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THE EVOLUTIONARY THEORY OF TIME PREFERENCES AND INTERGENERATIONAL
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ABSTRACT

At each age an organism produces energy by foraging and allocates this energy among reproduction, survival, growth, and intergenerational transfers. We characterize the optimal set of allocation decisions that maximizes reproductive fitness. Time preference (the discount rate) is derived from the marginal rate of substitution between energy obtained at two different times or ages in an individual's life, holding reproductive fitness constant. We show that the life history may have an initial immature phase during which there is body growth but no fertility, and a later mature phase with fertility but no growth, as with humans. During the immature phase, time preference depends only on the compounding effect of body growth, much like returns on a capital investment, but not on fertility, or the intrinsic population growth rate. During the mature phase, time preference depends on the costliness of fertility, and on endogenous survival and intrinsic growth rate, and not at all on body growth. During the transition between the two phases, fertility, mortality, body growth, and intrinsic growth rate all matter. Using these results, we conclude that time preference and discount rates are likely to be U-shaped across age. We compare our results to Hansson and Stuart (1990), Rogers (1994, 1997) and Sozou and Seymour (2003). Wastage and inefficiencies aside, in a single sex model a system of intergenerational transfers yields Samuelson's (1958) biological interest rate equal to the population growth rate. When the rate of time preference exceeds this biological rate, inter-generational transfers will raise fitness and evolve through natural selection, partially smoothing out the age variations in time preference.

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Once upon a time, there was a monkey-keeper who fed the monkeys with acorns. When he said that he would give them three bushels of acorns in the morning and four bushels of acorns in the evening, all the monkeys were angry with his arrangement. However, when he said he would give them four bushels of acorns in the morning and three bushels of acorns in the evening, all the monkeys were pleased with his arrangement.

Zhuangzi, Qiwu lun 233B.C.

1 Background

Economists generally take the framework of the human life cycle as given: the age patterns of fertility and mortality; the low level of fertility relative to other species and the long period of child dependency; bodily growth limited to the first part of life and fertility limited to a later period; extended parental support of their children, and the rate of time preference. Arguably, however, these features were shaped by natural selection in our evolutionary past and may be at least partially understood in an optimization framework, one approach to what biologists call “life history theory”. In the fable quoted above, even “ancient monkeys” had a time preference for (4,3) over (3,4). In this paper, we shall investigate how such preferences are shaped by evolution.

Robbins famously defined economics as “the science which studies human behaviour as a relationship between ends and scarce means which have alternative uses.” In evolutionary theory, the end is clear: reproductive fitness, or the propagation of genes into the future. Here we use economic reasoning to analyze how humans have evolved to allocate the scarce resource, energy, among the alternative uses of fertility, survival, body growth, and transfers to others so as to maximize the propagation of genes into the future, and how time preference emerges from this process. Economic reasoning thus

illuminates the evolutionary theory of life histories. But evolutionary theory, in turn, also sheds light on central problems in economics. Research in behavioral economics and neuroeconomics has found that intertemporal choices are governed by a set of disparate and conflicting emotions, cognitive processes, and neural functions (Frederick et al, 2002; Camerer et al, 2005). Evolutionary theory is a foundational approach to thinking about intertemporal choice in a unified way, leading to predictions about how this apparent hodgepodge of influences should lead to a coherent set of outcomes. For example, Sozou (1998) has shown how hyperbolic discounting and preference reversals may evolve through natural selection when discounting reflects risk. Intertemporal rates of preference and intergenerational transfers have an obvious relevance to economic growth.

1.1 Prior Literature

Economics increasingly recognizes that the biological nature of humans shapes their development, health, emotions, reproduction, altruism and cognitive processes. Evolutionary theory provides a fundamental organizing theory for understanding the interrelations of such human traits, and economists have begun to use their tools to analyze the evolutionary processes that shaped them. This paper seeks to understand the evolution of time preference, and it joins a growing number of papers that have taken an economic approach to the evolution of the life cycle or life history (Hansson and Stuart, 1990; Rogers, 1994; Sozou, 1998; Sozou and Seymour, 2003; Kaplan and Robson, 2002; Robson and Kaplan, 2003; Lee, 2003; Galor and Moav, 2002, 2004; Chu and Lee, 2006; Lee, 2008; Robson and Szentes, 2008). They ask what patterns of these life history traits would maximize reproductive fitness, typically measured either by the steady state population growth rate or by the expected number of births over a life time. In this paper we focus on the

evolution of time preferences, but we begin by analyzing the optimal life cycle. The general idea, as developed by Hansson and Stuart (1990), Rogers (1994), and Sozou and Seymour (2003) is that time preferences should have evolved in the past so that the marginal rate of substitution (MRS) between a good received at two different ages should be the MRS in fitness. We assess the MRS in fitness by analyzing the optimal life history.

Of course, economists' concept of human time preference does not refer to reproductive fitness, but rather to the variation of utility that is associated with different sequences of consumption amounts. But one may argue that the association of utility with consumption sequences evolved to guide individual decision making so as to enhance reproductive fitness. It is in this sense that our analysis informs the evolution of time preference. As Camerer et al (2005 p.27) remind us, "... humans did not evolve to be happy, but to survive and reproduce". Economists typically represent the objective function for intertemporal choice as an atemporal utility function multiplied by an age-time discount factor derived from a cumulated rate of time preference. It is this latter that we seek to understand here. Of course, the level of energy use and consumption is vastly higher now than in our evolutionary past, but we believe that human discounting today has some biological commonality with our ancient relatives, and it is this that we attempt to characterize.

We analyze and discuss intertemporal tradeoffs in terms of energy, but the actual tradeoffs are between the things into which energy can be converted: fertility, survival, bodily growth, and transfers to others. By way of illustration, consider human hunter-gatherers who chose between immediate childbearing versus building up somatic reserves of self and earlier born children to raise the probability of longer term survival and future reproduction. That was a decision about long term intertemporal tradeoffs. Short birth intervals undermined the health of both the mother and her previously born child, so these decisions were pervasive for humans in our evolution-

ary past. Consider individual members of some species of birds that must choose as yearlings whether to disperse, risking mortality from predation but gaining a shot at reproducing during the current breeding season, versus staying as “helpers at the nest” to assist their parents to raise new generations of siblings. Staying reduces their mortality risk while allowing them to gain experience before dispersing the following year, and keeping them in the running to inherit the breeding site if their parents die. These kinds of decisions involve intertemporal tradeoffs.

Hansson and Stuart (1990) considered individuals living a single period and investing in their offspring through intergenerational transfers in order to maximize their steady state population growth rate. They showed that such individuals would optimally discount the future at that maximum rate. We can view the saving and capital accumulation in the Hansson-Stuart model as investment in the body and particularly the brain of the developing offspring (Robson and Kaplan 2003). Other kinds of investment such as heritable dwellings, storage facilities, dams, and food stocks occur in some non-human species but do not seem relevant for most human hunter-gatherers in the evolutionary past. Because individuals lived only one period in Hansson and Stuart’s analysis, generations did not overlap and variations within the individual life cycle were not considered.

