

An Evolutionary Approach Towards Time Preferences*

Arthur Robson[†]
Simon Fraser University

Balázs Szentes[‡]
University of Chicago

Emil Iantchev[§]
Syracuse University

January 16, 2008

Abstract

We consider how choice behavior would be genetically determined when there are intertemporal and intergenerational tradeoffs. A particular gene is the result of evolution 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 such a resulting gene by a preference relation. We show that if choices affect the number of offspring but not the descendants' reproductive ability, such a representation is given by discounted expected utility, where the discount factor is the population growth factor, and the utility function is the product of the fertility function at each age and the survival functions to that age.

We then consider the case where newborn offspring are heterogeneous due to receiving transfers from parents. Now the preference representation is more subtle. The discount factor is still the population growth factor, but the utility function is the sum of the expected discounted *reproductive values* of the individuals whom the parent's choices directly affect.

Key words: evolution, time preferences.

*We have benefited from discussions with Gary Becker, Harold Cole, Larry Epstein, Drew Fudenberg, Edward Glaser, Faruk Gul, David Laibson, Mark Machina, Casey Mulligan, Kevin Murphy, Lionel McKenzie, Efe Ök, Wolfgang Pesendorfer, Marcin Peski, Phil Reny, Hugo Sonnenschein, Nancy Stokey, and Gábor Virág. We have also received valuable comments from seminar participants at Arizona, Berkeley, Chicago, Princeton, Rochester, San Diego, Stanford, UCLA, Yale, and Western Ontario. Robson thanks the Canada Research Chair program for support, and Szentes is grateful for financial support from the NSF.

[†]Department of Economics, 8888 University Drive, Burnaby, V56 1S6, CA. Email: robson@sfu.ca.

[‡]Department of Economics, 1126 E. 59th St, Chicago, IL 60637. Email: szentes@uchicago.edu.

[§]Department of Economics, 110D Eggers Hall, Syracuse, NY 13244. Email: iantchev@syr.edu.

1 Introduction

Most models in economics take preferences as given and then derive the choices induced by these preferences. We turn this around, first characterizing the choice behavior that would result from evolution, and then supporting this choice behavior with preferences. That is, we identify the preferences that induce evolutionarily stable choices.

We make the stark assumption that each choice behavior derives from a particular genetic type. Hence, the choices an individual makes during her lifetime are determined by her genetic type, where this is inherited from her parents. In the simplest case, without sexual reproduction, this inheritance is without modification, so populations can be defined as a group of individuals having the same genes. Populations with different genetic types may grow at different rates. Only those types inducing the highest feasible population growth rate survive evolution.

Our focus is on time preferences. Hence, individuals in our model face intertemporal trade-offs. In the simplest case we consider, current choices may affect not only current reproduction but also reproduction in the future. We show that the behavior that results from evolution 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 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 $f'(0) = \infty$. A gene is identified with a choice $x \in [0, 1]$, the use of the endowment in the first period, so the endowment available in the second period is $1 - x$. Offspring use the same rule as their parent.

Fix a choice, 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 :

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

Indeed, 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 $g > 0$ 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 might be in the population, the choice 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 unique positive solution of this equation for g . Then

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

Differentiating this identity,

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

Let x^* denote the choice generating the largest possible growth rate and set $g^* = g(x^*)$. Assuming an interior solution, x^* 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^* must be the unique solution of

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

Equation (1) means that an individual 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 of an offspring tomorrow, as measured by the relative contribution to the gene pool, is less, by this factor of g , than the value of an offspring today.

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

The present paper first 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 idiosyncratic 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 further generalize the argument by introducing a *carrying capacity constraint* into our basic model. The constraint is that per capita reproduction is a decreasing function of total population and converges to zero as the total population tends 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, so impatience depends merely on the functions involved in constructing expected fertility.

