The Co-evolution of Intergenerational Transfers and Longevity: An Optimal Life History Approach[1]

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[1] Lee's research for this paper was funded by two grants from NIA, R37-AG11761 and P01 AG022500-01. Marc Mangel, David Steinsaltz and conference participants at Rostock provided useful comments on an earlier draft.

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Abstract

How would resources be allocated among fertility, survival, and growth in an optimal life history? The budget constraint assumed by past treatments limits the energy used by each individual at each instant to what it produces at that instant. We develop explicit solutions for the optimal life history in this case, extending the current literature that presents numerical solutions and permitting comparative static analysis. Then we consider under what conditions energy transfers from adults, which relax the rigid constraint by permitting energetic dependency and faster growth for the offspring, would be advantageous. In a sense, such transfers permit borrowing and lending across the life history. Higher survival and greater efficiency in energy production at older ages than younger both favor the evolution of transfers. We show that if such transfers are advantageous, then increased survival up to the age of making the transfers must co-evolve with the transfers themselves.

Key words: evolution, longevity, mortality, intergenerational transfers, life history, optimal energy allocation.

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1 Introduction

A growing literature seeks the optimal solution to the "general life history problem", how to allocate resources among fertility, mortality and growth from birth to death.[3] Studies assume that the individual can use only the energy that it produces (forages) in each period, and optimize the life history subject to this strict budget constraint. But what if individuals were permitted to borrow and lend over their life cycles? That would permit a stage of nutritional/energetic dependence early in life with rapid growth and development, followed by a corresponding adult stage of "repayment" in which transfers are made to the young. The steady state constraint for transfers is that the survival-weighted and discounted sum of transfers received minus transfers made over the life cycle must be zero, similar to a life cycle budget constraint with borrowing and lending at an interest rate equal to the population growth rate. Many species have life histories of this sort, including all mammals, most birds, many insects, and some fish and reptiles (see Clutton-Brock [1991]). Here we will consider how the optimal life history changes shape when intergenerational transfers are permitted and confer a selective advantage. Lee (2003) took the existence of transfers as given, and did not consider physiological tradeoffs. In this paper we will examine the conditions under which transfer behavior (parental care) evolves, and consider how mortality co-evolves, when tradeoffs are explicitly modeled through the energy budget constraint.

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[3] See for instance Taylor et al. (1974), Goodman (1982), Schaffer (1983), Stearns (1992), Abram and Ludwig (1993), Cichon (1997), Cichon and Kozlowski (2000), Clark and Mangel (2000), and Kaplan and Robson (2002).

The analysis we present is formally applicable to cooperative breeders, that is, groups of individuals in which some members across the age spectrum potentially provide food and care to young that are not necessarily their own offspring.[4] In such cases, we can imagine a lineage carrying a mutation forming a stable population in aggregate, and fissioning into cooperatively breeding groups. Within each group, transfers of food take place. Each group can be viewed as a microcosm of the lineage, with random departures from its stable age distribution.[5] Humans are cooperative breeders, and the idea is well-established that their exceptional longevity, particularly in postreproductive years, is related to their transfer behavior.[6] There is also evidence (Brown [1987]) that cooperatively breeding bird species live longer than others.

We begin by considering what life history for a lineage-founding individual would produce the greatest number of living descendants at a specified future date, optimizing subject to the usual budget constraint that does not allow transfers (section 2). We show that the appropriate measure of fitness to be maximized for this individual turns out to be the Euler-Lotka parameter (section 3). This sets the stage for considering the conditions under which intergenerational transfers would be selected. We investigate when such transfers increase fitness (section 4), and if they do, how low mortality coevolves with them (section 5). The last two sections contain extensions

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[4] Whether or not cooperative breeding evolved to facilitate intergenerational transfers, the demography of cooperative breeding groups provides an analytic setting in which stable population methods can be appropriately used.

[5] The analysis for transfers within parent-offspring sets is more difficult, because their age distributions cannot plausibly be viewed as microcosms of the lineage. However, the technical difficulties in analyzing the parent-offspring case do not seem to point to substantive differences in the explanation of transfer behavior between this and the cooperative breeding contexts.

[6] See Clutton-Brock (1991), Kaplan and Robson (2002), Lee (2003) and Lahdenpera et al. (2004).

and conclusions.

2 A New Model of Optimal Life History

We first consider the case in which transfers are not an evolutionary option. The analysis could be carried out for a life history of potentially unlimited length, but we will instead consider the more realistic case of an individual who is not fertile past age y.[7] To avoid the complications of mating and sexual reproduction, we will consider a population of females reproducing asexually. To unify the terminology and notation, we call the age interval $[a, a+1)$ age $a+1$, and assume that all decisions affecting age $a+1$ are made at time a. The probability that a person survives from a toward the point $a+1$ (that is, toward the end of the open age interval) is denoted p_{a+1}. Fertility at age $(a+1)$ takes place toward the point $a+1$, and is denoted m_{a+1}.

At age a, a typical individual expects to have energy or resources which, following Abram and Ludwig (1995), Cichon (1997) and Vaupel et al. (2004), she allocates to fertility (m_a), maintenance (p_a) and growth (z_a). We can think of growth as increase in body size, but we could also think of it as other kinds of physical investment such as development of the brain, as in Kaplan and Robson (2002) and Robson and Kaplan (2003). Because the individual can potentially reproduce in all periods before y, there is a tradeoff

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[7] It is not necessary to assume that fertility is 0 past some age y. However, absent this assumption, fertility and survival would never reach zero in our optimization setup. As long as fertility and survival are not infinitely costly, death will never be optimal in our model setup. This is because fertility m_a occurs only after survival p_a, so it can never be optimal to spend all energy on fertility at some age and none on survival. For this reason, our analysis focuses on survival rather than on life span. We could define the end of life as that age at which the probability of survival to the next period drops below some specified level, such as .001. Perhaps for similar reasons, Cichon and Kozlowski (2000) adopted this approach.

between energies devoted to reproduction, growth and maintenance: Having more children early in life comes at the expense of her growth and survival probability, which in turn affects her later fertility.

