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Intergenerational Transfers, Life Histories and the Evolution of Sociality

Rough and preliminary draft

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Abstract of “Intergenerational Transfers, Life Histories and the Evolution of Sociality”

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For species that provide extensive parental care after birth, one potential advantage of living in social groups larger than the immediate family is that such groups may provide a form of life insurance for offspring who would otherwise die following the death of one or both parents. We use a stochastic micro-simulation to investigate whether varieties of a species living in larger kin based or mixed social groups have a selective advantage. To our surprise, we find that given our model specifications, detailed in the paper, those living in nuclear family groups beat those in larger social groups. However, when the level of consumption in childhood does not affect foraging productivity as an adult, then the results are reversed and consistent with our original expectations. The general lesson is that social groups as we construct them smooth out variability, and under some circumstances variability can be advantageous. In a second part of the paper we investigate how different social contexts modify evolutionary forces in ways that lead to different life history outcomes, finding that sharing with non-kin leads to lower infant mortality because the resources that would have been spent on the dead infant in the future can be fully captured by the surviving relatives in kin-based groups, but not in sharing groups with non-kin.

“If offspring require extended care, but adults risk high mortality, then a large fraction of independently nesting adults will fail to raise any young...” (Queller 1994:105)

Introduction and Theory

Sociality and Parental Life Insurance

There are many reasons why it may be advantageous for individuals of a species to live in groups with some elements of food sharing or task-sharing. For species that provide extensive parental care after birth, one advantage of group living is that it may provide a form of life insurance for offspring who would otherwise die following the death of one or both parents. Lee (2003) analyzes the consequences of parental care and other transfers for the evolution of life histories, taking transfer behavior as given, and showing that post-reproductive survival and declining childhood mortality would evolve in a mutation accumulation framework. Chu and Lee (2006a) use an optimal life history approach to consider the conditions under which transfers from adults to young might evolve, and show that if transfers evolve then longer life would co-evolve. In both cases, parental care or more extensive transfers to the young lead to the evolution of increased longevity, because the life cycle stage during which the young receive transfers and could not survive on their own is a stage during which the death of the parent or of other adults would risk the death of her offspring. Chu and Lee (2006b) shows that a U-shaped mortality curve will evolve for species with determinate growth, particularly if they make post-birth transfers to offspring. For parents that invest heavily after birth in the care of their offspring, all the investments in the offspring up to that point would be lost if the parent died (Queller, 1994). By contrast, in a species without parental care, once the offspring is born the subsequent death of the parent would not endanger the survival of her young. So the dependence of offspring survival on parental survival is an important cost of parental care, a cost that could be diminished by a social arrangement that might provide surrogate care for an orphan. Pavard et al (2005) have calculated the fitness advantages of female survival by age, taking into account the indirect effects of maternal survival on offspring survival, in an historical agricultural setting.

The risk entailed by the death of a parent means that any form of life insurance would be strongly selected, other things equal. One possibility is for the adult to accumulate a stock of nutritious food of some sort that can be bequeathed to the offspring as a way of providing some degree of limited parental care without requiring the presence of the parent. Whereas parental provision to young leads to inefficient wastage of previously invested resources if a particular offspring dies, at least the parent can then terminate the flow of transfers and redirect the food energy to herself or to siblings of the dead offspring. When the parent leaves a bequest, however, if the offspring dies then that entire bequest may be wasted generating another large inefficiency.

Another possibility is to provide life insurance by “making a deal” with some other parent, such that if one parent dies the remaining parent will care for the dead parent’s offspring. One way to bring this about is through a form of cooperative breeding in which the parentage of the offspring is unknown, as when acorn woodpeckers lay their eggs in the same nest. Another way is to cooperatively rear the young in some sort of sharing

group in which adults are willing to care for the young of other, perhaps unrelated, parents. Human cooperative breeding arrangements may be a mixture of these two approaches. On the one hand hunter-gatherer women are sometimes reported to have sex with men other than their long term mates in order to create paternity uncertainty, or in some cases in the context of a reported belief that an infant draws strength from many fathers. On the other hand if a father or mother dies sometimes a relative or a non-relative will step forward to assume responsibility for the care of a child or children, while at other times the children, if young, may be killed by the group (Hill and Hurtado, 1996). Thus extended offspring dependence and parental care combined with a risk of parental death generates a potential efficiency gain for sociality (Queller, 1994).

The Lee (2003) and Chu and Lee (2006a and b) analyses approximate the age distribution of breeding groups by a stable population age distribution. The age distribution of even a small group will indeed be stable if averaged over time or across many similar groups at a given time, provided that the total population has a stable age distribution. However, for a particular group at a particular time, the population will necessarily be far from stable if the group is small. The death of the parent in a parent-offspring set leads to a particularly stark example of a non-stable population age distribution, one in which there are dependent young but not a single adult or, in the case of bi-parental care, the age distribution would be tilted strongly toward the young. But the phenomenon is more general. Even without the death of a parent, the effective dependency ratio (consumption needs of the group relative to the productive capacity of the group) will vary in systematic ways over the life history.

For humans, this family life cycle was first described by Chayanov (1925:1986). He showed that the effective dependency ratio or “Chayanov Ratio” doubles over the first fifteen years of marriage before declining at a later life cycle stage when children have outgrown dependency (see also Lee and Kramer, 2002). In the Ukrainian peasant households that Chayanov studied the working age members of the household adjusted their efforts in proportion to the consumption demands of the household so as to maintain consumption at a relatively constant level relative to needs. Other options are to save and accumulate resources when dependency is low and then to decumulate when the ratio is high. For other species this could be accomplished by caching food (e.g. acorn woodpeckers) or by storing energy somatically, although such strategies are probably employed more for seasonal purposes than for coping with long term dependency variations.

Sociality can also smooth across the peaks and hollows of the family dependency cycle, although this feature of social living may be of most use for species that have both extended offspring dependency and relatively short birth intervals so there are multiple dependents at the same time. If families join together and share food and work in larger social groupings then within these groups the population age distribution and dependency burden will more closely approximate the constancy of a stable age distribution. This would achieve a more even distribution of work load and consumption over time, and do so at a lower cost than storing food (which involves substantial work and also loss through decay and theft by individuals of the same or a different species).

It is easy enough to see why individuals might be willing to share food with close relatives who have a high dependency burden, motivated by evolved feelings according to Hamilton's Law. But why should unrelated individuals do this? Yet this behavior has been observed repeatedly in human sharing groups, even when membership in the group was relatively transitory so that a quid pro quo claimed at a later date could not be the explanation (Gurven, 2004; Kaplan and Gurven, 2005).

Human hunter-gatherers lived in social groups that were large in the season when food was abundant but in the lean season shrank to about four families joined in mobile groups with 8 to 25 members. Within these groups some kinds of food were extensively shared, particularly large game and honey, while gathered food was predominantly kept within the family. Some of this sharing can be viewed as contingent and reciprocal, and therefore similar to informal loans. Another part of it cannot be understood in these terms and might be termed altruistic.

Because of this sharing, the whole group was affected by the presence of dependent children. Following the death of a parent, among the Ache of Paraguay there might be heated argument about whether to kill that parent's younger children, or to let some or all live. These arguments could become violent, and sometimes children were pulled in half by the rival factions. When another adult was willing to assume responsibility for feeding an orphaned child, its probability of survival was increased. At such times, a male who had had sexual relations with the mother might either believe a child might be his own, or might believe himself to be one of a number of fathers. It was not uncommon in Latin America for pregnant women to engage in sex with other males, a practice that has been interpreted as a risk hedging strategy of the mother.

A surprise result in the simulations to be reported below leads us to consider an additional possibility. Perhaps variability is good rather than bad. In larger social groups, the dependency ratio in any year is going to be fairly close to the stable population value, whereas in a simple matriarchal group it will fluctuate widely. If there is positive feedback, then the gains from the favorable fluctuations may exceed the losses from the unfavorable ones, and the greater variability of matriarchal groups might lead to greater average fitness.

In this paper we will use microsimulation to investigate the advantages of cooperative breeding in sharing groups as a means of insurance against offspring death following parental death.

Sociality and How it Affects Evolution of Life Histories

We have argued that the risk of parental death and fluctuations in the effective dependency ratio across the life history generate problems that social living arrangements can effectively solve. But social living arrangements, if they evolve, will themselves influence the evolution of the life histories of their members. Presumably that is how eusociality emerged as the result of a long process of coevolution of various attributes within a social setting that was itself evolving.

Here is one example that will be discussed in more detail later. If food is shared within a group that includes distant relatives or non-relatives, then the cost of a dependent child is born not only by its relatives but also by non-relatives. A species organized into closely related kin groups each living alone would evolve to an optimal point on the quantity-quality tradeoff. This optimal point would take into account that an extra offspring would take resources from all other members of the group, and that the early death of an offspring would in a sense release those resources that would otherwise have been devoted to its care at older juvenile ages. In a group of close relatives, these released resources would be fully recaptured by the relatives and would be available to nourish the siblings and cousins of the deceased child or its parents and other adult relatives. The benefit to rearing a well-nourished offspring would be a stronger and more fit adult who would contribute more to the fitness of all the other members of the group who were her close relatives.

Now consider a species organized into larger sharing groups that include non-relatives. The birth of an offspring imposes costs not only on its relatives but also on non-relatives in the group. In this case, the death of an offspring releases resources that are not fully recaptured by its kin group, but rather are shared with non-kin. Thus the birth is less costly and the death is more costly. We would expect, then, that the force of selection against childhood mortality would be more intense in the broader sharing group than in the kin group, and consequently that child mortality would be higher in the kin group than in the broader sharing group. Similarly, we would expect that fertility would be higher, other things equal, in the broader sharing group. Of course, resource constraints would force equilibration at a zero growth rate, but in that equilibrium we would expect the proportion of children to be higher in the social group than in the kin group.

