

THE EVOLUTION OF THE POST-REPRODUCTIVE LIFESPAN

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INTRODUCTION

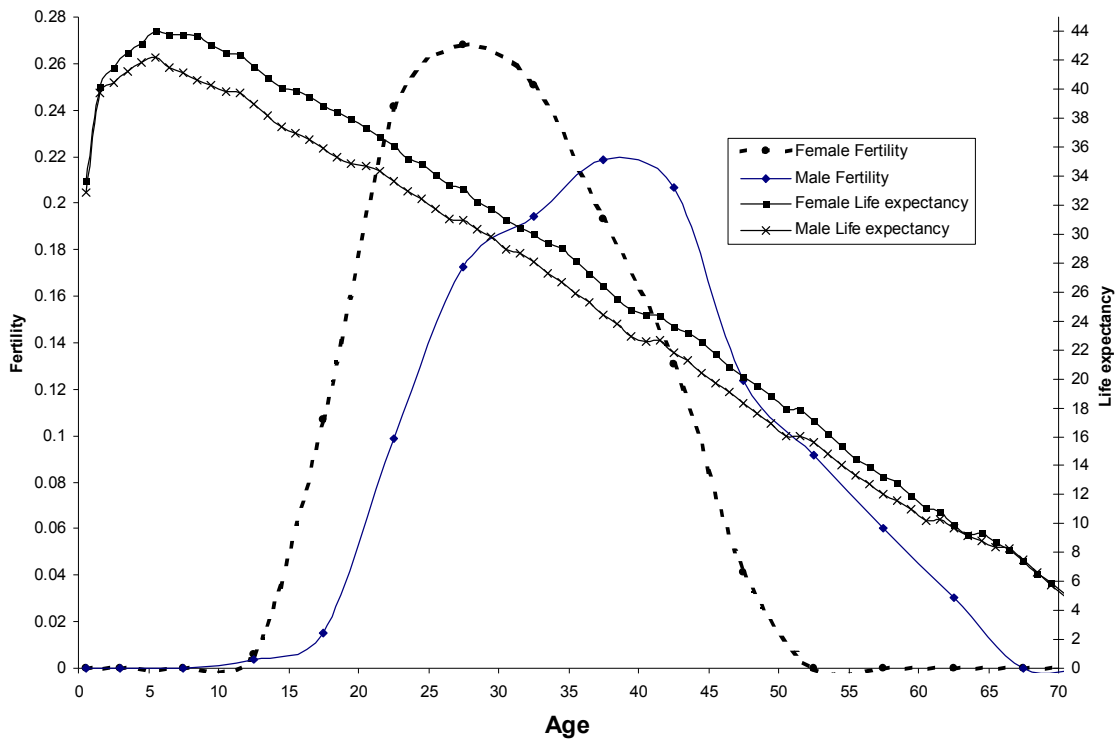
The Problem: Post-reproductive longevity

A recent cross-cultural analysis of contemporary hunting and gathering groups and of peoples who practice a mix of foraging and simple horticulture (Gurven and Kaplan 2006) reveals that those populations exhibit some very robust characteristics to their life course.

One of the most robust characteristics is a long, expected post-reproductive lifespan. For example, there are four hunter-gathering groups (the Hadza, Ache, !Kung, and Hiwi) for which there are reliable estimates of age-specific mortality rates. Although average life expectancy at birth (e_0) is only 34.5 years in these groups (s.d. 2.6), those who survive to adulthood (age 15) can expect a long adult lifespan. Life expectancy at age 15 is a mean of an additional 39 years (s.d. 5) such that the expected age at death is 54 years. Even more revealing is that life expectancy at 45 (e_{45}) is more than two decades (mean=21 years, s.d. 2.3). About 60% of hunter-gatherers born survive to age 15, but of those who survive, two thirds will survive to age 45 with an expected age at death of 66 years.

By age 45, however, most women have ceased to reproduce. Moreover, it appears that among contemporary hunter-gatherers and many forager-horticulturalists, most men cease reproducing when their wife has their last child. Among Ache hunter-gatherers, for example, if a couple had at least two children together, the woman's last birth was the same as her husband's last child in 90 percent of cases (Kaplan, Hill et al. 2000). Figure 1 illustrates the age-specific relationship between life expectancy and fertility for hunter-gatherer men and women. From the perspective of natural selection, the significant period of human life spent in a post-reproductive state is a conundrum, because sterility is equivalent to death. Its occurrence in humans (and absence in most other mammals) is one of the most challenging puzzles of evolutionary biology. Recent data from chimpanzees and other primates suggest that menopause itself is not unusual among mammals (and appears to occur roughly at the same age among chimpanzees and humans, Treolar 1981; Gould et al. 1981); rather it is the extended lifespan of humans after reproduction has ceased that is rare (occurring in only a few other species such as pilot whales). For example, chimpanzees in the wild have an expected age at death of 27 years upon reaching reproductive maturity at age 13, yet their age at menopause appears to be about the same as in humans. Thus, almost no chimpanzees in the wild reach menopause. The next section reviews several proposals for explaining the evolution of the two decades of post-reproductive life.

Figure 1. Fertility and Life Expectancy by Age among Foragers



Four Theories of Post-reproductive Longevity

Several theories have been proposed to explain this remarkable extension of the human lifespan. The classic theory of senescence in evolutionary biology was first suggested by Haldane (1942), proposed by Medawar (1957), developed further by Williams (1957) and then formalized by Hamilton (Hamilton 1966). It proposes that as individuals age, they contribute less to reproductive fitness because less of their expected lifetime fertility remains. Consequently, natural selection acts more weakly to reduce mortality at older ages. The existence of substantial post-reproductive life among humans therefore suggests that older individuals have “reproductive value” by increasing fitness through non-reproductive means.

George Williams (1957) was first to propose that beginning at ages 45-50, mothers may benefit more from investing their energy and resources in existing children rather than from producing new ones. This idea became known thirty years later as the “grandmother hypothesis” [hereafter **GMH**] (Hurtado & Hill, 1991). A specific version of the GMH has been proposed by

Hawkes et al. (1998) and explained more fully by Hawkes (2003). Their model focuses on intergenerational transfers among women and proposes that older women can increase their inclusive fitness by raising offspring fertility and grandoffspring survivorship through provisioning. The resources acquired by women foragers are strength-intensive, disadvantaging young children and increasing the value of the older women's contributions. According to this view, extensions in the human lifespan are driven by selection on women, and the value of resource transfers from grandmothers to grandchildren.

Peccei (1995; 2001) proposes an amendment to this view. She points out that long-term juvenile dependence among humans implies that adults who cease reproducing in their 40s will not finish parenting until they are 60 or older (see also Lancaster and King 1985). The notion that most of the benefits to longevity derive from helping offspring rather than grandoffspring has been called the mother hypothesis [hereafter **MH**].

An alternative view focuses on men. Marlowe (2000) argues that the extension of the lifespan is driven by selection on men, stressing the fact that men do not experience menopause and can have children into the 7th and 8th decades of life. His argument, called the patriarch hypothesis (hereafter **PH**), is that men accrue status and power as they age and this selects for their greater longevity.

A fourth view, the embodied capital model [hereafter **ECM**] (Kaplan et al. 2000; Kaplan and Robson 2002; Robson and Kaplan 2003) proposes that timing of life events is best understood as an 'embodied capital' investment process. In a physical sense, embodied capital is organized somatic tissue—muscles, brains, etc. In a functional sense, embodied capital includes strength, skill, knowledge and other abilities. Humans are specialists in brain-based capital. High levels of knowledge and skill are required to exploit the suite of high-quality, difficult-to-acquire resources humans consume. Those abilities require a large brain and a long time commitment to development. This extended learning phase during which productivity is low is compensated for by higher productivity during the adult period. Since productivity increases with age, the time investment in skill acquisition and knowledge leads to selection for lowered mortality rates and greater longevity, because the returns on the investments in development occur at older ages. Thus, the long human lifespan co-evolved with the lengthening of the juvenile period, increased brain capacities for information processing and storage, and intergenerational resource flows. This theory also proposes that meat acquisition and extractive foraging generate complementary roles for men and women, where both invest directly in offspring and grandoffspring in long-term unions. In fact, Kaplan et al.