2.1 The Maximization Problem

The disposable resource or energy of an individual aged a depends on her body size, denoted w_a. Specifically, her age-a budget (energy) constraint is written as

$$b_a p_a + c_a m_a + d_a z_a \leq \zeta_a w_a, \quad \forall a \tag{1}$$

where b_a, c_a, d_a are constant coefficients, which express the rate at which energy can be used to achieve various levels of survival, fertility or growth. ζ_a is a production coefficient linking body-size with the net production, or acquisition through foraging, of disposable energy. It is easy to see that one of the four coefficients (b_a, c_a, d_a, ζ_a) in (1) is redundant, and so at each age a, we normalize ζ_a to be 1 . This simplifies the expressions in what follows, but note that whenever we need to combine units of energy from different ages, we will have to convert the units appropriately. When this happens we will alert the reader.

The body size of an individual grows according to the following rule: $w_{a+1} \equiv w_a + z_a$. Note that given the same body size w, an older individual may still be weaker and more vulnerable, as reflected in a larger b_a (higher costs of achieving survival level p_a). The initial body size w_1 is itself an important intergenerational transfer from the mother. In our analysis, w_1 is given, while the adult size is part of the optimization problem through allocation of energy to growth. Thus the ratio of birth size to adult size is endogenous in our analysis. Given our linear homogeneous budget constraint, scale is irrelevant, so only this ratio matters. In this paper our emphasis is on intergenerational transfers occurring after birth.[8]

We expect that natural selection will maximize reproductive fitness, measured as the representation of an individual's genes at some future date τ. Since we are assuming clonal reproduction, this is equivalent to maximizing the number of living descendants at some date τ, which may be far beyond the individual's finite lifespan.[9] Consider an individual age a at time t. Let $V_{a,t}(.)$ be her contribution to the number of descendants at time τ. Here t will measure the remaining length of time until τ, when fitness is assessed, so for individuals closer to τ, t will be smaller. Bellman's (1957) *principle of optimality* can be used to maximize the expected number of future descendants at τ. According to this principle, energy is allocated at age a and period t so as to maximize the contribution to fitness assessed at τ, assuming that the energy in all future ages and periods is also allocated optimally.

2.2 The Solution

We shall first fix age 1 as the benchmark and try to solve the dynamics in terms of the age-1 value function. For any $a \in \{1, 2, ..., y\}$, let the age-a strategy be $\theta_a \equiv (p_a, m_a, z_a)$ and its feasible set be $\Omega(w_a)$. For any t, the

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[8] The linear form of the budget constraint, as in Taylor et al. (1974) and Vaupel et al. (2004), is to some extent restrictive. Appropriate nonlinear effects would include an upper bound of unity for p_a, with increasing costs as this limit is approached; a dependence of p_a on body weight w_a; and a dependence of fertility on body weight.

[9] As we shall see, once the population reaches steady state, the fitness measure is also stable. For this reason, τ should exceed the approximate number of periods from the time in question until the steady state is reached.

Bellman equations can be written as[10]

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\begin{aligned}
V_{1,t}(w_1) &= \max_{\theta_1 \in \Omega(w_1)} [p_1 m_1 V_{1,t-1}(w_1) + p_1 V_{2,t-1}(w_1 + z_1)] \qquad (2)\\
&\vdots \\
V_{y-1,t}(w_{y-1}) &= \max_{\theta_{y-1} \in \Omega(w_{y-1})} [p_{y-1} m_{y-1} V_{1,t-1}(w_1) + p_{y-1} V_{y,t-1}(w_{y-1} + z_{y-1})] \\
V_{y,t}(w_y) &= \max_{\theta_y \in \Omega(w_y)} [p_y m_y V_{1,t-1}(w_1)].
\end{aligned}
$$

The interpretation of the above equations is as follows: $p_1 m_1$ in the first term on the right hand side of (2) characterizes the event that an age-1 individual survives (with probability p_1) and bears m_1 offspring. Since each of these offspring is valued $V_{1,t-1}$ in period $t-1$ (because the offspring is one period closer to τ), $V_{1,t-1}$ should be multiplied by $p_1 m_1$ to obtain the expected value. The $V_{2,t-1}$ in the second term of (2) is the value function of this individual at age-2. With probability p_1 the individual will survive to face this state, and so $V_{2,t-1}$ should be multiplied by probability p_1. The age-2 body size should be $w_2 = w_1 + z_1$ instead of w_1. The interpretations of other expressions are similar, so we move forward to the last equation. For an individual aged y in period t, p_y and m_y are chosen to maximize the expected value of the last birth. At age y, there is no gain from further growth.[11] This generates the age-y expected value $p_y m_y V_{1,t-1}$. Since y is the last fertile age by assumption, there is no second term for the last equation.

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[10] See Ross (1983) for more details of the technical background behind (2).

[11] The growth of a post-reproductive individual might still be valuable if she could transfer some wealth to her young offspring, but here we are considering the case in which this is not possible, reflected in the budget constraint in equation (1). See also Lee (2003).

