

**MORTALITY EXPERIENCE OF TSIMANE AMERINDIANS OF BOLIVIA:
REGIONAL VARIATION AND TEMPORAL TRENDS**

Running title: Tsimane mortality

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ABSTRACT

This paper examines regional and temporal trends in mortality patterns among the Tsimane, a population of small-scale forager-horticulturalists in lowland Bolivia. We compare age-specific mortality in remote forest and riverine regions with that in more acculturated villages and examine mortality changes among all age groups over the past fifty years. Discrete-time logistic regression is used to examine impacts of region, period, sex and age on mortality hazard. Villages in the remote forest and riverine regions show 2-4 times higher mortality rates from infancy until middle adulthood than in the acculturated region. While there was little change in mortality for most of the life course over the period 1950-89, overall life expectancy at birth improved by 8 years from 45 to 53 after 1990. In both periods, over half of all deaths were due to infectious disease, especially respiratory and gastrointestinal infections. Accidents and violence accounted for a quarter of all deaths. Unlike typical patterns described by epidemiologic transition theory, we find a much larger period reduction of death rates during middle and late adulthood than during infancy or childhood. In the remote villages, infant death rates changed little, whereas death rates among older adults decreased sharply. We hypothesize that this pattern is due to a combination of differential access to medical interventions, a continued lack of public health infrastructure and Tsimane cultural beliefs concerning sickness and dying.

Neel and Weiss' (1975) analysis of mortality patterns among the Yanomamo of Venezuela and Brazil was a bugle call to anthropologists to "produce comparable bodies of [demographic] data" of relatively isolated tribal populations. Thirty years later, and the number of thorough demographic studies remains few [see for example, Howell (1979) on !Kung, Hill and Hurtado (1996) on Ache, Blurton Jones et al. (2002b) on Hadza, Early and Headland (1998) on Agta, Layrisse et al. (1977) on Warao; Pennington and Harpending (1993) on Herero; Early and Peters (2000) on Yanomamo; Hill et al. (n.d.) on Hiwi]. Our understanding of mortality profiles among remote, relatively unacculturated people living in autarkic societies without the convenience and protection of public health and sanitation programs, modern medicine, access to hospitalization and predictable resources therefore relies heavily on few well-worn examples. Furthermore, there are even fewer cases for which the mortality experience of middle-aged and older individuals living in remote subsistence-oriented populations is well documented. The lack of focused studies is due in part to problems of age-estimation and small sample sizes of older individuals. Many studies tend to cluster adults into large age categories such as 40+ or 50+. As a result, we know very little about the traditional human aging process and how it varies among societies.

In a recent review of all available demographic data on mortality patterns among hunter-gatherers and forager horticulturalists, Gurven and Kaplan (2006) showed that prior to significant exposure to western medicine and public health, humans exhibit a characteristic mortality profile that differs dramatically from that of other non-human primates, including from our closest relative, the chimpanzee. A summary of our main findings follows: 1) Post-reproductive longevity is a robust feature of hunter-gatherers and forager-horticulturalists, appearing to be a fundamental feature of the life-cycle of *Homo sapiens*. Survivorship to

grandparental age is achieved by over two-thirds of people who reach sexual maturity, and lasts for two decades, on average; 2) life expectancies for modern foraging, and presumably ancestral populations, are typically low due to high infant and child mortality but adult mortality rates remain low through the fifth decade of life; 3) much of the variation across foraging and forager-horticultural populations in mortality hazards and life expectancy at birth is due to differences in infant and childhood mortality rates; 4) mortality rates across populations tend to converge during adulthood, especially during and after late middle age; 5) all populations show a modal age of adult deaths for hunter-gatherers in the range of 65-75 years, which we interpret as the closest functional equivalent of an “adaptive” human lifespan.

Departures from this general pattern in published estimates of life expectancy in historical and past populations are likely due to a combination of high levels of contact-related infectious disease, excessive violence or homicide, methodological problems that result in poor age estimates of older individuals and inappropriate use of model life tables (*ibid*). On average, we found that illnesses accounted for 70%, violence and accidents 20%, and degenerative diseases 9% of all deaths in the cross-cultural sample. Illnesses largely include infectious and gastrointestinal disease, although less than half of all deaths in our sample were contact-related disease.