By contrast, a pioneering paper by Rogers (1994, 1997) calculated the fitness preserving MRS for demographic outcomes at different ages, where fitness tradeoffs were assessed through analysis of demographic accounting identities. Rogers also argued that the relevant intergenerational MRS was not the population growth rate as in Hansson and Stuart, but rather should reflect the dilution of genetic relatedness across generations in sexually reproducing populations, concluding that the annual rate of evolved time preference should be about 2%. Robson and Szentes (2008), while supporting Rogers’ general approach, argue that this specific conclusion is not correct.

While Rogers took the age specific birth and death rates as given, an elegant paper by Sozou-Seymour (1993) extended Rogers by endogenizing the age patterns of fertility and mortality through life history optimization theory and assessed the evolution of time preference relative to these. They concluded that time preference rates should rise at older ages because of the accelerating decline in fertility and the increase in mortality, and that time preference rates should be higher for organisms that evolved in regimes of higher unavoidable background mortality.

1.2 Incorporating Energy, Somatic Investment and Intergenerational Transfers

In nature, energy is the closest thing to money, and time preference refers most generally and fundamentally to the allocation of energy over the life cycle or across time. Both Rogers and Sozou-Seymour calculated the fitness preserving MRS for demographic outcomes at different ages without explicitly introducing an energetic budget constraint. However, the same outcome at a different age might have quite different energetic costs. At older ages an incremental birth may require enduring several prior miscarriages and other health costs and mortality risks, and in early childhood no amount of energy can achieve a birth. Similarly, reducing mortality at older ages may be more energetically costly than at younger ages due to senescent decline. Thus fitness tradeoffs based on demographic accounting rather than resource inputs necessarily omit some relevant considerations. Furthermore, these demographic outcomes are not fungible and are non-tradable. Tradeoffs of this kind between demographic outcomes are relevant for some real-world choices, but arguably these are special cases. Here we will consider time preference in relation to the allocation of energy across age and time.

Time preference is not a feature of the underlying utility function alone.

It also depends on the initial age-time trajectory of consumption over the life course, since this enters into the marginal utility at each age and hence the MRS. If individuals at all ages had access to intertemporal markets in the evolutionary past, then we might expect that their typical age trajectory of resource use would have evolved so as to set the MRS equal to the market discount factor for all pairs of ages, in which case the rate of time preference would be constant across age. But even in the modern industrial world children do not have access to intertemporal credit markets, and typically markets are restricted, for example they do not permit negative net worth. These limitations prevent this equalization from occurring.

In nature, intertemporal markets do not exist at all. However, two non-market mechanisms for intertemporal reallocation might work toward this equalization. First, energy can be reallocated forward in age and time when an individual invests in its own somatic growth in body size or brain (Robson and Kaplan, 2003) or simply stores fat. However, if the optimal life cycle requires downward or backward reallocations of energy, somatic investment cannot help. Because young organisms are small and immature, and are in mortal danger from predation and environmental fluctuations, they should optimally borrow against the future. In this case, somatic growth has a limited role in equalizing the MRS across ages.

The second non-market mechanism in nature is downward intergenerational transfers to the young from older relatives, particularly parents, but also older siblings, grandparents, and other unrelated individuals. Humans appear to surpass all other species in this regard, with hunter-gatherer children receiving net transfers and remaining nutritionally dependent until around age 20 (Kaplan, 1994). However, there are also obstacles to evolving an efficient allocation of resources across ages through transfers. Transfers from fathers might be limited by their uncertainty about paternity. More general kinds of free-riding might arise in cooperative breeding groups. When

offspring are heavily dependent on continuing parental investment, offspring survival depends on parental survival, leading to inefficient resource wastage following parental death. The upshot is that the fitness MRS for the evolved human will vary with age.

In virtually all species individuals invest in their own growth, but while some species continue to grow throughout their lives, others such as humans exhibit “determinate growth”. That is, in the first life cycle stage there is growth but no fertility, and in the second stage there is fertility, but no growth. None of the preceding studies of the evolution of time preference incorporate body size and growth, so none incorporates the special case of determinate growth. Biologists classify all mammals including humans, all birds, most insects, and most annual plants as species exhibiting determinate growth, although some of them, like humans, may have a short transitional period that connects the two life cycle stages. Consistent with some prior literature (Taylor et al. 1974 and Vaupel et al. 2004), we find that the optimal life history may have a corner solution in which an organism first grows without reproducing and then reproduces without further growth. We find that incorporating growth and the determinate growth pattern changes the conclusions of the earlier studies.

In sum, this study breaks new ground by explicitly incorporating energy resource constraints, body growth and the corner solution known as determinate growth, transfers of energy from older to younger individuals as constrained by the population age distribution, and by considering the consequences of these life cycle features for the evolution of time preference.

1.3 Plan of Paper

The next section of the paper discusses some issues in modeling that are preliminary to the main analysis. The first analytic section, labeled Theory

I., specifies a model of physiological tradeoffs across age and time during the evolutionary process, with size and energy treated as exogenous and the budget constraint autarchic. The optimal solution to this model provides us with an age-specific path of energy allocations to fertility and maintenance. Along this optimal path, we evaluate the marginal rate of substitution for exchanging energy between any two age-time points, which reveals intertemporal time preferences or discount rates. We implicitly assume that the same tradeoffs that operated during evolutionary time also characterize the fitness costs and rewards of behavioral decisions. We confirm earlier results from the literature in this new model incorporating energy.

In the next section, Theory II, the mature size of an organism is endogenously determined by investments in growth but still with an autarchic budget constraint, leading to a possible corner solution in which there is first growth without fertility until sexual maturity, after which there is fertility without growth, as in humans and many other species. The discount rates derived here differ from the earlier literature and have richer interpretations. The final analytic section, Theory III, relaxes the autarchic budget constraint by permitting intergenerational transfers. The age-time MRS together with the marginal rate of transformation provided by a cooperative breeding group determines whether transfer behavior will be selected, smoothing across age generations in the MRS. The last section summarizes our conclusions and compares them to features of the standard discounted utility approach.

2 A Model of Selfish Genes

The standard approach in life history theory models a conflict between an individual's age-specific consumption of energy for its current reproduction and for its own maintenance and survival, which are preconditions for its future reproduction, as in Abrams and Ludwig (1995). Natural selection

by definition favors the life history configuration with the highest reproductive fitness, which is typically measured by the numerical predominance of replicates in the future. Most models assume asexual reproduction, so all descendants except mutants are clones, and it makes no difference whether we think of replicates of the phenotype (actual life history arrangement) or genotype (which produces that arrangement). In practice, theorists generally maximize the steady-state intrinsic growth rate, also known as the Euler-Lotka parameter. In what follows, we put more emphasis on the allocation of energy in different age-time spans, and this helps us envisage the time preferences behind such a maximization.

2.1 A Species' Dynamic Maximization

Let μ_a be the instantaneous mortality rate at age a (Table 1 summarizes our notation). The probability that an individual survives from birth to age a is denoted ℓ_a . By definition, ℓ_a is given by $\exp(-\int_0^a \mu_s ds)$. The fertility rate of an individual at age a is denoted m_a .

At age a , a typical individual expects to have energy or resources which, following Abrams and Ludwig (1995), she divides between fertility and reducing mortality through body maintenance and repair. There is typically a tradeoff between energies devoted to reproduction and to survival: Having higher fertility in early life reduces probability of survival to later life, which in turn reduces the probability of realizing later-life fertility.