3 Interpreting the Solution

We denote the optimum in (2) by $\theta_a^* = (p_a^*, m_a^*, z_a^*)$. Now, we try to write (2) in terms of $V_{1,t}$ for different t's. Let $\phi_a \equiv p_1^* \cdots p_a^* m_a^*$ be the net maternity function. Starting from the age-y equation, lagging each equation by one period, substituting it into the equation one line above, and iterating the process, we obtain

$$V_{1,t} = \phi_1 V_{1,t-1} + \phi_2 V_{1,t-2} + \cdots + \phi_y V_{1,t-y}. \tag{3}$$

In the steady state, expression (3) is a simple difference equation for $V_{1,t}$, of which the solution is $V_{1,t} = A_1\lambda_1^t + \cdots + A_y\lambda_y^t$, where the A_i's are constants, and λ's are solved from the characteristic equation of (3): $\lambda^t = \phi_1\lambda^{t-1} + \phi_2\lambda^{t-2} + \cdots + \phi_y\lambda^{t-y}$. Since the individual is maximizing clonal reproduction, only the largest root of the characteristic equation is relevant, call it λ^* and call the associated A_i simply A. Then we have: $V_{1,t} = A(\lambda^*)^t \quad \forall t$ in the steady state. From now on, we shall normalize A to be 1 to simplify the notation.

3.1 The Dynamics

For any given w_1, $V_{1,t}$ is actually a variable (instead of a function) to be solved. Let $\theta \equiv (\theta_1, ..., \theta_y)$. We rewrite the maximization problem in (2) as

$$V_{1,t} = \max_\theta \Big[p_1 m_1 V_{1,t-1} + p_1 p_2 m_2 V_{1,t-2} + ... + p_1 p_2 ... p_y m_y V_{1,t-y} \Big]. \tag{4}$$

Expecting that the solution of $V_{1,t}$ is a power function of λ, we imagine the following solution method. For any given λ_0, replace $V_{1,t}$ by $(\lambda_0)^t$, and solve for θ_0 from $\max_\theta g(\theta, \lambda_0)$, where $g(.,.)$ is such that

$$[g(\theta, \lambda_0)]^t \equiv p_1 m_1 (\lambda_0)^{t-1} + p_1 p_2 m_2 (\lambda_0)^{t-2} + ... + p_1 p_2 ... p_y m_y (\lambda_0)^{t-y}.$$

Let the θ that is obtained from the above maximization problem be θ_0. Then, for $s = 1, 2, ...$, we let

$$\lambda_s = \max_{\theta_{s-1}} g(\theta_{s-1}, \lambda_{s-1}). \tag{5}$$

The dynamic process described in (5) is similar to the one in McNamara (1991) and Houston and McNamara (1999), where it is shown that under some technical conditions, an iteration of (5) will converge to the stable-population λ^*. Our later comparative statics will also be analyzed based on the dynamic structure of (5).

3.2 The Meaning of the Value Function

An advantage of our approach is that the contribution of an individual to the future population of living descendants at τ can be solved analytically. Here we first illustrate the meaning of this solution.

What is $V_{1,t}(w_1)$? It is the individual's assessment at age 1 of the value of her resources (w_1), in terms of the contribution to future descendants. We also show in Part A of the Math. App. that the steady-state solution of $V_{a,t}$ for any a is given by:

$$V_{a,t} = \frac{\phi_a}{p_1 \cdots p_{a-1}} (\lambda^*)^{t-1} + \cdots + \frac{\phi_y}{p_1 \cdots p_{a-1}} (\lambda^*)^{t-y+(a-1)}. \tag{6}$$

Evidently, for all $a = 2, 3, ..., y$, $V_{a,t}$ is also discounted at the rate λ^*. Note that $V_{a,t}(.)$ is closely related to Fisher's (1930) concept of reproductive value.

What does it mean to have $V_{1,t} = (\lambda^*)^t$? We note that p_a is the probability that a child can survive through the interval $(a, a+1]$, given her initial size w_a. Let $l_a^* = p_1^* \cdots p_a^*$.be the probability of survival from birth to age a. In view of the definition of ϕ_a, we can rewrite (4) as

$$1 = \sum_{a=1}^{y} l_a^* m_a^* \lambda^{-a}, \tag{7}$$

This is the Euler-Lotka equation. Its largest root is the steady state population growth rate. Thus, we have

Proposition 1: The solution to the value function in (2) has the form $V_{1,t} = (\lambda^*)^t$, where λ^* is the Euler-Lotka parameter solved from (7).

Most previous literature on population evolution, to our knowledge, *assumes* that the Euler-Lotka parameter is the target of maximization. In the analysis above, we *derive* what a selfish agent, that maximizes its own clonal replication, would do, and show that the objective to be optimized turns out to be the Euler-Lotka parameter. The generic optimization problem characterized in (2) not only helps us understand the micro foundations of the Euler-Lotka parameter, but also specifies the framework for the comparative static analysis of the next section.

4 Optimal Life History and Transfers

4.1 A Corner Solution Pattern

In reality, many species first grow and then become fertile once they have reached their adult size. They cease growth or grow very slowly once they start bearing offspring. Our main interest is in species that make intergenerational transfers, such as mammals or birds, and these exhibit determinate growth of the sort described. The following proposition, proved in Part B of the Math. App., shows that the determinate growth pattern emerges in our model:[12]

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[12] Suppose with effort z_a there is probability $q(z_a)$ of achieving size $w_a + g_1$, and probability $1 - q(z_a)$ of achieving size $w_a + g_2$. In this case, our corner-solution argument will not hold. This may correspond to the case of *indeterminate* growth. An interior solution could also arise if the rates of converting energy into fertility and into body size were not constant, but rather varied with the amount of energy so converted. See Stearns (1992)

Proposition 2: m_a and z_a cannot be interior solutions at the same time.

Proposition 2 is intuitive, consistent with that found in Taylor et al. (1974), and Vaupel et al. (2004) and is convenient for our later analysis. Simple differentiation of (2) tells us that any growth in size at age a has the benefit of increasing future offspring at various ages by a constant factor: p_{a+1}/c_{a+1} at age $a+1$, $p_{a+1}p_{a+2}/c_{a+2}$ at age $a+2$, $\cdots$. Furthermore, in a steady state the value of a new-born at time t is proportional to λ^t. Thus the steady-state tradeoff between increasing size and bearing offspring is a constant, which depends on the parametric value of c_a's and d_a's. Therefore, a corner solution of either m_a or z_a must arise.

