

HUMAN EVOLUTIONARY DEMOGRAPHY

EDITED BY
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18. Sociality, Food Sharing, and the Evolution of Life Histories

Ronald Lee and Carl Boe

Life history theory has focused on the life cycle trade-offs faced by individuals who are constrained by the energy they can forage for themselves at each age. However, humans are deeply social and adults transfer food to children for many years, freeing them from this energy constraint but also bringing the risk that parental death could entail the death of all dependent offspring. Multiple simultaneously dependent offspring also bring a family life-cycle squeeze in which dependency ratio doubles. Food sharing and alloparenting ameliorate both problems, providing life insurance and smoothing the life-cycle squeeze, while permitting humans to rely on food resources that would be too uncertain for isolated individuals. Food sharing and intergenerational transfers in turn affect the way natural selection shapes life histories. We use microsimulations to study evolution of life histories. Births inherit the mother's genome subject to mutations. Individuals live under different social arrangements and forage with productivity depending on population density. Natural selection on life histories occurs. We examine the way the size and relatedness of sharing group arrangements alter the evolution of life history traits through mutation and natural selection. We consider which social arrangements, with their corresponding evolved life histories, are most successful in a group competition where all face the same density constraint. There is a trade-off between costs and benefits of sharing. We find that intermediate levels are most successful, unless childhood conditions strongly influence later life productivity.

Introduction

The life histories of some species might be understood through the constraints and opportunities they face as isolated individuals. In life history theory, an individual starting life allocates whatever energy it can acquire among the competing goals of survival, growth, and reproduction (Stearns, 1992; Urlacher et al, 2018, estimate the survival-growth trade-off for a group of Amazon Basin forager/horticulturalists). Each allocation strategy entails some level of reproductive fitness. The strategy generating the highest fitness would tend to evolve through natural selection. Under some simplifying assumptions, mathematical models find that the optimal strategy invests first in growth and survival, and then at some "age of maturity" switches to investment in reproduction and survival. This life history pattern is called "determinate growth", and it is approximately the strategy of mammals and birds, but generally not of fish and reptiles, or plants.

What about humans? In one sense, the determinate growth story fits us well. But in other ways it misses most of what is unusual and important about our life history strategy. Humans' life histories are deeply enmeshed in familial relationships and in broader social relationships as well (MacDonald and MacDonald, 2010). Like all mammals, a newborn human does not at first forage for its own food, but rather receives it as an intergenerational transfer, in the form of maternal lactation. This enables the offspring to invest much more in its growth and survival, beyond the limits of any meagre food it could have acquired on its own. The intergenerational transfer of food relaxes the constraints that limit the individualistic life history strategy and open up possibilities for slower and longer growth and development. The calorically hungry human brain (Kuzawa et al, 2014) is possible only through such intergenerational transfers (Lancaster et al, 2000; Kaplan and Robson, 2002).

But human parental investments continue for a very long time after lactation ends. In the Ache, Piro and Machiguenga (Kaplan, 1994, Lee, 2000), the Tsimane (Hooper et al, 2015) and the !Kung (Howell, 2010), the average child does not begin to produce the number of calories it consumes until age 18 or 20.¹ The net cost of raising one surviving child from birth to age 20 is around ten years of average consumption (average consumption over ages 0–50; Lee et al, 2002). Since average birth intervals were three or four years, a woman would often have multiple dependent children while her foraging productivity was limited by the energetic costs of lactating and/or carrying young offspring. She could not possibly manage this on her own and required and received help from others beyond her mate, such as single males (Hill and Hurtado, 2009) or grandparents and other older adults (Hawkes et al, 1998; Hawkes, 2003; Hooper et al, 2015). These simple and well-known features of the human life history then go hand in hand with other features of the life history and, particularly importantly, with human forms of sociality (Hrdy, 2009). The fitness benefits arising from different family members, which surely involve contributions of many kinds in addition to food, are critically reviewed by Sear and Mace (2008).

As we will discuss at greater length below, the basic demographic problem posed by the human life history strategy is the long and deep stage of child dependency, which on the one hand runs the risk of parental death wasting the entire prior investment in fitness, and on the other hand leads to a crushing dependency burden at certain life cycle stages even for a fully cooperating parental pair. These problems are solved by human sociality, which in turn may lead to further problems, as will be discussed later. The literature on these and related problems arises partly in the context of evolutionary studies, but also in the study of modern-day societies, and in what follows we will try to link these two contexts.

Age and Economic Roles in Hunter-Gatherer Societies

Figure 1 displays age profiles of caloric production and consumption by age, averaged for the Ache, Piro, Machiguenga² and !Kung (Kaplan, 1994; Howell, 2010), with males and females combined. We see that production first equals consumption around age 20, and that production

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- 1 This is an average of males and females. Tsimane female children become self-sufficient some years earlier than males (Hooper et al, 2015).
 - 2 Hillard Kaplan kindly sent me the data underlying the table in his (1994) paper. After some adjustments (Lee, 2000) the average of these three Amazon Basin groups was then averaged 50–50 with the !Kung data, to give equal weight to the Latin American and African experience. But results for each of these four

continues to rise until a peak around age 50.³ People continue to produce substantially more than they consume, on average, through to the last ages observed (age 65), and we note that in the larger sample of the Tsimane that has a larger sample at higher ages, net production is still positive at age 80 (Hooper et al, 2015, Figure 1(a)).

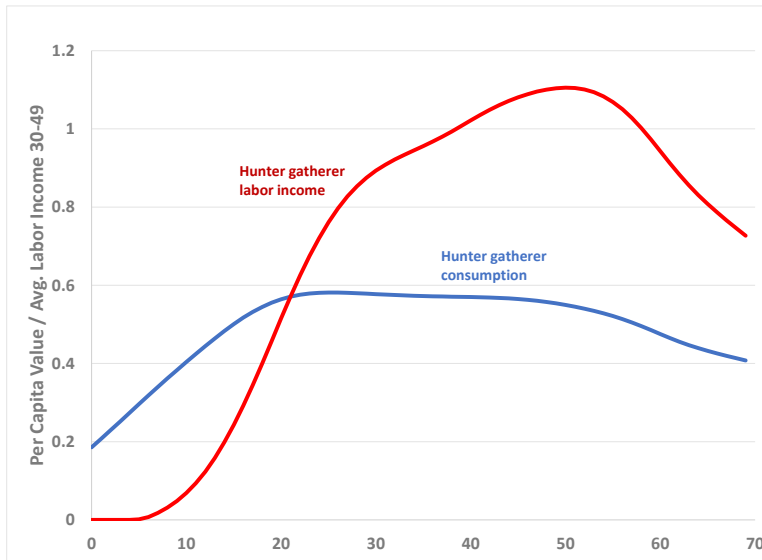


Fig. 1 Age profiles of hunter gatherer production and consumption: averages of estimated profiles for Amazon Basin Ache, Piro, Machiguenga (50%, based on Kaplan, 1994) and Botswana !Kung (50%, based on Howell, 2010).

The first problem posed by the substantial dependency of offspring, as compared to independent newborns who are on their own once born, is that the death of the mother entrains the death of the offspring (Queller, 1994) and the complete loss of the investment in fitness. If this is a problem for wasps (as in Queller) it is a much bigger problem for humans. The solution for insects and for humans is found in reproduction in a larger social group, in which others may take over if the mother or father dies.

