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**Intergenerational Transfers, Life Histories, and the Elderly**

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“Because of the historical emphasis on energy flow within individuals rather than among the members of a family, intra-individual tradeoffs have played a much larger role to date than intergenerational trade-offs….” (Stearns, 1992:80)

## INTRODUCTION

A transfer is a gift with no quid pro quo. It is not reciprocal; it is not an exchange. An intergenerational transfer is a gift of food or assistance by one generation to another, typically a descendant. The descendant, when mature, then herself makes a similar transfer to her offspring or grand-offspring. The chain of transfers continues downward from one generation to the next, never returning to earlier generations.

Reproduction is an intergenerational transfer. Building an offspring requires energy. Helping it survive and grow takes additional energy, provided in a seed or egg, or as a capital bequest (as when a dung beetle lays its egg on a dung ball, or a wasp lays its egg in prey) or through progressive feeding as the offspring grows over an extended period (as in mammalian lactation or a bird feeding its chick). In addition the parent incurs risks in reproduction and may provide services requiring energy expenditure such as building nests or burrows, guarding, ventilating, fanning, warming and training the offspring. While reproduction involves costly transfers, it lies at the very heart of evolution and natural selection, and does not require explanation through kin selection or inclusive fitness.

Yet many questions arise about the intergenerational transfers associated with reproduction. How many offspring versus how much investment in each (quantity versus quality)? For how long does an offspring receive transfers, and how are these related to growth and to the age of sexual and economic maturity? Is duration of offspring dependency related to adult longevity? What factors favor the co-evolution of transfers and longevity? How does the marginal fitness value of energy vary across the life span, and how is this age pattern related to transfers and fertility? How are transfers related to sexual dimorphism? Could upward transfers from adult child to older parent evolve? Are intergenerational transfers a form of cooperative behavior? Is menopause related to transfer behavior?

As Stearns (1992) suggested in his classic work, life history theory has focused mainly on intra-individual tradeoffs (the allocation of energy among growth, maintenance, survival and reproduction) and paid less attention to intergenerational tradeoffs. Yet intergenerational transfers can profoundly alter energetic budget constraint faced by the individual organism over its life course, since an offspring receiving transfers can consume more than it acquires through its own efforts, in which case adults must consume less than they acquire.

My own research, much of which is joint with Cyrus Chu, and sometimes also with HK Chien, has focused on the role of intergenerational transfers in life history theory. Here I will discuss this topic with heavy emphasis on my own research. In a nutshell, parents invest in the quality of their offspring when such investments yield a higher fitness rate of return than would parental consumption of those resources. Parental transfers permit offspring to grow faster for a longer time to a greater size or complexity (e.g. the brain or body armor), or to mature earlier. The balance between quantity and quality of offspring evolves as well, with orchids and oysters close to the “corner” of maximum number of seeds with minimum size of each, and humans and dung beetles at a low fertility interior optimum with great investment in each child.

When evolution raises or prolongs such investments, the age at maturity is postponed and nutritional dependency is extended to older ages. In this case parental death entails the wasteful death of offspring in whom much has already been invested, so selection favors longer adult life span, perhaps including postreproductive life span.

When there is long offspring dependency there is also a fitness reward for cooperative breeding as a form of life insurance, with other adults available to substitute for parents who die. Similarly, there is a fitness reward for cooperative food sharing because it eases the life cycle squeeze when there are multiple dependent offspring at the same time, a situation that is particularly important for humans (Lee and Kramer 2002). Thus investments in offspring quality through substantial and prolonged intergenerational transfers create conditions that favor the evolution of cooperative breeding. Cooperative breeding itself likewise alters the forces of selection on levels and age patterns of fertility and mortality, and provides some evolutionary opportunities for free-riding.

These basic ingredients provide a foundation for considering the evolution of menopause and postreproductive survival, time preference, specialization and division of labor between younger and older adults, sexual dimorphism, and some incentives for reproductive cooperation.

## Sensitivity and Selection

My personal starting point was Hamilton’s (1966) analysis how natural selection molds senescence. Hamilton’s study used sensitivity analysis, asking how much a perturbation in fertility or mortality at a given age would affect reproductive fitness measured by the intrinsic rate of natural increase (stable population growth rate). Hamilton assumed that deleterious mutations occur at some rate at birth, with each one raising mortality at a specific age. (He thought this approach was less applicable to fertility since it ignored tradeoffs.) If fitness at that age is highly sensitive to mortality, then such mutations would be deselected from the population rapidly. In the balance reached between arrival of new mutations raising mortality at that age and selection removing them, fewer mutations would mutations would be present in the genome, so mortality at that particular age would be lower than otherwise. The accumulation of mutations affecting mortality at a given age is inversely proportional to the strength of selection at that age (see Charlesworth, 1994). The mechanism at work is negative selection on deleterious mutations. Because the sensitivities are calculated based on the observed values of fertility and mortality at each age, which are taken as given, there is an element of circularity in the theory. Furthermore, it has now been shown that the linearity assumption underlying most such calculations leads to incorrect conclusions (Wachter, in this volume).

Hamilton’s analysis predicts that mortality will rise with age at a rate that is inversely proportional to expected remaining fertility at that age, and predicts very rapid increase in mortality at ages after reproduction ceases (menopause in human females). The long postreproductive survival of humans is a puzzle for the theory, although it was understood that post birth parental care probably played a role. Similarly, the theory predicts that mortality will be low and constant from birth until the age of start of reproduction, and the actual pattern in which it declines following birth is a puzzle for the theory.