Offspring in the example are homogeneous. An individual's decision affects only the number of her offspring, not their reproductive capacity. We now consider a model where individuals' choices influence the reproductive capacities of their descendants and, as a result, offspring are heterogeneous. Offspring with *rich* parents have more expected offspring themselves than do offspring with *poor* parents. In the presence of such intergenerational transfers, 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 first be generalized beyond just the discounted present value of the expected number of offspring. Evolutionary stability now means that the utility function at age t can be taken as the discounted sum of the reproductive values of all individuals directly affected by the choices an individual makes at age t , where the discount factor remains the population growth factor.

As a final 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, where 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, but parents cannot recognize the genetic type of the offspring. The surviving gene accordingly makes a smaller transfer to her offspring, diverting resources instead to improve her own reproductive value.

The surviving choice behavior maximizes its growth rate *as if its frequency was zero in the population*. Indeed, consider when a homogeneous population might be robust

to an invasion by a small number of mutant genes. Mutants grow fastest initially if they maximize their growth rate given that their frequency in the population is essentially zero. Mutants can also match the growth rate of the original population by adopting 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 were 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, so the probability an offspring has the same gene is one half, a grandchild one quarter, etc. All of this discounting arises even though, in the evolutionary equilibrium, all individuals have the same gene.²

Literature Review

There is a small but growing literature arguing that evolution can help explain preferences.³ Most of these papers 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 a few papers concerned with the evolution of time preferences.

The paper most closely related to ours is Rogers (1994). The author has 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, the preferences pinned down by Rogers do not generate evolutionarily optimal choice behavior, because he applies an inappropriate notion of reproductive value. We discuss these issues in Section 4.3. Robson and Szentes (2007) analyzes an example that fits to the framework of Rogers and provides a detailed discussion of these problems.

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

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.

³A key early paper is Becker (1976), who argues that economic arguments might be used instead of evolutionary ones in explaining altruistic behavior between relatives, for example.

capital and on the total population of all clans. The clans indeed face a carrying capacity constraint, meaning that per capita production decreases as total population rises. An individual is active for only one period, and each clan faces a consumption-saving decision. Higher consumption results in higher immediate population growth but a smaller capital stock, and hence smaller output, in the next generation. The carrying capacity constraint means that each clan's 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.

Hansson and Stuart (1990) and Robson and Wooders (1997) were motivated by concerns additional to time preference. Both papers are led then to consider choice problems that are too simple in the relevant dimensions for the present focus on time preference.

Two recent papers conclude that evolution might produce time-inconsistent preferences. First, 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 faced the following 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 paid off after some time, option B becomes more attractive. Thus it is optimal to choose option A at time zero but switch to option B after some time. The authors argue that in modern times, individuals face situations they did not face during the evolutionary process. They associate each modern option with an option available before, A or B , for example. This may generate actual time inconsistency. In other words, Maskin and Dasgupta take the view that individuals behave suboptimally in a modern society. Unlike Samuelson and Swinkels (2005) or 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 feasible set. These choices affect the individual's future choice sets, her probabilities of survival, and the expected number of her offspring.

The Choice Sets.— The feasible 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 be the choice of an individual at age t , and c^t be 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, but are independent across individuals. Let β_t denote (c^{t-1}, s^t) and let B_t denote the set of all possible realizations of β_t . Finally, let $b_t(\beta_t) \subset \Omega$ denote the feasible choice set for an individual at age t .

Fertility and Survival Probabilities.— An individual's choices and further 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 for 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. All the random events here are independent across individuals. 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}) .⁴ 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.

⁴Events more than one period before age t can influence the distribution of γ_t , since γ_{t-1} summarizes those events. We do not need a Markovian restriction on the random variables.

We have set up this model to illustrate the generality of the results in this section. The following examples 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 a trade-off of central biological interest—If an individual allocates more 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 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 $\alpha_2 = y_2$. ■

Returning to the general case, suppose that, at time zero, there is an arbitrary positive number of individuals of each age, but all individuals of all ages have the same genotype. We can apply the law of large numbers, since all the random variables described above are independent across individuals and there are no aggregate shocks. It will follow that the population growth rate corresponding to a particular genotype is asymptotically constant and independent of the initial population distribution. The evolutionarily optimal choices then maximize this long run population growth rate.