In what follows, we shall concentrate on analyzing the case in which an organism first grows for r periods, and then stops growing and reproduces. In our notation, the organism would have $m_a = 0$ in the first $a \leq r$ periods, and would have $z_a = 0$ when $a \geq r+1$.[13]

4.2 When Will Downward Transfers Be Selected?

In some species, parents invest in their offspring after birth by making transfers of food, guarding against predators, warming or ventilating them, and so on. We shall focus on the most prevalent form of transfers by mammals, when adult individuals aged $j \geq r+1$ transfer something to offspring aged $i \leq r$. We ask when such a transfer would raise the intrinsic growth rate λ, and therefore be selected.

Recall that equation (1) was normalized at each age a by dividing through by ζ_a. Because of this, when we consider transfers between ages i and j, we

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and Taylor et al. (1974).

[13] For instance, when $y = 3$ (three periods of life) and $r = 1$ (the first period being childhood), Part B of the Math. App. shows that the conditions for a switch of corner solutions at the junction of age 1 and age 2 are $d_1\lambda^2 < c_1p_2(\lambda/c_2 + p_3/c_3)$ and $d_2\lambda > c_2p_3/c_3$.

must use a conversion factor η_{ij} $(= \zeta_i/\zeta_j)$. Let the transfer given by an individual at age-j be T_j and the amount received by an age-i by R_i. The demography imposes a feasibility condition on these transfers in a steady state:

$$\eta_{ij}\lambda^{j-i}g(R_i) = p_i \cdots p_{j-1}T_j. \tag{8}$$

where $g(.)$ characterizes the technology for receiving transfers and converting them into the equivalent of energy directly produced by the age-i child recipient,[14] with $g(0) = 0$, and $g'(.) > 0$. If there is no difficulty in converting the transferred energy, then $g(R)$ simply equals R. We introduce $g(.)$ to reflect the likelihood that the transfer process becomes less efficient at very high rates. This nonlinearity makes it possible to consider interior optimal transfers.

Because fertility is zero in the first r periods of life, from (1) we have $z_s = (w_s - b_s p_s)/d_s,\ s \leq r$. For the age-$i$, $z_i = (w_i + R_i - b_i p_i)/d_i$ because the age-i agent receives transfer R_i. And because there is no body growth in periods $s \geq r+1$, we know from (1) that $m_s = (w_s - b_s p_s)/c_s\ \forall s \geq r+1$. For the age-$j$, $m_j = (w_j - T_j - b_j p_j)/c_j$, because the age-$j$ agent gives out transfer T_j. Finally, since body size does not grow after age $r+1$, we have $w_s = w_{r+1}\ \forall s \geq r+1$.

With this background information and assuming steady state, equation (4) can be rewritten as

$$\lambda^t = \max_{\theta_s} p_1 \cdots p_r[p_{r+1}m_{r+1}\lambda^{t-r-1} + \cdots + p_{r+1}\cdots p_y m_y \lambda^{t-y}], \tag{9}$$

where all p_s and m_s are evaluated at their optimal values. Note that the value of R_i is implicit in this equation, and is here taken as given and fixed.

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[14] We characterize the transfer by its energy cost to the individual making the transfer. The function $g(.)$ should have a subscript i to indicate that this is a function specific to age-i. However, since our analysis applies to any unspecified i, for the time being we drop this subscript i for simplicity of notation.

Note also that the form in which (9) is written assumes that r is given, whereas it is in fact endogenous, and varies as p_s, m_s and z_s vary. For small variations in the neighborhood of the optimum, however, r will not change. To see this, imagine that we carried out many optimizations of the form of (9), sequentially taking r equal to a for every possible discrete age group a. If we now choose the value of r with associated the greatest maximum value of λ, that will be the optimal r which occurs in (9). Note that this value of r is a function of the level of transfers R_i. However, due to the discreteness of the age groups, for small variations of R_i the value of the optimal r will not change. For this reason, we can differentiate (9) with respect to transfers R_i to determine the effect on λ of a marginal increase in transfers.

Starting from a scenario with no transfers ($R_i = 0$), we shall evaluate how the steady state selection criterion λ will be affected by the introduction of a marginal transfer. The case of optimal transfers will be discussed briefly later. We now differentiate (9), use the steady state condition $V_{1,t} = \lambda^t$, and evaluate the expression at $R_i = 0$ to obtain[15]

$$\begin{aligned} &\lambda^t \Big\{ \frac{t}{\lambda} - l_r \Big[\frac{p_{r+1}(t-r-1)m_{r+1}}{\lambda^{r+2}} + \cdots + \frac{(t-y)p_{r+1}\cdots p_y m_y}{\lambda^{y+1}} \Big] \Big\} d\lambda \qquad (10) \\ &= l_r \Big\{ K_i \Big[\frac{p_{r+1}\lambda^{t-r-1}}{c_{r+1}} + \cdots + \frac{p_{r+1}\cdots p_y \lambda^{t-y}}{c_y} \Big] - p_{r+1}\cdots p_j \frac{\lambda^{t-j}}{c_j} G_{ij} \Big\} dR_i, \end{aligned}$$

where

$$G_{ij}\Big|_{R_i=0} \equiv \frac{dT_j}{dR_i} \equiv \frac{\eta_{ij}\lambda^{j-i} g_i'(R_i)}{p_i \cdots p_{j-1}}\Big|_{R_i=0}$$

is the conversion factor between the transfer T_j and the effective value of the transfer received, and

$$K_i \equiv \frac{1}{d_i}\Big(1 + \frac{1}{d_{i+1}}\Big) \cdots \Big(1 + \frac{1}{d_r}\Big),$$

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[15] Note that the derivatives of the right hand side of (9) with respect to p_s ($s = 1, ..., y$) are zeros due to the first order conditions of maximizing over p_s, hence these terms do not appear in the differentiation. This is again an application of the envelope theorem.

which is the compound factor of accumulating size from age i to maturity (the end of age r).