The foraging success of an individual at age a is a function of her size, denoted w_a . Body size can be interpreted broadly to include development of the brain, for example (Kaplan and Robson, 2002; Robson and Kaplan, 2003). Specifically, her energy budget constraint at age a is:

$$f_a(\mu_a, m_a) \leq \zeta_a(w_a), \quad \forall a. \quad (1)$$

Let $f_{a,\mu}$ and $f_{a,m}$ denote the partial derivatives of f_a w.r.t. μ_a and m_a , respec-

tively. These derivatives represent the marginal energy costs of improving μ_a or m_a . The marginal increase in the net energy flow resulting from a marginal increase in body-size is given by $\zeta_{a,w} \equiv \zeta'_a$. For the time being, we treat w_a as given; later we shall allow the growth of w_a to be endogenous.

Consider how marginal survival costs $f_{a,\mu}$ might vary with age. Real time biological processes such as oxidative damage and somatic mutations will tend to raise the marginal costs of achieving a given level of mortality with age, which means that $-f_{a,\mu}$ is increasing in a . Higher levels of external risks due to predators, disease, or climate would raise $f_{a,\mu}$ at all ages. Reproduction may also become more costly for an older individual, as reflected in a larger $f_{a,m}$, due to the deterioration of quantity and quality of eggs in mammals, for example, and the deterioration of reproductive organs through the processes mentioned above. As for energy production per body weight, $\zeta_{a,w}$, this clearly first rises and then declines in old age in many species.² In applications of this optimal life history approach which start from a zero baseline, such variations might be treated as endogenous, while in other applications such features might be treated as having been fixed in an earlier evolutionary stage and therefore treated as constraints as we think about the evolutionary processes through which humans, for example, developed from an earlier primate form.

How do we characterize the optimal life history? Here we define a life history, $(\mu_a, m_a)_{a=0}^\infty$, as optimal if it maximizes the intrinsic rate of population growth, ρ . An alternative measure of an organism's ability to survive and reproduce is Fisher's reproductive value, $v_a \equiv (1/\ell_a) \int_a^\infty e^{-\rho(s-a)} \ell_s m_s ds$, for an age- a individual (Fisher, 1958). It is straightforward to demonstrate that an arbitrary life history corresponds to a certain steady state growth rate.

²Human infants are completely helpless, indicating that $\zeta_{a,w}$ is nearly zero for small a .

Evaluating v_a at $a = 0$ and equating it to 1, we have:

$$v_0 \equiv \int_0^\infty e^{-\rho s} \ell_s m_s ds = 1. \quad (2)$$

Consider that value of ρ for which the maximum value of v_0 is 1. That is, we seek the solution to:

$$\max \int_0^\infty e^{-\rho s} \ell_s m_s ds \quad \text{subject to} \quad (1). \quad (3)$$

Taylor et al. (1974) show that the corresponding life history is optimal. The solution to (3) will be presented in the following section.

2.2 The Solution

The state variable for the dynamic problem is ℓ_a , with dynamics specified by $d\ell_a/da = -\ell_a \mu_a$. The control variables are μ_a and m_a , which are regulated by the energy constraints in (1). Under appropriate regularity conditions, we can rewrite (1) as $\mu_a = \mu_a(m_a, w_a)$ and thereby eliminate the constraint. The present-value Hamiltonian is

$$\mathcal{H} = e^{-\rho a} \ell_a m_a - \phi_a \ell_a \mu_a, \quad (4)$$

where the costate variable ϕ_a satisfies

$$\frac{d\phi_a}{da} = -\frac{\partial \mathcal{H}}{\partial \ell_a} = -e^{-\rho a} m_a + \phi_a \mu_a. \quad (5)$$

Solving the differential equation (5) yields

$$\phi_a \ell_a = \int_a^\infty e^{-\rho s} \ell_s m_s ds + c, \quad (6)$$

which can be rewritten as $\phi_a = e^{-\rho a} v_a$ since the integration constant c equals zero.³ To maximize the Hamiltonian, the first order conditions are

$$\frac{\partial \mathcal{H}}{\partial m_a} = e^{-\rho a} \ell_a - \phi_a \ell_a \frac{\partial \mu_a}{\partial m_a} = e^{-\rho a} \ell_a + \phi_a \ell_a \frac{f_{a,m}}{f_{a,\mu}} \leq 0, \quad \text{and} \quad \frac{\partial \mathcal{H}}{\partial m_a} m_a = 0. \quad (7)$$

³An alternative approach to derive ϕ_a is to note that the value function $\int_a^\infty e^{-\rho s} \ell_s m_s ds$ can be written as $e^{-\rho a} \ell_a v_a$. Since ϕ_a is the derivative of the value function w.r.t. the corresponding state variable ℓ_a , we obtain $\phi_a = e^{-\rho a} v_a$.

The conditions in (7) reduce to $1 + v_a f_{a,m}/f_{a,\mu} \leq 0$ and $(1 + v_a f_{a,m}/f_{a,\mu})m_a = 0$, which provide the necessary conditions for the solution. These results can also be interpreted in terms of achieving the maximum population density in an environment and driving other gene lines extinct.⁴

3 Theory I: Time Preference and the Biological Discount Rate with Exogenous Body Growth

An advantage of our approach is that we can solve analytically for the use of energy, so that time preference by age and time can be studied without having to resort to arbitrary assumptions. We shall analyze the meaning of time preferences below.

⁴Consider the carrying capacity constraint imposed by the size and richness of the relevant environment. The solution to the optimization problem will only by chance be a growth rate of zero, yet we know that a positive growth rate is not possible in the long run and a negative one spells extinction. To address this problem, define density to be the ratio of the total body mass of a population to the environmental resource, call this ratio D . For a given body weight, the rate per capita at which energy can be extracted from the environment depends on D , say $\zeta(D)$, with $\zeta'(D) < 0$. Under suitable assumptions, for any given life history strategy there will be some equilibrium value of D for which the implied intrinsic growth rate is zero.

The life history strategy with the highest equilibrium density will be selected in the long run, because at that density, the growth rates of all other life history strategies will be negative. Searching for the strategy with the highest steady state growth rate will be equivalent to searching for the strategy capable of sustaining the highest equilibrium population density. More complicated situations are possible, as when some lines have faster growth at low densities but slower growth at high densities, and for these the basic argument should be modified.