Next consider adult and post-reproductive mortality. On the one hand, in the setting of a larger group, since infant mortality is expected to be lower, it is more likely that an adult mother will have a surviving child, which strengthens selection against her death and would lead to lower mortality. On the other hand, if she dies then there are likely to be other adults to care for her child (life insurance) so the force of selection against her death should be weaker and mortality higher. The net outcome for adult mortality is not clear.

The general point is that under individual selection (as opposed to group selection which we do not consider) sharing groups and sociality in general lead to problems of free riding. In part these occur at the level of strategic behavior of the usual overt sort, which may be countered in part by group monitoring and punishment of cheats. This problem has received a great deal of attention in the literature. But there is another aspect of free riding that we have not seen discussed: a subtle shaping of the life history in inefficient ways at the genetic level through evolution, as we described above. By this we do not mean a mutation that leads an individual not to share food or to cheat on life insurance. Rather we mean a mutation that might reduce the contraceptive effect of breastfeeding and thereby lead a female to have shorter birth intervals, higher fertility, and lower investment per child. Or in the mutation accumulation context, there might be the more rapid deselection of a mutation that raises child mortality, leading to an increased number

of surviving offspring. Similarly, a reduced fitness impact of maternal death might lead to higher female adult mortality than would occur if her death lead automatically to the death of her offspring. This topic of evolved free riding, not as a behavior but as a life history shape, will also be addressed below.

The design of the microsimulations

The basic model

The model is unisex, so reproduction is clonal.

Genome

The genome has genes at a site affecting mortality at each discrete five year age group. A birth inherits the genome of its mother, but mutations raising mortality at a given age occur with some probability at birth. The genome consists of a simple tally of the number of mutations at each site. The simulations start out with zero mutations at each site. However, we assume that there is a level of background mortality, the same at every age.

Production

We assume a base age schedule of production, $y(x)$. This age schedule is modified in three ways. First, the greater is the general level of population density the lower is age specific production. Second, the greater was consumption in childhood by a given individual, the greater will be production as an adult, to reflect a return to an investment in the quality of the offspring, most simply through body size. Production also depends on consumption in the previous period, so that a well-nourished individual is more productive.

Consumption

Individuals live in social units, the smallest and most basic of which is a mother and her offspring, but some of which can be much larger and more complex. We assume a basic age schedule of consumption, $c(x)$. We first calculate the total production in social unit based on the production by each individual as described above. Given this total production, the $c(x)$ base schedule is adjusted proportionately up or down until the implied level of total consumption for the social unit exactly equals the total production. The factor by which the $c(x)$ schedule is adjusted is called γ , which is a fundamental variable in the simulations.

Transfers

When production at an age exceeds consumption at that age some period, the surplus is transferred to others in the social group, and conversely. Thus production, consumption and their difference, intergenerational transfers, are all endogenous in this model, although only in a limited sense since the age-shapes of consumption and production are taken as given. This is discussed further below.

Mortality

We have already described the baseline mortality and the way that mutations affect mortality at each age. The mortality implied by these two factors is then modified according to consumption level relative to needs, that is γ , in the previous period.

Fertility

A baseline age schedule of fertility is assumed, and as with mortality it is modified according to consumption in the previous period, γ .

Selection

Genomes that imply higher mortality in the postreproductive years will be associated with worse dependency ratios and lower values of γ for the kin in their social groups. This will cause higher mortality, lower fertility, and lower future productivity for members of the social group, resulting in lower reproductive fitness for the individual with this genome. Therefore genomes of this sort will tend to be selected out of the population, whereas genomes with more postreproductive survival will do better. The force of selection against deleterious mutations will vary by age, depending on their impact on fitness, as analyzed for this general model by Lee (2003). At the same time, as the population grows, density rises, and γ will equilibrate at some level, and there will be some equilibrium frequency of mutations affecting each age. However, due to the operation of Mueller's ratchet, deleterious mutations will continue to accumulate at the older ages, so this is only a quasi-equilibrium.

In the data we use for age specific production and consumption, based on Kaplan (1994) and Lee (2002), adults produce more than they consume all the way through old age. However, in our model it is possible that consumption might be higher in some simulations and consequently some older ages may be net consumers. In this case there would be selection for higher mortality above the cross-over age. The simulations will automatically reflect these various forces at work.

Defining Kin groups

We define four different kin groupings. The matriarchal, designated M, has already been defined. M groups will primarily have mothers and offspring, or solo individuals, but occasionally they will contain a grandmother and then will contain all her surviving offspring and their offspring. The next grouping is K3, in which all individuals who are at least first cousins live together, whether or not there is a surviving grandmother. In K4, all individuals who are at least second cousins live together. In K5, all individuals who are at least second cousins together with all their offspring live together.

Defining Sharing groups

Based on a comprehensive survey by Binford (2001), we assume that kin groups as described above join together into sharing groups of size 8 to 25 individuals and typically around four M-type families. If the size of the sharing group grows above 25, then it fissions into two new sharing groups, keeping kin groups together. If its size falls below 8 individuals, then it fuses with some other small group to form a new sharing group.

Within these sharing groups, food is shared according to some specified rules. In a common specification, the kin groups retains half of its food production for its own consumption, and puts the other half in a common pot to be shared in the larger group. In some simulations this share is given different values.

In the real world, it appears that the membership of these sharing groups is quite fluid, at least so far as the unrelated individuals is concerned. In some simulations the sharing groups are reconstituted every few periods to capture this constant reshuffling.

Parameterization

The basic age schedule for fertility was taken from the Ache (Hill and Hurtado, 1996), and schedules for consumption and production were taken from empirical studies of the Ache, Piro and Macheguenga as reported in Kaplan (1994) and synthesized in Lee (2000). Assumptions about sharing behavior were based on research by Kaplan and by Gurven (Gurven, 2004; Kaplan and Gurven, 2005). Elasticities of fertility and mortality with respect to consumption were derived from a study of elasticities of fertility and mortality of landless laborers with respect to grain prices in Europe and Asia (Bengtsson et al, 200* and Lee and Steckel, 2006). The mutation rate was set at .01 per cycle for each age-specific site, and additive increment to an age specific death rate resulting from a single mutation was set at .02.

Basic Simulation Results

Matriarchy case

We will briefly describe the simulation results for the case where the only social group is the matriarchy, as defined above. We have defined the level of resources so that the population equilibrates at about 10,000 individuals. We have run this and the other simulations for 15,000 five year cycles, or for 75,000 years. We report the results at the end of this period. For mortality, we report the average value at each age, and its 95% probability interval based on the last 500 cycles observed to reduce the fluctuations.

Population size over time is shown in Figure 1. Its range of fluctuation is about 500 individuals, or about 5% of its mean value (that is, about $\pm 2.5\%$). The index of consumption level, γ , is shown over time in Figure 2. Its equilibrium value appears to be about 1.5, and its range of fluctuation is about .1, or 7%.

The size distribution of matriarchies is shown in Figure 3. Most have only one member, and the average size is 1.83. The average individual, however, is in a matriarchy of size 2.35.

Figure 4 plots consumption and production by age for the terminal cycle. We see that individuals do not produce as much as they consume until age 20 or so, which is what studies of contemporary hunter-gatherer groups have found. After this age, individuals on average remain net producers even into old age. In this particular plot there is an odd bump at age 55-59 which is just some sort of small population variation and is not typical.

Figure 5 shows the average level of γ by age. In a stable population, these γ 's would all be identical, but not here. Even averaging across individuals leaves systematic differences by age, which we now consider. The birth of an infant implies that the mother was alive recently to give birth, so typically the infant will have a mother to feed it. Note that γ declines to a minimum for ages 15-19. At this age, the mother has been exposed to the risk of death for 15-19 years, so there is a fair chance that she has died which reduces the average value of γ . Furthermore, a child at age 15-19 is likely to have siblings if the mother has survived, and those siblings will increase the consumption pressure in the matriarchy and depress γ . This is why γ is so low at this age. We also see that γ rises after this age group, roughly doubling by age 65-69. The reason γ is so high at that age is that the woman may well have no surviving offspring with whom to share her output.

Mortality by age is shown in Figure 6. The solid black line plots the age schedule of evolved mortality at the very end of the 15,000 simulation cycles. To reduce the role of random variation, the purple lines give averages over the past 500 cycles along with the 95% probability coverage. In addition, the blue line plots the predicted mortality according to the Hamilton theory. It is drawn as inversely proportional to the proportion of life time fertility remaining at each age. The tan line plots the prediction of the Transfer theory, and it is inversely proportional to the remaining transfers to be made after each age. The red line is a weighted average of the two. Given the tiny size of these matriarchies, and that the modal size of matriarchy is a single individual, it is remarkable that these simulated results match fairly closely the theoretical predictions derived by treating the age distributions of these small groups as stable.

On the whole, the relative levels of mortality by age reflect the relative frequency of mutations at each age. However, note the strange bulge in mortality in the late teen years. The generally low level of mortality at this age reflects the huge cumulative transfer that has been received to that point, and consequently the huge cumulative transfer that will be made to others over the remainder of the life cycle. The bulge in the late teen years reflects the exceptionally low level of γ for these ages as discussed earlier.

Social Arrangement distributions

We earlier defined the various kin groupings and sharing groups that are used in this paper. Figure 7 plots the average sizes of the different kinds of kin groupings for a given simulated population over 15,000 cycles. The smallest is M, with a mean of 1.84 as noted earlier. Then comes K3 at 3.3, K4 at 4.0 and K5 at 4.6. Evidently these mean sizes are quite stable over time. Note that the K5 mean size is about 2.5 times the mean size of M. We have already seen the distribution of sizes of M-groups (matriarchies). Figure 8 gives the comparable distributions for K3, K4 and K5 groups.

These kin groups are arranged into sharing groups according to differing sets of rules. Figure 9 shows the distributions of sharing group sizes, all of which lie between 8 and 25 as they should, with a mean size of 15. As explained earlier, sharing groups fission if they grow to exceed 25 and fuse if they fall below 8. Figure 10 shows the frequency of fissioning at about .026 and fusing at about .0125 over 15,000 cycles. These frequencies

imply that fissioning occurs on average about every 200 years, while fusion occurs about every 400 years. These are relatively rare events, permitting a substantial degree of relatedness to develop in the sharing groups beyond our defined kin groupings.