In the general case when $R_i \geq 0$, (10) only needs some minor revision. For $R_i \geq 0$, we can use (9) to cancel the terms associated with t, and multiply both sides by λ^{y-t}/l_r to obtain

$$-\Big[\frac{(r+1)p_{r+1}m_{r+1}}{\lambda^{r+2}}+\cdots+\frac{yp_{r+1}\cdots p_y m_y}{\lambda^{y+1}}-\frac{p_{r+1}\cdots p_j\eta_{ij}g(R_i)(j-i)}{c_j p_i\cdots p_{j-1}\lambda^{i+1}}\Big]\lambda^y d\lambda$$
$$+\Big\{K_i\Big[\frac{p_{r+1}\lambda^{y-r-1}}{c_{r+1}}+\cdots+\frac{p_{r+1}\cdots p_y\lambda^0}{c_y}\Big]-p_{r+1}\cdots p_j\frac{\lambda^{y-j}}{c_j}G_{ij}\Big\}dR_i=0$$

In this expression, the coefficient of $d\lambda$ is negative by the stability condition of λ. Substituting in the formula for G_{ij}, we have

Proposition 3: The sign of $d\lambda/dR_i$, which is the selection impact of a marginal transfer from age-j to age-i, depends on that of

$$B_{ij}\equiv K_i\Big[\frac{p_{r+1}\lambda^{y-r-1}}{c_{r+1}}+\cdots+\frac{p_{r+1}\cdots p_y\lambda^0}{c_y}\Big]-\frac{(p_{r+1}\cdots p_j)\eta_{ij}\lambda^{y-i}g'(R_i)}{c_j(p_i\cdots p_{j-1})}. \quad (11)$$

On the right hand side of (11), the first term ($K_i[.]$) is the lifetime expected sum of fertility increase, from age $r+1$ to age y, due to the increased body size. The second term captures the lost fertility at age j due to the out-transfer. Transfers to young individuals lead to larger adult body sizes, which in turn generate more energy for growth and other purposes. The envelope theorem (see footnote 14) tells us that the net marginal benefit of a change in R_i is evaluated by the net increase in reproduction. Because m_s is weighted by λ^s, we get B_{ij}, which must be > 0 for the transfer to be selected.

Examination reveals that $B_{ij} > 0$ is more likely to be met under the following conditions: 1) When there are more age-j adults relative to age-i offspring to share the costs of the transfer (either larger $p_i\cdots p_{j-1}$, or lower fertility, or both). Higher background mortality (larger coefficients b_a) would work against the evolution of transfers. It also follows from (11) that transfers are less likely to evolve in the context of rapid population growth (larger

λ), for example for an opportunistic species or under favorable climatic conditions, and more likely to evolve when carrying capacity is saturated. 2) When the adults are relatively more efficient than the child at generating energy per unit body size (smaller $\eta_{ij} \equiv \zeta_i/\zeta_j$). Perhaps this is more likely for carnivores than herbivores, since catching prey requires more skill, speed, strength, and weaponry (teeth, claws). 3) When there is a lower cost to augmenting body size between age i and age j (smaller $d_s,\ s = i, ..., r$ in K_i), which makes the investment from adults more rewarding. 4) When survival from age $r+1$ to j is high, so that low adult mortality is a predisposing factor for the evolution of transfers, at least up to the stage of the transferring age.[16]

Transfers might be concentrated on younger offspring or older offspring. In general, the compounded returns to early transfers (larger K_i for smaller i) favor transfers to the young, and the more so when the young convert energy more efficiently into body size (smaller d_a for small a's). Transfers to older juveniles might still evolve, if their survival were sufficiently high. Transfers to infants will be more likely if infants are relatively helpless, and unable to forage effectively (low ζ_i and hence low η_{ij}). This would be more likely true for carnivores but less so for herbivores. If older juvenile productivity relative to body weight increased, then transfers to that age would be less likely to evolve. Finally, a context of more rapid population growth favors transfers to older juveniles (as revealed by the λ^{y-i} term).

5 Coevolution of Transfers and Longevity

Natural selection should move the life history toward the optimal $\theta_s \equiv (p_s, m_s, z_s)$ to maximize the intrinsic growth rate λ. We now switch back

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[16] This can be seen by canceling the $(p_r \cdots p_{j-1})$ term in the numerator and denomenator of the second term of (11), and inspecting the remaining terms in B_{ij}.

to treating transfers, R_i, as given, and consider how the optimal levels of p_k depend on the level of transfers, for variations that are small enough such that the optimal age of sexual maturity r, corresponding to the given level of transfers R_i, does not change. We will develop one result (Proposition 4) that holds in the neighborhood of the optimal level of transfers, R_i^*, and another result (Proposition 5) that holds when transfers are below this optimal level.

>From the corner-solution pattern presented in section 4.1, it follows that the problem of finding the optimal life history reduces to searching for the optimal p_a's that maximize λ in equation (9). Given that the transfer in question is from age j to age i, it is natural to consider separately the first order conditions for p_k when $k \leq r$ and when $k \geq r+1$. We shall discuss these cases separately below.