Today, however, most of these and other small-scale subsistence-oriented groups have undergone or are undergoing dramatic change due to their increasing incorporation into modern state societies. While increased sedentism, intensive farming and greater market access are often clearly associated with higher fertility (Bentley and others 1993; Sellen and Mace 1997), the effects on health and mortality are more ambiguous (Godoy and others 2005b). A lack of micro- and macro-nutrient diversity and increased susceptibility to infectious disease are two pathways

by which morbidity and/or mortality can increase in transitional and acculturated populations (Cohen 1989; Eaton and others 1988). While the former may be due to a heavier reliance on carbohydrate-rich and protein-poor farm staples, the latter is usually attributed to increased sedentism and higher population densities that are typical of groups heavily reliant upon agriculture. On the other hand, however, access to vaccinations, improved hygiene, antibiotics and medical services may reduce morbidity and mortality. The total effects of these two processes remain largely unexplored. Furthermore, acculturation need not impact mortality on each age class in the same way. For example, immunizations can substantially reduce infant and child mortality, but might impact adult mortality mainly among the immunized cohort (Crimmins and Finch 2006).

Over the last four decades, demographers and epidemiologists have developed a body of theory and empirical data to explain patterns of change in mortality and morbidity rates that accompany modernization (Frederiksen 1969; Gribble and Preston 1993; McKeown 1976; Omran 1971; Preston 1976; Salomon and Murray 2002). Those changes have been termed the ‘epidemiological transition’ and were first described by Omran (1971). Omran (1971:510) defines the epidemiological transition as “the complex change in patterns of health and disease and on the interactions between these patterns and their demographic, economic and sociologic determinants and consequences”. It has generally been described as a pattern in which pandemics of infectious diseases are gradually replaced by chronic, degenerative diseases as the leading causes of death. Most of the original work on epidemiological transition was based on the experiences of Europe, North America, New Zealand, Australia and Japan during the early twentieth century (see references above). The most significant finding is that changes in public health had massive effects on reducing infant and early childhood mortality due to the lowered

exposure to infectious disease. Reductions in older age mortality were small, with major changes in late adult lifespan achieved only after 1960. In this paper, we argue that the mortality experience of small-scale indigenous populations in response to exposure to modern states today may be very different from that which occurred a century ago with the rise of public health.

Against this background, this paper has four principal goals. First, it contributes to the pool of demographic studies on small-scale societies by exploring mortality patterns among the Tsimane, a population of forager-horticulturalists living in the Bolivian Amazon (Figure 1). The Tsimane diet is a mix of wild game, fish, plantains and rice. Although agriculture provides approximately 3/4th of the caloric contribution to the diet, the relative abundance of protein and lipid sources varies depending on proximity to rivers, where fish is plentiful and primary forest where wild game is abundant. The mix of farming and foraging presents viable options for obtaining benefits of a diet rich in proteins, lipids and carbohydrates. If diet quality deteriorates with the shift to agriculture then a population with a mixed subsistence strategy should show improvements in health indicators in comparison to pure foragers or pure horticulturalists. By examining mortality at all ages, we hope to document and situate the Tsimane case in the larger body of Amazonian and other anthropological populations.

A second goal is to provide more precise estimates of mortality patterns among middle- and old age individuals. The Tsimane demographic sample contains the largest sample size of risk-years for older adults that we are aware of for a small-scale indigenous population, and therefore allows for a more thorough depiction of mortality in late adulthood.

Third, and most importantly, our goal is to examine regional and temporal variation in mortality rates in different Tsimane communities. The Tsimane are rapidly acculturating to national society and acculturation is an uneven process. The attraction of markets and other

features of national society has been and will continue to impact indigenous groups all over Amazonia and the rest of the world (see Godoy 2001). One enticement of acculturation may be the positive impact on health status. On the other hand, increased population density and food stress also appears to accompany acculturation among the Tsimane and other Amazonian populations. Increased population size and density is often associated with increased waste accumulation, macroparasites, gastrointestinal disease and higher rates of acute infections (Ewald 1994). If health worsens and morbidity increases, the question of why acculturate is even more salient (Godoy and others 2005a).