3.1 Deriving the Time Preference

Following Zhuangzi's fable quoted at the beginning of this paper, we can consider the following experiment. Suppose we take away some energy R_a when the individual is aged a , and give back some energy $R_{a+\tau}$ when she is aged $a + \tau$. Then, what is the $|dR_{a+\tau}/dR_a|$ ratio if we are to keep the fitness index ρ constant? Evidently, $|dR_{a+\tau}/dR_a|$ can be written as

$$\left| \frac{dR_{a+\tau}}{dR_a} \right| = \left| \left(\frac{\partial \rho}{\partial R_a} \right) / \left(\frac{\partial \rho}{\partial R_{a+\tau}} \right) \right|.$$

When variations in energy R_a are introduced, the constraint in (1) becomes:

$$f_a(\mu_a, m_a) \leq \zeta_a(w_a) + R_a, \quad \forall a. \quad (1')$$

The partial derivatives of ρ are proportional to those of \mathcal{H} :

$$\frac{\partial \mathcal{H}}{\partial R_a} = \left[\int_0^\infty s e^{-\rho s} \ell_s m_s ds \right] \frac{\partial \rho}{\partial R_a},$$

and thus the ratio $|dR_{a+\tau}/dR_a|$ can be expressed in terms of \mathcal{H} . Applying the envelope theorem to (4) and assuming that (7) leads to interior solutions, we have

$$\frac{\partial \mathcal{H}}{\partial R_a} = -\phi_a \ell_a \frac{\partial \mu_a}{\partial R_a} = -\frac{\phi_a \ell_a}{f_{a,\mu}} = \frac{e^{-\rho a} \ell_a}{f_{a,m}}. \quad (8)$$

Similarly, for the same individual who receives $R_{a+\tau}$ at age $a + \tau$, the impact is

$$\frac{\partial \mathcal{H}}{\partial R_{a+\tau}} = \frac{e^{-\rho(a+\tau)} \ell_{a+\tau}}{f_{a+\tau,m}},$$

which yields the following formula for the fitness-oriented time preference

$$\left| \frac{dR_{a+\tau}}{dR_a} \right| = \frac{\ell_a}{\ell_{a+\tau}} \cdot \frac{f_{a+\tau,m}}{f_{a,m}} \cdot e^{\rho \tau}. \quad (9)$$

In terms of the fitness index, expression (9) specifies how increments in R_a and $R_{a+\tau}$ are valued differently in the maximization process. In terms of economics, $|dR_{a+\tau}/dR_a|$ is the gene's MRS between the endowments of two

different periods, which should evidently be the gene's discount factor from one age to the other.

Since the current model is continuous, it is natural to consider the discount rate in continuous form: taking natural logarithm, dividing it by τ and then taking the limit with $\tau \rightarrow 0$, we obtain the instantaneous age specific discount rate:

$$\lambda_a = \mu_a + \frac{\dot{f}_{a,m}}{f_{a,m}} + \rho, \quad (9')$$

We will discuss the meaning of this result in relation to the existing literature.

Sometimes the discount rate may be expressed per generation rather than per year, equal to the annual rate multiplied by A_f , the average age of child-bearing in the steady state population. Note that we derived our formula for the discount factor based on the simple assumption of maximizing fitness, without relying on any assumption of stationary population or golden-rule growth, as in Hansson and Stuart (1990). Another feature of our approach is the explicit characterization of *fitness maximization*, which was not explicitly specified in the previous literature. Below we compare this result with the previous literature.

3.2 Comparison to the Literature

First, Hansson and Stuart (1990) found that the intergenerational discount rate should be the intrinsic growth rate ρ , which appears in (9'). Other factors also appear in (9), because in our *intragenerational* framework, ρ must be adjusted by some age-specific factors. As in Strotz (1956), the age and time separation factors are multiplied to form the discount rate: the factor depending only on the time separation between the two time points in question is our ρ , and the other factor depending on absolute age or time is the intragenerational discount rate between specific ages.

Second, Sozou and Seymour (2003 p.1047) correctly suggested that the

discount rate across age should depend on the mortality rate over the relevant age range. This is reflected by μ_a in (9'). It also follows that higher external mortality risks will lead to higher discount rates, since they will lead to lower survival in the optimal life history, again as suggested by Sozou and Seymour. In the context of the fable at the beginning of this paper, if the monkey expects a high mortality rate at noon, the discount factor will be small and the discount rate will be high.

Third, Rogers (1994 p.447) and Sozou and Seymour (2003 p.1049) also found that the discount rate should be higher when the rate of senescent decline in age-specific fertility is greater. This is reflected in our $\frac{\dot{f}_{a,m}}{f_{a,m}}$ in (9'). If $\frac{\dot{f}_{a,m}}{f_{a,m}} > 0$ then the energetic cost of fertility is rising with age due to senescent decline. If, however, $\frac{\dot{f}_{a,m}}{f_{a,m}} < 0$ as when fecundity is increasing in youth, then this declining cost of fertility reduces the discount rate.

Consider an age a just at sexual maturity. In the neighborhood of a , evidently $f_{a,m}$ and $f_{a+\tau,m}$ belong to different life-history regimes, and hence the formula in (9) must be revised to accommodate this important case, which we take up in a later section.

4 Theory II: Autarchic Energy Budget With Endogenous Body Size

The analysis so far has been based on the framework of Abrams and Ludwig (1995), which incorporates tradeoffs between fertility (m_a) and repair/maintenance (μ_a). In applying the envelope theorem to (4), we did not take into account the possible regime changes of the life-history maximization. But for humans and other mammals as well as birds and some other organisms, there is a long juvenile period in which individuals grow in size but do not reproduce followed by a period in which they reproduce but do not grow, a pattern known

as *determinate growth* which holds for “most insects, birds, mammals, and annual plants” (Stearns 1992:93) (although there may be some growth after sexual maturation, as with humans). In this section we shall show how the biological discount rate derived from this modified model may be different from the formula in (9).

4.1 A Revised Maximization Problem

Let us consider the same age-specific setup except that, following Cichon and Kozłowski (2000), individuals at each age are assumed to divide their energy use among fertility (m_a), repair and maintenance (μ_a) and body size increase (z_a). Introducing the additional variable z_a , we can write an individual’s energy budget constraint at age a as

$$f_a(\mu_a, m_a, z_a) \leq \zeta_a(w_a), \quad \forall a. \quad (10)$$

We expect the first derivatives of such functions to be positive for m_a and z_a and negative for μ_a . If reducing μ_a incurs increasing marginal cost, then $\partial^2 f_a / \partial \mu_a^2$ should be positive; other second derivatives can be specified similarly. The body size of an individual grows according to $dw_a/da = z_a$.

4.2 The Corner Solution Pattern

The determinate growth pattern described above implies that m_a and z_a cannot both be interior solutions at the same time. As is well known from Taylor et al (1974), Chu and Lee (2006) and Vaupel et al (2004), a sufficient condition for such a corner solution is that the constraints in (10) are linear. When (10) is nonlinear, determinate growth can still occur, as we will demonstrate below.

As in the previous section, we rewrite (10) as $\mu_a = \mu_a(m_a, z_a, w_a)$ to eliminate the budget constraint. The present-value Hamiltonian, which is

similar to (4), is:

$$\mathcal{H} = e^{-\rho a} \ell_a m_a - \phi_a \ell_a \mu_a + \psi_a z_a, \quad (11)$$

where ϕ_a and ψ_a are costate variables associated with ℓ_a and w_a , respectively. (11) differs from (4) in the extra term $\psi_a z_a$, which arises since we now allow the body size to grow endogenously with the dynamics characterized by $\dot{w}_a = z_a$.

The costate equations for the dynamic problem are:

$$\begin{aligned} \frac{d\phi_a}{da} &= -\frac{\partial \mathcal{H}}{\partial \ell_a} = -e^{-\rho a} m_a + \phi_a \mu_a, \\ \frac{d\psi_a}{da} &= -\frac{\partial \mathcal{H}}{\partial w_a} = \phi_a \ell_a \frac{\partial \mu_a}{\partial w_a} = \phi_a \ell_a \frac{\zeta_{a,w}}{f_{a,\mu}}. \end{aligned} \quad (12)$$

The first equation in (12) is identical to (5), which leads to $\phi_a = e^{-\rho a} v_a$. Substituting ϕ_a in the second equation yields the solution for ψ_a .