The second problem is that the simultaneously dependent offspring place an increasing burden on two collaborating parents up until around twelve to fifteen years after the start of mating. The Russian economist Chayanov (1925/1986) was first to analyse the economic life cycle of the family in this way using survey data from Ukrainian peasants in the early twentieth century. He considered a hypothetical couple marrying at age 20 and having a birth every two years. Combining this pattern of household age composition with age schedules for production and consumption, he found that the ratio of consumers to producers, now known as the “Chayanov ratio”, doubled after fourteen years of marriage. Similar results have been

groups were quite similar, and also quite consistent with the Tsimane age profiles for net production in Hooper et al (2015).

3 Caloric consumption is not completely satisfactory as a measure, because calories derived from fruits and vegetables are not regarded by these societies as being as nutritious as calories derived from meat. Older people may switch from hunting to gathering or horticulture, thereby maintaining a high caloric productivity, but with what may be some decline in nutrition and quality that is not shown on this graph.

found for calculations based on a group of Mayan subsistence swidden agriculturalists (Lee and Kramer, 2002), where the ratio more than doubled by the tenth year, and by Tobin (1967) for the US. In the relatively favourable conditions of the Ukraine, peasants met this rising ratio with increased hours of work, a result known as “Chayanov’s Law”, but in the harsher conditions of hunter gatherers that option would have been more restricted.

However, elder hunter gatherers continue to produce more than they consume on average, and the surplus is transferred to their children and grandchildren, helping to offset the rising dependency ratio — a possibility that Chayanov did not consider. Hawkes (2003) and her collaborators (Hawkes et al, 1998; Volland et al, 2005) have emphasized the importance of the grandmother’s role, while Gurven and Kaplan (2006) find greater contributions from older men, but the contributions of these elders was surely important in any case. Hunter-gatherers achieved further flattening of the rising Chayanov ratio by sharing food within groups of around three to five households and eight to twenty-five individuals containing both kin and non-kin (Binford, 2001; Gurven, 2004; Hooper, 2015).⁴ Of course, this sharing was not perfect, and households shared more generously with the households of others who were related to them, but non-kin participated to some degree as well (Hooper et al, 2015, provide detailed data and analysis). Within these sharing groups the household-to-household variations in Chayanov ratios tended to average out to a more stable level of dependency.

The economic role of children in the household economy is also potentially important. In settled agricultural societies there are safe and productive opportunities for children to contribute to household output. Cain (1977) found that male children in a Bangladesh village broke even by age 12, and Caldwell (1976) argued that the important economic contributions of children motivated parents in agricultural societies to have high fertility. These views have been questioned (Kaplan, 1994; Lee, 2000; Lee and Kramer, 2002; Robinson et al, 2008). In the Mayan subsistence agriculture group children began to breakeven around age 16, and actually contributed around 60% of the total family output from year twenty to year thirty-five of the average marriage, but, even so, the Chayanov ratio more than doubled as reported above. In hunter-gatherer settings, foraging was apparently more dangerous for children, and in any case they were not very efficient workers. Their limited contributions lead to a later break-even age near 20 (Figure 1).

The Evolution of Life Histories

With this background on the nature and importance of human sociality, we will now consider how this social context might have altered the forces of natural selection that shaped the human life history. Hamilton (1966) was the seminal mathematical study linking genetics and mutation to the evolution of the life history through natural selection. In his setup, each birth inherits a genome from its parents, but mutations also occur and each mutation can be thought of as a deleterious error that will raise mortality at some particular age. If a particular mutation raises mortality at an age before the start of reproduction, let’s say at age 11, then this mutation strongly reduces the recipient’s reproductive fitness and it would tend to be strongly

4 According to Binford (2001) hunter gatherers lived, travelled and foraged in these smaller groups during the lean season in each region, while congregating in larger groups of around 500 in seasons when food was plentiful.

selected out of the population. If instead the mutation raises mortality at age 35, when much of a female's potential reproduction is already behind her, it would reduce her fitness much less (in proportion to the small share of total lifetime reproduction remaining after this age), and the force of selection against it would be correspondingly weaker. If the mutation raises mortality at age 50 then, in Hamilton's theory, it would have no effect on reproductive fitness at all and so would not be deselected. Such mutations would accumulate, leading to a rapid increase in mortality after menopause. It seemed to Hamilton that this approach made more sense for mortality, where deleterious mutations might release no energy for other uses, than for fertility, where increases or decreases would entail trade-offs affecting other aspects of the life history. For this reason, we also will focus on mortality in what follows, although we believe that this problem of trade-offs also undermines Hamilton's analysis of mortality in ways that we hope to avoid with our approach — for example, the survival or death of a child affects the resources available to siblings and the parents, thereby indirectly affecting their survival.

In reality, human mortality does not rise explosively after the age of menopause, but rather continues its gradual Gompertzian ascent, and Hamilton recognized that this posed a problem for his theory (see Burger, 2017, on the evolution of human mortality schedules). Hunter-gatherer females have substantial post-reproductive survival, as has been well documented (Gurven and Kaplan, 2007) and as is widely accepted by demographers and anthropologists. According to the grandmother hypothesis (Hawkes et al, 1998; Hawkes, 2003) post-reproductive females continue to enhance their reproductive fitness by assisting their children and grandchildren. A similar argument can be made for older men, as discussed earlier.

Hamilton's theory also implied that mortality following birth would be low and flat until the age of reproductive maturity,⁵ whereas (as he discussed) actual mortality is very high following birth and then declines to a low point near reproductive maturity. This is a second problem for his theory.

Lee (2003) developed a mathematical model that sought to extend Hamilton's theory by incorporating the role of intergenerational transfers of food in promoting fertility and survival, and showed that in this case the force of selection against mutations affecting mortality at any age would be proportional to a weighted sum of the Hamilton effect (the proportion of lifetime fertility remaining) plus a transfer effect (the proportion of lifetime net transfers remaining to be made to kin). If this species makes no transfers after birth, then the Hamilton weight is 1.0 and the transfer weight is zero. In a species making transfers after birth, however, evolution would move the system toward the level of fertility that optimized the quality-quantity trade-off for births, at which point the transfer effect weight would be unity and the Hamilton effect weight zero, as for humans. In this theory, as in the grandmother hypothesis, there is post-reproductive survival because older people continue to enhance their reproductive fitness. Mortality is high at birth because expected net future transfers are zero, with expected future transfers to be received by a baby balanced by expected future transfers to be made by it to its own offspring. But as children grow older, transfers already received increase with no change

5 It is sometimes thought that in Hamilton's theory, evolved childhood mortality should be inversely proportional to Fisher's reproductive value, which would closely match the actual pattern of child mortality, but this is not correct. It should be inversely proportional to the share of lifetime reproduction remaining after each age, and that share remains 100 percent from birth until the age of reproductive maturity.

yet in those to be made in the future, so the expected future net transfers turn positive, and selection against deleterious mutations rises, so mortality falls. This is one explanation for why mortality declines following birth. Another way of putting this is that when an infant dies, all the transfers that would have been made to it in the future are saved and can be used for a replacement birth, so the death is not costly. But when a 12-year-old dies, all that has already been invested in that child is lost and cannot be replaced, so the death is very costly.