Simulation Experiments on the Benefits of Social Arrangements

The starting point for this study was the claim that social groups would provide a kind of life insurance which, for species that invest heavily in offspring over a prolonged period of juvenile dependency, would make the death of a parent less disastrous for the offspring. This is illustrated in Figure 0, which plots the probability of death over a five year period for an individual initially age 0-4 whose mother had died between giving birth and the start of the interval. Calculations based on the same simulations indicate that the relative risk of mortality when the mother has died is 7 in matriarchal groups, 1.4 in K5 groups, and 1.3 in 8-25 sharing groups. For the forest dwelling Ache (Hill and Hurtado, 1996:424 and 452) a mother's death raises mortality of children age 0-9 by a factor of 5 and the father's death by a factor of 3. The death of a mother in the first year of life leads to the infant's death 100% of the time. Since the Ache social arrangement is close to K5.50-50 which in our simulations has a relative risk of 1.3 it appears that we are underestimating the impact of parental death by taking account only of the effect of food sharing and not other aspects of the mother's care. Nor do we take account of direct mortality due to killing of children following the death of a parent which is fairly common among the Ache. Pavard et al (2005) and Pavard et al (2007) report estimates for historical Quebec indicating a 75% increase in the probability of death before age 15 if the mother dies when the child is age 0, but this is in an agricultural society with social support available, as they discuss.

We can calculate the impact on overall infant mortality by factoring in the probability of maternal death within a five year period. In our simulations this is about .035. This implies that the maternal death effect adds about .025 to the infant mortality rate, which is substantial. Kaplan and Gurven (2007) synthesize mortality data for contemporary hunter-gatherer groups and these estimates indicate that about .07 of mothers would die within a five year period, twice the simulation result. Using this figure would double the importance of the maternal death effect to .05. Since the Ache live in social groups and share food, it is likely that the counterfactual mortality of hunter-gatherer mothers living alone should be substantially higher than this, further increasing the size of the effect.

Earlier we suggested that larger groups in which food was shared would even out the irregularities in the age distributions and dependency ratios of smaller groups. Figure 11 illustrates this point by plotting the average γ by age for the Matriarchal, K5, and 8-25 sharing groups. The black line (group sharing) is quite horizontal, indicating that groups with a mean size of 15 achieve close to the smoothness of a stable population. The green line for K5 fluctuates more than the 8-25 group line but substantially less than the red line. The max to min ratio for M is around 2; for K5 it is around 1.5; and for SG it is below 1.2. This summarizes the across age variation.

There is also important variation within each age group across the individual groups, and this is described by the standard deviation at each age, plotted as dashed lines. For the Sharing Group (SG) this standard deviation is about .3, and quite constant across age. The standard deviations are considerably greater for M and K5, and they mirror the variations in the mean γ . The standard deviations for K5 are roughly 20% lower on average than for M up to age 60 or so. Clearly the larger groupings do exactly what we expect: they smooth out the variations both across age and across individual groups within ages.

Our basic argument has been that smoothing out the age distribution in this way and avoiding the wasted resources when a maternal death causes the death of her offspring would confer important fitness advantages. To investigate whether this is true, we compare results of simulations for different social group configurations. The first is the M case that we examined in detail earlier. Next comes the K5 case. After this comes Sharing Groups (8-25) formed from K5 kin groupings, with three or four separate K5 component groups. In this and the next group, it is assumed that the individual K5 groups each keep 50% of the food they produce and share 50%. Following this comes the same configuration but now the K5 groups are reshuffled into new Sharing Groups every five cycles. The last arrangement is sharing at the level of the total population, a case that would never happen for humans outside of modern industrial states, but it is included as a kind of benchmark. These social arrangements differ on two dimensions: size of group and degree of relatedness of group. Moving from first, M, to the last, population level sharing, the groups get larger and/or the degree of relatedness declines.

For each social arrangement, Figure 12 plots the equilibrium dependency ratio, calculated from the equilibrium life table as person years lived at ages 0-19 divided by person years lived at ages 20 and over $((T_0 - T_{20})/T_{20}$ in life table notation). We see that the dependency ratio declines slightly from M through K5.50-50 with dispersion, and then rises very sharply for the last group with population level sharing. If all arrangements had the same mortality, then their dependency ratios would be identical. They differ because different levels and age-shapes of mortality evolve under the different social arrangements, as we will consider in detail later.

Under population level sharing, the survival of offspring is entirely independent of the survival of the mother, because the offspring is provisioned by the population as a whole. Therefore there is no selective advantage to post-reproductive survival, and all that matters is bearing children, not rearing them. In this circumstance the evolution of mortality follows Hamilton's (1966) analysis and it rises explosively after menopause. Consequently the dependency ratios are very high in this case, because there are few post-reproductive adults to share the burden of caring for the young.

The figure also shows the mean value of γ . Recall that γ depends in part on the dependency ratio, calculated using the production and consumption weights; in part on earlier values of γ that affect the productivity of current adults, and in part on density which affects the productivity of everyone. Somewhat surprisingly, we see that γ is

highest for M, next highest is K5, and after that all the arrangements that involve sharing with non-kin have substantially lower γ .

Equilibrium density is the best measure among these three of fitness and evolutionary advantage. Here, density is calculated simply as Total Population divided by E, environmental resources. Again surprisingly M decisively achieves the highest density. All the other sharing groups achieve similar levels of density, while the population level sharing has substantially lower density. Contrary to our expectations and hypothesis, this suggests that the M arrangement confers the highest reproductive fitness despite the presumed wastage of resources through child death.

Before jumping to this conclusion, however, we note that the density measure we have plotted is not quite right, or at least cannot be compared across social arrangements. A young child does not exert the same pressure on the environment as a prime age adult, yet this kind of age composition effect has not been taken into account. To try to settle the matter, we try another experiment in which we pit M, K5, and K5.50-50 against one another in a head to head evolutionary competition. For this purpose we define a new density measure: (Total consumption in the aggregate population) divided by E, total environmental resources. This measure reflects our intuition that more food is extracted from the environment the more difficult it becomes to extract an additional calorie. This improved measure will reflect the relative prosperity of different groups as well as their age compositions.

In the next experiment, then, we will start with three separate populations that are arranged in matriarchal social groups; three more separate populations that are arranged in K5 social groups; and three more that are arranged in food sharing social groups based on K5 components with 50-50 sharing. Thus nine separate and non-interacting populations will compete only through their effects on density, where density is calculated based on the total consumption summed over all nine subpopulations.

The results of this experiment are shown in Figure 13, and the results could not be clearer. All three matriarchal societies beat all three K5 and all three K5.50-50 arrangements. The K5.50-50 groups die out first, with all three populations shrinking at about .5% per year and vanishing after about one thousand years. The K5 kin groups disappear next, a thousand years later, declining at about .25% per year. After five thousand years all three matriarchal groups are still thriving.

How can this be? As we saw earlier, there is a lot of variation in the gamma for matriarchal kin groups, both random and systematic with age, because they are so small. In larger sharing groups, γ is closer to its global mean. Could it be that this variation promotes reproductive fitness rather than undermining it? Some factors work against this. Over a longer time horizon the greater variability would reduce the expected time to extinction, but that is not an issue here. In a model that incorporated individual stochastic variation in production, which is very important for hunter gatherers, the production smoothing achieved by groups could enhance fitness, but our model does not include this.

One way that variability could be advantageous within the confines of our model is through the positive feedback in levels of γ : if γ is high today it will promote greater productivity and higher γ in future years. To see how this might work, consider a highly simplified example. Suppose that variations in γ cause the group NRR in matriarchies to be either 1.1 or .9 with equal probability. In larger sharing groups these variations are averaged out so that the NRR is always 1.0. If the variations in NRR are independent across time for matriarchies, then their average NRR will be 1.0 just like in the sharing groups. If, however, the γ variations come in runs due to the effect on later productivity then the outcome after two cycles would be $[1.1*1.1 + .9*.9]/2 = (1.21 + .81)/2 = 1.01$. The matriarchal groups will grow by 1% on average while the larger group will remain constant. Might this be what is happening?

Figure 14 shows age-specific productivity at various durations of the simulations by social arrangement. We see that after 100 years, productivity is clearly higher in the matriarchal populations than in the others, and after 500 years it is about 20% higher than the K5 arrangement and about 33% higher than the K5.50-50. Since all are facing the same density and we are controlling for age, this could be due only to higher consumption in childhood.

If this is so, it should show up in the age specific γ schedules, which are shown in Figure 15 for selected periods. There we see that after 500 years γ for ages 0-4 is about 20% higher under M arrangements than under K5 arrangements, and about 33% higher than under K5.50-50 arrangements. These advantages should compound over time. To quote Clutton-Brock (1991): "...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..." p.255 Nonetheless, our simple model may exaggerate these potential effects by ignoring limits to the size of gain that nutrition in youth can confer.

To investigate the importance of the influence of early life consumption on later life production, we set this effect to zero and reran the last set of simulations. The striking result is shown in Figure 15B. The outcome is the mirror image of the previous. Now the K5.50-50 arrangements all win while the M arrangements all lose, with the K5 as intermediate. Now the age-productivity schedules are identical for the different arrangements in the same period, in contrast to the previous experiment. Similarly, now the γ age profiles remain very similar over time, again in contrast to the previous result.

There are two important aspects of this result. First, the simple matriarchy arrangement M goes from being most successful to least successful. Second, the social grouping that involves non-kin does even better than the K5 arrangement. This seems to suggest that the greater smoothing of age distributions and consumption that is achieved by larger groups is sufficient to outweigh any loss in evolutionary efficiency that arises from dilution of the effect of an individual's genes on her success and thereby weakens and

distorts selection. It would be premature to draw this conclusion, however, because the inter-relatedness within the K5.50-50 sharing group is most likely much greater than its definition would suggest.