In Lee (2003) I developed a model that added food to the purely demographic model of Hamilton. In my model, fertility is a positive function of lifetime consumption and mortality is negatively related to it. Foraging productivity is also positively related to higher lifetime consumption levels, since these would lead to bigger body size, better health, and perhaps better brains. Individuals of all ages live in food sharing groups in which population age distributions are on average stable and depend on the levels of fertility and mortality determined by the model. Foraging success depends also on overall population density relative to a given resource, so population equilibrates eventually at a particular density, foraging productivity, fertility, mortality, and age distribution. At young ages individuals may receive transfers made by adults, and therefore consume more than they produce. The overall population age distribution is stable and the analysis is comparative static.

I then find an expression for sensitivities to perturbations in mortality and fertility in the neighborhood of the equilibrium, drawing conclusions about age patterns of mortality using arguments similar to Hamilton’s as described above in Lee (2003). In this model higher survival at postreproductive ages contributes to reproductive fitness if older individuals make net transfers of food to young members of the population (perhaps offspring or grand-offspring). In this model the force of selection against mortality starts at a low level at birth and rises up to an age between reproductive and economic maturity, so mortality is high following birth and declines until maturity..

The general conclusion is that the force of selection against higher mortality at a given age is proportional to a weighted average of the share of lifetime fertility remaining above that age (as in Hamilton) and the share of remaining lifetime net transfers to others above that age. If the species in question makes no transfers after birth, then the weight on remaining fertility is unity and the weight on remaining transfers is zero, giving the classical result of Hamilton (1966). If the species in question makes transfers to the point where the tradeoff between quantity and quality of offspring is optimal, then the remaining-fertility component gets zero weight and the force of selection depends entirely on remaining transfers which get a weight of unity. Intermediate weights can also occur according to explicit expressions in the analysis.

Based on observed fertility, mortality, and patterns of intergenerational transfers for some hunter gatherer groups, Figure 1 plots actual age specific mortality, the mortality predicted by the Hamilton analysis, and the mortality predicted by the theory of Lee (2003) incorporating intergenerational transfers. {I hope to redraw this based on the Kaplan-Gurven HG mortality schedules drawn from a collection of groups, and intergenerational transfer profiles that are an average of the Ache and !Kung}. The agreement with the transfer theory is quite striking, but I view this as in good part coincidental. There are many empirical difficulties with the estimates of food transfers, and food transfers are only one aspect of the ways older humans help younger ones, and surely many other forces are at play besides those incorporated in the model. Nonetheless, the figure is encouraging.

## Microsimulation of the Transfer Model with Explicit Food Sharing Groups and Rules

Some questions were raised about features of the 2003 paper. How could the populations of sharing groups be stable when individual families would have been tiny, perhaps with only one or two or three members? How could the catastrophic effects of a parental death be reflected in the analysis when in stable populations all ages are always present? How could comparative analysis of outcomes for gene lines be appropriate in the context of a mutation accumulation mechanism which would mean that every individual had a different mix of deleterious genes? While there are responses to each of these points[[1]](#endnote-1), these questions motivated me to investigate the same model using microsimulation (Lee 2008). While the model described earlier refers to any species, the microsimulation analysis is designed to reflect the situation of human hunter-gatherers.

In the simulations, individuals inherit the genome of their mothers, but experience random mutations at birth. They live together in small food sharing groups within which intergenerational transfers take place. Group membership is built up from membership in “matriarchies” consisting of all the living descendants of a single living female. Different rules for membership in sharing groups are considered, for example a) sharing only within matriarchies, and so strongly kin based; or b) sharing within groups containing up to third cousins, and so bigger groups with weaker kin ties; or c) sharing within groups that contain relatives up to third cousins plus sufficient non-related other cousin groups to achieve group sizes bounded between 8 and 25 members, numbers based on hunter-gatherer ethnographies. When group sizes fall below 8 members two groups fuse, and when they rise above 25 members they fission. Within these sharing groups the completeness of sharing among the constituent matriarchies can be specified. Fertility and mortality by age depend on food consumption by each individual, with this relationship calibrated on estimated relations in historical demographic data. The general setup is guided by descriptions such as Hill and Hurtado (2009) “food provisioning is ubiquitous, generally biased in favour of helping families with large dependency loads and not limited to kin assistance.”

These age distributions within the sharing groups are not assumed stable and mutations occur randomly at every birth so there is genetic heterogeneity within groups and among kin. Catastrophic effects of maternal death may occur, or the consequences of maternal death may be buffered by the presence of other adults in the sharing groups. In these ways the simulations avoid the questions raised above, but do not avoid a degree of circularity. They can assess the underlying coherence and consistency of an age-patterned set of behaviors – fertility, mortality and transfers. However, they are based on the observed age profiles of fertility and productivity as inputs.

The basic result is that starting from a flat and very low mortality schedule, after 75,000 years of simulated evolution along the lines described above, the age specific mortality schedule assumes a shape much like that derived analytically in Lee (2003) and shown in Figure 1. The simulated mortality schedules are shown in Figure 2, each corresponding to a different assumed social sharing rule. The schedule labeled Pop.100 assumes that all food sharing takes place at the level of the population. In this case there is no selective advantage to postreproductive life since sharing is not at all kin-based, and evolved mortality conforms to Hamilton’s theory: it is shaped solely by remaining lifetime fertility, rising sharply in the 40s and completely flat up to sexual maturity. The schedule labeled M.100 assumes that 100% of food sharing takes place within matriarchal groups, as defined earlier. In this case, mortality declines after birth and postreproductive survival emerges. The bulge in mortality from 10 to 20 reflects child death following maternal death. The schedule labeled K5.100 assumes that 100% of food sharing takes place within groups of kin up to third cousins. Because there are more adults in these groups, maternal deaths are buffered by help from other relatives, and the mortality bulge disappears, while postreproductive survival is again selected for. K5.50 refers to larger sharing groups composed of several K5 groups, but only 50% of food is shared with other unrelated K5 subgroups. K5.50.D5 is similar to the previous, except that the K5 groups disperse and join new sharing groups every 25 years, diluting the relatedness within the group since more relatives are not included.

