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The evolution of transfers and life histories☆

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ABSTRACT

Much of life history theory analyzes life histories of independent, isolated individuals, who grow, forage, reproduce, and die. However, in many species social interactions such as food sharing are a key part of the life history strategy, altering the energetic budget constraint. Transfers and sharing raise reproductive success and also alter the fitness impact of other aspects of the life history. We discuss a variety of traits and behaviors for which transfers are important, synthesizing results from a number of earlier papers. Topics include the U-shaped mortality curve, post reproductive survival, causes of early life mortality decline, why intergenerational transfers evolve and co-evolve with longevity, time preference, sexual dimorphism and sexual differences in transfers, menopause, demographic advantages of social sharing, and consequences of social sharing for life history evolution.

1. Introduction

Much of life history theory analyzes independent, isolated individuals who grow, forage, reproduce, and die. However, in many species individuals interact in ways that increase reproductive success, such as parental care of offspring or broader forms of social cooperation or sharing. These behaviors then alter the fitness impact of other aspects of the life history and expand the life history options by altering the energetic budget constraint. Transfers of energy or time are a key aspect of these behaviors. Some transfers are intergenerational, between adults and their descendants. Other transfers can occur among related or unrelated individuals of the same generation.

In humans, as in many species, these vertical and horizontal aspects of sociality are intertwined. Humans invest heavily in a small number of offspring who are nutritionally dependent on adults until around age 20 (Kaplan, 1994). Provisioning is mainly by parents, but there are periods in the family life cycle when the child dependency burden exceeds parental capacities and broader social transfers are necessary. Hill and Hurtado (2009) summarize: “food provisioning is ubiquitous, generally biased in favour of helping families with large dependency loads and not limited to kin assistance”.

Here we synthesize our papers that analyze the conditions under which intergenerational transfers or social sharing may evolve, and we consider how these transfers and sharing influence the coevolution of other life history traits including fertility, mortality, time preference, the intergenerational division of labor, menopause, and sexual dimorphism. Our analytic approaches include fitness impacts, microsimulation, and optimal life histories. We emphasize our own theoretical work, and regrettably do not have space for a balanced overview of all research on these topics.

We explicitly model intergenerational transfers of food, subject to a social budget constraint based on the average population age distribution in the cooperative breeding group rather than on the presence of particular biological relatives. This approach is consistent with some empirical and ethnographic studies of humans that find that food is shared within small groups, often with little or no kin-bias, and that relatives and friends other than parents and grandparents often make transfers or share in child care (Hill and Hurtado, 2009; Hrdy, 2009; Sear and Mace, 2008). The special importance of the mother is not reflected in this approach, and our approach is less consistent with other empirical research that finds a strong kin-bias in intergenerational transfers (Gurven, 2004; Gurven et al., 2000, 2002). Kin-bias would strengthen our substantive conclusions but undermine our analytic use of stable populations.

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2. The Basic Optimal Life History Model

In our optimal analysis (Chu et al., 2010), we view natural selection as tending to maximize reproductive fitness as measured by the intrinsic rate of natural increase or sometimes the Net Reproduction Rate, subject to an energy constraint. The constraint *f* describes the total energy required to achieve a given combination of life history traits at a particular age: mortality risk, fertility risk, and body growth. *f* is generally nonlinear, reflecting possible diminishing returns to investment in reducing mortality (μ_a), raising fertility (m_a), or accelerating body growth (z_a), where w_a is the body size attained by age *a* (or other form of somatic capital, see Kaplan and Robson, 2002; Robson and Kaplan, 2003). A foraging function ζ_a describes the available energy (net of energy costs of foraging) depending on the body size (or other somatic measure such as brain size) at each age *a*. The energy constraint defines the life history trait tradeoff frontier at each age.

$$f_a(\mu_a, m_a, z_a) \leq \zeta_a(w_a), \forall a \tag{1.1}$$

The partial derivative of the tradeoff function at age *x* with respect to fertility *m*, $f_{x,m}$ (for example), is the energy cost of raising fertility at age *x*. If *f* were linear, this derivative would just be the cost coefficient on fertility, giving the constant cost of raising fertility by one birth.

The literature has established that if *f* is linear (as in Chu and Lee, 2006), the optimal life history exhibits determinate growth: until some age *J* the organism invests in growth and maintenance/survival but not in fertility; after *J* it invests in maintenance/survival and fertility but not in growth. With a nonlinear tradeoff function the optimal life history is not necessarily determinate growth. However, most organisms that make substantial intergenerational transfers, such as mammals and birds, do have determinate growth. Even with determinate growth, foraging output might continue to increase for a while after age *J* due to accumulating experience and knowledge (Promislow, 1991).

Consider a determinate growth organism in which an adult at age *a* transfers a total amount T_a to young, while a young individual at age *a* receives a total transfer (from adults of all ages) of R_a. Now the new budget constraints are:

$$f_a(\mu_a, m_a, 0) \leq \zeta_a(w_r) - T_a, \text{ for adults} \tag{1.2}$$

$$f_a(\mu_a, 0, z_a) \leq \zeta_a(w_a) + R_a, \text{ for juveniles} \tag{1.3}$$

These constraints will depend on environmental context, presence of predator and prey species, competitors, and so on. The social budget constraint requires that the population-weighted sum of T_a equals the population weighted sum of R_a.