(2001) present data suggesting that men often experience ‘effective menopause’, because their last reproductive event is tied to their wife’s last reproduction.

Goals and Organization of the Paper

With the exception of the patriarch theory, which is purely demographic and focused on men only, each of the theories discussed above depends on the ability of older individuals to increase the survival and fertility of younger kin through intergenerational transfers of goods and services. Such transfers have not, however, traditionally been measured. Empirical studies have tended to focus instead on relationships between demographic variables, particularly upon the relationship between whether an older individual is alive or dead and either the fertility or survival of their descendants (see, for example, Hill and Hurtado 1996, Mace’s articles, voland, French Canadian studies).

The study of kin effects using purely demographic indicators suffers from several potential limitations, however. First, selection biases, due to the fact that older individuals who survive or die are not selected randomly from the population, may yield incorrect estimates of kin effects. Second, as pointed out by Hill and Hurtado (1996), when people die, other kin often provide additional assistance to their children that they would not have provided, had they not died. This tends to lead to underestimations of kin effects. Third, several demographic studies have yielded counter-intuitive findings. For example, sometimes living grandparents are actually associated with lower survival rates of grandchildren (Sear and Mace, Canadian studies). However, it is not known whether such results are due to estimation bias, error, or truly negative kin effects. Lastly, purely demographic studies are inherently unsatisfying, since they do not show the pathways through which older post-reproductive individuals affect the fitness of their descendants. While statistical associations between whether or not a grandparent is alive or dead and improvements in child survivorship or fertility are suggestive, they alone do not reveal any underlying design features of an old age geared towards kin assistance.

This paper is designed to provide information on intergenerational transfers for one forager-horticultural group, the Tsimane of lowland Bolivia. It intends to answer the following questions. At each age, how much is transferred to descendants and to which descendants are they transferred? What kinds of transfers do they make in the way of services? How do those transfers differ for men and women? At what ages do individuals receive those transfers? Knowing the answers to such

questions will help evaluate the alternative hypotheses about the evolution of the post-reproductive lifespan.

The mother and grandmother models focus exclusively on the contributions of women, and predict that during the post-reproductive period resource flows and childcare will be directed to children and grandchildren, respectively. Proponents of the GMH predict that men will distribute their food widely and that significant biases towards children and grandchildren are unlikely. The patriarch hypothesis predicts that men will maintain high levels of reproduction through old age, and does not expect major fitness returns to parental and grandparental investment, by either men or women. The embodied capital model predicts that low productivity prior to adulthood is compensated by higher productivity through adulthood until death. Accordingly, it predicts positive resource transfers downward along generational lines. Being a two sex model, it predicts that both men and women will invest in their joint descendants, but with a division of labor in the nature of those investments. Embodied capital theory is largely silent about the mix of investments in children and grandchildren, except that individuals are expected to invest optimally across descendants of different ages and degrees of relatedness, so as to maximize the marginal gains from those transfers.

The paper is organized as follows. First, we provide information about the Tsimane people, including the ecological and socio-historical context in which they live. Second, we discuss the data collection and analysis procedures upon which the analysis of transfers is based. Next, we present demographic data on Tsimane age-specific life expectancy and fertility for men and women, showing that their life histories are very similar to the pure hunter-gatherers, discussed above. This is followed by estimation of number of children and grandchildren under age 5 and under 15 that men and women will have at each age. This is a measure of number of possible recipients for transfers. Then, we analyze the work effort of both sexes as a function of age.

The analysis of transfers proceeds next, which primarily take the form of childcare and food energy (since the Tsimane own few heritable goods). Transfers are analyzed in three ways. First, we examine the sources of childcare provided to children, including mothers, fathers, siblings, grandparents and others. The second and third analyses deal with food transfers from the perspective of producers and recipients, respectively. From the perspective of the producer, we analyze the proportion of food going to recipients of different kin categories, as a function of the producer's age. From the perspective of the consumer, we analyze the proportion of food coming from producers of different kin categories, as a function of the consumer's age.

The paper concludes with a summary of the results and a brief discussion of their implications for alternative theories for the evolution of human longevity.

METHODS

The Study Population

The Tsimane are lowland forager-horticulturalists living in small villages composed of extended family clusters, located primarily in the Maniqui river system in the Ballivián and Yacuma Provinces of the Beni region of Bolivia (14° 35' S - 15° 30' S, 66° 23' W - 67° 10' W). Approximately 8,000 Tsimane inhabit 80 villages in the forest and savanna regions between the towns of San Borja, the foothills of the Andes and San Ignacio de Mojos (VAIPO 1998). Almost all of the food the Tsimane consume derives from slash and burn agriculture, fishing, hunting, and gathering. They cultivate plantains, rice, corn, and sweet manioc in small swiddens and regularly fish and hunt for meat. Subsistence tasks are primarily performed by all adults within a group of kin-related households, although group fishing, cooperative hunting and field clearance are not uncommon.

Although the Tsimane' were exposed to Jesuit missionaries since before the 17th century, they were never successfully settled in missions and remain relatively unacculturated (Chicchón 1992; Reyes-Garcia 2001). Other lowland Bolivian groups such as the Mojeño and Yuracaré, who engaged in more intensive agriculture were more easily concentrated in centralized missions. Some degree of their isolation is suggested by the fact that their language is an isolate, even within Bolivia, sharing a similar vocabulary and grammar only with the Mosesten, who inhabit the southern and northern stretches of Tsimane territory. They share distant genetic affiliation with the Yuracare, Trinitario and Quechua ethnic populations, and little affiliation with the Aymara (Bert et al. 2002). It is likely that Tsimane interacted with Incas (Saigne 1985).

New mission posts in several different villages only began in the 1950s (Chicchón 1992). The greatest influence of the 20-year-old New Tribes Mission was to create a system of bilingual schools with trained Tsimane' teachers and an elected village chief in each village downstream from the Catholic mission, Fátima. In 1989, a central representative organization, the Gran Consejo Tsimane was founded with assistance of the New Tribes Mission. The New Tribes Mission also maintains a small health clinic on the outskirts of San Borja, and has provided minimal and variable access to medicines in exchange for labor since 1990.

Tsimane villages vary in their degree of market access and interaction with outsiders. Acculturation occurs in several ways: visits to the main market town, San Borja (pop'n ~18,000),

wage labor with loggers or colonists, debt peonage with river merchants, and schools which exist in over 2/3rd of all Tsimane villages. Market items which are highly valued by the Tsimane include clothing, aluminum pots, salt, sugar, kerosene, utensils, and school supplies. Schools have existed anywhere from two to twenty years. Since the 1970s, Tsimane have come into greater contact with outsiders as new roads were built, inviting a burst of logging, trading, and encroachment by lowland and highland colonists (Ellis, 1996; Chicchón, 1992). Tsimane make occasional visits to San Borja during town festivals, and some sell agricultural produce or handicrafts. On average, however, only 2-6% of the diet derives from market purchases. Near San Borja, some Tsimane work as farm hands for local ranchers. Along the upper Maniqui River, Tsimane often collect jatata palm leaves and weave them into roofing panels. These panels are then traded with itinerant merchants who provide market goods and alcohol. The exchange rates vary among merchants, but most are unfavorably low. Goods are usually given in advance of payment, and Tsimane rarely refuse these 'gift' advances, which positions many households in a cycle of debt with the merchants.

Chicchón (1992) and Reyes-Garcia (2001) report a lack of any serious epidemics in Tsimane history, and based on rough historical estimates of Tsimane censuses over the past two hundred years. Nonetheless there is some evidence of a smallpox epidemic in the mid 1800's shortly after two missions, San Pedro and San Pablo, were formed along the Maniqui River. San Pablo was subsequently abandoned shortly after the murder of a Catholic priest who worked there (Cardús 1886, cited in Chicchon 1992). Demographic interviews revealed several waves of measles or rubeola that killed a large number of small children over the past sixty years, but due to the dispersion characteristic of Tsimane residence patterns, it is unlikely that any epidemic would have globally impacted all Tsimane.