It is interesting that infant and child mortality is substantially higher in the more closely related groups with 100% sharing than in those with less sharing. This results because with 100% sharing within a kin group, when an infant dies all the foregone future costs of rearing that child are recaptured and reabsorbed by kin and can be used to rear siblings or to better nourish the adults. When 50% of resources are shared outside the group and received from the other groups, only 50% of the foregone future costs of rearing a young child can be recovered by the kin if it dies. There is therefore greater selective pressure to avoid the child death. We would similarly expect fertility to be higher when there is sharing outside the kin group, because the costs of raising an incremental child are partially born by non-kin.

## WHICH SOCIAL ARRANGEMENTS HAVE THE HIGHEST FITNESS?

In Lee and Boe (2007) we simulated co-existing sub-populations with different social arrangements that interacted only through sharing the same foraging function, which as in other simulations depended negatively on population density. The sub populations remained totally separate and competed only through their abilities to reproduce and grow at a given density. There were three Matriarchal subpopulations, three Third Cousin subpopulations, and three Sharing Groups with Third Cousin components sharing 50-50 with total membership of 8-25 individuals. The simulations were run for 5000 years. Inclusion of three groups of each kind allows us to assess the role of randomness in the success of the social arrangement.

The clear but surprising results are shown in Figure 3. The larger the group and more extensive the sharing, the more rapidly the group declines in population size and goes extinct. The three Matriarchal groups, with average size of 1.8 members, win out over the Third Cousin groups that average 4.8 members, and these in turn win out over the Sharing Groups with Third Cousin components, averaging 15 members and 3 component groups. Our hypothesis was that sharing would raise fitness through maternal life insurance and smoothing of dependency burdens, but instead Figure 3 shows that the larger the group and broader the sharing, the less success there is in the competition, and this same result holds for all three instances of each kind of social arrangement.

Through analysis of the detailed simulation results we learned the reason: smoothing reduces variance, but variance can be useful, particularly when there is positive feedback. In this model, Matriarchal offspring have high variance consumption while young. For example, high consumption could arise when demographic randomness generates a low dependency ratio due to few or none surviving siblings and perhaps both a mother and grandmother surviving, and perhaps an aunt. When a juvenile has high consumption in the model it grows up to be more successful at foraging. To quote Clutton-Brock (1991:255): “…the effects of variation in parental investment are rarely confined to a single stage of the offspring’s life history or a single component of its fitness and can frequently be identified throughout its entire breeding career. Some studies show that the benefits … can be transferred across generations, influencing the phenotype and fitness of grandchildren….”. Such intergenerational transmission happens, on average, in the simulation model, and it is strong enough to reward the higher variance in offspring consumption in the Matriarchal units.

When this feature of the model is turned off, so that early life consumption does not affect later life foraging, the simulated competition yields the hypothesized result: The Matriarchal arrangements does worst, the Third Cousin arrangement also goes extinct but more slowly, and the Sharing Groups with Third Cousin components win out.

The message is that social smoothing of risks can indeed raise fitness, but it can also ensure mediocrity by smoothing out both high success and dismal failure, and in some circumstances mediocrity may lose.

## Optimal Life Histories with Intergenerational Transfers

To get at the more fundamental forces shaping the observed age patterns we turn to a different approach: finding the optimal life history using analytic methods. This approach avoids the circularity of the mutation accumulation and sensitivity analysis approach. However, one must begin by assuming underlying biological constraints and relationships, and consider how the organism acquires energy and allocates it among growth, survival, reproduction and transfers over its lifetime. Here deleterious mutations are ignored, and the implicit assumption is that a species can evolve to the optimal life history by positive selection on a sufficient variety of mutations. Because evolution through positive selection of beneficial mutations is implicitly assumed and the analysis is atemporal, the strength of selection does not matter. Only the sign and not the magnitude of sensitivities matters. Furthermore, selection is always forward looking and is therefore conditional on survival to a given age, whereas sensitivities are assessed at birth, as in Hamilton’s (1966) analysis. Some baseline conditions for the optimization must be assumed, such as that the organism has a deterministic growth pattern (first growth with no reproduction and then reproduction with no growth) or that the organism has oocytes that tend to decay with age and therefore faces rising costs of fertility with age.

This optimal life history approach is taken in my work with Chu and Chien. While the earlier literature on optimal life histories assumes optimization is carried out over an individual life history, with an organism constrained to consume no more than it produces at each moment, our approach is distinctive in relaxing this constraint by permitting intergenerational transfers. Despite the very different theoretical approaches and assumptions relative to the transfer model described earlier, there are many formal similarities in the results, and the central elements that emerge from the sensitivity approach occur again in the optimal life history approach.

Here are some basic results on the age-shape of mortality across the life span (Chu, Chien and Lee, 2008). If we assume a linear energy budget constraint for energy expenditures on survival, fertility, and growth, then the optimal life history involves growth without fertility up to some age of maturity, and fertility without growth thereafter, as has been known for some time. This is known as determinate growth which is characteristic of mammals and birds among others, in contrast to most fish, reptiles, and plants. The results described below are also true of a model with nonlinear budget constraints, provided these entail determinate growth.