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.⁵ 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 characteristic rate that is independent of the initial conditions, so that $y_\tau/y_{\tau-1} \equiv g(c)$ 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 desired population growth factor is the unique real root, which exceeds the modulus of any other of these roots (Pollard (1973) Chapter 4.6). Given equation (3): 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 sufficient that Ω and C_t are compact and p_t, f_t are continuous for $t = 1, \dots, T$.⁶

⁵Formally,

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

⁶Alternatively, one can assume that Ω and C_t are finite sets for $t = 1, \dots, T$.

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 mapping from choices to real numbers, that is maximized by these choices.

Recursive utility representation. — The collection of utility functions $\{U_t\}$ represents the 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 implies a form of time consistency. That is, a solution to an individual's maximization problem at age t involves expectations about her decisions at ages $t+1, \dots, T$, which 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.⁷

Theorem 1 *The optimal evolutionary choice is supported by the utility function:*

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

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

Theorem 1 implies that an individual with the surviving gene maximizes expected utility 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.⁸

Note that an age- t individual then maximizes

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

⁷Allowing β_t to influence f_t would be similar to letting prices enter preferences in standard consumer theory.

⁸Usually, the pure rate of time preference incorporates mortality. The advantage of the present definition is that the discount factor does not vary with age, even if mortality rates and reproduction functions do so. This definition is for convenience only, and has no substantive implications.

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 $\underline{\mathcal{C}}$ denote the set of choices that maximize the utility function defined by (6). Let $\overline{\mathcal{C}}$ denote the choices that maximize the growth factor, g , characterized by (3). It follows that $\underline{\mathcal{C}} = \overline{\mathcal{C}}$.

The definition of recursive utility yields that $\{U_t\}_{t=1}^T$ represents the choice $c = \{c_t\}_{t=1}^T$ 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 additional discounting. It is well-known that c is a solution for this problem if and only if c maximizes

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

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

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

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

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 since the right-hand side of (3) is weakly decreasing in g and $g^* \geq g(\underline{c})$. 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 $\underline{c} \in \overline{\mathcal{C}}$. ■

Identification of preferences. — A natural question is: Under what circumstances is this utility representation unique? Any preferences of a consumer can be deduced from her

behavior only if she faces enough choice problems. Our utility representation is unique, in particular, if and only if there is enough variation in the resource constraints. Instead of developing a general uniqueness theorem, we illuminate this issue by means of an example.

Of course, if $\{U_t\}_{t=1}^T$ is a utility representation and $V_t = \theta U_t + \theta_t$, where $\theta \in \mathbb{R}_+$, θ and $\theta_1, \dots, \theta_T \in \mathbb{R}$, 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 factor $R \in (0, \infty)$. The numbers b and R are realizations of independent random variables with full support on \mathbb{R}_+ , that are revealed to the individual prior to her choice. These random variables 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 choice function is $c: (0, \infty)^2 \rightarrow [0, 1]$. 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 $R(b - c(b, R))$ 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 determines the optimal choice:

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

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 $R(b - c(b, R)) = y$.⁹ Let $R(x, y)$ denote the interest factor corresponding to x and y . The first-order condition, (8), can be rewritten as

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

Now suppose that $\{U_1, U_2\}$ are the instantaneous utilities in the preference representation. Then $\{U_1, U_2\}$ 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 $x_0 \in (0, \infty)$. If we normalize $U'_1(x_0)$ to be $f'(x_0)$ we then need to show that $U'_1(x) = f'(x)$, and $U'_2(y) = pf'(y)$, for all $x \in (0, \infty)$. Indeed, for all $y \in (0, \infty)$,

$$U'_2(y) = \frac{g^*U'_1(x_0)}{R(x_0, y)} = \frac{g^*f'(x_0)}{R(x_0, y)} = pf'(y),$$

⁹Note that, if $R = f'(x) / [g^*pf'(y)]$ and $b = x + y/R$, the first-order condition in (8) is satisfied.