3. Optimal Juvenile Mortality

The first order condition for an optimal juvenile mortality trajectory is that the marginal energy cost of reducing mortality at age *a* must equal the net marginal fitness gain of reducing mortality at that age:

$$-f_{a,\mu} = \frac{\int_J^\omega e^{-\rho x} l_x m_x dx + \int_J^\omega \frac{1}{f_{x,m}} \int_0^a e^{-\rho s} l_s R_{s,x} ds dx}{\frac{1}{f_{a,z}} \exp\left(\int_a^J \frac{\zeta_{x,w}}{f_{x,z}} dx\right) \int_r^\infty e^{-\rho x} l_x \frac{\zeta_{x,w}}{f_{x,m}} dx} = \frac{M + \tilde{T}_a}{K_a N} \tag{1.4}$$

Here ρ is the intrinsic rate of natural increase, and letters at the far right name the corresponding integrals. This complicated expression is not an explicit solution for the age path of juvenile mortality, because l_x (survival from birth to age x) also occurs on the right side of the equation in the various terms. However, this expression helps us understand the shape of the optimal age trajectory of juvenile mortality and the forces generating it.

The LHS is the cost of reducing the death rate at age *a*, that is the negative of the "cost" (or energy released) of raising mortality. On the RHS, M is the expected lifetime births for an individual who survives to the age of reproductive maturity, *J*. *M* does not vary by age before *J*. Because *M* is the sole influence on juvenile mortality in Hamilton's (1966) theory, it predicts that juvenile mortality is low and constant across juvenile ages, in contrast to Fisher's (1930) result that juvenile mortality falls until the age of reproductive maturity based on reproductive value. $\tilde{T}_a$ is the expected total energy to be transferred by an age *a* individual over the remainder of life, expressed in units of the fertility cost of those transfers, as is *M*. This equals the fertility value of all the transfers *R* received by the birth cohort up to age *a*, per juvenile surviving to age *a*, including the wasted transfers to other juveniles who died before reaching age *a*.

The RHS denominator includes K_a, which is the effect of an additional unit of energy invested in body weight at age *a* on mature size at age *J*. *N* is the effect of an increase in body weight at age *J* on remaining lifetime fertility, an effect which is independent of juvenile age. So the product K_aN is the lifetime fertility cost of spending a unit of energy on reducing mortality rather than on raising body weight.

As *a* rises from 0 to *J*, *M* remains constant, T_a rises, and K_aN declines. The right hand side, therefore, rises with age. Thus the energetic cost of reducing mortality rises with juvenile age in the optimal life history, and from this we can infer that the level of mortality declines with juvenile age, from 0 to *J*. This decline reflects the Hamilton Effect, Transfer Effect, Compounded Effect of Growth, and any variations by age in the tradeoff cost of reducing mortality, $-f_{a,\mu}$.

4. Optimal Adult Mortality

For adult mortality, the corresponding first order condition for an optimum (see Chu et al., 2008: Eq. (9)) is:

$$\begin{aligned} -f_{a,\mu} &= \frac{e^{\rho a} f_{a,m}}{l_a} \left[\int_a^\infty e^{-\rho x} l_x m_x dx + \int_a^\infty e^{-\rho x} l_x \frac{T_x}{f_{x,m}} dx\right] \\ &= \frac{e^{\rho a} f_{a,m}}{l_a} \left(M_a + \tilde{T}_a\right) \end{aligned} \tag{1.5}$$

Here $M_a + \tilde{T}$ represents the gross (ignoring costs) benefit of investing in continuing adult survival. M_a is expected future fertility (the Hamilton effect) and $\tilde{T}_a$ is the expected cumulated transfers to be made above age *a* as in Lee (2003), expressed in units of fertility to convert to units commensurate with M_a. The $M_a + \tilde{T}$ in the numerator corresponds closely to the weighted average of the Hamilton and transfer effects as in Lee (2003). As noted by Hamilton, M_a goes to zero as *a* approaches menopause. However, the transfer term $\tilde{T}_a$ continues positive past the reproductive ages, reflecting the transfers that older men and women continue to make in hunter-gatherer societies. This component indicates that human postreproductive survival is explained by the continuing role of postreproductive adults in assisting the reproductive efforts of their offspring and other kin through transfers of energy.

However, there are important differences from Lee (2003). First, $M_a + \tilde{T}$ is multiplied by the energy cost of fertility at age *a*, which we expect to rise with age due to deterioration of oocytes and general aging. Second, the RHS is calculated conditional on surviving to age *a* (l_x/l_a) in the optimal approach, whereas in Hamilton and in Lee, multiplication is by l_x alone. This reflects a key difference between the mutation accumulation-strength of selection approach and the optimization approach based on positive selection. The optimization approach is always forward looking, so that the optimal approach is chosen for age *a* conditional on having reached age *a*. But in the mutation accumulation-deselection approach, effects are evaluated at birth, and consequences that are farther in the future at more advanced ages are consequently discounted.