Data Collection

Demography: Mortality and Fertility

Demographic interviews were conducted in the Tsimane language among all available adults over age 18 by Gurven during fourteen months from July 2002-August 2005 with the assistant of a bilingual Tsimane (Zelada) as a central component of a project focused on Tsimane life history and health. Deaths were elicited from retrospective reproductive histories of interviewees, their parents and siblings, whether alive or dead. This process yields redundant reproductive histories (e.g. if more than one sibling is interviewed), allowing for cross-validation of data. Years of birth and death were assigned based on a combination of methodologies employed by researchers among the !Kung

(Howell 1979), Ache (Hill and Hurtado 1996) and Hadza (Blurton Jones, Hawkes et al. 2002). These include using known ages from written records, relative age lists, dated events, photo comparisons of people with known ages and cross-checking of information from independent interviews of kin. Methods are described at length in Gurven et al. (n.d.). The methods provide roughly independent estimates of age. When all estimates yield a date of birth within a 3-year range, the average was used unless one or two estimates were judged to be superior to the others. Since the sampling procedure yielded redundant reproductive histories (e.g. if more than one sibling is interviewed), data were cross-checked for consistency and inconsistencies were resolved. On the basis of those data, all living and deceased 'Tsimane' in the sample were assigned estimated ages. Individuals for which confident ages could not be ascertained are not included in this analysis.

Time Allocation

Activity budgets are based on spot observations made in four Tsimane communities from July 2002 to June 2003 and one other from February to August 2005. During 3 hour observation blocks, all activities of members from several groups of families were recorded by student researchers every half hour. Individuals present at or near the residential cluster were observed directly while the activities of absent individuals were obtained by informant interviews and many of these were later verified. Activities were coded based on a scheme of over 150 descriptive codes. These were grouped into macro-categories such as food processing, tool manufacture, food production and parental care. Frequent processing tasks include pounding rice, peeling, and grating sweet manioc, boiling water for cooking purposes, butchering animals and fish. Frequent manufacture activities include mat, fan and handbag weaving for women, and arrow, bow, and ax handle construction or repair for men. Both sexes in two of our sample communities collect jatata palm leaves for the purpose of assembling roofing panels that are traded with itinerant river merchants. Food production includes farming, hunting, fishing and collecting activities. Parental care includes tending, feeding, bathing, holding, or comforting children. Household chores commonly include water transport, firewood collection and chopping, fire tending, and interior and exterior house cleaning.

Sampling was done without replacement until all group clusters were sampled throughout the day (7-10am, 10-1pm, 1-4pm, 4-7pm). Total sample size includes xx,xxx person-observations. Overall, 299 individuals age 15 and above were observed, resulting in a total of 21,893 person scans and an average of 73.2 scans per person.

Consumption

During the collection of time allocation data, those individuals that were observed eating during the instantaneous scan were asked questions concerning the acquirer of food being eaten. Space was provided for up to three different ingredients (e.g. rice, meat, fish, etc.) and three acquirers for each ingredient (e.g. for food that was harvested by multiple people). Credit was equally divided among all three acquirers. For all agricultural ingredients, credit was divided among the harvester(s) and the husband and wife owners of the field. All harvesters received equal share of 55% of the credit, as this was the percent of all time in garden labor spent in harvesting. Husband owners received 32% and wife owners received 13% of the credit, as these were the respective proportions of non-harvesting labor performed by each based on time allocation. This credit was then multiplied by the caloric concentration of the food item (kCal/kg), in order to weigh more nutritional foodstuffs accordingly, and then divided by the number of ingredients in the food being consumed (each ingredient is typically substantial in Tsimane cuisine), resulting in a value termed food credit.

To determine the sources of individuals' food (providers), the sum of all caloric concentrations for all eating events for each individual was calculated, and proportional contributions from the sum of each relation's food credits was deduced. This resulted in a sample of 528 consumers with an average of 6.0 consumption events. To determine the consumers of one's production (distribution), food credits for which an individual was listed as acquirer were summed, and the proportions in which each relation was the consumer was calculated. Because only individuals that were listed as acquirers were included the sample decreased to 410 individuals, but because there were potentially multiple ingredients with multiple acquirers for each consumption event, these acquirers had an average of 19.0 food credits.

Production

Production was calculated using two interviews, a daily food production interview and an agricultural field interview. The daily food production interview was conducted regularly with all families within the focal communities. During these interviews, individuals were asked about the production events of all present family members over the previous two days, resulting in a sample of 536 individuals with an average of 20.2 sample days. This interview covered hunting, fishing and agricultural production (harvesting). Credit for agricultural foods was divided as described above for

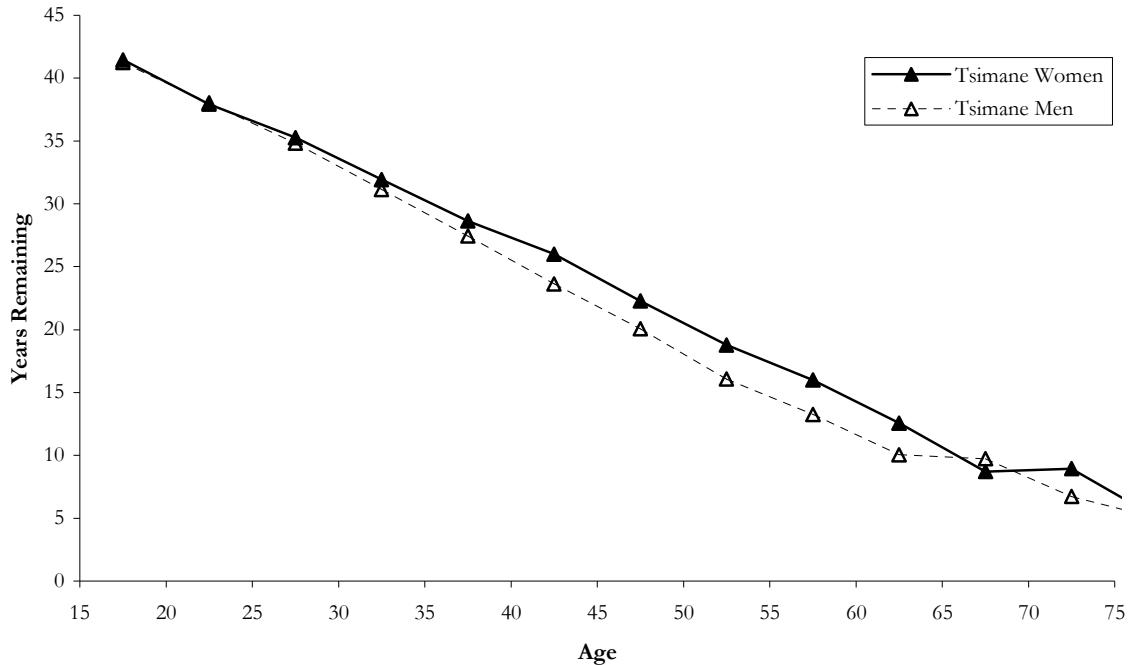
consumption. Unit weights were obtained from previous field measurements and these were multiplied by caloric concentrations to derive the total caloric production. Daily caloric productions were summed for all interviews and divided by the number of sample days.

A review of the daily production data revealed an over-sampling of the rice-harvest season. To correct for this, we looked to the agricultural field interviews to determine actual daily rice production over a year. Rice is the most important crop for the vast majority of Tsimane, and they are well aware of the amount of land devoted to the crop and the expected return in number of arrobas (11.5 kg). We divided the total caloric rice production from each field, and then used the daily production interviews to allocate harvest credits to family members. Owners were given the same credits as described above. This resulted in rice production estimates for 188 individuals. We performed a log-log-transformed regression of this new value from the field interviews onto the old values from the production interviews, and along with age, sex and community in the model, we obtained an R^2 of 0.77, which made us feel comfortable that these data were comparable. Because of such a high correspondence, we felt it was appropriate to use the regression equation to estimate daily rice harvest values from individuals for whom we had agricultural field interviews but no daily production data. This was done for only 44 individuals who were older than 50 in order to increase the small sample sizes in these age brackets. Daily rice production was estimated for each age bracket and added to that estimated for non-rice estimates.