Consider mortality from birth until maturity. We find that survival from age a to a+1, pa, will be proportional to an expression that has in the numerator the weighted sum of two terms. The first term is expected remaining lifetime fertility at age x, the *Hamilton* effect, which is constant across all juvenile ages. The second term is expected remaining lifetime transfers to others at age x, the *Transfer* effect, which rises with age since adult transfers to be made remain unchanged while fewer future transfers will be received as a juvenile approaches maturity. This weighted average is very close to the sensitivity analysis result of Lee (2003). However, there is additionally the possibility of investing in growth before maturity, which is in the denominator of the expression. An investment in growth has a compounded effect because size enables increased energy through foraging, and that increased energy is then optimally expended, perhaps on further growth. The compounding is greater for expenditures made at younger ages, with more time for compounding before adulthood. Thus the denominator declines with age. The rising numerator divided by the falling denominator implies rising survival with age, and therefore mortality declines from a high level at birth up to maturity. (The force of mortality at age a = *dln(pa)/da.*)

Now consider adult mortality. The numerator is exactly the same, a weighted sum of the *Hamilton* effect which declines to zero when fertility stops, and the *Transfer* effect which gradually declines but remains positive throughout adult life (unless there are net transfers from younger to older in old age). Thus the numerator declines with age but remains positive after fertility ceases. This points to continued survival after completion of fertility as older people raise, through transfers, the fertility and survival of their descendants and thereby raise their own fitness. By itself this would imply that survival rates at each age were declining and mortality rising.

However, in optimal life history analysis optimization is forward looking from each given age, unlike sensitivity analysis which evaluates a perturbation’s impact at birth. For this reason, impact sensitivities for mortality perturbations late in life tend to be small, since relatively few survive to be affected by the perturbation. By contrast, the optimization expression has the probability of survival from birth to age a in the denominator, and this survival declines with age. The declining denominator tends to offset the declining Hamilton and Transfer effects in the numerator, postponing the increase in mortality following maturity, and slowing the pace of mortality increase. While the U-shape of mortality remains a prediction of the model, the upswing may start later than maturity. The age schedule of optimal mortality may have a bathtub shape rather than a J shape, with flat mortality from (say) age 20 to 40, as often found for contemporary hunter-gatherer populations (Kaplan and Gurven, 2007). This flatness could also result from a violation of our determinate growth assumption. Foraging productivity may continue to rise during adult years due to accumulating skills and experience, rather than being fixed at maturity. For example, the hunting productivity of male hunter-gatherers has been found to rise to a peak at age 40.

## The Evolution of Transfers and Longevity

In Chu and Lee (2006) preconditions favoring the evolution of transfers include a) the initial ratio of adults to juveniles is high (and therefore life expectancy is high relative to age of maturity), b) greater productive efficiency of adults relative to juveniles per unit of body size (and therefore it is efficient when young to receive transfers of food that is easily acquired by adults), c) greater efficiency of juveniles in converting energy into body size. Initial low mortality and long life favors the selection of transfers from old to young through a), but lower mortality itself evolves farther when transfers are greater as discussed earlier. Therefore longevity and transfers co-evolve in a mutually reinforcing way, as argued in Lee (2003).

## The Evolution of Menopause and Inter-Adult Transfers

In Chu and Lee (2013) we consider the comparative advantages of younger women and older women, and the efficient division of labor between them. Suppose that for young women, the ratio of productivity in foraging to that in childcare is greater than the corresponding ratio for older women such as their mothers. (If the opposite is true, slightly different results follow but the principles involved are the same.) Then in a hypothetical state before the evolution of menopause, it would be efficient if the grandmother spent more time in camp rearing the children and reduced time spent foraging for herself and her children, while the younger mother increased her foraging time and left her children to the care of the grandmother. This efficient division of labor would raise the fitness of both grandmother and her adult daughter, and is the first stage of specialization.

However, the grandmother is less efficient in childbearing as well, with higher costs per birth or lower quality due to the declining quality of oocytes with age. Her continuing childbearing also limits her specialization in providing childcare for her daughter’s children. There could be fitness gains for both grandmother and mother if the older woman reduced her fertility and increased her childcare, with the younger mother providing more food. We show that evolution could move the human life history in this direction of further specialization, eventually reaching the reproductive “corner” outcome where the older woman has zero fertility (menopause) and the younger woman has higher fertility, shorter birth intervals, and greater reliance on the older woman’s assistance to cope with the increased dependency burden. The older woman would continue to forage for her own subsistence and have no dependent children of her own to feed. This is the second stage of specialization.

However, there is still room for further efficiency gain and increased fitness if the grandmother reduces her foraging even more and relies on food provided by the younger woman, in the limit ceasing to forage altogether and subsisting entirely on upward transfers of food from the younger woman. This is the third stage of specialization.

We show in Chu and Lee (2013) that such a life history pattern could yield higher fitness. Furthermore, under certain parameter restrictions in a two-sex population, the mutations causing this behavior could successfully invade the population. That is, we show that individual selection and not just group selection could lead to this outcome. In this way menopause, age specific division of labor, and intergenerational transfers among adults could evolve together. But has this ever in fact occurred?

Ethnographic evidence reviewed in Chu and Lee (2013) suggests that at younger old ages grandmothers may specialize in foraging rather than childcare, but at older old ages a pattern like the one described above does occur for both men and women. Some species of toothed whales appear to have menopause and extensive postreproductive survival. The older adults may guard the young while the parents dive to hunt. The adults bring up food to the surface for their young and if some were consumed by the grandparents (I know of no evidence on this point) this would be consistent with the scenario described for humans. However, although such behaviors appear possible and not inconsistent with known facts (for example for pilot whales, Orcas, or Sperm whales) they are very far from established, and research on whale life histories is very difficult. Life histories of some other species, such as African hunting dogs or naked mole rats, share some elements of the theory sketched above, although in these the division of labor and reproductive specialization are not based on age but on dominance that may be transitory or by size. There are also some similarities to the reproductive and foraging specialization in eusocial insects.

## Intergenerational Transfers and Sexual Dimorphism

The classic theory of sexual dimorphism, dating to Darwin, begins with the observation that females invest much more heavily in reproduction than do males, starting with the trivial cost of sperm compared to the female egg, and continuing with the costs of pregnancy for viviparous species and birds, and then post-birth care, mammalian lactation and transfers (although transfers are sometimes shared with males). Consequently, fitness is constrained by the female’s resources while the male has resources to spare. Here the evolutionary path forks. In one direction lie pair bonding, relative monogamy, greater paternity certainty, and male investment of his surplus resources in rearing the offspring, as in the case of humans and many other species.