This model captures the average effects of intergenerational transfers but it assumes that each sharing group has a stable population distribution, on average. This assumption would be harmless if the consequences of age distribution variations were linear, but they are not. A mother who survives until a child is halfway to independence will not leave half a surviving child, she will leave zero surviving children, for example. The stability-on-average assumption does not incorporate the catastrophic effect of maternal death. Another troubling assumption is homogeneous genetic lineages. The simulation model described next does not require these assumptions. It is also able to incorporate more ethnographic detail for social group living and food sharing.

Modelling and Simulating the Evolution of Life History in a Social Context⁶

The starting point is 100,000 single-sex individuals of different ages who are subject to probabilistic fertility and mortality at five-yearly simulation steps. Probability of death depends on age, genome and food consumption. Probability of giving birth depends on age (according to an initial hunter-gatherer age-specific fertility schedule) and food consumption in the previous five-year simulation cycle. Each birth inherits the genome of its mother (consisting of some number of deleterious alleles raising mortality at each age and setting an initial age schedule of mortality for that birth) but mutations also probabilistically occur, modifying the inherited age schedule by further raising mortality at certain ages.

Individuals live in households that share food. A matriarchal household contains all individuals descended from an oldest single living female, for example a grandmother, her two surviving daughters and the children of each. If the oldest household member dies, this household would split into two new matriarchies under each of the mothers. Food in such households derives from age-specific production (foraging) according to an age schedule like that in Figure 1, and the age-production profile is shifted downwards in inverse relation to population density. An individual's production also depends on her level of consumption in the prior period and on her level of consumption as a young child, which is assumed to influence her adult size, health and vigour. This turns out to be a key feature, and it will be discussed in more detail later.

Based on this treatment of production, each household will have a certain level of total output each simulation cycle. This output is allocated to the household members in proportion to a consumption age profile like the one in Figure 1, the level of which is adjusted so that total household consumption equals total household production. In this way the age composition and dependency structure of the household affects household production and the level of

6 The code in R for the microsimulation program used in this paper is posted at <https://github.com/carlboe/SocEvoSims>. We encourage others to experiment with this simulation program and to modify it for use in different ways.

consumption by every individual, which is the central feature of the simulation. Every individual in the simulation is in this way assigned a level of production and consumption, and the difference between these two indicates a transfer made to others or received from others. The simulation is then run for many five-year cycles, typically over a span of 75,000 years. Because productivity is inversely related to population size, and the population growth rate (through fertility and mortality) depends on productivity, population size converges to an equilibrium level and to a stable age distribution and age schedule of production, consumption, mortality and fertility.

As an aside, here I will briefly discuss the relevance of population equilibration for hunter-gatherer populations. In these simulations, populations do reach a stable equilibrium. The model underlying the simulations incorporates individual-level demographic uncertainty because fertility and survival are probabilistic. However, this form of individual-level uncertainty largely cancels out for population-level outcomes such as population size and age-specific death rates. The model does not incorporate other kinds of uncertainty, such as variation in food availability due to changes in weather or climate, or variation in mortality due to epidemics. Lee (1987:453) incorporated both equilibration and random macro-perturbation in simple population models calibrated to preindustrial human conditions. He found that population size swung widely around its hypothetical equilibrium, with a standard deviation from equilibrium of 7% and with swings away from equilibrium that last hundreds of years. Indeed, a simulated population size series with equilibration looked indistinguishable from another with no equilibration over a simulation period of one thousand years when both were subjected to the identical random shocks. It was only in the next thousand years that they diverged. Thus “the gentle nudge of homeostasis becomes a dominant force in the longer run” (1987:454). The presence or absence of a tendency toward equilibration could only be discerned through studying the mechanisms at work, and not through change or stability total population numbers. For this reason, I disagree with the “forager population paradox” based on observed boom-bust cycles in contemporary hunter-gatherer populations.

The matriarchal social system described above, which we will label “M.100”, is the simplest system simulated. Actual hunter-gatherer societies had larger and more complex food sharing groups as discussed earlier. In other simulated systems, related matriarchal households are grouped together. Here we will emphasize a system in which individuals group together if they are third cousins or closer (have a common great-great grandmother). We label this system “K5.100” because kin groups span five generations. Here and above, the “100” means that the M or K5 groups retain 100% of their output and do not share at all with other groups or households. Another system takes into account Binford’s (2001) conclusion that hunter gatherer sharing groups contained between eight and twenty-five individuals during the lean season. In this system, K5 households are grouped together to form sharing groups in this size range, and in the simulations this means that most of households in sharing groups have no kin ties with other households. We label these SG.K5 for “sharing group composed of K5 households”. As time passes, the groups may shrink below eight members, in which case they fuse with another small group, or may grow above twenty-five in which case they split into two sharing groups. Because food sharing was biased toward own kin in such sharing groups (Gurven, 2004; Hooper, 2015), the share of food placed in the common pool by each K5 group can be specified, and here we report results for SG.K5.50 which indicates that 50% of each household’s output is kept within it, with the remainder placed in the common pool of the sharing group. In some

variations there is reshuffling of the K5 components of a group every five years, indicated by a “D” for dispersion. This is intended to reflect the fact that membership in sharing groups is in fact fluid, and also that young adults would often leave the group to join a mate.

A reviewer suggests that it would be interesting to make the dispersion and reshuffling non-random. The reviewer points out that hunter-gatherers like to be in groups with good hunters, e.g. Ache (Wood and Hill, 2000) and Hadza (Wood, 2006) and with cooperators (Apicella et al, 2012). At the same time, since both the man and the woman in a couple want to live with their own kin (Dyble et al, 2015), sorting into groups based on genetic relatedness is limited. Our model has only one sex, and within each kind of social arrangement simulation, all are equally strong or weak cooperators. But there is heterogeneity in hunting ability arising from childhood nutrition, and sorting into groups based on hunting ability would certainly lead to the kind of positive feedback loop that we will discuss later.

Social Sharing and the Evolution of Age-Specific Mortality

With this background, consider Figure 2 which plots the long-run equilibrium evolved age schedules of mortality,⁷ averaged over the last 300 years at the end of the 75,000-year simulation period⁸ for different social arrangements. Experiments find that the same schedules evolve every time, over multiple trials, and that nearly identical mortality schedules evolve regardless of the initial mortality-age schedule assumed, including completely flat age schedules. All these average simulated age schedules have very tight confidence bounds, which are not shown.