Resource Flows

Resource flows were calculated by multiplying an individual's daily production by the sex and age-bracket specific predicted distribution to each relation. Estimates for distribution were estimated because the two datasets did not match one-to-one with respect to subjects, resulting in a reduction in sample size. Because distribution profiles did not vary greatly by community, these estimates were used. Net resource flows were calculated by subtracting the total resource flows from the reciprocal relation. For example, all resource flows towards fathers were summed for all individuals in which ego was named as the father, and this sum was subtracted from the ego's resource flow to children. This resulted in a sample size equivalent to the production dataset.

Figure 2. Tsimane Life Expectancy



Data Analysis

All data analysis was performed in SAS V8 or SPSS 12.0. Time allocation is presented as Loess curves, created using the proc loess procedure with a smoothing factor 0.5. Daily production estimates and resource flow estimates are presented as modified population marginal means, based on an ANOVA including sex, age category and community. Because consumption profiles did not differ greatly between communities, such measures are presented as sums of all numerators and denominators for each age bracket.

RESULTS

Survivorship

Figure 2 shows the remarkable correspondence between the male and female lifespan. Upon reaching age 15, Tsimane survivorship profiles for males and females are very similar throughout

much of the life course, and show a similar trajectory as in other hunter-gatherer and forager-farmer populations. Approximately 40% of Tsimane males and 39% of Tsimane females ever born live to the age of 60. The average 15 year-old Tsimane can expect to live to 58 years, and the 45 year-old, to 67.

Fertility

Women's age-specific fertility rate peaks very early during their reproductive careers, in the early to mid twenties (Figure 3a). It then declines slowly until the late thirties, after which it drops precipitously, ending in a total cessation of reproduction. Although the median age of menopause is 49 years old for Tsimane women, the median age of last birth is nine years prior at 40 years old (Table 2). These characteristics of Tsimane women's fertility—early peak in the twenties, accelerating monotonic decline thereafter, and cessation of reproduction well before menopause—comprise the typical pattern of female reproduction within natural fertility populations (Wood 1994; Peccei 2001).

The profile of Tsimane men's fertility is also quite typical of other non-contracepting groups. The onset of fertility is delayed by just over 5 years compared to women and is characterized by a less steep incline towards and decline from peak fertility in the mid 30's (Figure 3a). This decline may not be a direct result of men's reproductive or somatic senescence, but a reflection of the close link between of men's fertility and the declining fertility of their slightly younger wives. By the age of the 49, the median age of menopause for women, a Tsimane man can expect to have only 0.69 more children (Figure 3b). This represents 10.0% of men's total fertility rate (Table 2). By age 60, this number is down to 0.03 children, or 0.4% of men's total fertility rate. At this age, Tsimane men can expect to live an additional 11.7 years.

Using our estimates of age-specific fertility, we can estimate the cumulative number of children and grandchildren women have over the life course. Figures 4a and 4b presents this analysis for women. By the median age of last birth, women have on average 2.9 sub-adult children (<15 years) and 1.5 sub-adult grandchildren, and by age of menopause they have only 1.6 children and 5.8 grandchildren. Finally, by age 60, less than one out of ten women has a single sub-adult child, yet

Figure 4. Number of Sub-Adult Children and Grandchildren by Age for Tsimane Women

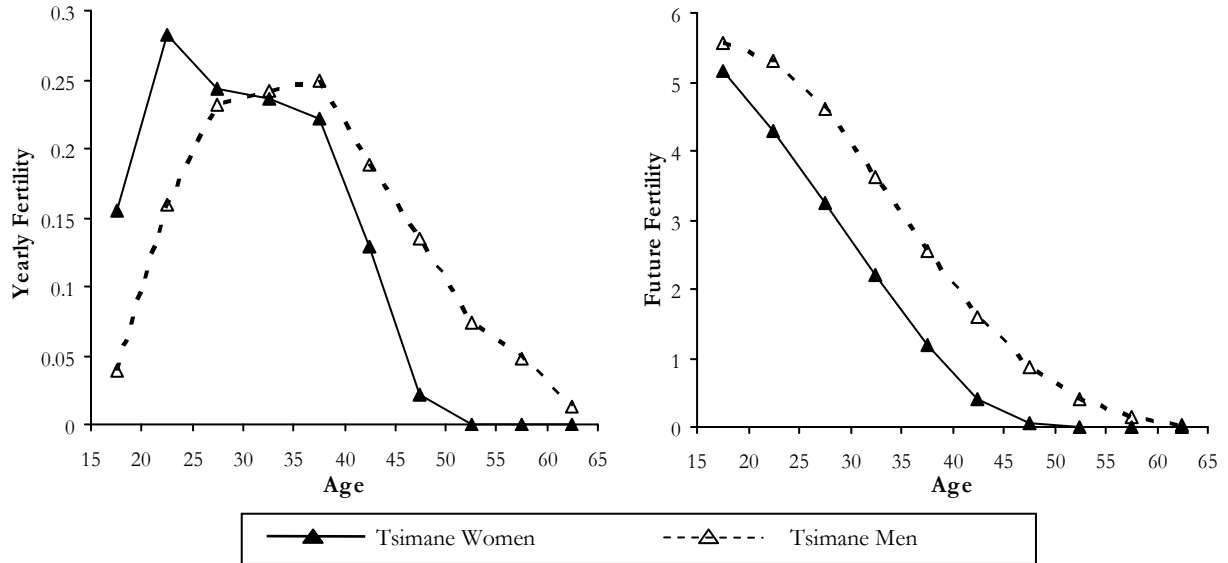


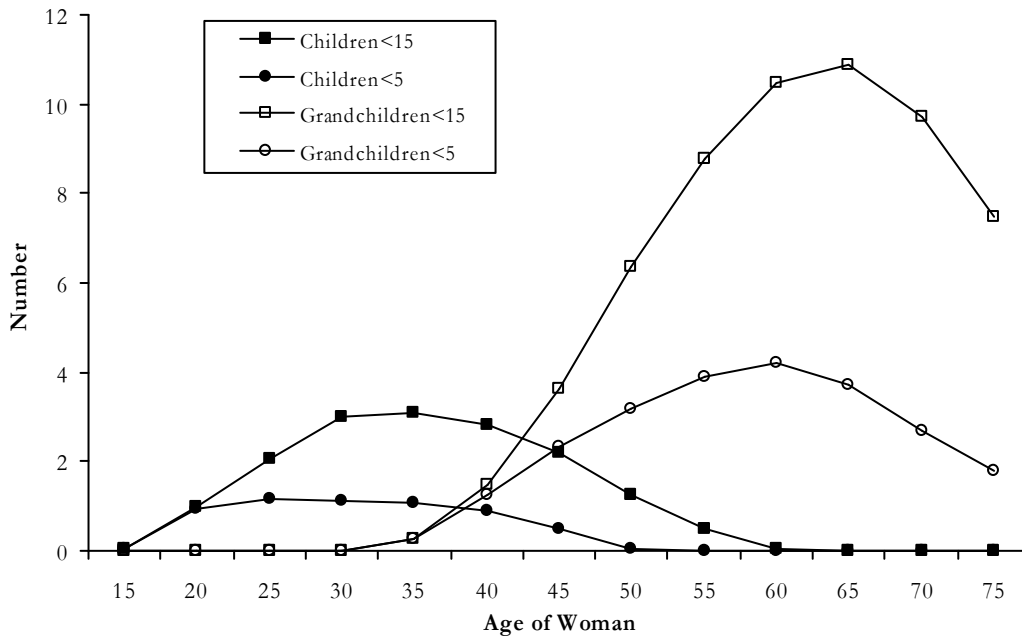
Table 1. Fertility Characteristics of Tsimane Population

Sex	TFR	Median Age of First Birth	Median Age of Last Birth	Median Age of Menopause	Fail to Reprod. By 40
Men	6.9	24.0	47.5	n/a	7.6%
Women	6.4	19.0	40.0	49.0	1.2%

they have an average of 10.5 sub-adult grandchildren. At this age, Tsimane women can expect to live an additional 12.2 years with no dependent children. The number of sub-adult grandchildren continues to rise to a peak of nearly 11 grandchildren by the age of 64.