Our tentative conclusion is that indeed variation can be an advantage, at least the way we have set up the model. The reduction of variation not only makes the loss of parents less disastrous, but also avoids some extraordinary successes that would be more likely to arise in small groups. This is the drag of mediocrity which might be a more general cost of sociality.

So far we have considered the potential advantages conferred by living in social groups. Now we ask a somewhat different question: how does living in social groups alter the force of selection by age and so shape the evolution of life histories.

Social Arrangements and the Evolution of Life Histories

The basis of our theoretical discussion and our simulations is selection operating at the individual level, not at the group level, even though much of the selected fitness is indirect, through promotion of the fitness of close kin. Once individuals are embedded in social groups, the way in which natural selection acts on their life history characteristics is subtly altered, as we discussed earlier. In this section of the paper we will explore the way that different kinds of social arrangements shape the evolution of life history characteristics.

Figure 16 plots the evolved age pattern of mortality under different social arrangements, similar to the earlier figure for the matriarchal case. First consider mortality at the youngest age. Recall the earlier discussion suggesting that this should be higher the greater the likelihood that relatives would capture the released resource costs following a child death. Here we see that mortality is highest under the K5 arrangement which is the largest group defined by relatedness, two and a half times as large as the M arrangement which is also defined by kinship and which has the next highest level of infant mortality. Infant mortality is lower in this group because there is a greater likelihood that if an infant dies there will be no other sibling to whom the unused future resources can be reallocated.

Mortality at ages 10-19 stands out for M as being particularly high, 60% higher than in the other arrangements. This is due not to mutations affecting these ages but rather to the influence of maternal deaths and sibling competition for resources. The mothers of children in this age group have been exposed to the risk of death for 10 to 20 years and also are more likely to have born additional offspring, younger than the reference child, who would reduce γ for this group and thereby raise mortality. Recall that γ is at its lowest value for ages 10-19 as we saw in Figure 5. Figure 3B shows that a relatively high proportion of singleton M groups consist of a child aged 10-19. This means that their mothers have died, and they are compelled to get by on what they can forage for themselves.

The next highest infant mortality occurs for the K5.50-50 sharing group, in which on average 70% are not members of a given K5 group, so there is substantial sharing of food with potential non-relatives. But under 50-50 sharing, at least 50% of the unused future resources can be captured and used for close kin.

Next we move to K5.50-50 with dispersion (shuffling) every five cycles. Members of individual K5 groups are kept together here, but more distant relatives in the sharing group are dispersed so under dispersion the actual relatedness in a group is well described by the K5 definition, and relatedness is therefore lower than in the K5.50-50 groups in which there may be a high proportion of phantom relatives with ties of K6 or higher order. Here infant mortality is very low, because now when an infant dies no more than 50% of resources will be recaptured. Finally we see that mortality is even lower under population level sharing, where no resources at all are recaptured following an infant death.

Now consider mortality during the adult years. Under population level sharing, an offspring's survival and success is independent of her parent's survival, so there is no selective pressure to preserve future transfers, and selection is as described by Hamilton (1966). This is illustrated by the age shape of mortality for population level sharing in Figure 16, which shows it rising throughout the childbearing years and turning sharply up by age 50-54 (we would need to simulate over a longer horizon for the mutations affecting old age mortality to accumulate sufficiently to show the vertical wall of death here). The contrast between this age trajectory and the others indicates the role of post-reproductive selection under other arrangements.

For the other social arrangements there is selection of varying intensities continuing throughout life well past reproduction. During the reproductive ages mortality is low in all arrangements at about .03 to .04 probability of death within five years and rising slightly. Mortality is notably lower at ages 40 to 55 in the K5.50-50 arrangement, which probably reflects the high likelihood that there will be closely related children to be supported by older survivors, and hence selection will be relatively strong. Mortality is notably higher in the K5.50-50.D5, that is with dispersal every five cycles. This is to be expected, because with the reshuffling survivors in this age range are mainly supporting the children of non-relatives, so the force of selection against bad mutations will be weaker and mortality higher.

Figure 17 shows selected results from Figure 16 for infant mortality (${}_5q_0$) alone, arranged by strength of relatedness within the group. It can be seen that the line declines from left to right: the highest the degree of relatedness, the higher is infant mortality. This is consistent with the argument that the costs of infant death are lower in a closely related group because unspent resources can be recaptured and reallocated to relatives.

Figure 18 shows evolved mortality for social groups built from K5 blocks by whether there is shuffling every five cycles and by the extent of sharing, measured by the proportion of food retained within the kin group rather than shared with the broader group. Infant mortality is highest in the group in which there is shuffling, but in which

95% of output is kept within kin groups. At 100%, shuffling would be irrelevant because there would be no sharing outside kin groups in any case. K5.50 has slightly lower infant mortality but is otherwise very similar. When there is shuffling of the groups then infant mortality is quite similar whether kin groups keep 50% of their output or 75%. At older ages mortality is lowest in K5.50 with no shuffling, presumably because of high relatedness. Mortality is highest under K5.50 with reshuffling, presumably because relatedness is lowest so surviving elderly individuals are providing for unrelated offspring to a considerable extent. A general observation is that shuffling and reduction of relatedness has a large effect on child mortality, flattening it out thoroughly. However, it does not seem to have a strong effect on post-reproductive mortality, for reasons we do not fully understand.

Summary and Conclusions

We began with the idea that when offspring are dependent on parental transfers for a substantial time then parental death would entrain the death of offspring and a loss of prior reproductive investments. In these circumstances there should be a payoff to some form of life insurance that would enable offspring to survive parental death. Living in social groups larger than the mother-offspring sets and sharing food and other tasks could potentially achieve this end. We used stochastic microsimulation of the deterministic model in Lee (2003) to explore this hypothesized role of social living.

We find that living in social sharing groups does smooth out the life cycle squeeze type variations in consumption across age, and in particular alleviates a period of relatively low consumption (low $\gamma(x)$) in the teen years. It also does provide an effective form of life insurance that substantially reduces the relative risk of offspring death following parental death. However, we found that in head to head competition in our original specification the smallest grouping, mother-offspring sets, quickly won out over larger groupings. We believe this is because when early life consumption influences later life productivity, the beneficial effects of exceptionally good demographic outcomes more than outweigh the adverse effects of exceptionally poor outcomes. (Time to extinction, and in a richer model production-smoothing through group sharing would work in the opposite direction). Larger groups average through the good and the bad, achieving a middling outcome while the small groups profit from their higher variability, and win out. When we knock out this persisting effect of childhood consumption then we get the result we initially expected: larger kin groups win over smaller ones, and still larger groups that include non-kin do best of all.

We then consider how social living arrangements shape the evolution of mortality by age. The simulations show that the closer the relatedness in a group, and the larger the group for a given relatedness (to generalize from our few experiments) the higher is infant mortality, because the kin can recapture and use the future resources not needed for the now dead infant, reducing the force of selection against infant death. The effects of social arrangements on post-reproductive mortality are more difficult to interpret.

Many related topics remain to be explored within these simulation results. Introducing a mutation that affects the level of fertility is also a high priority. Extension of the

simulation model to include two sexes and a geographic gradient in relatedness will be difficult, but will be an important step.

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Figure 0. Infant mortality (5q0) contingent on maternal death or survival, by social arrangement

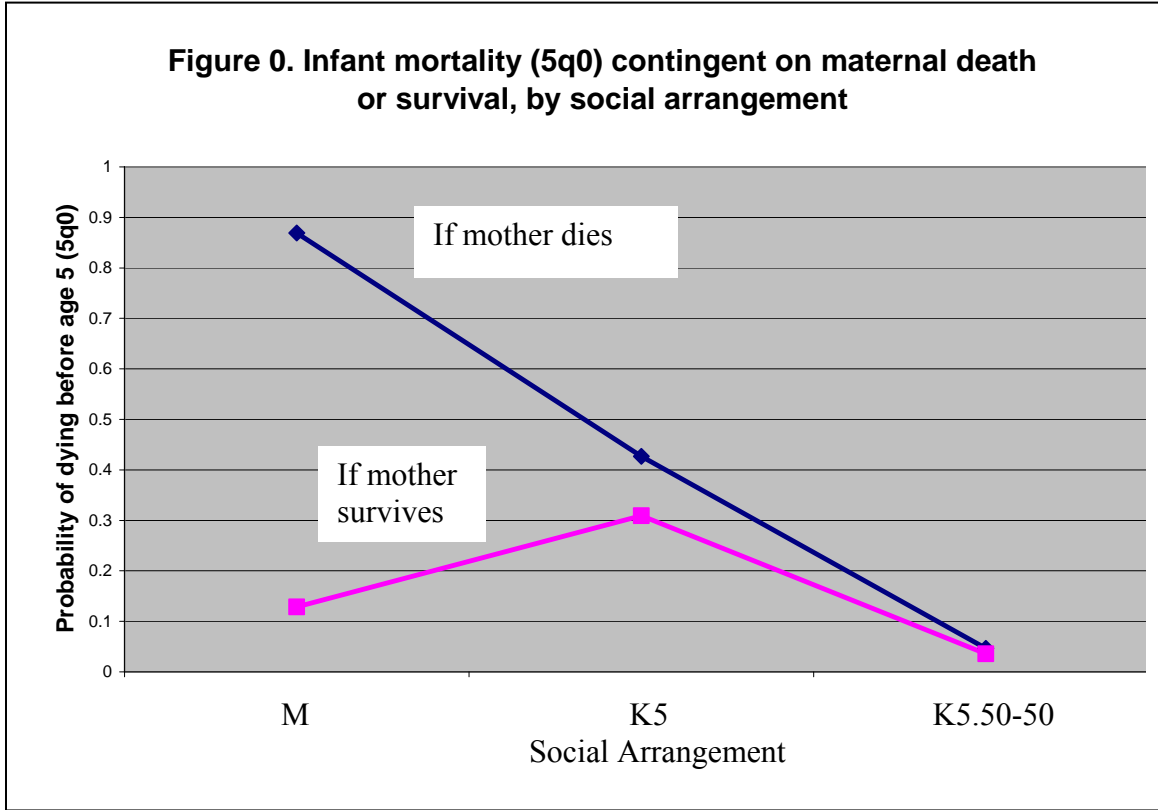


Figure 0B. Incremental infant death probability (5q0) due to maternal death by social arrangement