Down the other fork the males’ surplus energy is devoted to competition for reproductive access to females. Female preferences females shape the form of male-male competition which may be combat based on size, teeth, and horns; sperm competition with large testes and spermicidal weapons; competition by display of colors, claws, tails, dances, or noises; and so on. In this case the male seeks to mate with as multiple females and paternity is highly uncertain. Down the monogamous first fork, sexual dimorphism is slight. Down the second fork, dimorphism flourishes. In Chu and Lee (2012) we develop this classic theory in mathematical form, focusing on the second dimorphic fork, and draw out some new implications. Because successful males father many offspring while most males father none, and because of high paternity uncertainty, the father’s transfers would have small fitness value to him, and he has greater incentives to compete for more females, to guard access to the females he already has, and perhaps to protect his purported offspring from lethal assault by other males.

## Time Preference, Transfers, and the Marginal Value of Energy

Organisms must frequently make decisions about tradeoffs across time, or intertemporal allocations. Most of these are developmental and physiological, and have evolved, but others are strategic and a matter of choice and decision. Eat a nut now or store it for later? Wait to grow bigger or start reproduction now? Search longer for a mate or accept this one now? Bear another litter this year or wait until next?

In general, an incremental unit of energy may have different incremental fitness value at different ages over the life span. Often it would have greater fitness impact early in life when it can enhance survival and growth than it would in later adult life when energy is more easily acquired and the perils of early life have already been avoided. Time preference between ages i and j is measured by the number of incremental units of energy at age j an organism could trade for one unit of energy at age i, with no change in fitness. Intergenerational transfers evolve in species which have a high rate of time preference between early and adult years. The transfer of resources from the adult to the offspring raises the marginal value of energy to the giver and reduces it for the receiver, tending to equalize them and to move the rate of time preference towards one across all ages, although paternity uncertainty and parental death would likely prevent complete equalization. Chu, Chien and Lee (2010) develop these ideas in a formal analysis. This general line of theory was pioneered by Alan Rogers and followed by Sozou and Robson.

## Intergenerational Transfers and Cooperation

Individuals in many species cooperate with one-another, and their behavior is a mixture of competition and collaboration. A sizeable literature in various disciplines (Nowak, 2011; Bowles and Gintis, 2011) discusses how cooperation could evolve given that defection would often seem to give an advantage, at least in the short term. Cooperation is advantageous because it makes production more efficient, because risk sharing shifts some resources from those for whom they have a lower marginal value to those for whom it is higher, and because it aids in defense and in acquisition of territory.

The literature appears to be largely about cooperation among adults. An adult who cooperates will on average experience a net individual gain as a consequence. By contrast, an individual adult who makes an intergenerational transfer of food or care to her offspring is permanently worse off as an individual as a consequence. Of course, she raises her reproductive fitness thereby and is therefore better off indirectly, which is why the behavior of transferring to her offspring young was selected. But her transfer is not an effort to improve her individual situation. Her recipient offspring will not return the favor to her parent, but will instead herself grow and mature and later make similar transfers to her own offspring. To the extent that the parent and offspring do help one another reciprocally, the behavior is cooperative or an exchange, not a transfer.

Cooperation resembles a mutually advantageous exchange more than an altruistic act or transfer. Unlike market exchanges the terms of the exchange are not enforced by rules of the market, police, and a judicial and penal system. Instead, reciprocal behavior develops in the context of repeated interactions that are maintained through mutual benefits, an evolved sense of fairness, and occasional punishment of offenders.

Nowak (2011) discusses five mechanisms through which cooperation could evolve: reciprocity, indirect reciprocity, spatial selection, multilevel selection, and kin selection. Bowles and Gintis (2011:2) define cooperation as “…engaging with others in a mutually beneficial activity.” As an example, consider a pair of unrelated foragers with families to feed, who are each disabled by illness or injury on 20% of the potential foraging days (as estimated in Hill and Hurtado, 2009). They might agree to provide food for one another’s family on these days of disability, which would be an example of reciprocity, a form of cooperation that could evolve for foragers who were repeatedly in contact over a long time. (A similar outcome could be achieved in a different institutional setting through formal insurance markets or through money.) Both the foragers and their families are better off with this cooperative arrangement than without.

Intergenerational transfers benefit the recipient but not the giver – other than indirectly through reproductive fitness. Intergenerational transfers are never reciprocal, since by definition there is no quid pro quo. For example, young birds sometimes remain at their parents’ breeding site rather than dispersing, and assist their parents in rearing their younger siblings as so-called “helpers at the nest”. It appears that they do this in exchange for being allowed to avoid risky dispersal by staying at the breeding site, although they may gain a bit through inclusive fitness as well. This is not a true transfer.

In the literature on cooperation I find very little discussion of fertility, survival, or reproductive fitness (Nowak, 2011; Bowles and Gintis, 2011). To understand the evolution of life histories, in the sense of age-patterning of fertility, mortality, growth, investment in offspring and behavior over the life span, we need to consider the evolution of intergenerational relations. There is remarkably little overlap between this topic and the evolution of cooperation.

## Cooperation and Intergenerational Transfers as Reallocation Systems

At a general and abstract level we can consider the possible ways of shifting resources in a population across age and over time. There are only three ways (Bommier and Lee, 2002): 1) saving, accumulation, and then dissaving; 2) borrowing, lending, repaying – that is, intertemporal exchange; 3) transfers across ages or generations. The first, accumulation, can shift resources only forward in time: accumulation (of nuts, berries, a nest or beaver dam, or 401K account) necessarily precedes consumption of the asset or its services. This cannot help a juvenile to grow. The second, intertemporal exchange, is limited in its ability to shift resources from one age to another. It could shift resources to the young only if they repaid those resources at a later age to their elderly parents, and that is inconsistent with maximization of reproductive fitness and does not occur in nature although it does occur in agricultural and industrial human societies. The third possibility, intergenerational transfers, is the only mechanism capable of shifting resources to children to promote their survival and development. A parent may accumulate an asset or capital good, of course, and then give it as a lump sum transfer to an offspring at birth or at laying, for example a dung ball or paralyzed prey on which an egg is laid. This nonetheless remains an intergenerational transfer.