Time Allocation

Figure 3. Age Specific Fertility and Expected Future Children for Women (a) and Men (b)



Figures 5a through 5d show the average percentage of time men and women spend in different daily work activities by age. Although overall time spent in work varies relatively little across adult ages, the composition of work activities changes quite drastically throughout the lifespan.

Women spend a total of 15% of daily hours, or roughly 1.8 hrs per day in food production, and 35-45% of the day, or 4.2 to 5.4 hours per day in other work activities. The major change over time is the drastic decrease in time spent direct parental care as women's children become independent. Tsimane grandmothers appear to offer little help in the form of babysitting (at least for young children). Figure 5a shows that although women spend upwards of 30% of their time caring for children while in their twenties (when few older daughters are available to provide assistance), they spend less than 5% of their time providing direct care for their grandchildren despite the fact that most older women have many more grandchildren than they ever had children. The infrequent care that grandmothers provide is thus divided amongst a greater number of

Figure 5. Women's Time Allocation in Non-Productive Work (a) and Productive Work (b); Men's Time Allocation in Non-Productive Work (c) and Productive Work (d)

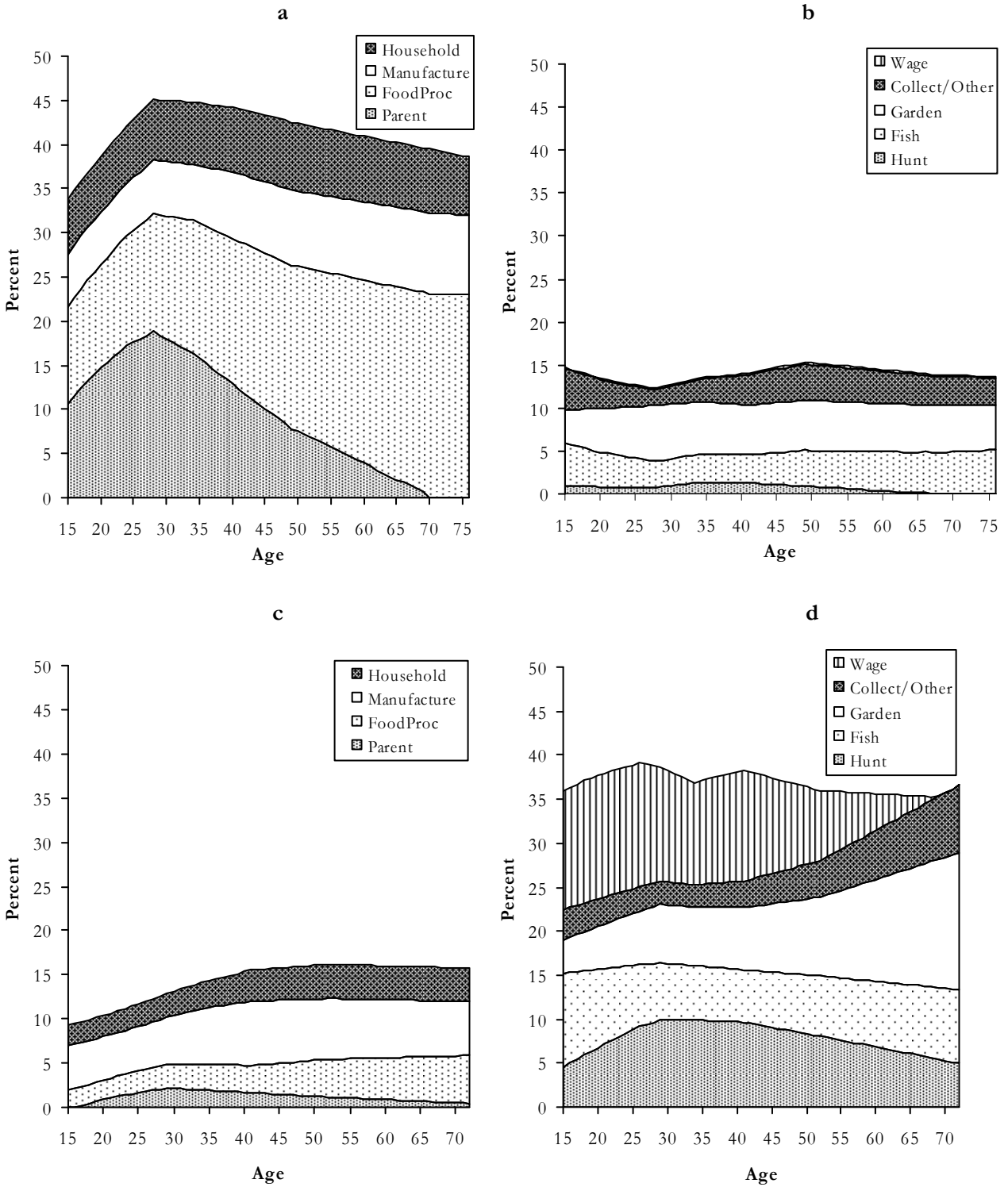
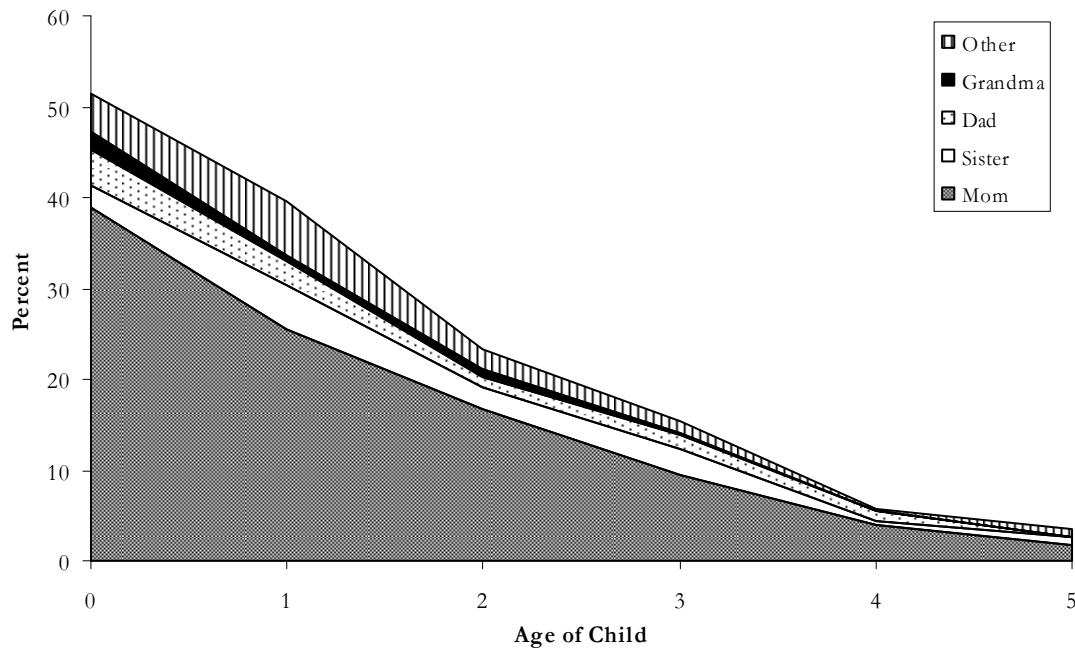