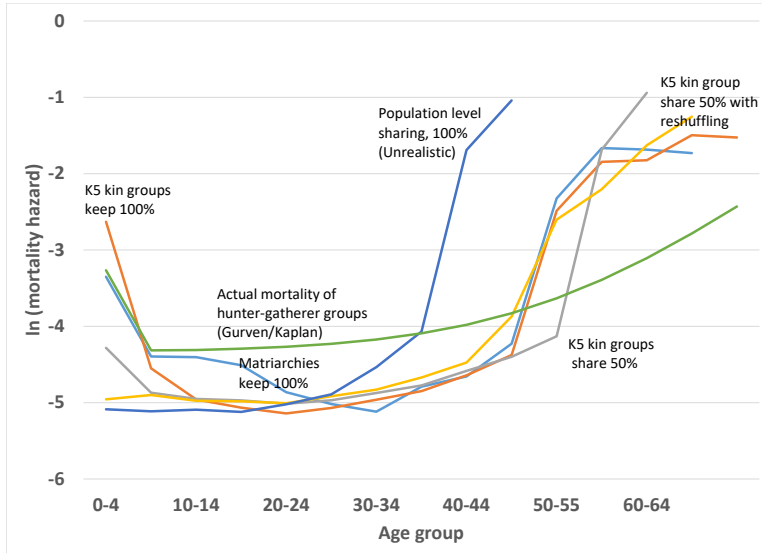


Fig. 2 Evolved mortality under different social arrangements after simulation runs 15,000 cycles (75,000 years), and contemporary hunter-gatherer mortality (Gurven and Kaplan, 2007, Siler fitted curve). Line of age-specific death rate plotted at midpoint of 5-year age group.

- 7 These are not strictly speaking equilibria, because at the highest ages mutations continue to accumulate despite the weak selection against them, but for practical purposes we may think of them as equilibria.
- 8 Averaging smooths out the jaggedness in cycle-to-cycle age schedules, which arises from randomness and the size of the simulated populations.

Note: “Actual mortality” is calculated from the parameters of the Siler curve for average non-acculturated hunter-gatherers given in Gurven and Kaplan, 2007, p. 327. K5 indicates all group members are at least third cousins. A matriarchy group contains all descendants of a single living female. Reshuffling indicates that the K5 components of a group are shuffled every five years. Keep or share refers to the proportion of a kin group’s output that is kept in the kin group rather than shared with others.

We can begin with the Pop.100 simulation which assumes a completely unrealistic social system in which 100% of output is shared with the total population. This simulation leads to the Hamilton (1966) outcome with almost no post-reproductive survival and low and flat infant/child mortality, as discussed earlier. The reason is that with universal sharing, there is no fitness advantage in any given female surviving past menopause since her offspring would be fed by the total population in the event of her death. By the same token, the rising expected net future transfers by older children do not lead to lower mortality, because they have no impact on the fitness of these children through kin selection. Kin selection is taken out of the picture by universal food sharing. This case is a convenient benchmark and deviations of simulation outcomes from this benchmark case will reflect differences in food sharing rules.

It is instructive to note that the Pop.100 system achieves perfect sharing, completely eliminating the life-cycle squeeze and providing complete life insurance since in the event of a mother’s death her children will be provisioned like all other children. Yet here we see that there is a downside to this complete sharing, because natural selection is unable to act on individual mortality variation, and consequently post-reproductive survival cannot evolve. As we shall see later, this means that Pop.100 leads to a chronically unfavourable dependency ratio, and equilibration at a low population density. As a result, this social arrangement would be vulnerable to deselection in intergroup competition.

The M.100 simulation corresponds most closely to the setup in Lee (2003). In it, matriarchal households retain 100% of their product, sharing none with other households. Mortality starts high at time of birth. One way to think of this is that if an infant dies, all the food that would have been used to rear it can now instead be used to feed siblings and the mother, the mother can soon get pregnant again, and the resource cost of the child death is consequently very low and has little impact on reproductive fitness. Mortality then declines from birth to a low point around age 30, after which it rises. This is quite different than a modern mortality-age schedule, but it is more consistent with the mortality patterns of hunter-gatherer groups studied over the past half century as summarized and analysed by Gurven and Kaplan (2007, Figures 2 and 10). They found that mortality remained quite low through mid-adult years until beginning a rapid rise at around age 40, after which it doubled every eight or nine years. Nonetheless, they find substantial post-reproductive survival. Remaining life expectancy at age 45 averages 20.7 years across hunter gatherer groups (Gurven and Kaplan, 2007:327), somewhat higher than in these simulation results.

There is an interesting bulge in M.100 mortality at ages 10–14 and 15–19. This reflects the reduced consumption during the family life-cycle squeeze when a mother and perhaps grandmother must also feed a number of children without help from a broader kin group. Put differently, this bulge is due to economic circumstances, not to a bulge in accumulated mutations affecting these ages, and therefore not heritable.

In the K5.100 simulation we see that infant mortality is even higher than in the M.100. The future resources freed by the death of child can be captured even more efficiently by the other kin, so the resource costs of the child death are even lower in this case, and the mutations leading to higher infant mortality are only weakly selected out of the population. However, starting at ages 5–9 the K5.100 mortality is lower than the M.100, because the family life cycle squeeze is much reduced by the larger size of the sharing group, and also because if the mother dies, other kin are available to raise her surviving offspring — the life insurance effect. After age 15–19, however, the M.100 and K5.100 are very close. Why does mortality at 60–64 and above flatten out in the M.100 and K5.100 results? We believe it is because at these higher ages it is more likely that surviving older women will have grandchildren in whom to invest, so selection against mutations promoting their death is stronger.

The SG.K5.50 groups are larger, with 8 to 25 members, consisting of multiple unrelated K5 families. These families keep half their output and put half in a common pool for broad sharing. In this case infant mortality is very much lower with less than one tenth as many accumulated harmful mutations affecting this age than in the K5.100 groups. Selection is stronger against these infant mortality mutations in the SG.K5.50 because when an infant dies the family recaptures only half of the food that would have fed this child in the future. The other half would have come from the common pool, and it is mostly lost to the family.

From age 25–29 to 45–49 mortality for M.100, K5.100 and SG.K5.50 is very similar. At 50–54 the SG.K5.50 mortality is much lower than the others, probably due to a greater likelihood of surviving related offspring to care for. Thereafter it is higher, perhaps because of the greater availability of other surviving elders to care for the dependent offspring, so the survival of any particular individual elder is less important.

The final social arrangement in Figure 2 is SG.K5.50.D, in which the K5 components of a larger sharing group are reassigned to these sharing groups every five years. This would only matter if the unshuffled groups were more highly interrelated than the shuffled ones, and we see in Figure 2 that this is indeed the case. The shuffled ones have much lower infant mortality because a far smaller portion of the resources released by an infant's death is recaptured by the kin group with shuffling. There are also differences above age 45–49, but the explanation is not clear.

Social Sharing and the Evolution of Other Aspects of Population and Life History

Although the genome in this simple model only directly affects age-specific mortality, it nonetheless has indirect effects that reverberate through the population and the life history. For example, when a broader sharing group bears half the costs of raising a child, then we would expect that natural selection would lead not only to lower infant/child mortality, as we saw above, but also to higher fertility, both through a kind of evolved (non-behavioral) free riding, other things equal.

Panel (a) of Figure 3 shows, for three simulations for each of M.100, K5.100, and SG.K5.50 (nine in total), the ratio of consumption at each age to the levels shown in Figure 1, after 500 years of simulation when these have stabilized. For each social arrangement the three simulations lie close together, showing that the results are consistent and systematic. In every case, average consumption is low at ages 5–9 to 15–19, when the dependency ratio (Chayanov

ratio) is unusually high, but the contrast between these younger ages and the later adult years is greatest for M.100, because in this case many adults end up with no surviving offspring with whom to share. This is much less true for the K5.100 group in which the life cycle squeeze is diluted by a larger kin group with a more diverse age distribution, and even less true for the K5.50 group with broader sharing among K5 groups.