Teasing apart the separate effects of dietary shifts and population size or density effects can therefore be difficult. Tsimane currently reside in both dispersed, small settlements and larger, more densely populated villages. Tsimane villages that are more acculturated and closer to town tend to be larger. Thus, the Tsimane case is useful for distilling mortality variation that might be due to broad differences in both diet and population density. Health care, immunizations and hospitalization are beneficial byproducts of increased access to market towns, whereas loss of traditional culture, alcoholism, sexually transmitted diseases, infectious disease, stress and depression are often unfortunate concomitants of acculturation. One key factor affecting the level of acculturation and exposure to modern medicine is the nearness and ease of access of different villages to markets by way of roads or rivers. Variation in acculturation by geographical area is therefore a natural experiment for investigating the effects of integration on mortality. By focusing attention on the distance of different villages to the nearest market town, San Borja, and on temporal changes in mortality, we can begin to understand the differential effects of modernization on overall and age-specific Tsimane' mortality. In addition, there have been changes in mortality rates over time, and those changes interact with both age and

community location. We will show that the Tsimane have had a very different pattern of mortality change than has previously been described for the epidemiologic transition.

Finally, a fourth goal is to describe and contrast the causes of mortality in older versus younger adults. An appreciation of mortality patterns is crucial for understanding aspects of Tsimane life history, such as growth, production, reproduction and aging. This paper thus lays the demographic groundwork for future studies of physical growth and maturation, age-related changes in economic production, inter-generational resource transfers and senescence.

The paper is organized as follows. We begin with a description of the Tsimane and their current situation, and discuss methods of data collection and analysis. The results are then presented, discussing first infancy, childhood and adolescence, and then early adulthood, middle-adulthood and old age. In each case, we examine the effects of proximity to town (comparing the more acculturated villages close to the town of San Borja, with a distant but missionized settlement, and then to the much more isolated communities living in riverine and forest environments, respectively). We also compare the early time period 1950-1989 with the more recent period, 1990-2002 to examine both secular trends in mortality and its interaction with proximity to San Borja. The results section concludes with a discussion of how the causes of mortality change with each of the six age groups mentioned above. The paper concludes with a discussion of the results and their implications for epidemiologic transition theory, particularly in Amazonia and among rural societies throughout the developing world.

MATERIALS AND METHODS

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 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.

Denevan (1966) estimated a population size of roughly 350,000 natives in the Beni region shortly after contact and a low population density of 2 per km². Although the Tsimane' were exposed to Jesuit missionaries before the 17th century, they were never successfully settled in missions and remain relatively unacculturated (Chicchón 1992). Rice and various citrus fruits were likely introduced by the Jesuits at this time. Other neighboring lowland groups such as the Mojeño and Yuracaré engaged in more intensive agriculture and were more easily concentrated in centralized missions. Some degree of the Tsimanes' isolation is suggested by the fact that their language is an isolate, even within Bolivia, sharing a similar vocabulary and grammar only with the Mosekene, who inhabit the southern and northern stretches of Tsimane territory. Tsimane share distant genetic affiliation with the Yuracaré, Trinitario and Quechua ethnic populations, and little affiliation with the Aymara (Bert and others 2001). However, there is some evidence that Tsimane likely interacted with Incas (Saignes 1985).

New mission posts in several villages began in the 1950s. The greatest influence of the 35-year-old New Tribes Mission was to create a system of bilingual schools with the goal of training Tsimane' as teachers, and organizing the election of chiefs in each village located 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 intermittent access to medicines in exchange for labor since 1990.

Tsimane villages vary in their degree of market access and interaction with Bolivian nationals. Acculturation takes several principal forms: visits to the main market town, San Borja (pop'n ~18,000), and the selling of agricultural produce, wage labor with loggers or colonists, debt peonage with river merchants and formal schooling. Portable radios that transmit messages and music from the New Tribes radio tower outside of San Borja are also available in many villages. The Tsimane came into greater contact with outsiders as new roads were built in the 1970s, inviting a burst of logging and trading interests, as well as encroachment by lowland and highland colonists (Ellis, 1996; Chicchón, 1992). Market items that are highly valued by the Tsimane include clothing, aluminum pots, utensils, salt, sugar, kerosene and school supplies. Schools exist in over 2/3rd of all Tsimane villages, having been established anywhere from two to twenty years ago.

