if \mathbf{s} maximizes g subject to (20). Notice that if $\bar{\mathbf{s}} = \mathbf{s}$, the mutant population grows exactly as fast as the original one. Therefore, in the evolutionary equilibrium, $\bar{\mathbf{s}} = \mathbf{s}$, and hence, $P_1^j = \bar{P}_1^j$ for all $j = 1, \dots, T-1$, for otherwise the mutants would invade the original population.

We emphasize that the gene that maximizes g subject to (20) is different from the one that maximizes g subject to (11). The reason is that, in the former maximization problem, the terms \bar{P}_1^j ($j = 1, \dots, T-1$) are treated as constants.

Intuition and reproductive values. — The maximization problem corresponding to the surviving gene is:

$$\max_{s \in [0, I_t]} p_t (I_t - s) \frac{V_{t+1}(g^*, \mathbf{s})}{g^*} + p^1(s) \frac{V_2(g^*, \mathbf{s})}{2g^{*2}}, \quad (21)$$

for all t and $I_t \in \mathbb{R}$. The function V_t is the same as the function of the previous subsection, defined by (14). The first term is the individual's own survival probability times her discounted reproductive value, the same as in (15). The second term is the survival probability of her newborn until the age of two times half of the discounted reproductive value of this offspring. The reproductive value of the offspring is multiplied by half in (21) because the gene of the offspring is inherited from the parent making the transfer only with probability half. This is because when the frequency of a gene is zero in a population, the probability that an offspring inherits this gene from a parent is one half, conditional on one of the parent having this gene.

It is easy to show that \mathbf{s} maximizes (21) for all t , I_t , if and only if, \mathbf{s} maximizes g subject to (20) with $\mathbf{s} = \bar{\mathbf{s}}$.¹⁵

¹⁵Since the proof of this result is identical to the proof of Lemma 1, we omit it.

The argument above implies that, although, in the evolutionary equilibrium, each individual has the same gene, she behaves as if their offspring inherit their genes with only probability one half. Individuals still maximize the discounted present value of the reproductive value of those descendants who are affected by their choices. But now, they further discount the reproductive value of their offspring by half. In a more general model, they would discount the reproductive value of their grandchildren by one fourth etc.

Recursive utility representation. — We again can find a utility representation for the surviving gene, that is, for the behavior defined by maximization problems in (21). The surviving gene has this utility representation:

$$U_t(s_t, s_1, \dots, s_{t-1}) = \frac{p_1(s_1) \cdots p_{t-1}(s_{t-1})}{g^{*t}} \left[\frac{\int_{\mathbb{R}} V_0(s_t(I_t)) dG_t(I_t) + V_0(s_t)}{2} \right].$$

This representation implies that at age t , the individual maximizes

$$\frac{V_0(s_t)}{2} + p_t(I_t - s_t) E \left[\frac{V_0(s_{t+1})}{g^*} + \sum_{i=t+1}^T \frac{p_{t+1} \cdots p_i}{(g^*)^{i-t+1}} V_0(s_{i+1}) \right]. \quad (22)$$

We omit the proof because it is essentially identical to the proof of Proposition 1. Notice that the only difference between (18) and (22) is that in the latter formula the reproductive value of the newborn offspring is discounted by two.

3.3 Discussion of Rogers

Rogers (1994) is a path-breaking paper deriving time preferences from natural selection. Here we summarize several problems that nevertheless arise in his analysis.

Domain of choice problems. — Rogers (1994) analyzes a deterministic model in which an individual faces a single choice problem.¹⁶ Any two individuals at the same age face the identical decision problem. This makes it impossible to identify the relevant indifference curves. A contribution of the present paper is to show how the introduction of suitable idiosyncratic uncertainty can help in this regard.

The two following issues are addressed in detail by Robson and Szentes (2007), who show they are sufficient to invalidate Rogers' key results.

¹⁶In Section III, Rogers (1994) introduces uncertainty, but even in that model, individuals face only a single choice problem.

Reproductive value and felicities. — Rogers assumes that the reproductive value of an individual is the discounted present value of the expected number of descendants. That is, Rogers assumes in his model of altruism what we derive in our model without altruism. With altruism, however, reproductive value must be extended, as we have explained it in this section. Robson and Szentes (2007), indeed, show that the preferences characterized by Rogers induce too little savings.

Long-term interest rate. — Rogers (1994) considers the key combination of transfers and savings to involve a sacrifice by a parent in favor of an offspring one generation later. That is, the recipient's age when she receives the benefit is the same as the donor's age when she gave it away, so the reproductive values of the donor and the recipient are the same. Rogers further assumes that there is an interior solution for the optimal transfer. Under this assumption, Rogers derives a numerical value for the real rate of interest. However, Robson and Szentes (2007) show that, in Rogers' model, such solutions are generally not interior, and no such clear-cut prediction for the real rate of interest can be made.

4 Concluding Remarks—Further Research

This paper seeks to understand what structure evolution imposes on time preferences. We have shown that one can always find a utility representation for choice behaviors that survive evolution. We have established strong relationships between utilities and fertilities, and between discount factors and population growth factors. In particular, we have shown that if offspring are indistinguishable then, in the utility representation, the instantaneous utility function is weighted sum of reproductive values and the discount factor is the inverse of the population growth factor. In our representation, utilities have a natural cardinal interpretation: When newborn individuals are identical, the instantaneous utility at a certain age is simply the expected number of offspring at this age. More generally, the utility of an individual is generated by the reproductive values of the descendants affected by the individual's choices.