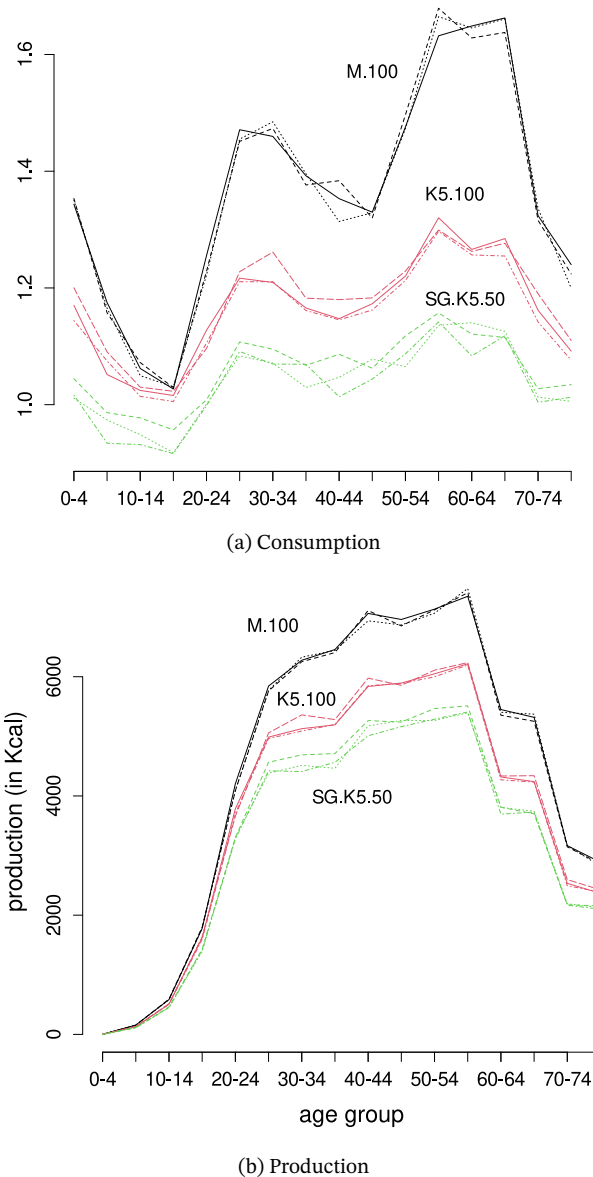
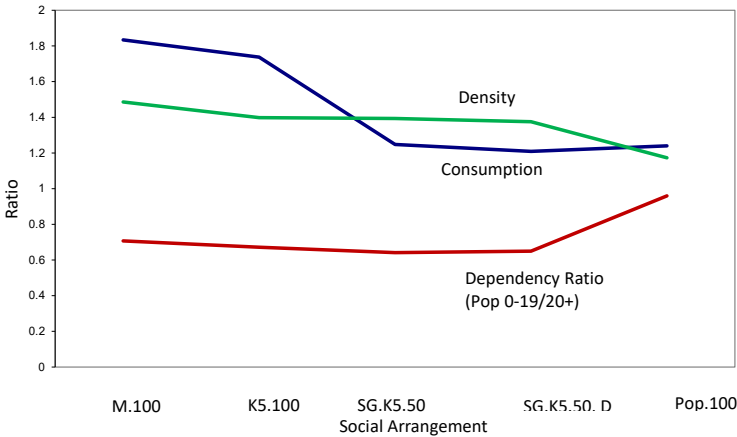
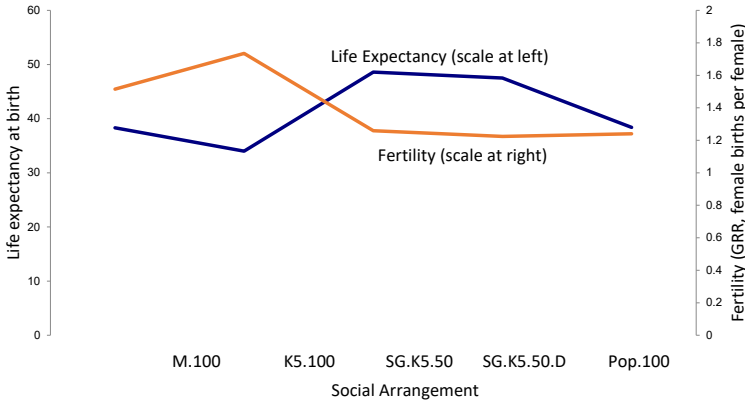


Fig. 3 Average age profiles of consumption and production by social arrangement. Consumption is expressed as a ratio of the age profile in Figure 1 and production is expressed in Kcal.

At the same time, it is striking that the average level of consumption is far higher in the M.100 group than the others, and the SG.K5.50 with broader sharing has the lowest consumption levels. Panel (b) of the figure shows the evolved level of production by age in the same way, which is clearly highest for the M.100 arrangement and lowest for the SG.K5.50. Why should consumption and production be highest in the M.100 group with the narrowest food sharing and closest relatedness? One possibility to consider is that the population density of this arrangement is lower, resulting in higher productivity and therefore higher consumption, a possibility we now consider.



(a) Density, Consumption and Dependency



(b) Life Expectancy and Fertility (GRR)

Fig. 4 Other outcomes by social arrangement.

Note: In Panels (a) and (b), Social Arrangements on the horizontal axis are arranged from least to most food sharing with less close kin or farther to right with non-kin, so the lines indicate the effect of food sharing on long-run equilibrium-evolved outcomes. In Panel (b), fertility is measured by the GRR or Gross Reproduction Rate which is lifetime female births per female. The simulated populations are in equilibrium with growth rates very near zero, so differences in fertility and life expectancy must be offset.

Figure 4 shows long-term equilibrium outcomes by social arrangement, with the arrangements listed on the horizontal axis in order from sharing in a narrowly defined highly interrelated group to a broader less interrelated group. Although the arrangements are categories, we plot the results as lines because with this ordering or categories it is easiest to see the association of outcome with sharing/relatedness. We see in Panel (a) that equilibrium population density is highest for the M.100 group and lowest for Pop.100. Nonetheless, consistent with Figure 3 (a), consumption is highest for the M.100 group. Clearly the explanation proposed just above is incorrect, since density is actually highest for the M.100 group, which in itself would reduce its level of consumption and production, other things equal. We also see that the dependency ratio for M.100 is slightly higher than that for K5.100 and SG.K5.50 which in itself would also lead to lower consumption.

In Panel (b) we see that fertility is highest for K5.100, but is also quite high for M.100 in contrast to broader sharing arrangements. Life expectancy varies inversely with fertility because in equilibrium the population growth rate is zero, and the Net Reproduction Rate must be 1.0. The outcomes shown here are interesting but they do not explain the patterns observed in Figure 3, so we now consider a different and unexpected possibility.