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 $x \in (0, \infty)$,

$$U'_1(x) = \frac{R(x, y) U'_2(y)}{g^*} = \frac{R(x, y) p f'(y)}{g^*} = f'(x).$$

■

Commonly used preferences. — Next, we investigate the conditions under which Theorem 1 implies various restrictions on preferences that are often used. One such property of preferences in dynamic models is time separability.

Remark 1 *Consider the case that survival is independent of consumption. The utility representation of the surviving gene is time separable if and only if the reproduction 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.

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.¹⁰ Assume that the reproduction function depends on total population, N ,

¹⁰Hansson and Stuart (1990), for example, also introduce such a constraint.

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.

Coexisting populations. — The premise of this paper is that a population growing more slowly than another population cannot survive evolution. If one accepts this premise, one can take it a step further and apply it to populations facing different physical environments. For example: What if two populations have different reproduction functions? Our logic implies that two populations can coexist only if they grow at the same rate.

A consequence of Theorem 1 is that the discount factor in the preferences representing surviving genes is the inverse of the growth factor. Coexisting populations must grow at the same rate. Thus:

Remark 4 *Individuals from different coexisting populations might have different felicity utility functions, but they must have the same discount factor.*¹¹

The remark implies that heterogeneity in preferences among individuals must be due to heterogeneity in felicity utility functions, not in discount factors.

If one specifies two different physical environments, the surviving genes corresponding to the two environments will generically grow at different rates. We argue, however, that if different populations interact, their growth rates can be forced to be the same in steady state equilibria.¹² Suppose that one environment is described by the reproduction functions $\{f_t\}_1^T$ and the other by $\{h_t\}_1^{T'}$. Further assume that growth of either population

¹¹We are grateful to Phil Reny for pointing out this consequence.

¹²We are grateful to Kevin Murphy for making this observation.

produces a positive externality for the other population. Formally, let ρ denote the ratio of population one to population two. Assume that f_t and h_t depend on ρ and satisfy $\partial f_t / \partial \rho < 0$ and $\partial h_t / \partial \rho > 0$. That is, an individual is more fertile if the other population is large relative to her own population. Further assume that $\lim_{\rho \rightarrow \infty} f_t = 0$, $\lim_{\rho \rightarrow 0} f_t = \infty$, and similarly $\lim_{\rho \rightarrow \infty} h_t = \infty$ and $\lim_{\rho \rightarrow 0} h_t = 0$. In steady state equilibria, ρ must be constant and, equivalently, the two populations must grow at the same rates. (Suppose, to the contrary, that population one grows faster than population two. Then ρ increases, and members of population one become less and less fertile while members of population two become more fertile. This decreases the growth rate of population one and increases the growth rate of population two.)

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 capacity at the cost of reducing her own. Such transfers derive from a parental endowment that varies 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 significant implications for the preferences representing the evolutionary optimal behavior.

3.1 Altruism

The utility representations must be modified when newborn individuals are not identical. When resources can be transferred to future generations, individuals with wealthy parents are likely to receive more transfers and reproduce more. We show that the surviving gene therefore does not simply maximize the discounted expected number of descendants. Two new born 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 she lives, the individual asexually produces exactly one offspring. Furthermore, at age t , an individual receives endowment I_t , a random variable distributed on \mathbb{R}_+ according to a c.d.f. G_t . For

simplicity, these random variables are independent over age. 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. In particular, a newborn offspring surely survives until age one. This means that a newborn will save all her resources that are transferred from her parent. 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 decides her transfer to her current newborn, she conditions neither on the income derived from her parent nor on her parent's age. This one year old then consumes all of her remaining income and the transfer from her parent. A gene is characterized by 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 an evolutionary perspective, it is often true that parents can make transfers to their newborns but not to their older offspring. Indeed, parents in most species are only in contact with their children at early ages. Note also that one could interpret saving, here and 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 capacities 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 .¹³ Let λ_j denote the steady state probability that an individual's