The first order conditions are

$$\begin{aligned} \frac{\partial \mathcal{H}}{\partial m_a} &= e^{-\rho a} \ell_a + \phi_a \ell_a \frac{f_{a,m}}{f_{a,\mu}} \leq 0, \quad \text{and} \quad \frac{\partial \mathcal{H}}{\partial m_a} m_a = 0, \\ \frac{\partial \mathcal{H}}{\partial z_a} &= \phi_a \ell_a \frac{f_{a,z}}{f_{a,\mu}} + \psi_a \leq 0, \quad \text{and} \quad \frac{\partial \mathcal{H}}{\partial z_a} z_a = 0. \end{aligned} \quad (13)$$

We can apply (13) to establish the pattern of determinate growth. Suppose the optimal m_a and z_a are both strictly positive. In this scenario, (13) implies that $\partial \mathcal{H} / \partial m_a = 0$ and $\partial \mathcal{H} / \partial z_a = 0$. These equations result in different value functions v_a :

$$v_a = -\frac{f_{a,\mu}}{f_{a,m}} \quad \text{and} \quad v_a = -\frac{f_{a,\mu}}{f_{a,z}} \cdot \frac{\psi_a}{e^{-\rho a} \ell_a} = -\frac{f_{a,\mu}}{f_{a,z}} \cdot \frac{c}{e^{-\rho a} \ell_a} \exp\left(\int_a \frac{\zeta_{s,w}}{f_{s,z}} ds\right), \quad (14)$$

which cannot hold simultaneously. The expression for ψ_a is derived as follows. $\psi_a = -\phi_a \ell_a f_{a,z} / f_{a,\mu}$ if $z_a > 0$. Along with the second equation in (12), we obtain $(\partial \psi_a / \partial a) / \psi_a = -\zeta_{a,w} / f_{a,z}$, and hence $\psi_a = c \cdot \exp[\int_a (\zeta_{s,w} / f_{s,z}) ds]$, where c is an integration constant to be determined later.

We have demonstrated that m_a and z_a cannot both be strictly positive. In what follows, we skip the technical discussion concerning which corner solutions arise, and concentrate on the scenario in which the organism grows until age J , and then stops growing. In this case, we have $m_a = 0$ ($z_a > 0$) for earlier ages ($a \leq J$), and $z_a = 0$ ($m_a > 0$) for subsequent ages ($a > J$).

We shall consider a transfer of resources (positive or negative) received at age- a , which we denote R_a . Because fertility is zero in the early periods of life, the budget constraint becomes

$$f_a(\mu_a, 0, z_a) \leq \zeta_a(w_a) + R_a, \quad \forall a \leq J.$$

And because growth stops for $a > J$, we know that

$$f_a(\mu_a, m_a, 0) \leq \zeta_a(w_J) + R_a, \quad \forall a > J.$$

The latter expression is similar to (1'), for which we assumed that the body size is exogenous and does not grow.

4.3 Discount Rates and Demography

Now let us consider the impact of R_a on the value functions, starting with $a \leq J$. Applying the same method as in Section 4.1, we obtain

$$\frac{\partial \mathcal{H}}{\partial R_a} = -\frac{\phi_a \ell_a}{f_{a,\mu}} = \frac{\psi_a}{f_{a,z}} = \frac{c}{f_{a,z}} \exp\left(\int_a^J \frac{\zeta_{s,w}}{f_{s,z}} ds\right) \quad \text{for } a \leq J. \quad (15)$$

The first equality holds true for any a , while the second equality follows from (13) and employs the fact that $z_a > 0$ for $a \leq J$. The expression for ψ_a in the final equality can be found in (14).

The first order conditions in (13) suggest that term $\phi_a \ell_a$ has different expressions depending on whether $z_a > 0$ or $m_a > 0$. With $m_a > 0$, we have

$$\frac{\partial \mathcal{H}}{\partial R_a} = -\frac{\phi_a \ell_a}{f_{a,\mu}} = \frac{e^{-\rho a} \ell_a}{f_{a,m}} \quad \text{for } a > J. \quad (16)$$

We first study the time preference within juvenile ages a to $a + \tau < J$. In this scenario, we have $\phi_a \ell_a = \phi_{a+\tau} \ell_{a+\tau}$ according to (6) since both terms equal $\int_J^\infty e^{-\rho s} \ell_s m_s ds$. It follows that

$$\left| \frac{dR_{a+\tau}}{dR_a} \right| = \frac{f_{a+\tau, \mu}}{f_{a, \mu}}. \quad (17)$$

As one can see from (17), the discount rate between two ages within the immature period depends neither on the intrinsic growth rate ρ nor on the survival probabilities ℓ_a or $\ell_{a+\tau}$, in sharp contrast to the previous literature. An energy increment affects the reproductive fitness of an immature individual only if she survives to reproductive age. The timing of mortality before that age is irrelevant, so neither ℓ_a nor $\ell_{a+\tau}$ enters the MRS expression directly. Similarly, postponing the energy increment from age a to age $a + \tau$ *does not postpone its effect on reproduction*, which in any case does not occur until after age J , hence ρ is irrelevant.⁵

However, an energy increment received earlier permits earlier body growth which has a compounding effect since it leads to more energy acquisition each instant and further increases in size which raise energy acquisition even more. Applying the last equality of (15) to both a and $a + \tau$ yields an alternative expression of the MRS, which illustrates such an effect.

$$\left| \frac{dR_{a+\tau}}{dR_a} \right| = \frac{f_{a+\tau, z}}{f_{a, z}} \exp \left(\int_a^{a+\tau} \frac{\zeta_{s, w}}{f_{s, z}} ds \right). \quad (17')$$

Getting the energy increment R_a at age a enlarges the feasible set *earlier* in life than an increment $R_{a+\tau}$ at age $a + \tau$, leading to a larger body size at

⁵In fact, a determinate growth pattern implies a *dichotomy* of optimal growing and fertility in the following sense. Suppose a mutation effectively reduces the marginal fertility cost of age J , so that $f_{J, m}$ decreases, and the intrinsic growth rate ρ increases. The organism's tradeoffs and strategies in the growing period will not be affected by this parameter change of the fertile period. This is intuitive, for under determinate growth, whatever marginal fertility cost the species is to face at age J is not going to affect its optimal strategy of somatic growth in its earlier ages of growing.

age $a + \tau$ and therefore greater energy production and a compounding of the gain as indicated in the exponential term.