Tsimane make occasional visits to San Borja during town festivals, and some sell agricultural produce or handicrafts. Near San Borja, some Tsimane work as farm hands for local ranchers. Along the upper Maniqui River, Tsimane sometimes 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, based partially on historical estimates of Tsimane population growth 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. However, it is unlikely that any epidemic would have globally impacted all Tsimane due to the highly dispersed character of Tsimane settlements.

Study villages

Demographic data were collected in 18 villages that span traditional Tsimane territory (Figure 1). These include distant villages on the upper Maniqui River (Cachuela, Cosincho, Munday, Fatima, Anachere, Donoy, Emeya, Catumare, Boreyo), villages situated along a private logging road in the interior forest (Aperecito, Uishiricansi, Cuverene, Nuevo Mundo, Campana, Moseruna) and two acculturated villages located near San Borja (Tacuaral de Mato, San Miguel). We separate Fatima from the rest of the riverine sample because of its unique association with a Catholic Redemptorist mission that has provided some medical assistance since its inception in 1952. Table 1 reports the numbers of interviewed adults, reproductive histories, deaths and risk-years resulting from interviews with members of each village.

The source study population, constituting about 31% of all Tsimane, has a very young age structure, as shown in the age-sex pyramid in Figure 2. Approximately 51% of the current population is under age 15 and only 10% over the age of 45. The sex ratio is male-biased during early childhood, and most of adulthood, with a slight female-bias present during adolescence and early adulthood (15-24) and after age 70.

Demographic interviews

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 and 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 information. On the basis of these interviews, all living and deceased Tsimane' in the sample were assigned estimated ages. The Tsimane' have no taboos against speaking the names of deceased relatives, including small children. In consultation with a team physician (Dr. Daniel Eid Rodriguez), causes of death were assigned using a system based on the International Classification of Disease version 10 (ICD-10) (WHO 1990). No cause could be determined for 17% of the 1,715 deaths in our complete sample, due more to a lack of information by informants than inexplicable symptoms. Percentages of deaths due to specific causes therefore only consider the set of deaths with known causes. Cause-specific death rates were calculated by dividing the number of deaths due to specific causes by the appropriate number of risk-years.

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 and others 2002a). 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. Catholic missionaries have recorded the dates of 1,110 births among the Tsimane since 1952, many of the deaths occurring during the same period, and age estimates for an additional 120 individuals who were baptized as small children or as young adults during the early 1950's. These records are invaluable because they include many residents of Fatima, three additional study villages, Cachuela, Munday and Cosincho, and other migrants now dispersed in other communities. We have also obtained birth records for an additional 310 individuals associated with the Evangelical Mission, La Cruz.

For individuals born prior to record keeping, four procedures were used to ascribe ages to individuals from the reproductive histories. For children, age at death was estimated using developmental stages (e.g. just born, still breastfeeding, crawling, walking), comparisons to living children of known ages, and seasons of birth and death. For each pair of consecutive siblings, the birth interval was estimated. For pairs in which the older sibling was alive when the younger one was born, the elder's age at birth was estimated, using the above methods for assigning age at death. For pairs in which the older sibling died before the birth, the time interval between death and birth was estimated using information on the ages of other living children in the family and seasonality.

The second method ranked all individuals, both living and deceased, in the sample of reproductive histories by relative age, beginning first with five-year estimated age classes for relative age rankings. Multiple informants were used for each age class and inconsistencies were investigated and resolved. In addition, significant age-related relationships were investigated to

augment the relative age lists. These include ‘hip-child’, hunting mentor, and playgroup companions.