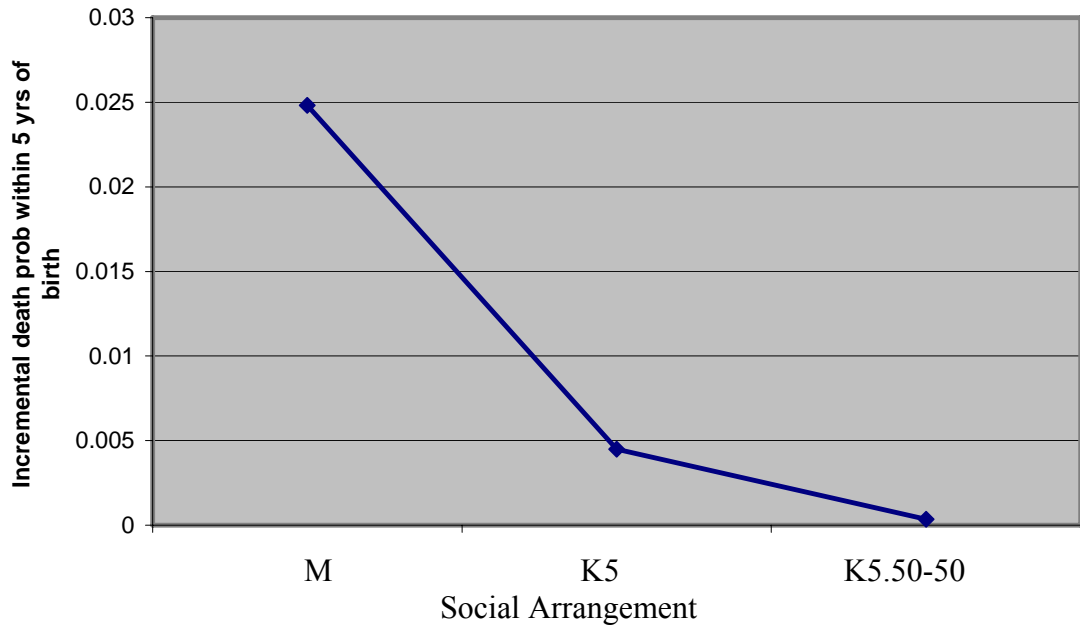


Figure 1. Simulated population size over 15,000 cycles (75,000 years) under matriarchal social arrangements (sim144).

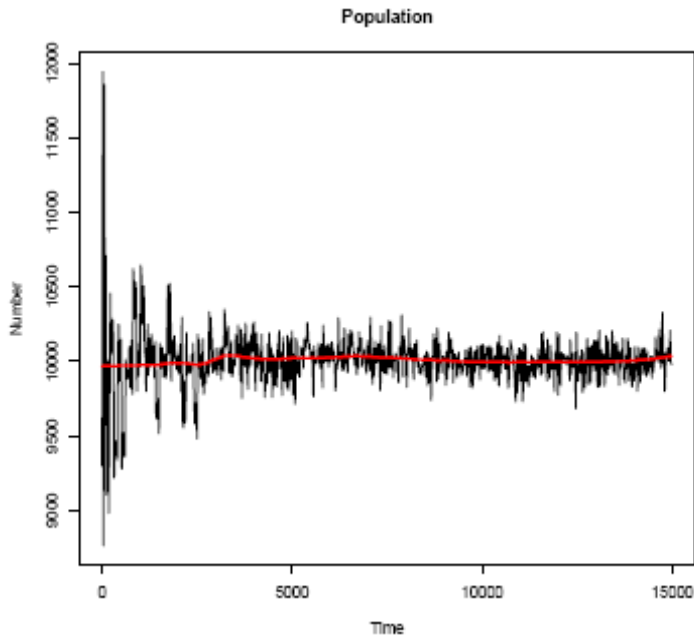


Figure 2. Average level of gamma (consumption index) across matriarchies over 15,000 cycles (75,000 years) under matriarchal social arrangements (sim144).

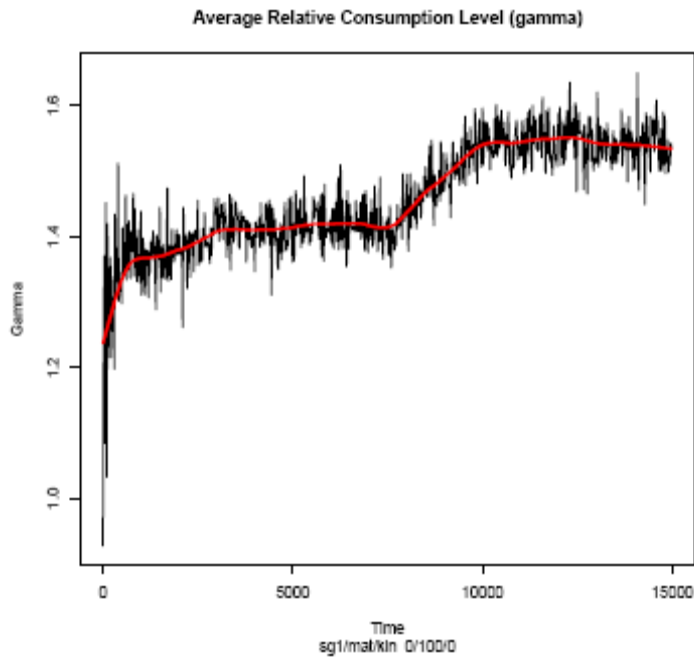


Figure 3. The distribution of size of matriarchies over 15,000 cycles (75,000 years) under matriarchal social arrangements (sim144).

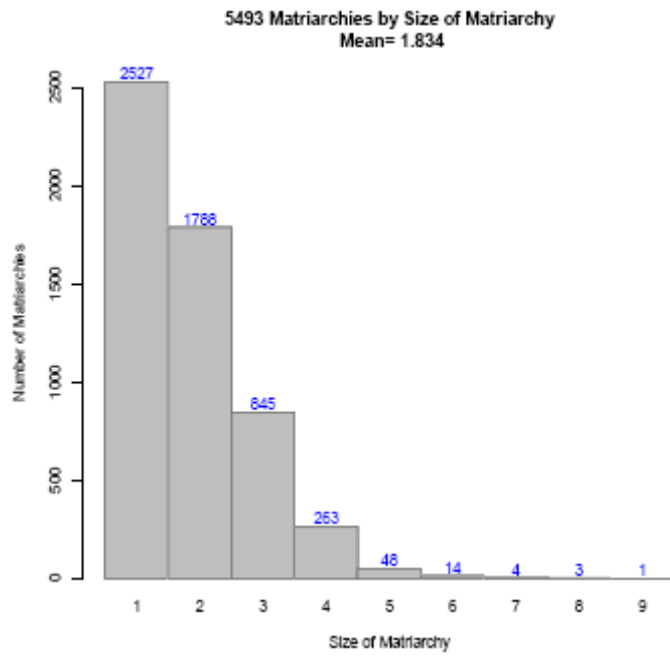


Figure 3B. Distribution by age of the singleton Matriarchal (M) groups

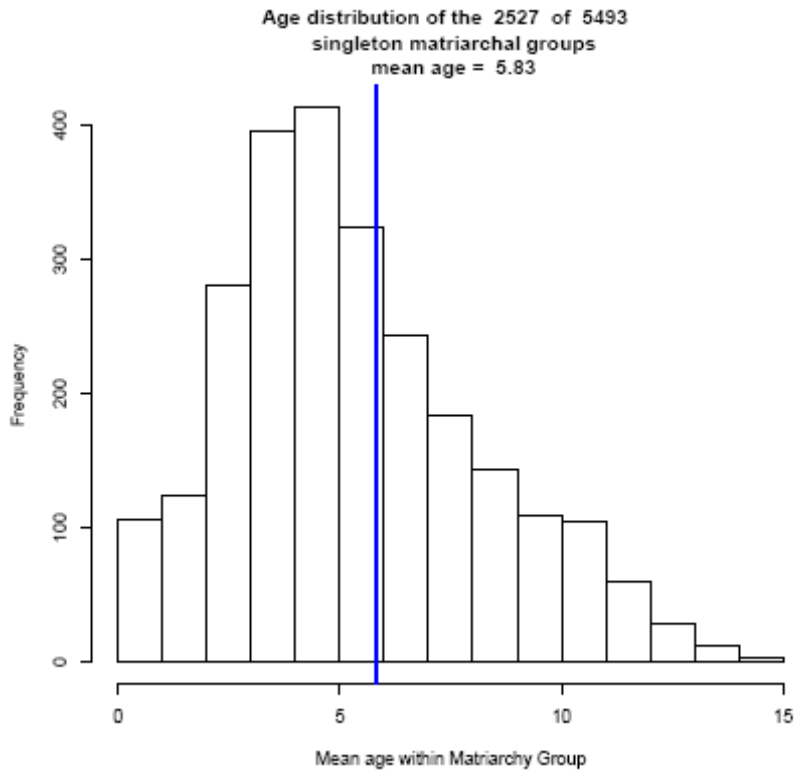


Figure 4. Average production and consumption by age in the simulated population after 15,000 cycles (75,000 years) under matriarchal social arrangements (sim144).