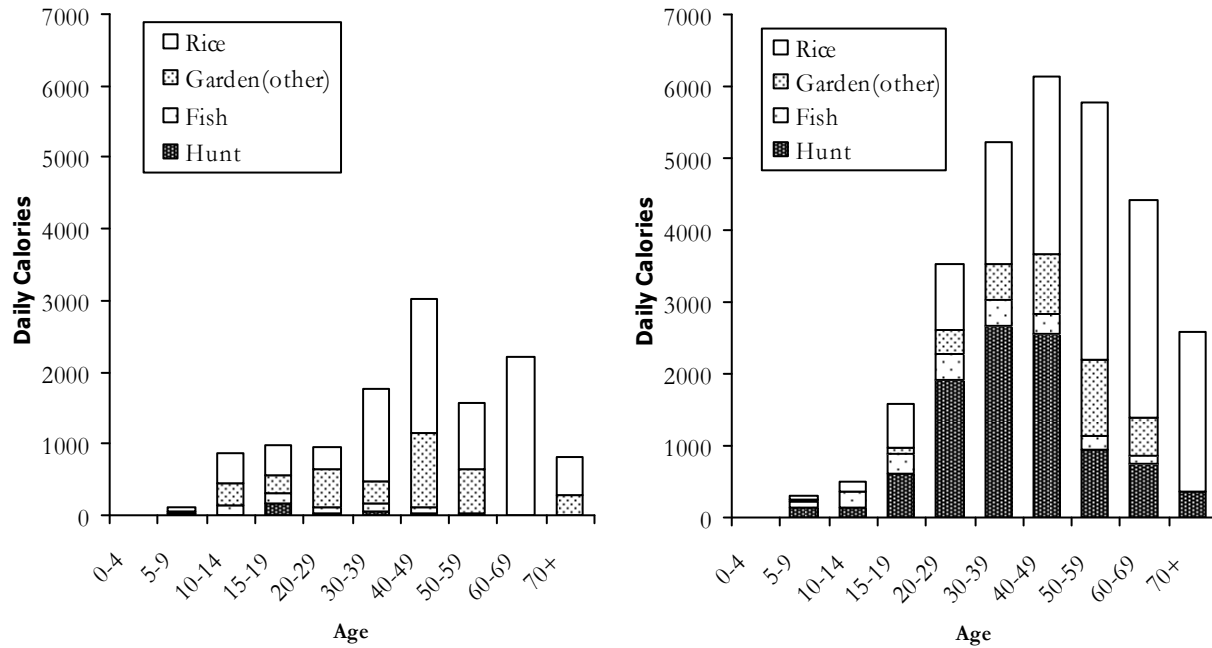
Figure 6. Percent of Time Being Cared for by Various Caretakers



children, resulting in each child receiving roughly nine minutes of grandmaternal care per day in the first three years of life (Figure 6). The decrease in parenting, however, is met with an almost equal increase in time spent either food processing or manufacturing. Time spent in various production activities remains relatively stable throughout women's lives.

Men's use of time is more heavily biased towards productive work, with engagement in the production of food or wages occupying more than twice as much time as among women. Men spend about 38% of daily time, or 4.6 hours per day, in food or wage production. Their time spent in non-productive work, however, is less than half that spent by women. Men spend only 10-15%, or 1.2-1.8 hours per day in non-productive work. The greatest shift through time for men is a decreasing reliance on hunting and wage labor and an increasing reliance on farming. Wage labor for the Tsimane usually consists of working for loggers, which is extremely arduous work. It is therefore no surprise that it, along with hunting—the other most physically demanding activity—display decreasing trends with age. The overall time men allot to non-productive labor increases as they age, with the greatest increase coming from time spent in food processing.

Figure 7. Daily Caloric Production of Women (a) and Men (b)



Production

Figures 7a and 7b present the daily caloric production of individuals throughout their lives. We see that Tsimane men are the main producers, accounting for 66% of all calories. Women's production comes almost exclusively from agricultural foods, with very few calories coming from animal sources. Men's production begins with a larger contribution from animal foods in early adulthood, and switches to a greater emphasis on agriculture in the forties—a finding that mirrors the time allocation. Production from fish appears smaller than the time allocation data would suggest; this is due to the fact that the time allocation dataset contains two riverine communities that are not present in the production dataset.

Remarkably, men and women are able to maintain substantial levels of production into their sixties, even producing greater amounts than young adults in their twenties. As stated above,

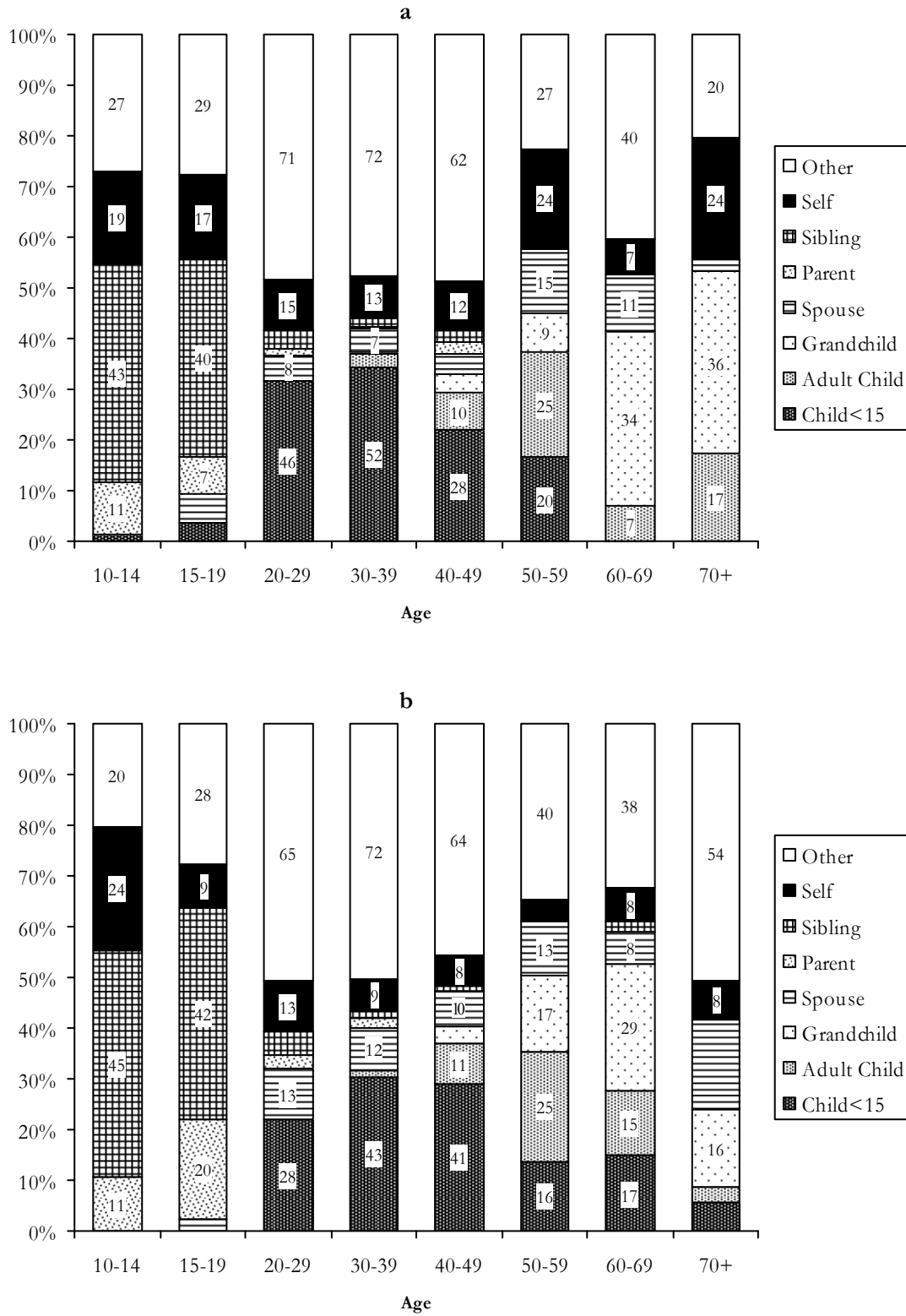
however, young men may be producing slightly less than their sixty year-old counterparts, but 65% of their calories are coming from more highly valued animal sources, compared to only 19% for the older men. Even the small contributions from animal sources seen in young women's production are essentially absent by the fifties.