Third, ages were also estimated using historical information and known historical events. A Catholic missionary, Father Marcelino, began working with the Tsimane’ in 1952, and Father Martin Bauer in 1958. Both missionaries are widely known among most Tsimane in the Maniqui region. Another missionary was murdered in 1848, and many Tsimane scattered to other regions downstream and in the interior forest back in the late 1920s. The first dirt highway was cleared in the interior forest in 1970 and then refurbished again in 1985. The Tsimane government organization started in 1989. We investigate which people were born (and which were not born) and approximate ages of other individuals, such as younger siblings, or smallest child, with respect to these events. When interbirth intervals are short, as is common among the Tsimane, the use of sibling comparisons and dated events can be an effective tool in age estimation.

A final method used a sample of seventy photos of individuals with known ages. For older individuals, fifty photos of men and women from ages 50 through 75 were used. These photos were used as a means of aging dead individuals at the time of their death, and for aging old interviewees. This method worked in conjunction with comparisons of dead individuals to known individuals in the community and surrounding region.

Each of the above methods provides a roughly independent estimate 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. Individuals for which confident ages could not be ascertained are not included in this analysis. These individuals are mostly people whose name appeared only once in the interviews, distant siblings without other interviewed kin in the sample, and estranged individuals not seen or heard from in many years.

All research was conducted with the approval of the Institutional Review Boards of the University of California-Santa Barbara and University of New Mexico, and with approval by the Tsimane government in San Borja (*Gran Consejo Tsimane*). Approval by village leaders and members was given in community meetings and before each interview.

Data analysis

Period life tables stratified by sex, region or time period are calculated by considering the total number of deaths within a specific category (e.g. females living near San Borja in the 1950's) with respect to the total number of person-years at risk of death in that same category. Age-specific probabilities of death (q_x), cumulative probability of living from birth to age x (l_x), and the yearly mortality hazard (h_x) are estimated from these life tables. We estimate infant (IMR) and child mortality rates using a restricted dataset that includes only births or risk-years from directly interviewed individuals.

We smooth l_x and h_x functions using a Siler competing hazards model (Gage 1989; Siler 1979). The Siler model includes three components: a negative Gompertz exponential function to capture juvenile mortality, a Makeham constant hazard and a positive Gompertz function to capture late age mortality. The hazard has the following functional form:

$$h(x) = a_1 \exp(-b_1 x) + a_2 + a_3 \exp(b_3 t)$$

We produce Siler-based l_x and h_x curves using the non-linear regression procedure (NLIN) in SAS version 9.1.

The statistical comparison of mortality rates is facilitated by the use of discrete-time logistic regression models (Allison 1995). We use fixed effects models for examining temporal trends from the 1950's through 1990's and geographical variation in age-specific mortality in

forest, riverine and acculturated regions. Due to the similarity in mortality rates from 1950-89, we primarily compare temporal trends between 1950-89 and 1990-2002 time periods¹. These regressions are implemented with the LOGISTIC procedure in SAS v. 9.1 and applied separately for six life stages: infancy (<1 year old), early childhood (1-4), late childhood (5-15), early adulthood (16-39), middle adulthood (40-59) and late adulthood (60+). All regressions produce partial estimates that examine the effects of age, sex, region and period simultaneously. We test for interactions and report these effects when statistically significant at the 5% level.

RESULTS

Infancy (age <1)

Figure 3 shows infant mortality rates (IMR) grouped in five year intervals from 1950 through 2000, and makes comparisons with national Bolivian IMR (UN Common Database, UNICEF). While, at the national level, Bolivia experienced a significant decline in infant mortality of 2.41/1,000 per year ($p < 0.0001$) during the fifty year period, Tsimane infant mortality did not decrease significantly (0.91/1,000 per year, $p = 0.14$).

Using the most reliable data derived from focal-person reproductive histories, the IMR for the Tsimane population as a whole is 137/1,000 for the period 1950-1989.² This estimate is derived from live births only, and does not include reported cases of abortions or miscarriages. Overall, 2.9% of pregnancies were reported as miscarriages or abortions. However, ethnographic experience and informant reports suggest that some of these reported miscarriages are probably premature births or babies killed by infanticide, which would lead to a slight underestimate of

IMR. If we assume that a conservative 20% of reported abortions are legitimate births, then the IMR increases from 137 to 144. Moreover, from 1990-99, 4.8% of all pregnancies from directly interviewed adults were reported as miscarriages, suggesting that some miscarriages in the past were forgotten as well.