Recall that the simulation model assumed that the childhood consumption level had a positive effect on later-life productivity, through the well-established effects of early childhood wellbeing on later-life outcomes. Similarly, adult consumption levels affect adult productivity in the next cycle. These are features of the model for all social arrangements, but they turn out to favour the M.100 group precisely because its narrower sharing base makes consumption outcomes more variable. Sometimes a child's mother dies, and then it consumes little or nothing and dies too. But other times a child has a surviving mother and a surviving grandmother, and everyone in the family eats exceptionally well. In this case the child grows up to become a strong producer who can feed her own children better and survive better, and this efficient production continues with positive feedback since her children are consequently better fed. The broader social sharing in K5.100 and even more so in SG.K5.50 reduces this variability in consumption and thereby reduces the chance of entering the positive feedback loop. Variance can be good! And stable mediocrity can be bad.

Figure 5 presents box plots displaying the dispersion of consumption by social arrangement, assessed in the standard group selection simulations (which will be explained below in reference to Figure 6 (a)) after 2,500 years (500 cycles) of simulation. Although we started with M.100, K5.100 and SG.K5.50, by 2,500 years the three SG.K5.50 groups were extinct so the figure only compares the M.100 and K5.100. It shows box plots for six simulations, three for each social arrangement. The horizontal line gives the median, the box indicates the interquartile range (from 25th to 75th percentiles), the top and bottom lines indicate the 75th and 25th quartiles plus and minus 1.5 times the interquartile range, and the circles indicate outcomes outside that range. We see that there are many more circles outside that range for M.100 consumption than for K5.100, reflecting the greater smoothing of consumption variation in the K5.100 arrangement.

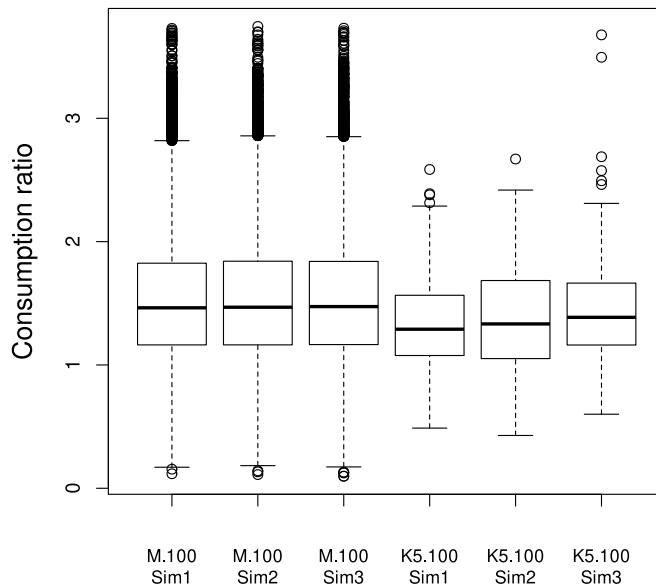


Fig. 5 Dispersion of individual child consumption outcomes after 2,500 years (500 cycles) of simulation according to social food sharing arrangement, M.100, K5.100 and SG.K5.50. However, by 500 cycles all three SG.K5.50 simulated populations had gone extinct, so are not shown here.

Note: Child consumption is measured as a ratio to the level of consumption in Figure 1 within a family unit (M or K5). The box shows the interquartile range (Q2 to Q3) and the horizontal line in the box is the median outcome. The vertical lines outside the boxes extend to 1.5 times the interquartile range above and below the upper and lower edges of the box. The circles fall outside that range. The boxes for M.100 are considerably longer than those for K5.100, and many more points fall outside the range of the vertical lines, showing that the distribution of child consumption in M.100 is much wider than for K5.100.

We will pause here to consider the plausibility of this unforeseen process. Among actual hunter-gatherers there is a great deal of heterogeneity in ability, and some of this might result from childhood conditions. A study found that among Ache hunters at the age of peak productivity (around age 40), the worst hunters got zero on 70% of days they hunted and the best hunters on only 30% of their hunting days (Koster and McElreath, 2014:117). There is a vast literature on the effects of childhood environment on later health, education, and wages. Perhaps most relevant and most persuasive are studies of long-term outcomes based on earlier randomized childhood interventions. One such study (Parker and Vogl, 2018) of the PROGRESA contingent cash-transfer program in Mexico found that wages were 50% higher for girls in households that had earlier received the randomized cash transfer, while the effect for males was the same size but was not statistically significant. Another study (Hoddinott et al, 2008) found that a randomized nutritional intervention program in Guatemala boosted men's wages by 46% decades later. These studies make clear that improved childhood conditions can lead to big increases in later productivity. However, it is not clear how to translate such findings into the context of hunter-gatherer children raised with higher levels of consumption. Nor is it clear what upper limits there may be to the size of such effects, but evidently a 50% increase is possible, and that is large. The simulated mean differences in productivity levels in Figure 3 (b) are certainly less than 50%, but those also reflect other factors such as population density.

Natural Selection at the Level of the Individual and the Group

The idea that natural selection operates simultaneously at many different levels, including group selection, has gained wider acceptance in recent years (Boyd and Richerson, 1990; Richerson and Boyd, 2004; Nowak, 2006; Okasha, 2009). Cultural evolution has also increasingly been recognized as an important process in humans and other animals (Cavalli-Sforza and Feldman, 1981; Whiten et al, 2017). Here we will ask which of the social arrangements we have described would prevail if they coexisted and foraged in the same environment, subject to the same overall population density effect on their foraging productivity, but without any other form of interaction. Assuming that somehow these sharing arrangements came into existence through cultural or biological evolution, which would be most successful?

The social arrangements we have considered differ by the size and stability of the group within which food is shared and by the closeness of kin with whom food is shared. Such different arrangements could either reflect genes or cultures. In head-to-head competition through their shared population density, some groups will do better than others. Under stable environmental conditions, the winning social arrangement would be able to equilibrate at a higher density than the other groups which would then have negative growth rates and eventually die out.

We implemented this idea by running nine concurrent simulations, three each for populations with M.100 social arrangements, three with K5.100, and three with SG.K5.50. All nine groups are assumed to forage in the same area and therefore the productivity of foraging in each group is affected by the total population size (sum of the nine individual simulated populations) and overall density, updated at each simulation cycle. Simulating three populations for each social arrangement helps us to assess whether outcomes are systematic and not accidental. The groups able to equilibrate at the highest density will win out as the others decline toward extinction.

Figure 6 plots the log of population size against time measured in cycles for each of nine simulations. Panel (a) shows the standard model specification which includes the effect of childhood consumption on later life productivity. The outcome is opposite to our expectations, although it was foreshadowed by the densities shown in Figure 4 (a). The M.100 arrangement quickly and completely dominates K5.100, which in turn dominates SG.K5.50. This outcome reflects both evolutionary processes within each social arrangement and also group selection operating on each of the nine simulated populations as they compete through their abilities to sustain themselves at each density. Looking closely at the first cycles shown in Panel (a) we can see that M.100 does worse than the other specifications for the first 100 years or so as expected, because the other arrangements do benefit from broader sharing in a larger group and from the life insurance that protects child survival. But thereafter the M.100 populations grow.