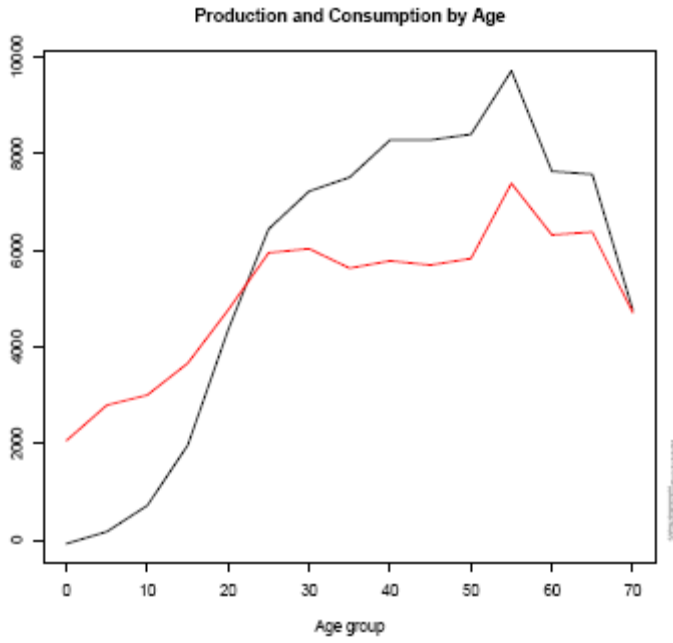


Figure 5. Average gamma by age in the simulated population after 15,000 cycles (75,000 years) under matriarchal social arrangements (sim144).

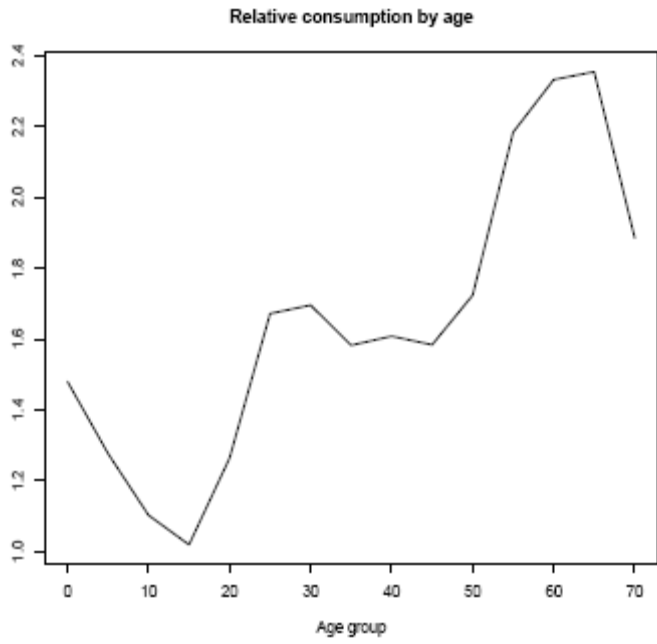


Figure 6. Age specific mortality after 15,000 cycles (75,000 years) for a matriarchal social arrangement. Log of ASDR over the past 500 cycles, with 95% probability interval. Also shown are the Hamilton theoretical mortality schedule, the Transfer theory schedule, and a mix of 20% Hamilton and 80% transfer. (Sim 144).

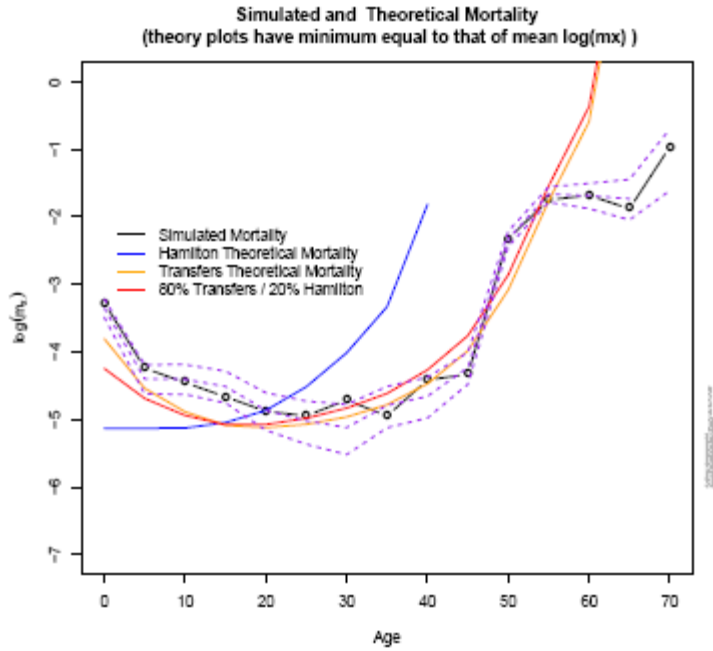


Figure 7. Average size of each kin group for simulated matriarchal population after 15,000 cycles. From bottom to top: M=2, K3= 3.5, K4=4.0 and K5= 4.8. (Sim 141).

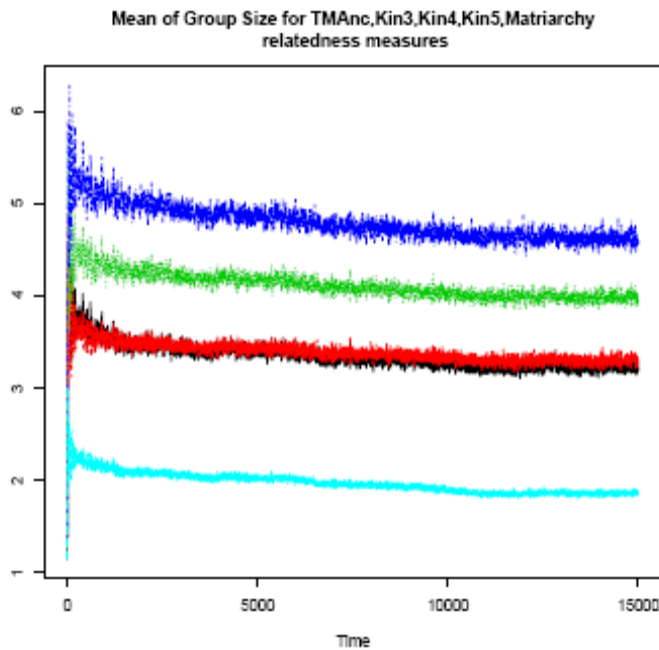


Figure 8. Distribution of kin group sizes according to different definitions after 15,000 cycles. (Sim 141)

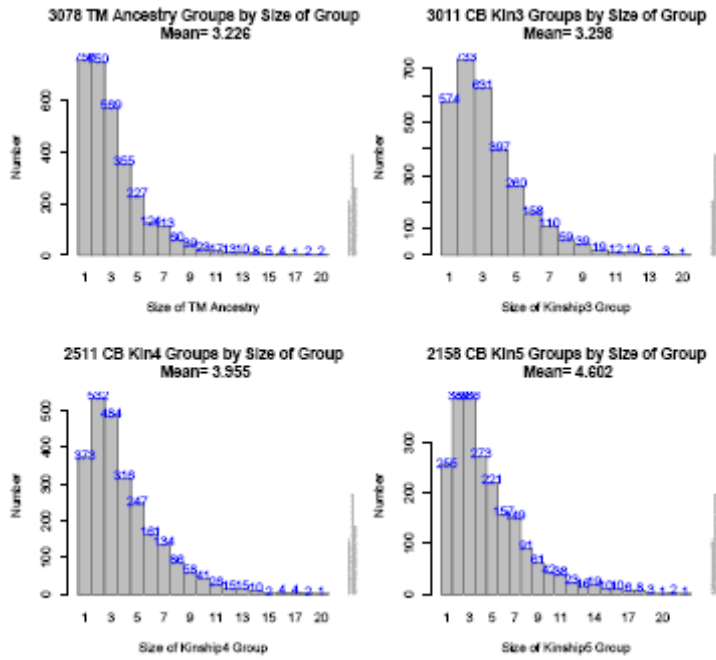


Figure 9. The Distribution of Sharing Groups by Size after 15,000 cycles.

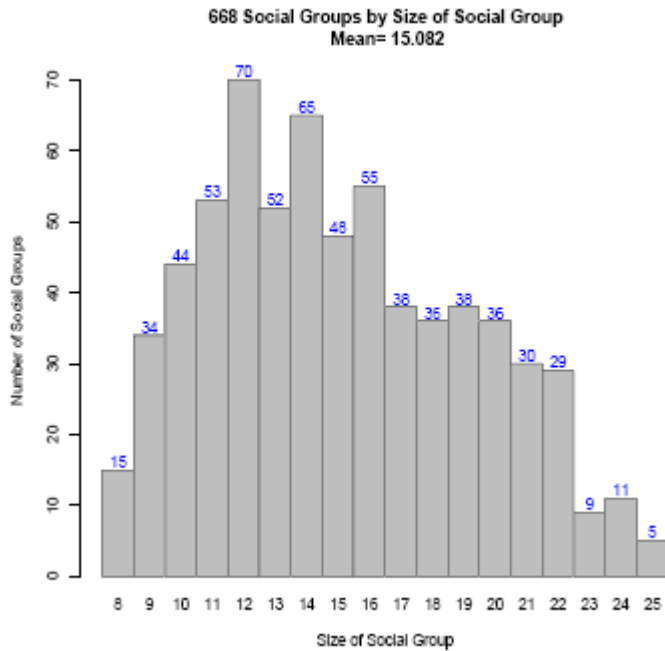


Figure 10. The raw and smoothed frequencies of social group fissioning and fusing over 15,000 cycles. (Social groups vary between 8 and 25 individuals). (sim 144).