Table 2 (part A) reports the IMR among Tsimane regions and by period. The more isolated communities located along the upper Maniqui River and in the interior forest show the highest rate of infant deaths (177 and 178, respectively). Although Fatima is located along the upper Maniqui River, it shows a lower IMR of 142. The lowest IMR occurs among acculturated communities living in close proximity to San Borja (100). Thus we find an almost two-fold difference in infant mortality rates among Tsimane communities.

Logistic regression analysis of infant mortality confirms a significant main effect only for region, where infants born in remote communities experience about 1.5 times the risk of dying than those born near San Borja (Table 3:A). IMR does not significantly vary between females and males, although we do find that female infants die at slightly higher rate (14.8% versus 13.7% dying during the first year of life, respectively). IMR does not change significantly over time and there are also no significant two-way or three-way interactions between sex, geographical region and period of birth. The mean rates reported in Table 2 show that IMR actually increased somewhat in the least acculturated villages in the riverine and forest ecologies, whereas rates tended to decrease somewhat in the Fatima mission and even more so near San Borja.

Early childhood (ages 1-4)

Average survivorship to age five (l_5) is 79.3% (80.8% for males, 77.7% for females – see Figure 4). The total probability of dying from ages 1 to 5 is 9.8%, 8.7%, 7.5%, and 3.6%, for forest, riverine, Fatima and near San Borja samples, respectively, with average rates per year shown in Table 2. Logistic regression analysis shows that expected mortality decreases by about 30% with each advancing year over the age range 1 to 4 as children grow and their immune systems develop.

Again, there are no significant effects of sex. Mortality appears to have improved over time, with mortality prior to 1990 being 1.6 times higher than after 1990 (Table 2). However, there is a stronger effect of region. Controlling for sex and time period, mortality is 2.4 times greater in the remote villages than in the villages near San Borja (Table 3:B).

Late childhood (ages 5-15)

Survivorship to age fifteen (l_{15}) is 74.2% (75.2% for males, 73.1% for females – see Figure 4), indicating that one-fourth of children ever born die before the age of fifteen. Mortality rate continues to decrease by about 7% each advancing year from ages 6 to 15 (Table 3:C). By age 15, mortality rate is below 1% per year (Figure 4).

There are significant and similar effects of period and region on mortality, with odds ratios of about 1.63. This suggests a smaller regional effect than at the earlier ages. There is a marginally significant region by period effect ($p=.066$), as can be seen in Table 2, where the gains in survivorship seem to be greater in the more acculturated communities near San Borja. The highest mortality rates in late childhood appear to be in the riverine communities.

Early adulthood (ages 15-39)

Survivorship to age 39 is 60.9% (57.8% for females, 63.8% for males – Figure 5). Mortality rates for both men and women during early adulthood are low and fairly flat, at about 1%, with increases beginning at around age 30 (Figure 5). In a multiple logistic regression, the mortality rate increases by less than 3% per year (Table 5:A). During these critical reproductive years, women show a 35% higher mortality rate than men, with most of the difference being in the age range of 26-39, where the odds ratio is 1.5. Presumably much of this difference is due to death in childbirth and related complications.

The multiple logistic regression also reveals large regional differences, where the odds ratio is 2.5 in remote riverine and forest villages, and smaller but significant for period differences, with an odds ratio of 1.63 (Table 5:A, Table 2). Further analysis reveals that almost all the regional effect is due to the 15-25 year age bracket (odds ratio=4.0).

Middle adulthood (ages 40-59)

Survivorship to age 59 is about 41.0% (40.5% for women, 41.4% for men- Figure 5). During middle adulthood, the mortality rate increases by about 6% per year (Table 5:B, Figure 5). There are no significant differences between the sexes during this period, although the point estimates in Table 2 show a slightly lower mortality rate for women.

Interestingly, the overall regional effect is in the opposite direction from the common pattern encountered among other age groups, with the more remote communities exhibiting lower mortality than those near San Borja, with an odds ratio of 0.66. Mortality of middle aged adults at Fatima is about half that in the acculturated region (Table 5:E). There is a very strong period effect, however. Mortality is much higher prior to 1990 than after, with an odds ratio of 2.5. This can be seen especially in the more remote villages (Tables 2 and 5).