Why does M.100 win? Recall our earlier discussion of why the M.100 arrangement achieved a greater equilibrium density than other arrangements in Figure 4 (a), due to the greater variability of childhood consumption across families and its effect on later life production. To explore this effect, we turn off the child-consumption-productivity feature of the simulation model. The new result is shown in Panel (b). Now M.100 goes quickly to extinction as originally expected, while the broadest sharing arrangement, SG.K5.50, triumphs completely. Evidently the surprising success of M.100 in group competition is indeed due to the effect of child consumption on productivity. The greater variance combined with nonlinear positive feedback help the M.100 to recoup its early losses and dominate the others.

In a series of experiments, of which two are shown in Figure 7, we limited the boost to adult production that could derive from elevated consumption in childhood. Panel (a) shows that with a limiting factor of 1.35 the M.100 arrangement continued to win out decisively. However, with a slightly lower limiting factor of 1.25, the SG.K5.50 social arrangement won out decisively. The tipping point is evidently close to 1.30. These experiments and the literature reviewed earlier suggest that variability in child wellbeing could perhaps have conferred some evolutionary advantages for hunter-gatherers in the past through non-genetic inheritance of nutritional status and productivity.

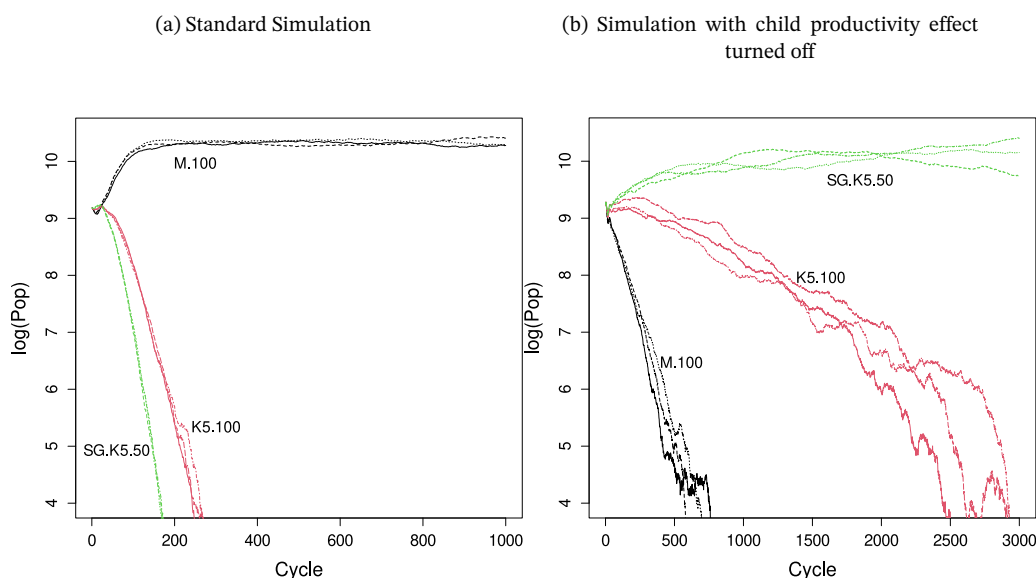


Fig. 6 Evolutionary competition among nine simulated subpopulations initially of 5,000 each, with three each of M.100, K5.50 and SG.K5.50. Plot shows the log of total population size for first 1,000 cycles (5,000 years). Initial population age distributions and mutational distributions are taken from evolved states in individual runs for each social arrangement.

Key: Black=M.100; Red=K5.100; Green=SG.K5.50. For definitions of M=Matriarchy, K5 and proportion shared (here 100% or 50%), see Note to Figure 2 or the text.

Sociality in the Modern World: The Family and the State

We have explored how different social settings alter the way that natural selection shapes the evolution of mortality and may lead to post-reproductive survival in the hunter-gatherer setting. These results depend on the shapes of the age profiles of production and consumption that are assumed in the simulations. In particular, the evolution of post-reproductive survival derives from the empirical finding by anthropological studies that on average, adults at all ages produced more than they consumed, including in old age. For hunter-gatherers, longer life and higher proportions of elderly were beneficial because elders helped with the costly task of raising the young through their long period of dependency.

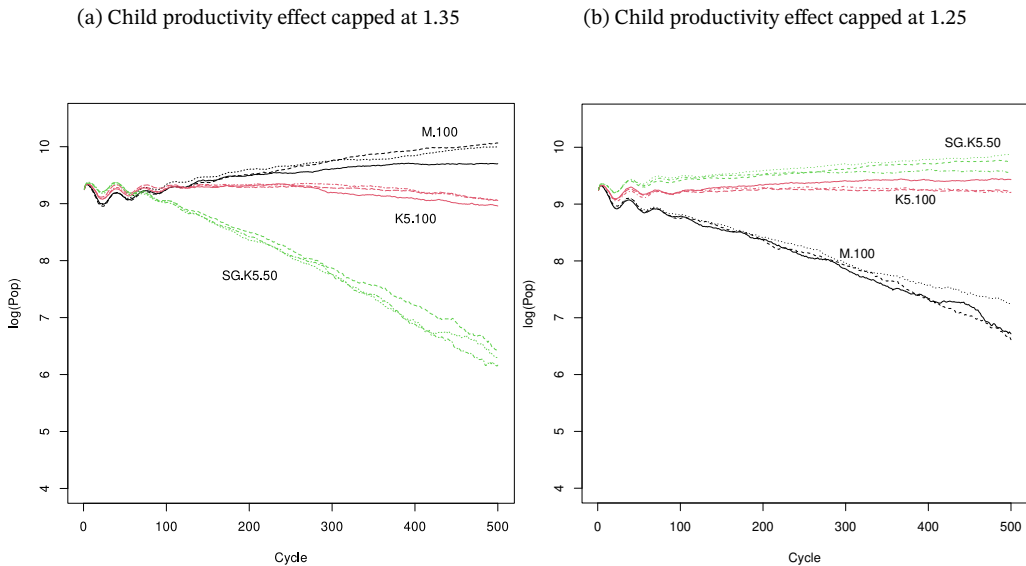


Fig. 7 Evolutionary competition among nine simulated subpopulations when effect of child consumption level on production is constrained to be no greater than a) 1.35 or b) 1.25. Populations are initially 5,000 each, with three each of M.100, K5.50 and SG.K5.50. Plot shows log of total population size for first 500 cycles (2,500 years). Initial population age distributions and mutational distributions are taken from evolved states in individual runs for each social arrangement.

As societies moved toward settled agriculture and developed property rights in land and dwellings, the elderly came to control valuable assets. Perhaps for this reason, age patterns of labour changed dramatically, altering the shape of the economic life cycle as older people reduced their hours of work and came to rely on transfers from their children to support their consumption. This is seen in the National Transfer Accounts (NTA) data (Lee and Mason et al, 2011) for low-income agricultural countries. In Figure 8, to facilitate comparison of the shapes of the age profiles across groups, each profile is divided by the average level of labour income in its group between ages 30 and 49. As shown in Figure 8, in low- and lower-middle-income countries labour income drops below the level of consumption by age 59, and thereafter older people consume far more than they produce. Nonetheless, they earn asset income as a return on the farms or other property they own, even if it is the labour of their children or other younger people that makes those assets productive. (Consumption here includes public transfers of goods and services such as health care and public education, but not public pensions because these are just income and need not be consumed.)