Consumption

The distribution of resources from men and women is remarkably similar (Figures 8a and 8b) with the sexes being significantly different in only the percent given to spouse and to self (ANOVA, Spouse $p=0.045$; Self $p=0.004$). At their peaks, both men (in their forties) and women (in their thirties) share over half of their production with their children. After these peaks, the proportion directed towards children declines as that towards grandchildren increases. By the sixties, women are directing much more of their production to grandchildren than to children, and no longer have any sub-adult children to invest in. Men, on the other hand, are providing comparable amounts to children and grandchildren in their sixties, with grandchildren receiving slightly greater amounts only when men are in their seventies. Towards later ages, small sample sizes may unfortunately be resulting in spurious noise, particularly with regards to the group of men in their seventies. This group consisted of only three men, two of whom had step-children and step-grandchildren living nearby, which account for a large proportion of the 'Other' category.

Figures 9a and 9b shows what these actual distributions mean from a consumer's point of view, as although an individual may be sharing a large proportion of his or her production with children, the actual benefit to children depends also on the amount produced. Again, we see an overall correspondence between males and females, with percents coming from children and self presenting the only sex differences (ANOVA, Spouse $p<0.001$, Children $p<0.001$). Sub-adult children receive roughly half of their calories from food acquired by their parents, and between 5% and 10% from food acquired by their grandparents. Men experience a substantial decline in the number of calories from their relations during the twenties—the time during which they live for a number of years with the families of their wives. We also see that during the reproductive years, women are receiving relatively little caloric contribution from their parents. Mothers account for an average of less than 3% of their daughters' consumption over the three decades. Again, the effect of the small sample sizes at older ages presents itself. For the two men in their seventies discussed above, much of the food is coming from their step-families.

Figure 8. Consumers of Produced Food for Women (a) and Men (b)



Resource Flows

As a final exercise, the net resource flows were calculated by multiplying the individual's daily production by the expected contributions to each relation, and subtracting the reciprocal flow (Figure 10). For instance, although Figure 8a shows over a quarter of women's food coming from their husbands over the reproductive years, the fact that men are receiving food from their wives must be taken into account by subtracting this amount from the amount the wife receives. Figure 9 displays the results of these calculations. Men's net contribution to their wives peaks in the twenties and declines slowly over time, ranging between 524 and 344 calories from the twenties to the fifties. It precedes to drop more rapidly as spouse production falls and more individuals are widowed. Parents' caloric contribution to their children peaks in the forties, when they provide a combined 3963 calories to their children everyday. Men and women continue to contribute to their descendents into their sixties, during which men provide a combined 2558 calories to all descendents and women provide 831 calories. Finally, these data show that although Tsimane men and women in their seventies do not contribute substantial sums of calories to their descendents, nor are they great burdens to them.

DISCUSSION

The data presented here represent an effort to illuminate the many hypothesized pathways through which individuals can accrue fitness benefits at later ages in an attempt to isolate those that are maintaining the long lifespan in this population (and others by extension) and ultimately, which factors led to its evolution. Each type of data speaks differently to each of the four hypotheses presented at the beginning of this paper and will be reviewed below.

The demographic profiles of Tsimane fertility and survivorship reveal a number of important insights. The first is the remarkable correspondence between men and women's life histories. At age 15, both men and women can expect to live to the age of 58; by age 45 and 60, respectively, the expected age of death is 65 and 70 for men, and 67 and 72 for women. Male fertility tracks female fertility with a lag of roughly 5 to 6 years (the approximate age differences between ages of first birth and between spouses). By age 60, men have effectively ceased to reproduce, contrary to the prediction of the PH. The logic of the PH implies that a) a marginal increase in the lifespan of the ancestral short-lived male resulted in a greater marginal increase in the

Figure 9. Providers of Consumed Food for Women (a) and Men (b)

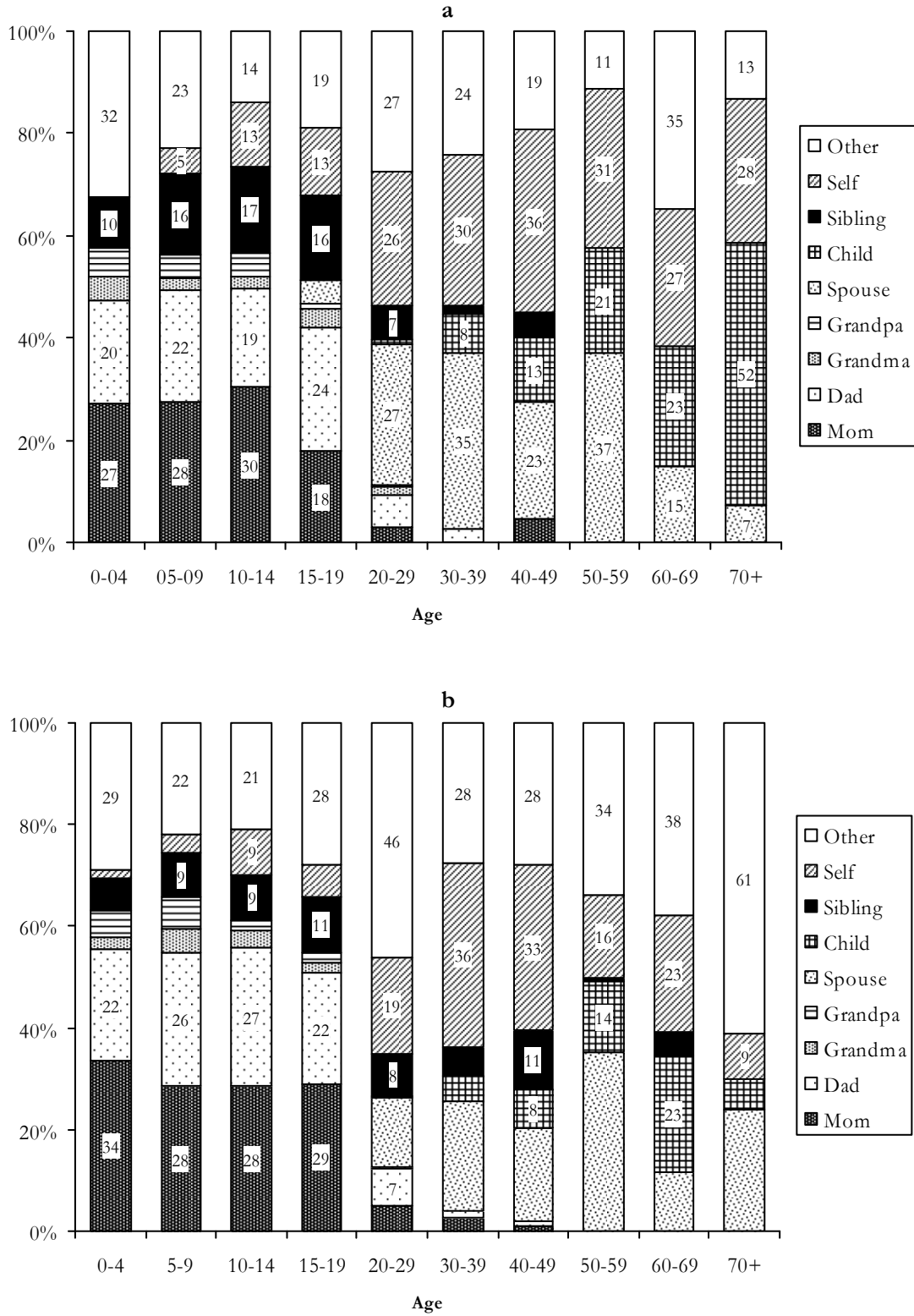
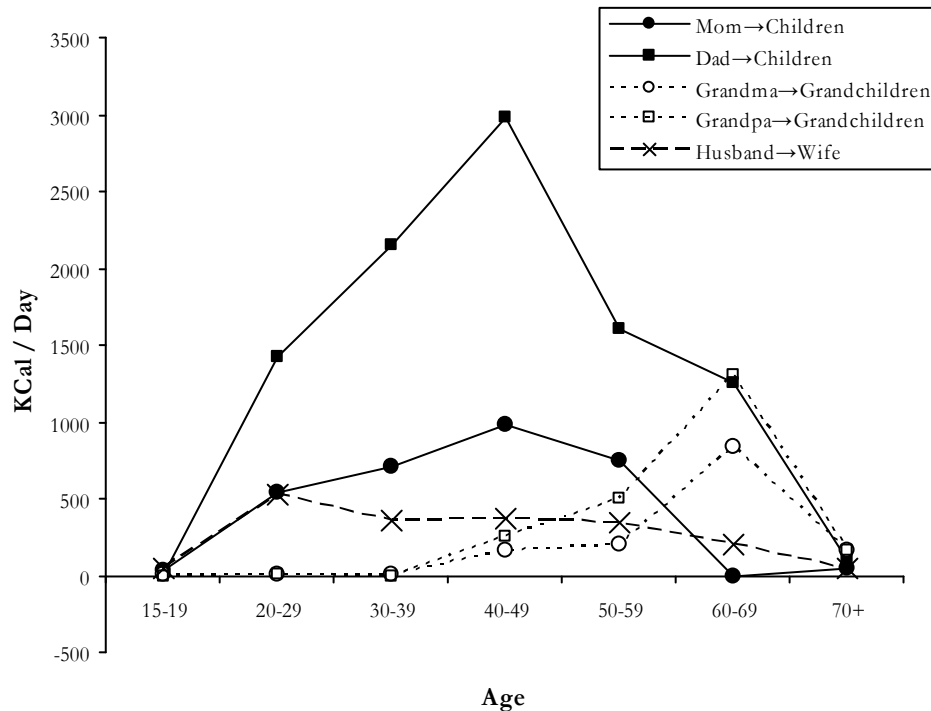