The premature age range corresponds to $k \leq r$. Differentiating the right hand side of (9) with respect to p_k and using the envelope theorem, we see that its first order condition is proportional to the following expression:

$$\begin{aligned}\Delta_{p_k} \equiv\ & [p_{r+1}m_{r+1}\lambda^{y-r} + \cdots + p_{r+1}\cdots p_y m_y \lambda] \\ & - p_k b_k K_k \Big[\frac{p_{r+1}\lambda^{y-r}}{c_{r+1}} + \cdots \frac{p_{r+1}\cdots p_y\lambda}{c_y}\Big] \\ & + \frac{(p_{r+1}\cdots p_j)\lambda^{y-i+1}\eta_{ij}g(R_i)}{c_j(p_i\cdots p_{j-1})}\cdot I(k) = 0, \quad k \leq r \qquad (12)\end{aligned}$$

where $I(k) = 1$ if $r \geq k \geq i$, and $I(k) = 0$ otherwise. The term associated with $I(k)$ is from the differentiation of (8) (dT_j/dR_i), which is nonzero only if k is in the range between i and j. The K_k factor enters (12) because it is the relevant compound growth factor up to age-k.

The sexually mature range corresponds to $k \geq r+1$. Differentiating (9) and using the envelope theorem yields the following first order condition:

$$\begin{aligned}\Delta_{p_k} \equiv & (m_k\lambda^{y-k+1} + p_{k+1}m_{k+1}\lambda^{y-k} + \cdots p_{k+1}\cdots p_y m_y \lambda) \\ & - \frac{p_k b_k \lambda^{y-k+1}}{c_k} + \frac{(p_k \cdots p_j)\lambda^{y-i+1}\eta_{ij} g(R_i)}{c_j p_k (p_i \cdots p_{j-1})} \cdot I(k) = 0, \quad k \geq r+1 \end{aligned} \tag{13}$$

where $I(k) = 1$ only if $r+1 \leq k \leq j-1$, and $I(k) = 0$ otherwise. In what follows, we shall ask the following comparative static question: how does the optimal p_k change when R_i increases toward its optimum R_i^*?

We note that in the ongoing process of evolution, the cumulation of marginal changes should eventually maximize a species' fitness and hence exhaust the selection advantage of increasing transfers by choosing the optimal R_i^* such that

$$d\lambda / dR_i = 0. \tag{14}$$

Suppose the optimal transfer from age j to age i, denoted R_i^*, has been attained. Totally differentiating (12) we have

$$\frac{\partial \Delta_{p_k}}{\partial R_i} dR_i + \frac{\partial \Delta_{p_k}}{\partial \lambda} d\lambda + \frac{\partial \Delta_{p_k}}{\partial p_k} dp_k = 0. \tag{15}$$

If we evaluate the derivative around the optimal R_i^*, we know from (14) that $d\lambda = 0$. The coefficient of dp_k is negative by the second order condition. Thus, we know that as R_i increases towards the optimum R_i^*, whether p_k moves in the same or opposite direction hinges on the sign of $\partial \Delta_{p_k} / \partial R_i$.

Partially differentiating (12) with respect to R_i, we get

$$\begin{aligned}\frac{\partial \Delta_{p_k}}{\partial R_i} &= K_i \Big[\frac{p_{r+1}\lambda^{y-r}}{c_{r+1}} + \cdots + \frac{p_{r+1}\cdots p_y \lambda}{c_y} \Big] \qquad k \leq r \\ & - \frac{(p_{r+1}\cdots p_j)\lambda^{y-i+1}\eta_{ij} g'(R_i)}{c_j (p_i \cdots p_j)} + \frac{(p_{r+1}\cdots p_j)\lambda^{y-i+1}\eta_{ij} g'(R_i)}{c_j (p_i \cdots p_j)} \cdot I(k).\end{aligned}$$

For $r \geq k \geq i$, $I(k) = 1$, the last two terms of the above expression cancel, and hence the we see that $\partial \Delta_{p_k} / \partial R_i$ is indeed positive. This means that if R_i increases towards its optimum R_i^*, then p_k is also increasing.

Following similar steps we see from (13) that for $k \geq r+1$, p_k moves in the same direction as R_i around the optimum R_i^* if and only if $\partial\Delta_{p_k}/\partial R_i$ is positive. Partially differentiating Δ_{p_k} in (13) with respect to R_i, we have

$$\begin{aligned}\frac{\partial\Delta_{p_k}}{\partial R_i} = {} & K_i\Big[\frac{\lambda^{y-k+1}}{c_k} + \frac{p_{k+1}\lambda^{y-k}}{c_{k+1}} + \cdots + \frac{p_{k+1}\cdots p_y\lambda}{c_y}\Big] \qquad k \geq r+1 \\ & + \frac{p_k\cdots p_j\lambda^{y-i+1}\eta_{ij}g'(R_i)}{c_j p_k(p_i\cdots p_{j-1})} \cdot I(k) - \frac{p_{k+1}\cdots p_j\lambda^{y-i+1}\eta_{ij}g'(R_i)}{c_j(p_i\cdots p_{j-1})}.\end{aligned}$$

For $r+1 \leq k \leq j-1$, $I(k)=1$, the last two terms in the above expression cancel, and hence $\partial\Delta_{p_k}/\partial R_i$ is positive. As such, we know that p_k and R_i also move in the same direction for $r+1 \leq k \leq j-1$ as R_i moves toward the optimum, R_i^*. Summarizing the above discussion, we have

Proposition 4: Consider a transfer R_i from age j to age i. As R_i increases towards the optimum within the neighborhood of the optimal R_i^* that maximizes the fitness index, survival from age i to age j must increase.

What about the evolution of survival before age i? We show the results for this case below. For $k \leq i-1$, the first order condition for p_k is similar to that in (12), except that $I(k) = 0\ \forall k \leq i-1$:

$$\begin{aligned}\Delta_{p_k} \equiv {} & [p_{r+1}m_{r+1}\lambda^{y-r} + \cdots + p_{r+1}\cdots p_y m_y\lambda] \\ & - p_k b_k K_k\Big[\frac{p_{r+1}\lambda^{y-r}}{c_{r+1}} + \cdots \frac{p_{r+1}\cdots p_y\lambda}{c_y}\Big], \quad k \leq i-1\end{aligned}$$

Partially differentiating the above expression with respect to R_i yields

$$\frac{\partial\Delta_{p_k}}{\partial R_i} = \lambda B_{ij}$$

where B_{ij} is given in (11). We know that $d\lambda/dR_i = 0$, and hence $B_{ij} = 0$, around the optimum R_i^*. Thus, dp_k/dR_i, $k \leq i-1$ is close to zero around the optimum transfer. But we are able to say more about the change of p_k in the process when R_i increases toward R_i^*.