As before, we can also express this as an instantaneous rate of time preference

$$\lambda_a = \frac{\dot{f}_{a,z}}{f_{a,z}} + \frac{\zeta_{a,w}}{f_{a,z}}. \quad (17'')$$

>From (17''), one observes that the discount rate λ during immature ages is independent of age-specific mortality and fertility, and depends only on the rate of return to investment in growth (the second term) and the rate of change in the costliness of growth (the first term). We have no reason to expect any particular age pattern in the proportional rate of change in the costliness of growth; our expectation is that it is constant. However, we do expect diminishing fitness returns to body size, $\zeta_{a,w}$, as the optimal size w_J is approached. We also expect that the costs of increasing body size, $f_{a,z}$, will rise as the optimal body size is approached. For these reasons, we expect that the discount rate will be high following birth, when the returns to growth are large, and energetic inputs are readily converted into weight gains, and will then decline to lower levels as the age of maturity is approached.⁶

To be more precise, assume that body size increases with age up to maturity. Assume that the costs of growth do not grow at more than an exponential rate during the juvenile years, so that the first term declines with a or is constant. Assume further that $\frac{\zeta_{a,w}}{f_{a,z}}$ is decreasing in age. This would be so, for example, if the marginal effect of body weight on productivity is decreasing with body size, or if the marginal cost of body growth is increas-

⁶This conclusion hinges upon an implicit assumption in (10) that the energy constraint only contains flow variables but not stock variables, such as the size of body. If this is taken into account, the formula in (17) will be more complicated. Right now we assume that the stock variable is embodied in the age subscript a , but not independently as an argument.

ing with body size, or both. In addition, we must assume that the partial derivatives of $f\{a, z\}$ w.r.t. μ_a , m_a , and z_a are negligible in comparison to the partial derivative of $f\{a, z\}$ w.r.t. a (i.e., $\dot{f}\{a, z\}$). A similar condition should also be true for $f\{a, m\}$. These conditions are sufficient for λ_a to decline from birth to maturity.

Now let us look at the discount rate within mature ages between a and $a + \tau$ for $a > J$. Since both m_a and $m_{a+\tau}$ are strictly positive, the formula is identical to (9) derived in Section 3.1:

$$\left| \frac{dR_{a+\tau}}{dR_a} \right| = \frac{\ell_a}{\ell_{a+\tau}} \cdot \frac{f_{a+\tau, m}}{f_{a, m}} \cdot e^{\rho\tau}. \quad (18)$$

and the instantaneous discount rate is

$$\lambda_a = \mu_a + \frac{\dot{f}_{a, m}}{f_{a, m}} + \rho, \quad (9'')$$

The term $\frac{\dot{f}_{a, m}}{f_{a, m}}$ is the proportional rate of change of the marginal energetic cost with age of fertility, similar to the observation by Sozou and Seymour (2003 p.1049). This may initially be negative following J but will eventually rise as a result of deteriorating ovarian function which causes conception delay and more frequent fetal loss.⁷ If the marginal cost rises more than exponentially with age, then λ tends to rise as well. The authors have shown elsewhere (Chu et al, 2008). that the endogenous death rate, μ_a , also may decline or remain steady until some age after J , reflecting continuing maturation and the effects on productivity of increasing foraging experience. Thereafter, however, it rises at all ages. Therefore λ , the rate of time preference, also eventually rises with age after maturity. consistent with Sozou and Seymour (2003).

⁷The declining marginal cost of fertility phase in humans is reflected in early reproductive ages when fecundity (biological potential fertility or natural fertility) rises. The rising marginal cost phase clearly holds for mammals which move toward deterioration and exhaustion of their oocyte stores as they age (Finch 1990).

To put these conditions more precisely, if the proportional rate of increase with age in marginal fertility costs declines more slowly than μ_a , declines, and given the earlier conditions on the partial derivatives of f , then λ_a rises with age starting at some point after sexual maturity. Together, these two sets of conditions for the ages before and after sexual maturity are sufficient to establish that the instantaneous rate of time preference is U-shaped.

We conclude, therefore, that the discount rate will be U-shaped, declining from birth to the age of maturity and perhaps a bit longer, and rising thereafter. In reality, the transition between immaturity and maturity may be blurred, as it surely is in humans, where a few years of adolescent growth overlap with the early reproductive ages.

Finally, let us consider a transfer from a mature individual to a juvenile, that is the case where $a < J$ and $a + \tau > J$. From (15) and (16), the discount factor between ages a and $a + \tau$ is given by

$$\left| \frac{dR_{a+\tau}}{dR_a} \right| = \frac{c(a)}{e^{-\rho(a+\tau)} \ell_{a+\tau} / f_{a+\tau, m}}, \quad (19)$$

where the coefficient $c(a)$ equals $\frac{1}{f_{a, z}} \exp(\int_a^J \frac{\zeta_{s, w}}{f_{s, z}} ds) \cdot \int_J^\infty e^{-\rho s} \ell_s \frac{\zeta_{s, w}}{f_{s, m}} ds$,⁸ which is the effect of a unit of energy received at age a . The initial factor is the increase in size that results from the unit of energy, with the exponential factor as the compounding impact of increase in size at age a on the recipient's continuing growth of body size from age a up to age J ; and the last factor accounts for the effect of this ultimate increase in body size on the donor's reproduction from J until death, weighted by probability of survival at each

⁸ $c(a) = \partial \mathcal{H} / \partial R_a$, which equals $\psi_a / f_{a, z}$ with $a < J$. The solution to the costate variable ψ_a is given by $c \cdot \exp \int_a^J \frac{\zeta_{s, w}}{f_{s, z}} ds$ as shown in (14). Substituting $a = J$ in the formula, we find that $c = \psi_J$. In order to derive ψ_J , recall that ψ_J is the derivative of the value function w.r.t. w_J : $\psi_J \equiv \partial(\int_J^\infty e^{-\rho s} \ell_s m_s ds) / \partial w_J$. Moreover, m_s can be considered as a function of w_J , which in effect eliminates the energy constraints. Since the constraint implies that $\partial m_s / \partial w_J = \zeta_{s, w} / f_{s, m}$, we obtain $\psi_J = \int_J^\infty e^{-\rho s} \ell_s \frac{\zeta_{s, w}}{f_{s, m}} ds$.

age and discounted to birth. The denominator of (19) is the effect of a unit of energy received at age $a + \tau$ which raises fertility at that age by $\frac{1}{f_{a+\tau,m}}$ and this is weighted by the probability of surviving to this age and discounted back to birth. Thus (19) provides the discount rate bridging the age-ranges of growing size and reproducing.

There are a couple of points about this result that are worth mentioning. If the energy increment is received at age $a + \tau$ it has no effect on body size, and the sole effect is on fertility or survival at age $a + \tau$. However, if it is received at age a then it affects size, and therefore affects fertility or survival at all ages beyond J and indeed beyond $a + \tau$ as well. In contrast to previous results in (18), it is only survival from J to $a + \tau$ that matters; survival from a to J is irrelevant. As explained earlier, unless the individual survives from a to J it does not reproduce at all, and conditional on survival to J , the age pattern of earlier mortality is irrelevant.

The earlier literature found that the MRS was positively related to ρ , the intrinsic growth rate. Our result is different, since an energy increment at age a increases body size and therefore raises fertility at every age above age J . If most of this survival weighted and discounted incremental fertility occurs before age $a + \tau$, then the MRS is positively related to ρ as in the previous literature. However, if most of it occurs after age $a + \tau$, then the MRS is negatively related to ρ , contrary to the previous literature. Thus when the mature age $a + \tau$ is closer to sexual maturity J the effect of ρ on the MRS is more likely to be negative (because most of the fertility increment comes at later ages), and when the mature age under consideration is farther beyond sexual maturity, then this effect is more likely to be positive (because more of the increment to fertility comes at earlier ages).