Cooperation is based on reciprocity. One consequence is that at any instant, the average age of all those contributing and all those benefiting from a cooperative situation are equal. This is obviously true when every participant also simultaneously benefits, since the ages of the contributor and beneficiary are then one and the same. Consider the less obvious case of sharing the risk of disability through food sharing as described above. Suppose hunter X is age Ax, and y is age Ay. On one day X gives food to Y, and d days later Y gives equal food to X. The average age of givers is [Ax + (Ay + d)]/2. The average age of receiving food is [Ay + (Ax+d)]/2. Clearly these are equal, and this will be so no matter how circuitous and indirect is the path by which X eventually receives the reciprocal gift. (I call these “gifts” here, but clearly they are not gifts; they are essentially loans to be repaid, directly or indirectly.)

Contrast the case of intergenerational transfers. Suppose each generation is g years older than the next. A parent in generation X makes a transfer to her offspring in generation Y who eventually makes a transfer to her offspring in generation Z. The transfer is always made to someone g years younger than the donor parent. The average age of donors is g years greater than the average age of recipients.

The average participant in the cooperative arrangement, looking to the future, expects to contribute and receive equal amounts. In the language of reallocation systems we would say that there is a zero aggregate credit balance in this system (Lee, 1994; Bommier and Lee, 2002). Individuals who have contributed more in the past than they received, and therefore who expect to receive more in the future than they will contribute, are exactly balanced by those in the opposite situation. The aggregate credit balance is proportional to the difference in average ages of receiving and contributing, which is zero.

The situation is different in the case of intergenerational transfers. Juveniles have already received transfers from their parents, and even if they expect to receive more in the future, at every age after birth these expectations will be outweighed by the transfers they expect to make later when they are themselves parents. For this reason the young have a negative credit balance. As for adults, they expect to continue to make transfers themselves for the rest of their lives so they also have a negative credit balance. In fact, every member of the population expects to make more transfers in the future than will be received. The aggregate credit balance is therefore negative, and indeed is proportional to the difference in average ages of receiving and donating, which is g – one generation. The system of intergenerational transfers enables what would be impossible through exchange, cooperation and reciprocity. It enables the young to consume more than they produce through their own foraging efforts and therefore to grow faster, larger and more complex than otherwise. As adults they will never repay their parents, since they received a transfer with no quid pro quo. Instead they will enable their own children in the same was as they were earlier enabled themselves. These points are established in mathematical models and analyses in Lee, 1994, and elsewhere.

And what about cooperative breeding? The part of cooperative breeding that involves relatives of the parents and offspring is intergenerational transfers, not cooperation. But in some species, including humans (Gurven 2004; Hrdy 2009)), African hunting dogs (Creel and Creel 2002), and acorn woodpeckers (Koenig and Mumme 1987), for example, non-kin may assist in provisioning and caring for the young of others. This is a form of cooperative behavior in which the non-kin will expect to receive similar support when they are in similar circumstances, although not necessarily from the same adults that they assisted. In human hunter-gatherer sharing groups, for example, families with higher dependency ratios (more children relative to adults) often receive extra help from others including non-kin (Gurven 2004).

## Direct and Indirect Genetic Effects and Intergenerational Transfers

Intergenerational transfers are all instances of indirect genetic effects, to the extent that the transfer behavior is genetically influenced and therefore heritable. Review articles on indirect gene effects often give maternal care of offspring, the most basic kind of intergenerational transfer, as a lead example of an indirect genetic effect (Wolf, 1998; Cheverud, 2003). Certainly the quality and quantity of this care influences the survival, growth and development of the offspring, in addition to the direct genetic effects operating in the offspring to influence height, speed of growth, body mass, and so on. Later in life the continued survival and presence of the mother influences her daughters’ fertility and the survival and growth of the mother’s grandoffspring (Sear and Mace, 2008; Coall and Hertwig, 2011). When the effects of the presence of the mother or grandmother on the survival, growth, development and reproduction of the offspring are not additive but involve interactions, then there are gene-on-gene (GxG) epigenetic effects that arise through intergenerational transfers. In this case selection acts on both genes, e.g. of mother and offspring, through the offspring trait in question. Therefore the evolution of intergenerational transfer behavior will act through both direct and indirect genetic effects.