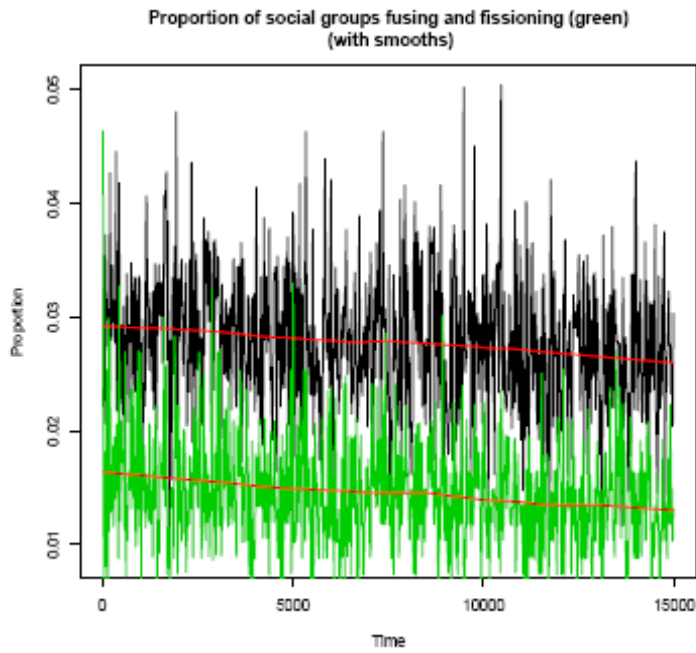


Figure 11A. Distribution of the number of K5 kin groups per 8-25 sharing group after 15,000 cycles (Sim 141).

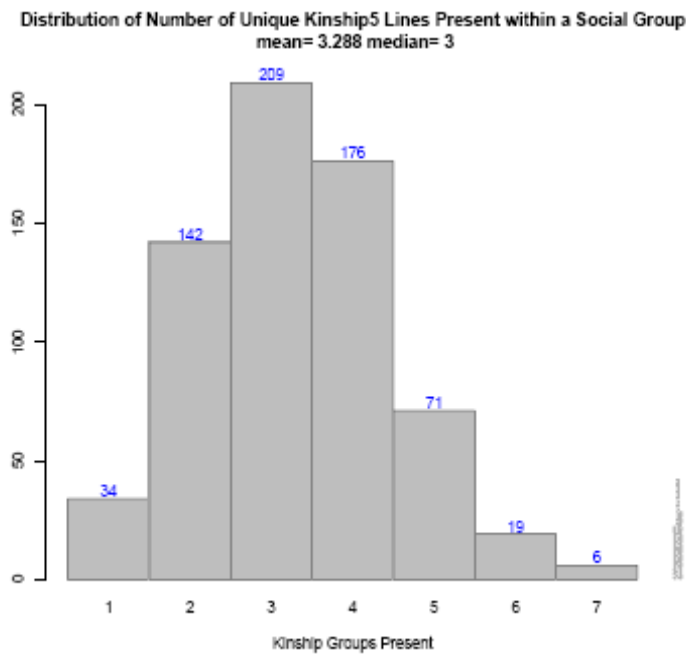


Figure 11B. Level (solid line) and standard deviation (dashed line) of γ by age averaged across all individuals in a population for different social arrangements. M (red); K5 (green); 8-25 Sharing group (black). (sim 141).

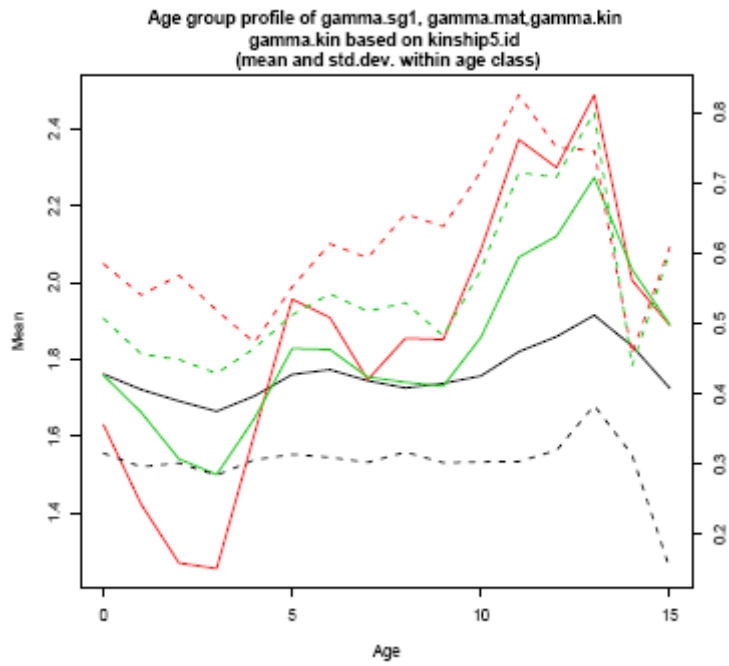


Figure 12. How simulated density, γ and dependency vary across five different social arrangements, ranked by increasing size of group and decreasing degree of relatedness in group.

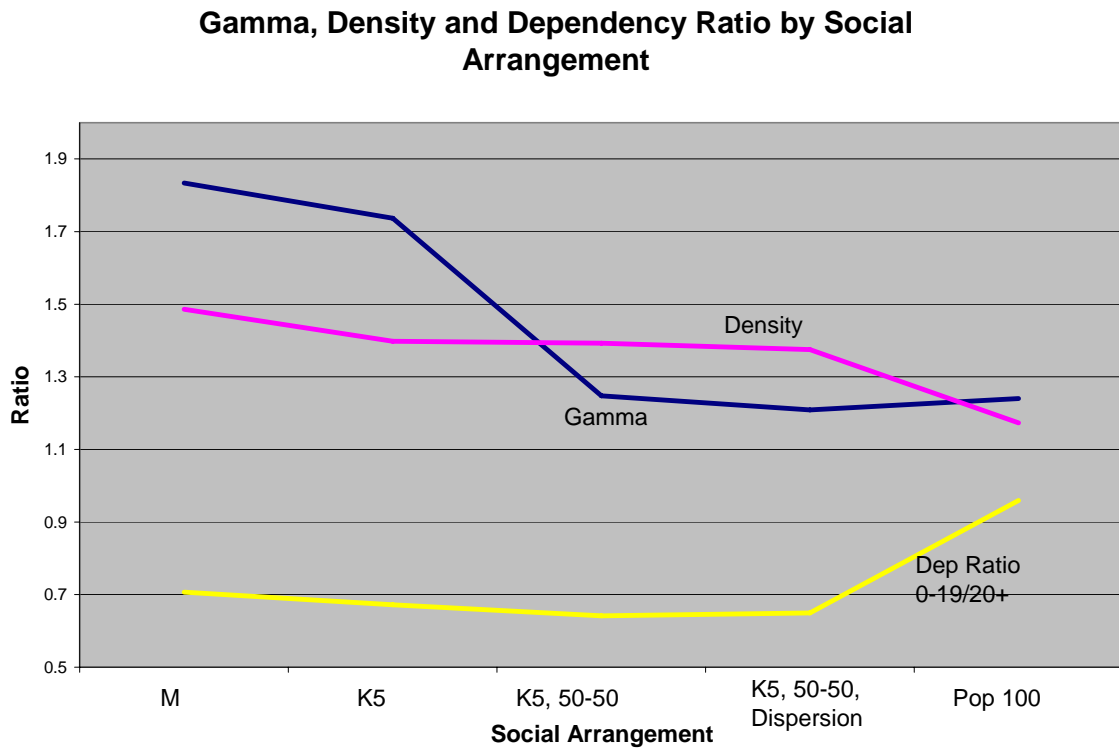
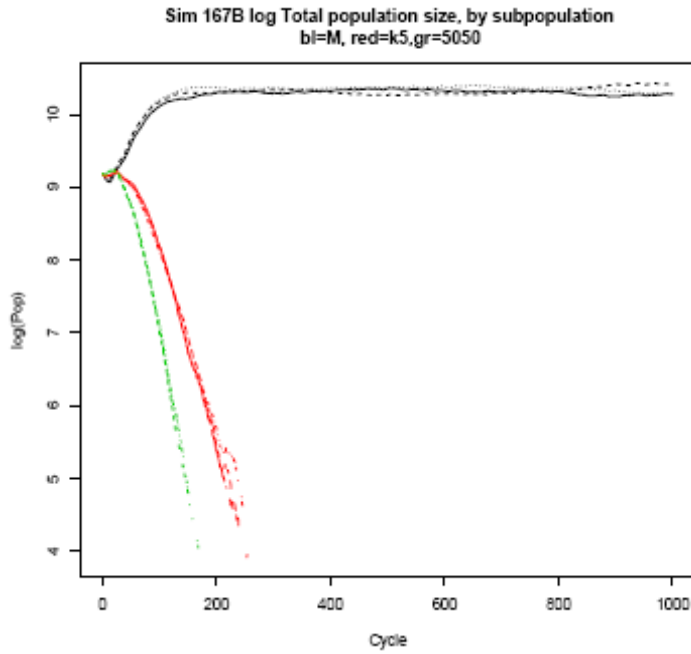


Figure 13. Evolutionary competition among nine subpopulations initially of 5 thousand each, with 3 matriarchal societies, 3 K5 societies, and 3 K5.50-50 societies. Plot shows the log of total population size for first 1000 cycles (5000 years). Initial population age distributions and mutational distributions are taken from evolved states in individual runs for each social arrangement. (sim 167B).



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

Figure 14. Age Specific Production after 0, 5, 20 and 100 cycles by social arrangement. Key: Black=Matriarchy; Red=K5; Green=K5.50-50. (sim 168B).

