

The co-evolution of intergenerational transfers and longevity: An optimal life history approach[☆]

C.Y. Cyrus Chu^a, Ronald D. Lee^{b,*}

^a*Institute of Economics, Academia Sinica*

^b*Department of Demography, University of California, 2232 Piedmont Avenue, Berkeley, CA 94720-2120, USA*

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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 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.

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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. Most optimal life history studies of which we are aware assume that the individual can use only the energy that it produces (forages) in each period, and the life history is optimized subject to this strict budget constraint (Cichon, 1997; Cichon and Kozłowski, 2000; Vaupel et al., 2004; Abrams and Ludwig, 1995; Taylor et al., 1974; Goodman, 1982; Schaffer, 1983; Stearns, 1992; Clark and Mangel, 2000; the important exceptions are Kaplan and Robson, 2002 and Robson and Kaplan, 2003). But what if individuals were permitted to borrow and lend over their

life cycles? Markets for loans do not, of course, exist in nature, but intergenerational transfers from adults to juveniles are common and serve a similar function. Transfers 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 strict period-by-period energy constraint is then replaced by a looser version which, in a steady state, requires 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.¹

Many species, including all mammals, most birds, many insects, and some fish and reptiles, make various forms of intergenerational transfers (see Clutton-Brock, 1991). The duration and magnitude of such transfers are extraordinary in the case of human beings and some dolphins and whales,

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*Corresponding author. Fax: +510 643 8558.

E-mail addresses: cyruschu@gate.sinica.edu.tw (C.Y. Cyrus Chu), rllee@demog.berkeley.edu (R.D. Lee).

¹Some transfers take the form of stored output, for example paralyzed prey, and therefore occur with a delay. In steady state, this constraint will still hold: the survival-weighted and discounted transfers made and received over the life cycle must be equal. Out of steady state, the budget constraint would be more complicated to accommodate storage.

and the longevity of these species (see Carey and Gruenfelder, 1997) motivates our exploration of the possible correlation between intergenerational transfers and the optimal life history strategies. We will consider how the 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.

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.² In such cases, we can imagine a lineage carrying a mutation forming a stable population in aggregate, and living in small cooperatively breeding groups. Each group can be viewed as a microcosm of the lineage, with random departures from its stable age distribution. To obtain analytic results, we need the stable age distribution to write the balancing constraint on transfers.³ Within each group, all members share the same genotype which might include a gene promoting longevity, transfer behavior, or punishment of freeriding, for example. Transfers take place within these groups. Humans are cooperative breeders, and it has been argued that their longevity, particularly in postreproductive years, is related to their transfer behavior.⁴ There is also evidence (Brown, 1987) that cooperatively breeding bird species live longer than others.

The evolution of altruistic behavior raises difficult questions addressed by a large literature. We acknowledge these difficulties, but here we simply assume that some genotype can solve these difficulties and support transfer behavior. Although humans and other species we have in mind do not reproduce clonally, we believe that our analysis captures the central forces at play.

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 is the Malthusian parameter. This sets the stage for

considering the conditions under which intergenerational transfers would be selected. We investigate when such transfers increase fitness (Section 3), and if they do, how low mortality coevolves with them (Section 4). The last two sections contain extensions and conclusions.

2. A 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 .⁵ 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 to age just below $a + 1$ is denoted p_{a+1} . Fertility at age $(a + 1)$ takes place just before $a + 1$, conditional on survival, and is denoted m_{a+1} .

At age a , a typical individual expects to have energy or resources which, following Abrams 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 an 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 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

$$b_a p_a + c_a m_a + d_a z_a \leq \zeta_a w_a \quad \forall a, \quad (1)$$

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

²Whether 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.

³The 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.

⁴See Clutton-Brock (1991), Kaplan and Robson (2002), Lee (2003), Hawkes (2003) and Lahdenpera et al. (2004).

⁵It 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 Kozłowski (2000) adopted this approach.

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