¹³Recall that an offspring survives for sure until age one.

parent is of age j . Then the unconditional probability of surviving until age two is

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

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 from age j 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 :

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

Lemma 1 *The growth factor of the population in steady state is implicitly defined by the following equation¹⁴*

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

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

$$\lambda_1 = \frac{y_{\tau-1}}{y_\tau} = \frac{1}{g}.$$

Furthermore,

$$\lambda_t = \frac{\lambda_2 \prod_{i=2}^{t-1} P_i}{g^{t-2}}, \quad t = 3, \dots, T.$$

Since $\lambda_1 + \dots + \lambda_T = 1$, it follows that

$$\lambda_2 \left(1 + \sum_{t=3}^T \frac{\prod_{i=2}^{t-1} P_i}{g^{t-2}} \right) = 1 - \frac{1}{g} = \frac{g-1}{g}.$$

¹⁴In what follows, we adopt the convention: $\prod_{i=a}^b x_i = 1$ if $a > b$.

Let Q denote the coefficient of λ_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). ■

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 not immediately 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, however, 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 choice $\mathbf{s} = \{s_t\}_1^{T-1}$. Let $V_t(g, \mathbf{s})$ denote the reproductive value of an individual at age t , 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 be age two in two periods, 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 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 discounted reproductive value of the individuals whom her choices directly affect. That is, she apparently 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. We now show that this intuitive prediction indeed holds.

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

Lemma 2 $\underline{\mathcal{S}} = \overline{\mathcal{S}}$.

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 $\underline{\mathbf{s}} = \{\underline{s}_i\}_1^{T-1} \in \underline{\mathcal{S}}$ and $\bar{\mathbf{s}} = \{\bar{s}_i\}_1^{T-1} \in \bar{\mathcal{S}}$. 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

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

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 yields 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:*

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

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

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

Proof. By Lemma 2 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. ■

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 sum of the expected reproductive values of direct descendants at age- t .

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 the discounted sum of the expected reproductive values of all descendants directly affected by the individual's choices at age t .¹⁵

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. More generally, the

¹⁵In the model of this section, the choice of an individual of a particular 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.

reproductive value of an individual of each age is the relative contribution the descendants of that individual make to the limiting population. Suppose the evolution of the age structured population is cast as linear first order differential equation, for an appropriate constant matrix (the “Leslie matrix”). The steady state reproductive values are then the right eigenvector of this matrix corresponding to the eigenvalue yielding the maximum growth rate. The heuristic argument here is consistent with this more general framework. For a discussion of generalized reproductive values, see Robson and Szentes (2007).

3.2 Sex

Consider the following modification of the current model. 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 and transfers resources to her.¹⁶ When the parent decides how much to transfer to 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 the mutant gene s might be, s grows no faster than the original gene \bar{s} ?

An intuitive description of the surviving gene. — The gene that results from evolution maximizes the growth factor as if its frequency in the population were zero. Although every individual has the same gene in equilibrium, this gene acts as if it were rare.

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 at the same rate as the rest of the population.

Now, let us instead color an infinitesimal fraction of the population yellow, which is tied to a possibly different choice of savings. Consider the maximization of the growth rate of the yellow population, given it remains a small fraction of the overall population. Since one option for the yellow population is to mimic the original population, the yellow mutant

¹⁶Thus, the model departs as little as possible from 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. This leads to substantially the same results.

invades if the optimal yellow choice differs from the choice of the original population. If this optimal behavior must be 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 as does the yellow gene.