Extrapolation. — Our theory implies that time preferences surviving evolution must be time consistent. We think that one must be careful when using evolutionary arguments to analyze consumption-saving decisions in modern times. It is not straightforward to draw conclusions based on evolutionary arguments about individuals' choices unless similar choices were offered during the evolutionary process. Nonetheless, there is a strong

evolutionary force in favor of time-consistent behavior. Perhaps time-inconsistent behaviors were associated with choices that populations have not faced before, so that the optimal behavior has not yet evolved.

To extrapolate results based on evolutionary arguments to choice problems faced only in modern civilizations, one must go beyond interpreting a gene merely as a choice behavior. One way to extrapolate is to assume a principal-agent relationship between gene and individual. The gene is interpreted as a principal that rewards and punishes the individual (agent) for her choices. The individual's objective is to maximize rewards. One can think of rewards as food, sexual satisfaction, etc. The utility identified in this paper can be interpreted as the reward scheme corresponding to the surviving gene. Extrapolation then becomes less problematic. By way of illustration, suppose that during evolution, individuals could save only at a zero interest rate and the optimal reward for consumption turned out to be the reproduction function. In modern times, individuals might have access to better saving technology. However, if the reward scheme is hardwired in individuals, they could adapt the new regime, if they intelligently accounted for the novel effect of positive interest.

Social discounting. — Our model also has important implications for social discounting. An interesting yet unsettled question in economic theory is: How should a social planner weight future generations?

In our model, in the absence of sex, individuals who have the surviving gene make choices that maximize the population growth rate. When making choices, individuals appropriately account for the impact of their decisions on future generations. In this case, there may be no divergence between the private and social rate of discount.

Sexual reproduction, however, seems to introduce a motive for private discounting that is absent from social discounting. Namely, individuals also deflate the worth of resources that are transferred to offspring in the future by the degree of relatedness. Perhaps, then, the appropriate social rate of discount might be less than the private rate of discount.

Social norms. — We have maintained a literally biological interpretation in our derivation of intertemporal preferences—choice behavior is genetically hard-wired into individuals. An alternative interpretation might be that learning from parents shapes individual behavior. Corresponding to the most general model here, with altruism and sex, each offspring would then copy the behavior of a randomly chosen parent with respect to transfers to descendants. Although some such process is inherently plausible, malleable preferences

in this sense are far from conventional economics, and we have not yet considered this alternative interpretation in detail.

5 Appendix

The Derivation of Equation (11)

In steady state, the population grows at a fixed factor g , and μ_t ($t = 1, \dots, T$) does not change. Notice from (10) that

$$\mu_1 = \frac{y_{T-1}}{y_T} = \frac{1}{g}.$$

Furthermore,

$$\mu_t = \frac{\mu_2 \prod_{i=2}^{t-1} P_i}{g^{t-2}}, \quad t = 3, \dots, T.$$

Since $\mu_1 + \dots + \mu_T = 1$, it follows that

$$\mu_2 \left(1 + \sum_{t=3}^T \frac{\prod_{i=2}^{t-1} P_i}{g^{t-2}} \right) = 1 - \frac{1}{g} = \frac{g-1}{g}.$$

Let Q denote the coefficient of μ_2 in the previous equation. Then (10) can be rewritten as follows:

$$\begin{aligned} g &= 1 + \left(\frac{P_1^1}{g} + \frac{P_1^2(g-1)}{gQ} + \dots + \frac{P_1^T(g-1)P_2 \cdots P_{T-1}}{g^{T-1}Q} \right) \left(\frac{1}{g} + \frac{P_2}{g^2} + \dots + \frac{P_2 \cdots P_T}{g^{T-1}} \right) \\ &= 1 + \left(\frac{P_1^1}{g} + \frac{P_1^2(g-1)}{gQ} + \dots + \frac{P_1^T(g-1)P_2 \cdots P_{T-1}}{g^{T-1}Q} \right) \frac{Q}{g} \\ &= 1 + \frac{P_1^1 Q}{g^2} + \frac{P_1^2(g-1)}{g^2} + \dots + \frac{P_1^T(g-1)P_2 \cdots P_{T-1}}{g^T}. \end{aligned}$$

After multiplying both sides by g^T :

$$g^{T+1} = g^T + P_1^1 Q g^{T-2} + (g-1) P_1^2 g^{T-2} + \dots + (g-1) P_1^T P_2 \cdots P_{T-1}.$$

Finally, using the definition of Q yields

$$g^{T+1} = g^T + P_1^1 \left(g^{T-2} + \sum_{j=3}^T g^{T-j} \prod_{k=2}^{j-1} P_k \right) + (g-1) \sum_{j=2}^T P_1^j g^{T-j} \prod_{k=2}^{j-1} P_k.$$

After subtracting g^T from both sides and dividing through by $g^{T-1}(1-g)$ we get (11).

Proof of Proposition 1. By Lemma 1 it is enough to show that the maximization problems in (15) with $g = g^*$ and in (18) are identical. Notice that

$$V_0(s) = p^1(s) \frac{V_2(g, \mathbf{s})}{g^2} + \frac{P_1^1}{g^{*3}} \frac{g^*}{g^* - 1}$$

and by (13)

$$V_{t+1}(g, \mathbf{s}) = p_t(I_t - s_t) E \left[\frac{V_0(s_{t+1})}{g^*} + \sum_{i=t+1}^T \frac{p_{t+1} \cdots p_i}{(g^*)^{i-t+1}} V_0(s_i) \right].$$

Since $(P_1^1/g^{*3}) / (g^*/(g^* - 1))$ does not depend on s_t the solutions to the two problems are indeed identical. ■

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