## HYPOTHESES

1. Longer nutritional and other dependence of offspring on one or both parents is associated across species with longer postreproductive survival. The length of dependence must be substantial in relation to the life span of the mother or parents. In the case of humans, years of dependence for a child, say 18-20 years, is about half of total life expectancy of individuals surviving to maturity. When offspring care is limited to a short time followed by more reproduction it will be difficult or impossible to separate its effects on longevity from the effects of fertility itself.
2. The male or female parent that is more heavily involved in care and transfers to offspring (if either) will have longer life expectancy, with due allowance for mortality risks incurred through care and foraging, and for mortality risks incurred in intraspecific competition for access to the other sex. For example, when only the female bird cares for the chicks she thereby exposes herself to risks of predation while obtaining food for chicks and while attempting to defend the nest against predators. Whether or not she has evolved a lower level of senescent mortality, she typically has higher overall mortality. Unfortunately, it will typically be impossible to make “due allowance” (although analysis of animals in captivity may help), so it may be impossible to test this hypothesis. A study of sex differences in longevity of apes did find that the sex mainly responsible for offspring care did live longer.
3. The period of time in which mortality falls following birth should be associated with the duration of dependency. Unfortunately, it will be difficult to distinguish this hypothesis from the hypothesis that mortality is lowest when reproductive value is highest.
4. In species in which mothers or parents are fully responsible for provisioning and caring for their offspring in contrast to otherwise similar species in which provisioning and care are provided cooperatively, infant and juvenile mortality are intrinsically lower in the cooperative groups, by which I mean that mortality is genetically lower, and therefore lower than the sharing of food and care could itself explain.
5. Mortality follows a U-shaped pattern, declining from a high level at birth to a low point at sexual/economic maturity, rising to early adulthood and either continuing to rise throughout the rest of life or possibly having a flatter segment for a while following maturity. The flatness may arise in an optimal life history because even in species with deterministic growth like mammals, the accumulation of skills and knowledge may continue after somatic growth has ceased (for example, peak hunting output is reached by human hunters in their 40s), so the opportunity set may continue to expand (Chu, Chien and Lee 2008 and references therein). This is not relevant for late life plateaus in mortality.
6. Intergenerational transfers are more likely to evolve in species that a) have higher ratios of person years lived in adulthood to juvenile person years lived; b) have higher ratios of adult foraging productivity to juvenile productivity; c) have more efficient conversion of calories received through transfers into somatic growth.

## EMPIRICAL ANALYSIS

Consider conspecifics of varying ages and sex, living in a group. They may compete for breeding sites and for food, and members of some age-sex groups may tend to kill members of other age-sex groups. Offspring in a family may compete with one another for parental care. Some members may assist all others as sentinels or combatting other groups, or defending the group from predators. Some age-sex members may store information and use it to guide group decisions. Others may lead the group. Some may provide food or care for others. It would be impossible to account for all the relevant pathways through which one individual affects the survival and fertility of another. However, the interaction of all these different influences will be a net effect of an incremental member of age x and sex s on the fertility or mortality or fitness of the average member of age a and sex j. We can form a matrix with all these net effect parameters, for example for the case of fertility f, where the i,j element is df(i)/dN(j), where N(j) is the number or proportion of group members of age j and f(i) is the average fertility of females age i. This describes an effect evaluated at some given number or population share by age and sex, but the effect may vary depending on the absolute and relative sizes of the cells of the matrix, so we may need more elaborate functions as elements of the matrix. Information on kinship could be added as well, leading to a three dimensional matrix. In principle such a matrix could be estimated from data, although there are many pitfalls. A matrix like this expresses the sensitivities described earlier. These sensitivities might then be argued to shape the evolution of life histories.

We could develop the matrix of effects from theory combined with focused experiments or field studies, as has been done in a partial way focusing on optimal clutch size for birds. We could also try to estimate the matrix of effects empirically from observations on a group over time. A coefficient matrix of this sort is what economists would call a “reduced form”. It does not incorporate theoretical insights. The virtue of this approach is that it is comprehensive. It measures the net outcome of all ways in which the size of one subgroup affects the other. Instead of simple derivatives in each cell, the cells could contain quadratic or other functions, and population shares or ratios instead of absolute numbers could be used to compute sensitivities.

There is a substantial literature for humans on the effect of the presence of specific kin on the survival or fertility of a reference individual in historical and anthropological populations, as surveyed by Coall and Hertwig (2011) and Sear and Mace (2008). The consistent finding is that the mother has a large beneficial effect on outcomes for children while the father does not, and for grandparents the ranking by size of beneficial effect is maternal grandmother, maternal grandfather, paternal grandmother, paternal grandfather, generally interpreted as reflecting degrees of certainty about relatedness. Some years ago, I estimated matrices for acorn woodpeckers based on a large longitudinal data set created by Walter Koenig covering many breeding sites and individuals, to which he generously gave me access. However, there are serious issues of identification in studies of this sort – shared genes, shared environment, and so on.

This sketch of population dynamics as it is influenced by numbers in different age-sex bins is very general. We can focus on particular theories and accounting frameworks. The Leslie matrix incorporates only demographic accounting identities, on the assumption that vital rates are independent of the numbers in the bins. This approach is based on Lotka’s equation and its precursors. It was used by Hamilton (1966) to develop his theory of how natural selection molds senescence, based on the idea that the force of selection against deleterious mutations would be proportional to the sensitivity of the intrinsic rate of natural increase to a perturbation in the vital rate affected by the mutation. The optimal clutch size analysis would go a step beyond this Hamilton-Lotka approach by taking into account the inter-sibling competition for parental resources and quality of average offspring as a function of the number of offspring. But there are many other kinds of effects that could be incorporated, such as those arising from density dependence if the territory is bounded.

Earlier I described the model of Lee (2003, 2008) which spelled out a structural theoretical model in which incremental individuals affected others not only through the classic demographic accounting identities but also through density dependence in food acquisition and dependency in kin groups and broader sharing groups, which indirectly affected fertility and mortality of all members of the broader population as well as having stronger and more focused effects on kin and sharing group members.

Based on these models a specific matrix of sensitivities could be constructed. Unlike the Leslie matrix it would have no zeros because it would be filled by indirect effects operating through density, inter-age transfers, and competition for transferred resources. In this setup, genes have both direct and indirect genetic effects on reproductive fitness (Cheverud, 2003; Wolf, 2003), unlike the Lotka setup used by Hamilton in which only direct effects occur. However, other theories could also be considered, each bringing its own set of constraints on the elements of the matrix. It is possible that an empirical approach of this sort would have sufficient power to distinguish between different theories.