These results modify the previous wisdom on the relationship between ageing and the discount rate. Sozou and Seymour (2003 p.1047) argued that ageing is partly a consequence of a life-history strategy that discounts the

future. This is particularly correct for mature ages. In view of (17)–(19), however, we need to modify the previous results if we want to consider the whole range of a species' life cycle. When individuals are still growing, the mortality factors (ℓ_a 's) do not affect the marginal rate of substitution between age-specific resources, and the population growth rate has no effect on the rate of time preference.

5 Theory III: Arbitrage in Nature? The Evolution of Intergenerational Transfers

For many species, this is the end of the story. The young, particularly newborns, have a very high rate of time preference, because increased investments in their body growth would substantially raise reproductive fitness. While the young would do better if they could borrow from the old, repayment could never evolve because it would diminish reproductive fitness rather than improving it. But as in Samuelson's (1958) classic analysis of a consumption loan economy, intergenerational transfers (here from old to young rather than the reverse) can lead to a better outcome. In Samuelson, intergenerational transfers yield the biological interest rate ρ which is the marginal rate of transformation (MRT). In the context of energy transfers within a cooperative breeding group, the MRT is determined by the energy transformation technology between the adults and the juveniles, which in turn depends on the age structure of the group. If $MRS > MRT$ then transfers would be enhance fitness and therefore might evolve. In the limit, transfers would evolve to the point where they would equalize the MRS across the entire life cycle, equating it to the MRT.

Many species, including mammals, birds, many insects and some fish invest in their young after birth through transfers from one or both parents,

older siblings, grandparents, or others. The simplest case is parental care, but more complicated arrangements occur for cooperatively breeding species, including humans. We shall investigate when this kind of transfer behavior will be selected and its relationship to the age-specific MRS.

The optimal life history satisfies the identity (2): $\int_J^\infty e^{-\rho s} \ell_s m_s ds = 1$. Totally differentiating this equation⁹ leads to

$$\begin{aligned}
\int_J^\infty s e^{-\rho s} \ell_s m_s ds \cdot \frac{d\rho}{dR_a} &= \int_J^\infty e^{-\rho s} \ell_s \frac{\partial m_s}{\partial w_J} \frac{dw_J}{dR_a} ds + e^{-\rho(a+\tau)} \ell_{a+\tau} \frac{\partial m_{a+\tau}}{\partial R_{a+\tau}} \frac{dR_{a+\tau}}{dR_a} \\
&= \int_J^\infty e^{-\rho s} \ell_s \frac{\zeta_{s,w}}{f_{s,m}} ds \cdot \frac{dw_J}{dR_a} + \frac{e^{-\rho(a+\tau)} \ell_{a+\tau}}{f_{a+\tau,m}} \frac{dR_{a+\tau}}{dR_a} \\
&= \frac{\psi_a}{f_{a,z}} + \frac{e^{-\rho(a+\tau)} \ell_{a+\tau}}{f_{a+\tau,m}} \frac{dR_{a+\tau}}{dR_a}.
\end{aligned} \tag{20}$$

The integral on the left equals the average age of fertility, denoted A_f , which measures the length of a generation. Multiplying this by $\frac{d\rho}{dR_a}$ converts the effect of dR_a from an annual rate of change to a change per generation, which is expressed on the right side of the equation. The second equality follows from the energy constraints, with $\frac{\partial m_s}{\partial w_J} = \frac{\zeta_{s,w}}{f_{s,m}}$ and $\frac{\partial m_s}{\partial R_s} = \frac{1}{f_{s,m}}$. Meanwhile, the marginal effect of the transfer on size, $\frac{dw_J}{dR_a}$, is given by $\frac{1}{f_{a,z}} \exp(\int_a^J \frac{\zeta_{s,w}}{f_{s,z}} ds)$ from the argument in Section 4.3. The expression, along with the argument in footnote 8, yields the last equality in (20).

For $\frac{dR_{a+\tau}}{dR_a}$ we first consider how the population age distribution constrains the size of the transfers given relative to the transfer received, which depends on the relative number of individuals making transfers at age $a + \tau$ and

⁹To understand the meaning of $\frac{d\rho}{dR_a}$, given that in the long run the steady state growth rate must be zero in any case, refer back to footnote 4 on carrying capacity, density, and the steady state growth rate. If intergenerational transfers can generate a more rapid population growth rate in a context without carrying capacity constraints, then in the presence of constraints they should lead to equilibration at a denser population that would crowd out the rival genetic line.

receiving them at age a . We introduce a function $g_a(\cdot)$ which characterizes the efficiency with which an organism at age a converts a transfer that it receives into a usable form of energy, in the same units as $\zeta_a(w_a)$. In a stable population if each surviving adult at age $(a + \tau)$ gives out one unit of energy to its offspring at age a then each offspring receives a proportional share equal to $e^{-\rho\tau}\ell_{a+\tau}/\ell_a$ of the energy given by each adult.¹⁰ However, a juvenile at age a cannot be fed too much or too fast in a given period without wastage. This constraint on the ability of an individual to utilize a transfer is characterized by $g_a(\cdot)$, with $g_a(\cdot) > 0$ and $g'_a(\cdot) > 0$.¹¹ For an individual at age a to acquire R_a units of usable energy, $g_a(R_a)$ units must be received.

Taking into account the stable (steady state) population constraint on relative numbers at the two ages,¹² the transfers $R_{a+\tau}$ made by adults at age $a + \tau$ to juveniles at age a who receive R_a , are linked by the following identity:

$$-\ell_{a+\tau}dR_{a+\tau} = e^{\rho\tau}\ell_a dg_a(R_a) = e^{\rho\tau}\ell_a g'_a(R_a)dR_a. \quad (21)$$

Let us define K as the RHS of (20) multiplied by $e^{\rho a}$. Substituting the derivatives obtained so far, we can compute K with simple algebra:

$$K = \frac{e^{\rho a}\psi_a}{f_{a,z}} - \frac{\ell_a}{f_{a+\tau,m}}g'_a(R_a),$$

where $\psi_a/f_{a,z}$ is the numerator in (19). We know from (20) that K has the

¹⁰Here we assume that transfers go from parents to offspring, but in cooperative breeding groups the relatedness between donor and recipient is often less close, which we ignore here for simplicity.

¹¹ $g'_a > 0$ since a transfer outlet from age- $(a + \tau)$ (negative $dR_{a+\tau}$) is needed to produce an increase of R_a at age- a (positive dR_a). That $g''_a > 0$ is needed for an interior solution of transfers.

¹²The stable population assumption is appropriate for cooperative breeding groups involving multiple related adults, but for the case of simple parental care it should be viewed as a necessary simplification for characterizing the relative numbers of those in the two age groups in parent-offspring sets.

same sign as $d\rho/dR_a$. Therefore a transfer from age $a + \tau$ to age a will be selected ($d\rho > 0$) if and only if $K > 0$.

The first term of K is the weighted fertility increase at ages beyond J arising from the increase in weight at age a , which is in turn caused by the transfer of energy from the adult aged $a + \tau$. The second term of K is the fertility loss to the adult aged $a + \tau$ caused by her energy transfer to an offspring aged a . The net benefit is positive if the net fertility gain is positive.