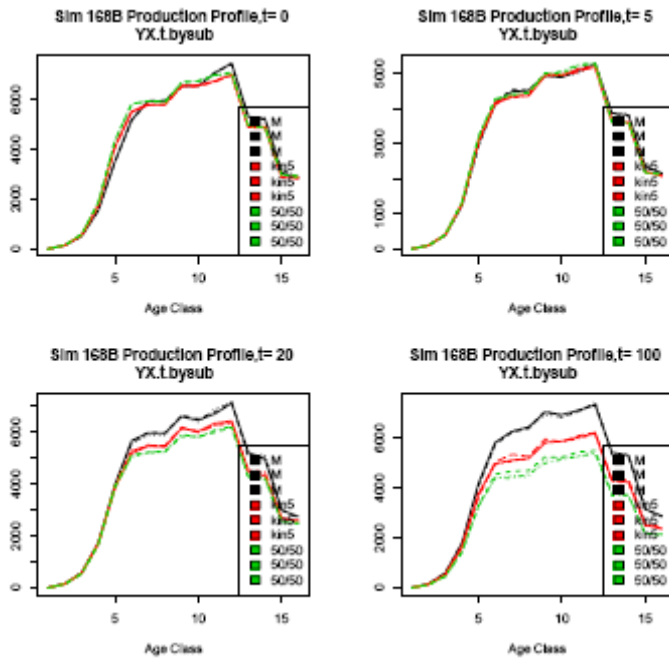


Figure 15. Gamma (consumption level) at 0, 5, 50 and 100 cycles by social arrangement. Key: Black=Matriarchy; Red=K5; Green=K5.50-50. (Sim 168B)

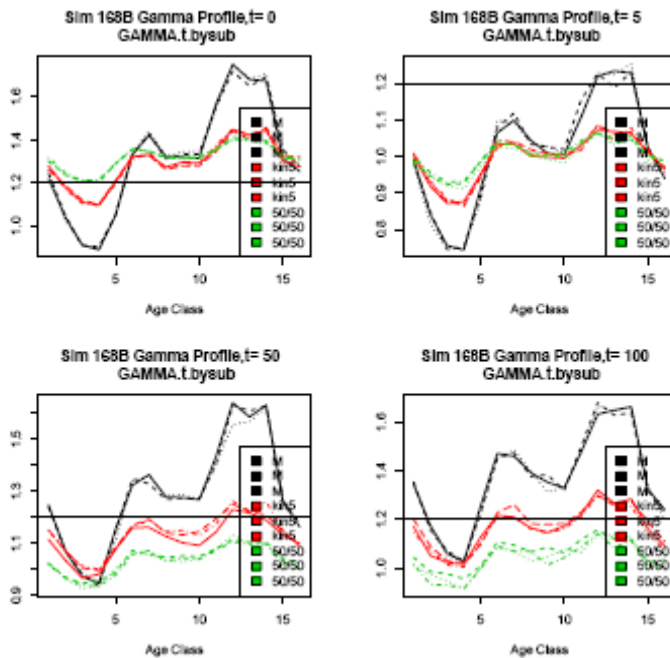


Figure 15B. Evolutionary competition with childhood consumption effect on later life production turned off. Nine subpopulations initially of 5 thousand each, with 3 matriarchal societies, 3 K5 societies, and 3 K5.50-50 societies. Plot shows the log of total population size for first 3000 cycles (15,000 years). Initial population age distributions and mutational distributions are taken from evolved states in individual runs for each social arrangement. (sim 168C).

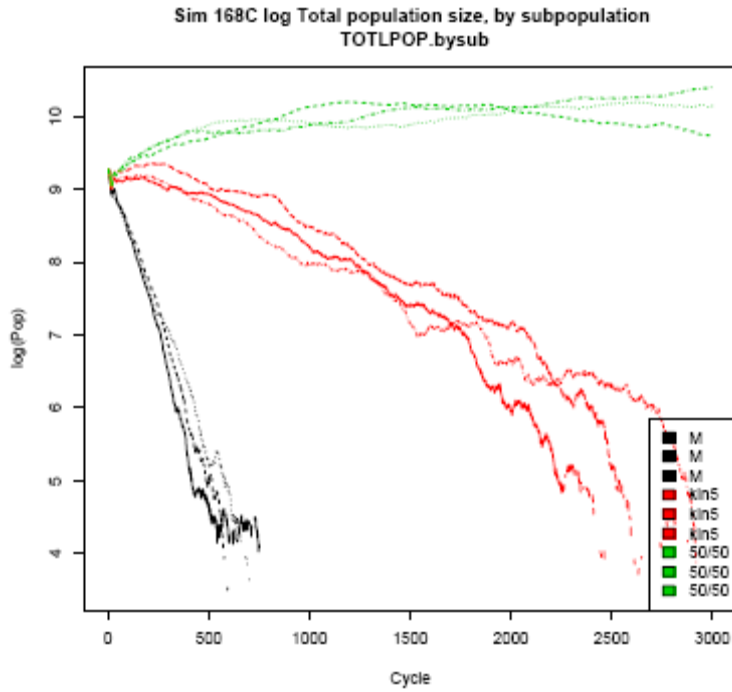


Figure 16. Evolved mortality by social arrangement after 15,000 cycles (75,000 years). (Various sims).

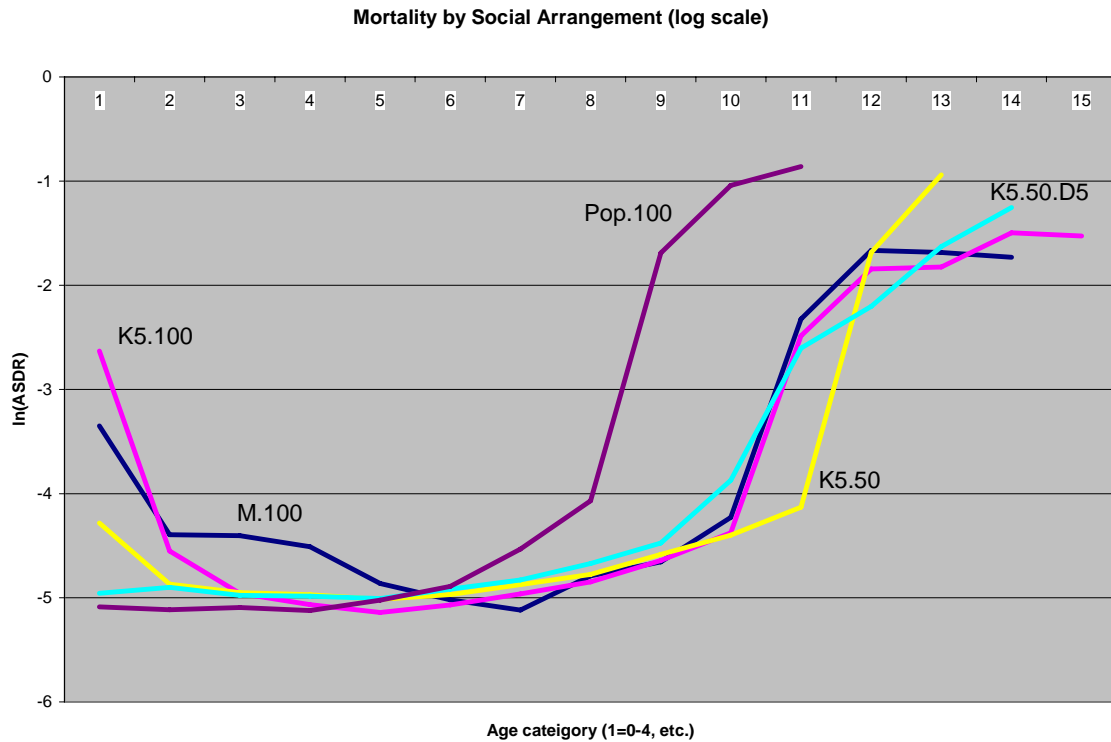


Figure 17. Evolved mortality at age 0-4 by social arrangement

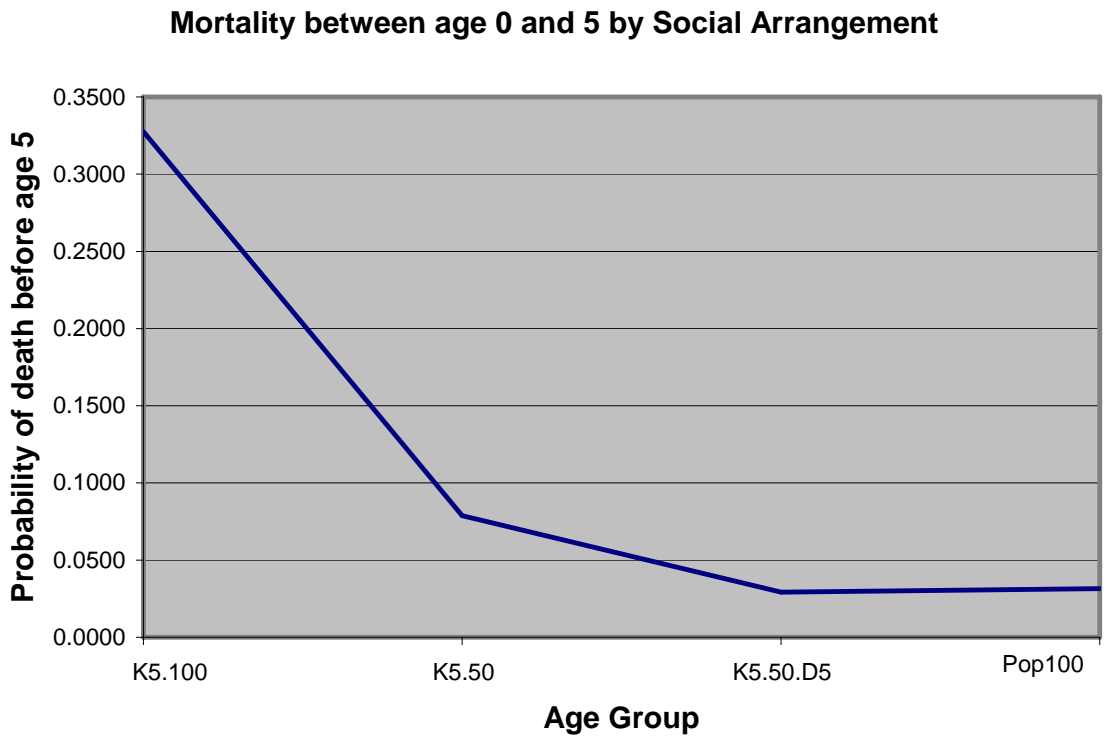


Figure 18. Evolved mortality in 8-25 sharing groups with K5 components based on whether the groups are shuffled every five cycles (D5) and on the extent to which food is kept in the K5 groups (50, 75, or 95 percent). (Various simulations).