Equation (15) says that for any dR_i, the sign of dp_k/dR_i is the same as that of $[\partial\Delta_{p_k}/\partial R_i]+[\partial\Delta_{p_k}/\partial\lambda]\cdot[d\lambda/dR_i]$. Partially differentiating $\partial\Delta_{p_k}$ with respect to λ, using (12) to simplify the result, and substituting in the $d\lambda/dR_i$ formula from (10) and (11), we have

$$\begin{aligned}\frac{\partial\Delta_{p_k}}{\partial R_i}+\frac{\partial\Delta_{p_k}}{\partial\lambda}\cdot\frac{d\lambda}{dR_i} &= \lambda B_{ij}E \\ &+ \lambda B_{ij}\Big[1-\frac{\frac{p_{r+2}m_{r+2}}{\lambda^{r+2}}+\cdots+\frac{(y-r-1)p_{r+2}\cdots p_y m_y}{\lambda^y}-F}{\frac{(r+1)m_{r+1}}{\lambda^{r+1}}+\cdots+\frac{y p_{r+2}\cdots p_y m_y}{\lambda^y}-F}\Big],\end{aligned} \qquad (16)$$

where

$$E \equiv p_k b_k K_k\Big[\frac{p_{r+2}}{c_{r+2}\lambda^{r+2}}+\cdots\frac{p_{r+2}\cdots p_y}{c_y\lambda^y}\Big]>0,$$

and

$$F \equiv \frac{p_{r+2}\cdots p_j g(R_i)(j-i)}{c_j p_i\cdots p_{j-1}\lambda^i}.$$

It is easy to see that terms in the square brackets of (16) are positive. We showed in section 4 that whenever the increase of R_i improves fitness, B_{ij} must be positive. Thus, if R_i moves toward the optimum R_i^* to improve fitness, $B_{ij}>0$ must hold in the process, which means that $dp_k/dR_i > 0\ \forall k\le i-1$. Thus, we have

Proposition 5: If an increased transfer from age j to age i improves fitness, the survival probability up to age i must also co-evolve. As R_i approaches R_i^*, $\partial p_k/\partial R_i \to 0,\ \forall k\le i-1$.

Why is it that Proposition 4 applies only to survival improvements between the age of receiving and the age of giving the transfer, while in Proposition 5 survival also improves at ages from birth to i? Improved survival from age i to j always imparts an efficiency gain when transfers are increased, so it is selected either at the optimum or away from it. Increased survival from birth to age i does nothing to conserve the investment in transfers, and in this sense does not impart any efficiency gains when transfers increase. However, it raises the number of births surviving to age i, and thus raises λ, other things equal. In the neighborhood of the optimal transfer, the effect of this increase in survivors to age i is exactly offset by a reduction in transfers per offspring age i, so λ is unaffected, and the survival improvement to i is not selected.

Once an adult is both past the age of providing transfers and no longer fertile, her continuing survival makes no contribution, positive or negative, to reproductive fitness. Mathematically, with respect to a transfer from age j to age i, we can say nothing about the comparative statics with respect to p_s for $s \geq j$.

6 Extension and Discussion

6.1 General Optimal Transfers

So far we have discussed the impact of a transfer from one age j to one age i, but of course transfers may be provided by adults of various ages, and received by children of various ages. The feasibility constraint in (8) need not hold for each (i, j) pair, but rather resources must be balanced over the life-cycle. Specifically, let $g(R_i)$ indicate the energy cost of all transfers received by an individual at age i. The life cycle feasibility constraint is:

$$\sum_i \zeta_i g_i(R_i)\lambda^{-i} = \sum_j \zeta_j p_i \cdots p_{j-1} T_j \lambda^{-j},$$

similar to that in Lee (2003).

In general it will be optimal for adults of many ages to make transfers, and then the marginal benefit of transferring *from* each age must be equalized. Likewise, the marginal benefit at each age of receiving must be equalized. As long as we have interior solutions, we should have a system of equations to solve for such optimal transfers. Details will not be provided here, but one should note that the co-evolution result of transfers and longevity we derived in the previous section would not be affected by such complications.

6.2 Selection and Population Density

For a given set of the parameters b_a, c_a, d_a and ζ_a, for all a, there will be some optimal growth rate associated with the optimal life history, and only by chance will it be zero. If the growth rate is positive, then nothing in our model prevents population density from increasing without limit. It is beyond the scope of this paper to consider the dynamic trajectory as density changes. However, we will sketch the way density could be introduced into the model and provided that density is at an unchanging equilibrium level, no change in the analysis would be required. Density is measured as the total body mass of the population per environmental resource. The main effect of greater density would be to make foraging more difficult and thereby to reduce the energy yield for a given body weight, that is to reduce the coefficients ζ_a. The conversion of energy into body weight, fertility, or survival as expressed by the other parameters would not be affected to a first approximation, although a more elaborate analysis might permit density to affect mortality (through contagion) and fertility (through limited breeding sites) directly, in addition to the indirect effect through energy production that is now included. So long as the relationship is monotonic, its precise functional form need not concern us. We can simply multiply ζ_a at every age by some factor that makes the corresponding optimal growth rate λ^* equal unity.