There is a close relationship between the the $MRS_{a,a+\tau}$ we derived in (19) and the condition for transfers to be selected. On the one hand, we have the time preference result derived earlier, which is analogous to the MRS in an intertemporal utility function. It describes the slope of an iso-fitness contour for energy increments at age a and age $a + \tau$, R_a and $R_{a+\tau}$. On the other hand, we have $MRT_{a,a+\tau} \equiv e^{\rho\tau} g'_a(R_a) \cdot \ell_a/\ell_{a+\tau}$ from (11), which is analogous to a market rate of interest earned by participation in parental care or the cooperative breeding group. It describes the rate at which energy given up at age $a + \tau$ can be converted into energy received by individuals at age a through intergenerational transfers, given the demographic constraints and the transfer conversion constraint. If the $MRS_{a,a+\tau}$ in fitness is greater than the $MRT_{a,a+\tau}$ through the intergenerational transfer technology, then intergenerational transfers from age $a + \tau$ to age a can raise reproductive fitness and a mutation causing this transfer behavior will be selected. It is easy to see that this difference is given by:

$$MRS_{a,a+\tau} - MRT_{a,a+\tau} = e^{\rho\tau} \frac{f_{a+\tau,m}}{\ell_{a+\tau}} K.$$

Thus, the transfer will be selected if and only if $K > 0$. If the second order condition is satisfied, there is an optimal level of transfers from individuals age $(a + \tau)$ to age a , when the $MRS_{a,a+\tau} = MRT_{a,a+\tau}$.

>From the expression for K we can infer the factors that favor larger K

and therefore favor the evolution of intergenerational transfers in a species. Lower costs of juvenile body growth and larger productivity gains from body size favor the evolution of transfers as do lower costs of fertility across the adult ages. However, high costs of fertility at the specific age making the transfers also favors the evolution of transfers at that age, with menopause an extreme example. Higher adult survival across the fertile ages also promotes the evolution of transfers, as does a low population growth rate. Of course, these very features of a life history are endogenous. But thinking of evolution as a sequential process which works to improve existing life histories, these features favoring the evolution of intergenerational transfers are of interest.¹³

6 Discussion

The neurological equipment that guides our intertemporal decisions evolved to enhance fitness in our pre-Neolithic past (Camerer et al, 2005), before capital and storage were important features of our economic life. We have built on an earlier literature to explore what patterns of time preference could be inferred from this premise. Our approach integrates optimal life history theory with time preference theory, explicitly incorporating energy constraints, resource tradeoffs, and intergenerational transfers that were not included previously and consequently reaching rather different conclusions.

Beginning with a framework in which body size and energy constraints by age are exogenous (**Theory I**), we have confirmed earlier results: 1) The rate of time preference *across generations* equals the population growth rate (Hansson and Stuart, 1994). 2) Higher mortality between two ages implies

¹³Interpretations of this sort are based on a feature of the life history that from a *tabula rasa* (0-base) analysis would be viewed as endogenous. However, actual evolutionary processes are heavily constrained by the preceding life history on which they build, and from this perspective, these statements about $f_{a,z}$ and $\zeta_{a,w}$ have causal force.

a higher rate of discount between them (Sozou and Seymour, 2003). 3) The discount rate should be higher when the rate of senescent fertility decline between two ages is higher (Rogers, 1994; Sozou and Seymour, 2003).

We then developed a more general model with endogenous body size and energy production so that fertility and survival tradeoff not only against each other but also against growth and future body size (**Theory II**). This framework leads to quite different conclusions. Now the optimal life history can involve two corner solutions: first growth with zero fertility (the immature stage), and then fertility with zero growth (the mature stage), a pattern called determinate growth, which is in fact characteristic of many animals including mammals. In particular, we find that:

1) Before reproductive maturity, neither survival nor the intrinsic growth rate enters into time preference, in both respects contrary to earlier results. Reallocating resources within the immature ages does not directly advance or retard fertility, and therefore the intrinsic growth rate does not directly influence discounting. To be sure, the intrinsic growth rate is endogenous and depends on allocations during the premature phase, but our result is different than the previous literature where the intrinsic growth rate enters the MRS formula directly.¹⁴ And reproduction depends on not dying before maturity, but within immaturity there is no tradeoff between dying earlier or later. Instead, the discount rate derives from differences in the ability to convert energy into body growth, and then to convert body size into energy.

2) For tradeoffs between immature and mature ages, only survival up to and beyond sexual mortality (ℓ_J) matters, and the age pattern of mortality before J is irrelevant, consistent with the previous discussion. Furthermore, when the older age is not long after sexual maturity then a higher intrinsic growth rate actually reduces the MRS rather than raising it, contrary to all

¹⁴For example, if $f_{a,m}$ for $a > J$ changes then the intrinsic growth rate will also change, but the MRS between juveniles will not change.

previous literature. The reason is that resources received during the immature stage raise fertility throughout the entire mature reproductive life span by raising body size, and on average this increase may actually occur later than the mature age under consideration.

3) Within the mature ages, the discount rate depends on the rate of reproductive senescence, on the intrinsic growth rate, and on survival, as suggested by the earlier literature (Rogers, 1994; Sozou and Seymour, 2003).

4) We find that the optimal discount rate is U-shaped with age: high at birth, declining until the age of maturity and perhaps a bit longer (depending on whether and for how long after maturity the marginal energetic costs of fertility continue to fall), and then rising thereafter as the pace of fertility decline and mortality increase accelerates.

A high and variable rate of time preference across the life cycle suggests that autarchy is inefficient and that intergenerational transfers could raise reproductive fitness (**Theory III**). In the limiting evolutionary equilibrium the MRS would equal the MRT with a discount rate equal to the steady state population growth rate, typically zero. But as discussed earlier, various frictions such as paternity uncertainty and parental mortality would prevent this limit from being reached. The outcome, therefore, will be a flatter U shape for the rate of time preference than in the world without transfers.

Understanding how people actually make intertemporal choices is an important topic on the agenda of behavioral economics (Frederick et al, 2002; Camerer et al, 2005). Life history theory can provide a foundation for further work. Building on a valuable earlier literature we have found that the relationship between the discount rate and demography is more complicated than has been previously realized.

Table 1. Definitions of variables and functions.

$f_a(\mu_a, m_a, z_a)$	Energy budget constraint at age a excluding transfers.
$f_{a,\mu}; f_{a,m}; f_{a,z}$	Partial derivatives of f_a with respect to μ, m, z
m_a	Birth rate
μ_a	Instantaneous death rate = $d \ln(l_a) / da$
l_a	Probability of surviving from birth to age $a = \exp(-\int_0^a \mu_s ds)$
$\zeta_a(w_a)$	Energy flow generated as a function of body size
ρ	Steady state population growth rate or intrinsic rate of natural increase.
ϕ_a	Costate variable associated with l_a
ψ_a	Costate variable associated with w_a
w_a	Body size
z_a	Rate of change of body size, \dot{w}_a
λ_a	Rate of instantaneous time preference at age a
R_a	Transfer made or received
$g_a(R_a)$	Amount of usable energy derived from receipt of a transfer R_a
K	If $K > 0$ then transfers raise reproductive fitness (for specific pair of ages)

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