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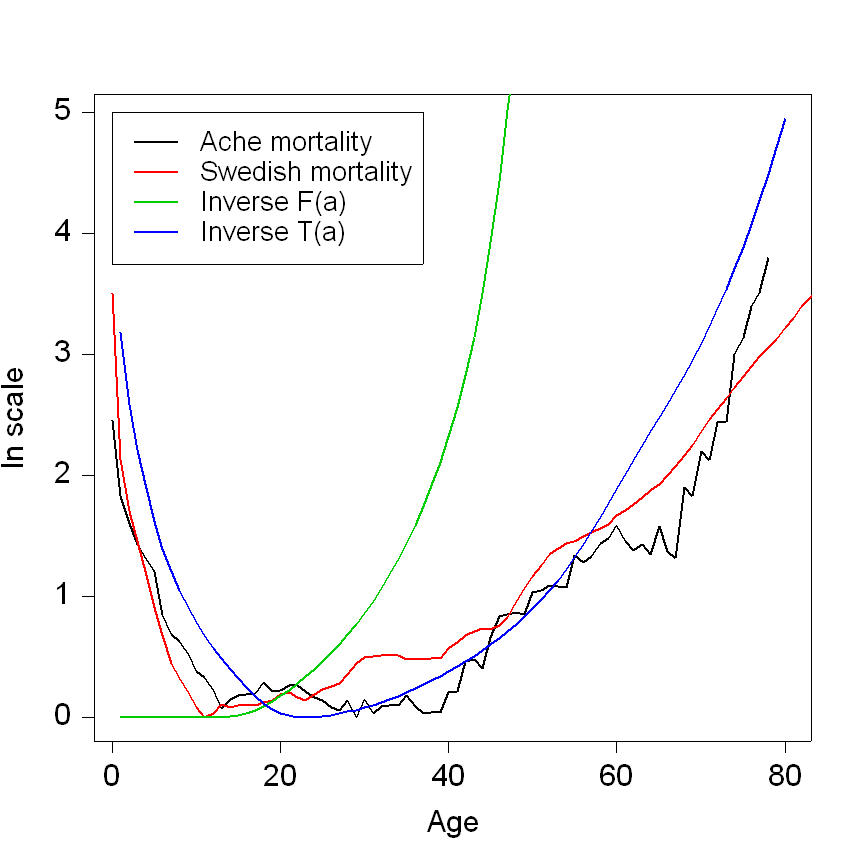
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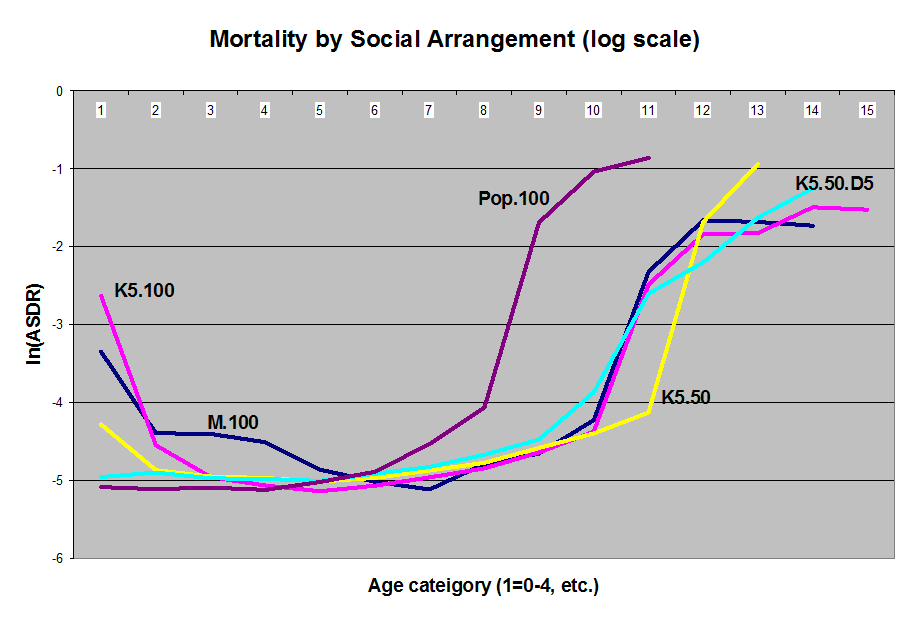
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Figure 1. Comparison of actual mortality schedules for Ache and historical Sweden  
with those predicted by force of selection for Hamilton theory and theory including transfers.



Note. F(a) is the share of lifetime net maternity remaining at age a, ranging from 1.0 until the age of sexual maturity to 0 at the first age at which fertility reaches 0, at some time before menopause. T(a) is the share of lifetime net transfers to others remaining at age a. At birth (or conception) this zero, since transfers made and received over the remainder of life are equal. From zero this share rises until it peaks at the age when the average child becomes nutritionally self-sufficient and then begins to make net transfers to others, which happens around age 18 or 20 for hunter-gatherers. After this the share remaining declines with age until death.

Figure 2. Simulated Evolution of Mortality by Social Arrangement after 75,000 years (ln of age specific death rates)



Age group, in years

Age group, in years

0-4 5-9 10-14 15-19 20-24 25-29 30-34 35-39 40-44 45-49 50-54 55-59 60-64 65-69 70-74

Note to self: Azores.

Figure 3. Evolutionary competition through density pressure on foraging among three types of sharing groups: Matriarchal, Third Cousins, and Sharing Groups with Third Cousin components sharing 50-50 in groups of 8-25. Three sub-populations of each kind were simulated, for a total of nine, over 1000 cycles (5000 years).



Key: Black=Matriarchy; Red=K5; Green=K5.50-50

Note to self: (sim 167B); Figure 13 from Azores paper by Lee and Boe.

1. The average age distribution within sharing groups must indeed be stable. Catastrophic outcomes would indeed be missed, but they must be averaged with the more common outcomes in which a parent survives despite having a positive probability of death. It is not clear that this would much alter the results. As for the relevance of comparative statics across gene lines when each birth experiences mutations, the point is surely correct but its effect on the conclusions via the sensitivity analysis is unclear. This argument would seem to apply equally to any use of sensitivity analysis in life history theory. [↑](#endnote-ref-1)