With this setup, suppose that lineage A equilibrates at some density D_A (that is, $\lambda^*_A(D_A) = 1$), whereas mutant lineage B has a positive growth rate at that same density ($\lambda^*_B(D_A) > 1$). Then we know that B will out-compete A and be selected. In the analysis reported above, we can assume that the population without transfers has equilibrated in this manner, and then the analysis indicates the conditions under which transfers would lead to more rapid growth at this particular density (D_A), and increased longevity at this density. Lineage B, with transfers, will now grow until it equilibrates with $\lambda_B^*(D_B)$ equaling 1.0 at some higher density D_B. At this higher density, lineage A would have a negative population growth rate, and go extinct.

7 Conclusion

The optimal life history approach seems well suited for exploring the positive selection of life history characteristics. Earlier studies have generally assumed that the Euler-Lotka parameter (steady state growth rate) or the net reproduction ratio (NRR) was the measure of fitness to be maximized (Goodman (1982) and Cichon and Kozlowski (2000) are exceptions). Here, rather than assume a measure, we have derived it from the goal of maximizing the number of living descendants at some future date. If that future date is sufficiently distant, then we show that indeed the Euler-Lotka parameter should be maximized. We are able to connect formally the optimization problem for an individual life history and the aggregate criterion of the growth rate. We also find analytic expressions for the value of the contribution of individuals by age and time period to the maximization, as a function of the parameters constraining the production of energy and its uses. This enables us to carry out a comparative static analysis of the effects of these parameters, in contrast to the previous literature which has explored optimal life histories through numerical solutions.

Previous applications of the optimal life history approach have assumed that the individual's energy budget must balance at every age. Intergenerational transfers replace this instantaneous budget constraint with one that holds over the life cycle. Here we model intergenerational transfers, and ask under what conditions they would improve reproductive fitness and be selected. With transfers, a period of juvenile dependency with more rapid growth and development can be funded by contributions from adults. We consider what features of an initial life history without transfers would make it more likely that intergenerational transfers would confer a selective advantage. Factors favoring the selection of transfers include the ratio of adults to juveniles, greater efficiency of the old relative to the young in producing energy per unit of body size, and the efficiency of juveniles in converting energy into body size. We also discussed the factors favoring transfers to younger versus older offspring, and favoring transfers *from* older versus younger adults. Because lower mortality favors the selection of transfers from old to young, and because lower mortality coevolves with increased transfers, we find the longevity and transfers should increase in a mutually reenforcing way, as argued in Carey and Judge (2001) and Lee (2003).

When transfer behavior evolves, the founder of the mutant line actually experiences a lower NRR than otherwise, because she foregoes some adult fertility and survival in order to divert energy to caring for her existing offspring, although she received no such care in her youth. In this way she gets the lineage started, and subsequent members of the lineage realize a higher NRR as a result of her initial sacrifice and the improved life history it made possible. Of course, the inclusive reproductive fitness of the first individual is also raised thereby, even though her own NRR is reduced.

A central finding is that on the one hand, lower mortality makes the evolution of transfers more likely, and on the other hand, if increased transfers do evolve than longevity should coevolve. With transfers from adults to juveniles, costly resources are diverted from immediate reproduction to care for existing offspring, and concurrent life history investments in reducing mortality serve to protect these investments.

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Mathematical Appendix

Part A

Lagging $V_{y,t}$ one period, substituting it back into the previous age and iterating until we reach equation $V_{a,t}$, we have

$$V_{a,t} = \frac{\phi_a}{p_1 \cdots p_{a-1}} V_{1,t-1} + \frac{\phi_{a+1}}{p_1 \cdots p_{a-1}} V_{1,t-2} + \cdots + \frac{\phi_y}{p_1 \cdots p_{a-1}} V_{1,t-y+(a-1)}.$$

Given the solution $V_{1,t} = (\lambda^*)^t$, we obtain (6) in the text. That $V_{a,t}$ deflates at a stable population growth rate for all ages is not surprising. The best that the optimal life history can achieve is to grow at the maximum possible intrinsic growth rate. Thus, at the optimum, although the *value* of the contribution of an individual at different ages may be different, this value deflates at the same *rate*.

Part B

Let $g(\alpha) \equiv \max_x f(x, \alpha)$. The envelope theorem (see Simon [1976]) says that when x has an interior solution, $dg/d\alpha = \partial g/\partial \alpha$ around the neighborhood of the maximum, for the indirect effect through x is absorbed by the first order condition of x. Applying the envelope theorem to (2), we see that

$$V'_{a,t} = p^*_a\{V_{1,t-1}/c_a + p^*_{a+1}[V_{1,t-2}/c_{a+1} + p^*_{a+2}(V_{1,t-3}/c_{a+2} + ...]\}. \qquad [A1]$$

For the age-a problem, concerning the trade-off between m_a and z_a, we have the following first order condition (in terms of economics, MRS equals price ratio) for an interior solution:

$$\frac{p_a^* V_{1,t-1}}{p_a^* p_{a+1}^* \{V_{1,t-2}/c_{a+1} + p_{a+2}^*[V_{1,t-3}/c_{a+2} + p_{a+3}^*(V_{1,t-4}/c_{a+3} + ...)]\}} = \frac{c_a}{d_a}.$$

In the steady state, $V_{1,t}$ is a constant of power λ for all t, as shown in the text, and so the above expression can be further rewritten as

$$\frac{p_a^* \lambda^{t-1}}{p_a^* p_{a+1}^* \{\lambda^{t-2}/c_{a+1} + p_{a+2}^*[\lambda^{t-3}/c_{a+2} + p_{a+3}^*(\lambda^{t-4}/c_{a+3} + ...)]\}} = \frac{c_a}{d_a}. \qquad [A2]$$

Canceling p_a^* in the numerator and the denominator of $[A2]$, we see that both sides of $[A2]$ are not dependent on any age-a choice variable. Thus, expression $[A2]$ could hold only by accident in a steady state, which in turn implies that m_a and z_a cannot be interior solutions at the same time.