The formal characterization of the surviving gene. — Consider a population described by the gene $\bar{\mathbf{s}}$. Suppose that a small proportion of mutants is now introduced into this population. 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 $\tilde{P}_1 = \sum_{t=1}^T \lambda_t (P_1^t + \bar{P}_1^t) / 2$. Here, λ_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 a transfer from her mutant parent only with probability one half. With probability one half the offspring receives the transfer from the other parent. Similarly to (11), the limiting growth factor of the mutant population satisfies

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

The mutant population maximizes its initial growth factor if and only if \mathbf{s} maximizes g subject to (20). Furthermore, in the evolutionary equilibrium, $\bar{\mathbf{s}} = \mathbf{s}$, and hence, $P_1^j = \bar{P}_1^j$ for all $j = 1, \dots, T-1$.

We emphasize that the choice that maximizes g subject to (20) is different from the one that maximizes g subject to (11).

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, 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.

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 $\mathbf{s} = \bar{\mathbf{s}}$.¹⁷

Although, in the evolutionary equilibrium, each individual has the same gene, she behaves as if her offspring inherited her gene with probability one half. Individuals still maximize the discounted present value of the reproductive value of those descendants who are directly affected by their choices, but now 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.

¹⁷Since the proof of this result is identical to the proof of Lemma 2, we omit it.

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.¹⁸ Any two individuals of 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 invalidate Rogers' key results.

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 with 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) show that the preferences assumed by Rogers are not evolutionary optimal and, indeed, 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

¹⁸In Section III, Rogers (1994) introduces uncertainty, but even in that model, individuals face only a single choice problem.

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 the utility function is the appropriately discounted sum of reproductive values and the discount factor is the inverse of the population growth factor. If offspring are identical, the instantaneous utility at a certain age is simply the expected number of offspring at this age. More generally, when offspring differ due to altruism, utility is the sum of the reproductive values of the descendants affected by the individual's choices, discounted by the degree of relatedness and the population growth rate.

Extrapolation. — One must be careful when using evolutionary arguments to analyze consumption-saving decisions in modern times. It is not straightforward to do such analysis unless similar choices were offered during the evolutionary process. Nonetheless, there is general evolutionary pressure 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 was 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, introduces 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 in economics, and we have not yet considered this alternative interpretation in detail.

References

- [1] Becker, G. (1976): “Altruism, Egoism, and Genetic Fitness: Economics and Sociobiology,” *Journal of Economic Literature*, **14**, 817-826.
- [2] Bergstrom, T. (1995): “On the Evolution of Altruistic Ethical Rules for Siblings,” *American Economic Review*, **85**(1), 58-81.
- [3] Dasgupta, P and E. Maskin (2005): “Uncertainty and Hyperbolic Discounting,” *American Economic Review*, **95**(4), 1290-1299.
- [4] Fisher, I. (1958): *The theory of interest*. New York: Kelley and Millman.
- [5] Hansson, I. and C. Stuart (1990): “Malthusian Selection of Preferences,” *American Economic Review*, **80**(3), 529-544.
- [6] Pollard, J.H.: *Mathematical models for the growth of human populations*. New York: Cambridge University Press, 1973.
- [7] Robson, A. (2001): “The Biological Basis of Economic Behavior,” *Journal of Economic Literature*, **39**, 11-33.
- [8] Robson, A. (2002): “Evolution and Human Nature,” *Journal of Economic Perspectives*, **16**(2), 89-106.

- [9] Robson, A. and M. Wooders (1997): “The Growth-Maximizing Distribution of Income,” *International Economic Review*, **38**, 511-526.
- [10] Robson, A. and B. Szentes (2007): “On the Evolution of Time Preference,” *Mimeo*.
- [11] Rogers, A.R. (1994): “Evolution of Time Preference by Natural Selection,” *American Economic Review*, **84**(3), 460-481.
- [12] Samuelson, L. and J. Swinkels (2005): “Information, Evolution and Utility,” *Mimeo*, University of Wisconsin – Madison.