Figure 8 also shows the average labour income and consumption profiles for a group of rich industrial nations. Labour income is even lower in old age than in the lower income group, and consumption which had been flat or falling with age there is strongly rising in the rich countries so that the gap has greatly expanded. The rise of the welfare state, with its high and rising level of public transfers to the elderly for pensions, health care and long-term care, has played a big role in these changes, particularly in the relative increase in consumption at older ages.

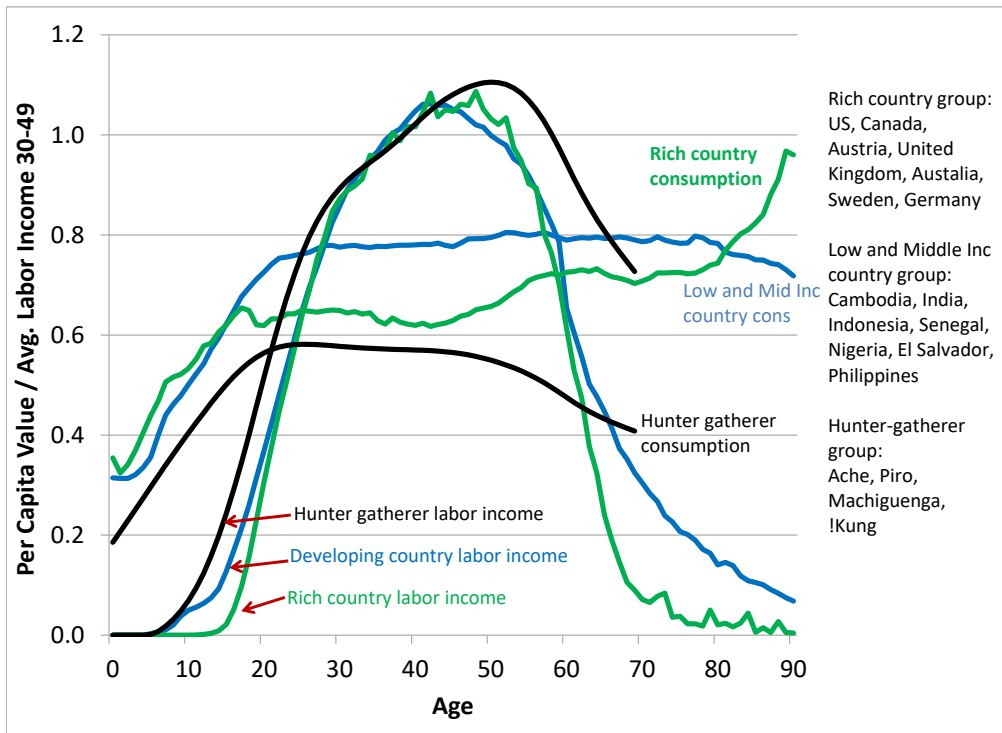


Fig. 8 The hunter-gatherer economic life cycle compared to rich and lower-income countries. Source: Hunter-gatherer age profiles are same as Figure 1. The other age profiles are calculated from National Transfer Accounts data: ntaccounts.org (see text).

Post-reproductive survival and old age most likely evolved in humans to improve the dependency ratio and help to provision and care for dependent children. It is ironic that population aging in the modern world has turned into a great cost due to altered economic behaviour of the elderly. Until the last few decades income flowed downward within virtually all societies, from older to younger ages. The average age of earning labour income was always many years greater than the average age of consuming. The public sector was small, as were pensions and publicly provided health care, and it was through the family that income was transferred to children in the form of consumption goods. This pattern persists everywhere, in that familial transfers still do flow downward in all countries of the world (Lee and Mason et al, 2011). In the rare countries where families do provide net support to the elderly, this support is dwarfed by the transfers to children. Although net familial transfers remain downward to children, public transfers have begun to flow upward in many countries, and in a growing number of countries the net direction of total transfers, public plus private, is now upward. This is a sea change, and it points to the need for very large adjustments to public policy and individual behaviour as populations age.

Discussion

Sociality and intergenerational transfers bring evolutionary advantages as we have discussed. But they also alter the forces of natural selection acting on life history traits. The matriarchal system has strong kin ties between givers and receivers of intergenerational transfers but the individual

matriarchies vary widely in their dependency ratios and life-cycle squeezes. The matriarchal arrangement leads to an evolved age schedule of mortality rather similar to the hunter-gatherer schedule and similar to historical age schedules, for example for Sweden (see Lee, 2003). Remarkably, this same general mortality pattern also evolves for older ages under social arrangements involving weaker kin ties including with sharing groups of the kind observed ethnographically, although levels of infant and child mortality differ considerably due to free riding.

The degrees of genetic relatedness within sharing groups engender different evolved life histories including levels of investment in offspring and differing evolutionary free riding. Some of these combinations of social arrangements and evolved life histories are more efficient than others, in the sense that each can attain and sustain a different maximum population density. The one able to sustain the highest density eventually wins out and is selected in inter-group competition. In general, social sharing confers benefits through life insurance and smoothing the life-cycle squeeze, but incurs costs by distorting the evolution of life histories in the direction of inefficient traits and free riding. The clearest example is the polar case of complete population level sharing in which post-reproductive survival does not evolve, and consequently the population-level dependency ratio is very high and only modest densities can be sustained.

This study has many limitations. Here are some that seem most important. 1) The models and simulations are single-sex with no mating market and no corresponding recombination of the genome at birth. This means that our kin groups are too highly interrelated. Mating would also raise the possibility of some in-migration from neighbouring populations, which would affect interrelatedness. It would be very useful to have some DNA evidence for hunter-gatherer/forager groups like the Tsimane to assess the degree of relatedness in these groups. 2) Mortality at each age is governed by genes/mutations as well as by productivity of the family and sharing groups and the dependency ratios which together determine the level of consumption at each age. However, genes only affect the level of fertility indirectly. Given the age-shape of fertility, its level is determined by consumption, which in turn depends on dependency ratios, productivity levels and sharing rules. It would be possible to introduce a mutation affecting the level of fertility but making the age shape subject to natural selection would be more complex. 3) The age shapes for fertility, consumption needs and baseline productivity are predetermined. The simulated age profiles differ from these due to differences in dependency ratios at different stages of the life cycle, levels of prior childhood consumption, population density experienced at different ages over the life cycle and so on. With our current modelling approach, it would not be possible to relax the need for baseline age profiles. This is not a perfectly general model. It is a model for humans. 4) The social group membership is taken to be given and is not governed by mutating genes governing degrees of sociality. We could instead introduce a mutation similar to mortality that raises preferences for food sharing in larger groups and assume that individuals seek out others with similar preferences to form groups. We could then see what sort of social arrangement and food sharing evolved. A more general approach might start with an optimal life history model like Chu and Lee (2013) and simulate it subject to mutations, which would permit the evolution of transfer behaviour, levels of fertility and mortality, age at maturity, menopause and so on.

This study illustrates the potential for simulation studies that incorporate mutation and natural selection in an age-structured environment with both individual and group selection. The simulations complement the more static analytic solutions of models by Hamilton (1966)

and Lee (2003) by allowing a much richer and more realistic set of assumptions, dynamic interactions of highly nonlinear processes and selection at multiple levels.

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⁹ Note this chapter has been posted on the Open Science Framework website since 28/06/2019, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

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