Figure 10. Net Caloric Resource Flows



number of grandoffspring through direct fertility than it did through increasing offspring fertility and grandoffspring survivorship, and b) the increase was greater than the marginal decrease it caused in the number of grandoffspring for women, who were unwittingly carried along. By age 60, a Tsimane male can expect to have 0.03 children in the subsequent 11.7 years he can expect to live, accounting for only 0.4% of his TFR. It is difficult to imagine that the caloric surpluses men continue to produce in their sixties increase the combined offspring fertility times grandoffspring survivorship by only 0.4%. Perhaps, however, the Tsimane are a poor example to test this hypothesis, as marriages are remarkably stable, and older men may thus be hindered in any attempts to pursue additional fertility at older ages.

Another important observation is that women live long past the age at which their last child reaches adulthood. The median age of last birth was only 40 years old, yet at this age, Tsimane women can expect to live an additional 27 years. The MH, which holds that menopause was selected to enable the parenting of later-born sub-adult children, is unable to account for the fact

that women live for so long after the age of menopause. By age 45, women have more sub-adult grandchildren than sub-adult children, and this number continues to rise to a peak of over 10 juvenile grandchildren in the sixties, by which time a woman's children have all reached adulthood. According to the logic of the MH, women would either be expected not to live past their late fifties, or to experience menopause much later. Clearly, the role of providing support to reproducing children and to grandchildren must be taken into account.

The MH, GMH and ECH all propose that the main fitness benefits enjoyed by older individuals are realized through their investing in their descendents. The other data presented in this paper cover the various ways that they can invest and to whom they invest. The MH emphasizes the benefits conferred through investing in sub-adult children, while the GH focuses on the aiding of adult children and grandchildren. The ECH is relatively silent with respect to the recipients of investment, but predicts that production and downward resource flows should peak relatively later in life, as increasing productivity from on-the-job training is cancelled out by declining strength, and that these rates should continue on to old ages in order to pay for the extended learning phase. It also proposes that men should be (almost as) equally concerned with the wellbeing of descendents as are women, and that investments from men and women could take different forms as a result of a division of labor.

Women and men work comparable amounts of time, roughly 50-60% of their time from early adulthood until old age. Women focus on household chores that are compatible with childcare (35-45%) and spend less time in productive activities away from the house (10-15%). The reverse trend is true for men. Through time, women maintain their comparatively low levels of productive work, and although they provide little aide in the form of direct grandparental care, they double the amount of time spent in household tasks, particularly food processing. Tsimane men increase the amount of time spent in non-wage production as they age, with an ever increasing emphasis on agriculture, and exhibit a slight increase in non-productive work. Consistent with the ECH, men and women appear to be employing different strategies with respect to investment at older ages, with men focusing on direct provisioning and women on increasing the productivity of descendents by performing other essential tasks.

The production data also point to this fact. Tsimane men continue to produce substantial surpluses into their sixties, accounting overall for twice as many calories as women. As predicted by the ECH, production peaks relatively late in life—for men, production levels in the forties and fifties are higher than they are at any other decade of life. Women's peak is also in the forties and remains

relatively high into the sixties. Children, on the other hand, are producing very little. Additionally, daily production rates increase more rapidly through time than the time allocated to productive activities, indicating increasing productivity within these activities. This speaks to the importance of investing in embodied capital and the extended time frames required to realize the full returns from such investments.

The consumption and resource flow data perhaps best capture the benefits that descendants enjoy from the investment of older individuals. We see the majority of calories produced by pre-reproductive individuals stay within one's natal family, being distributed to siblings, parents and to self, but that by the twenties, children and spouses are the major receivers any produced food. During the fifties, resource flows to children remain high and sub-adult children remain significant beneficiaries of produced food. By the sixties, however, women have ceased to provide net caloric benefits to their children, and in fact have no sub-adult children to invest in. During this decade, both men and women appear to switch their focus to investing in grandchildren over children, in both percentages of produced food given and overall net flows. These distributions result in children receiving roughly half of their calories from parents, with siblings (~15%) and then grandparents (~10%) being the two next important contributors. Downward resource flows to all descendants peak in the forties for both men and women. Although grandparents are not very substantial contributors to individual grandchildren, when this is multiplied by all grandchildren, the assistance is by no means insignificant. By the seventies, men and women have essentially ceased to provide any significant surplus to their descendants, but are not great caloric burdens, at least to their children. It is interesting to note that this is the first decade for which an individual upon entry cannot expect to live to the next decade.

CONCLUSIONS

All of the proposed hypotheses provide pathways through which true benefits are undoubtedly realized, and the important question is really one of magnitude. The MH and PH can account for the fitness benefits realized in the forties and fifties, but fail to explain the extension of the lifespan beyond that. The levels of investment shown by older men, matched with their low fertility, seems to imply that they are more concerned with investing in their existing progeny than pursuing additional fertility, contrary to the predictions of the PH. Although the MH and GMH emphasize the role of women in the evolution of a long lifespan, among the Tsimane, men are

providing much greater caloric contributions at later ages. Sixty year-old men are actually providing both their children and grandchildren with amounts that surpass the total downward resource flow of women at *any* age. Instead, women appeared to be focusing on aiding their families by boosting time spent in non-productive work. It was surprising, however, just how little direct parenting grandmothers were offering. This may be a result, however, of grandmothers acting perhaps more as supervisors of older children—something that will have to be determined through future analyses. Despite the low levels of production from older women, the logic of the GMH may still hold, that longevity was selected specifically to allow for the investment in descendents, but it must be qualified by the fact that men may have played just as important a role, or more, in driving this. Overall, the predictions of the ECH were best supported. Daily production peaked relatively late in life, mainly due to increasing productivity levels, and net downward resource flows continued until the sixties in men and the fifties in women. Although women did not remain productive as long as men, as stated above, they increased the time they spent in other household chores—a reflection of the different types of investment also predicted by the ECH. Finally, the fertility and resource flow profiles of men and women displayed remarkable correspondence, indicating a tight link between their reproductive careers and the goals of their reproductive efforts.

The greatest limitations of this research came from the small sample sizes at older ages—an artifact of the traditional pyramidal demographic profile of the Tsimane. Only 3.3% of our entire sample of nearly 2800 individuals was over 60 and only 1.4% over 70. This problem should be alleviated by future research, which will most likely involve biased sampling of older individuals. Additionally, we hope to include affinal kin in future analyses and to explore the actual effects that the reported investments have on descendent fitness. Despite the challenges, we believe that the data presented here provide strong evidence for the fact that post-reproductive periods are significant for both women *and* men, consisting of a shifting mix of investments in both children and grandchildren. The female-biased mother and grandmother hypothesis and the male-biased patriarch hypothesis received little support and are unappealing in the fact that they largely ignore one sex. The results presented here best support the predictions produced by the only two-sex model, the embodied capital hypothesis.

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