Late adulthood (ages 60+)

About 40% of men and women survive to age 60 (Figure 5). Late adulthood shows a 9% increase with each advancing year from age 60. For late ages, men are about 50% more likely to die than women. Upon reaching age 60, women and men show a mean of 12.3 and 9.9 years remaining, respectively (Table 6). There are no reliable cases of individuals surviving past the age of 80.

As in middle adulthood, the period effect is stronger than the region effect. Only Fatima shows a significantly higher mortality rate in late adulthood than in other regions, with an odds ratio of 2.5. When region is dichotomized as those villages located far versus those near San Borja, the region effect is borderline significant ($p=.06$ with an odds-ratio of 1.76). The odds ratio for the period effect is 2.47, $p<0.0001$. Thus, as in middle adulthood, there are large significant gains in survivorship in recent years. There are no significant sex, period or region interactions, but from Table 2, it is clear that the large absolute effects are in the more remote communities.

Population size and distance to town

So far we have examined regional differences in mortality, especially during high mortality phases of infancy and childhood. Two dimensions of the regional differences are the size of villages and the distance from San Borja. We now attempt to use direct measures of these two *village*-level features to see if they further explain differences in mortality during infancy and early childhood. We can only crudely examine the effect of population size on infant and child mortality because our estimates of population size are based on censuses from 2002 while

we estimate mortality based on a larger sample stretching back thirty years from 1970-2002 to generate a sufficient sample at the village level. It is likely that census counts in specific villages in different areas have increased at different rates over the past thirty years, with numerous fissions, fusions and migrations, particularly in small communities. Nonetheless, based on retrospective interviews of residence histories, we suspect that the rank order of village sizes should not have changed significantly over this time period.

Contrary to expectations based on the notion of a higher transmission rate of infectious diseases in more populated areas, we find that larger communities exhibit a lower infant mortality rate (IMR) ($r=-0.50, p=0.03$) and a lower probability of dying by age 5 (${}_5q_0=1-l_5$) ($r=-0.51, p=0.03$) (Figure 7).

Distance to the town of San Borja is measured both as the straight-shot distance between a village center and San Borja using a handheld GPS unit, and as the actual travel distance along roads or the Maniqui River. Using straight-shot distance, more distant villages show higher IMR ($r=0.49, p=0.04$) and higher ${}_5q_0$ ($r=0.49, p=0.04$) (Figure 8). However, these relationships lose significance when using travel distance by road or river.

Village size and distance to market are not independent variables. More people choose to live in villages that provide easier access to the market town. In our 18 village sample, there is a significant negative association between distance from San Borja and village size ($r=0.48, p=0.04$), and this relationship increases when excluding Fatima ($r=0.75, p=0.0006$). We find that population size and distance each lose statistical significance when analyzed simultaneously as predictors of IMR and ${}_5q_0$ in multiple regression analyses.

Mortality and its causes across the life course

Table 6 presents an annual life-table for males and females, covering the early period from 1950-89, based on all deaths and risk-years from this forty year period. Life expectancy at birth for males and females is 44.8 and 45.4, respectively. Siler-based mortality hazard and survivorship curves are shown in Figure 6. The mortality hazard curves illustrate the cross-over whereby older males are more likely to die than older females, whereas female mortality is modestly higher than male mortality for the rest of the life course.

During the 1990's, life expectancy at birth for males and females increased to 53.5 and 52.8, respectively. Table 7 shows the abridged life table for 1990-2002 and Figure 6 compares the Siler-smoothed mortality hazard from the combined 1950-89 sample with that from the 1990's. The regional differences in mortality mirror, to a large extent, the period differences in mortality, with the villages closer to San Borja exhibiting lower mortality than the more distant ones. The distant Fatima mission village falls somewhere in between the more acculturated villages and the unattended forest and remote riverine villages. Despite Fatima's remote location, some medical support has been provided by the Mission staff, and on occasion, there have been emergency departures to San Borja by small propeller plane through use of an airstrip. The general pattern, however, is that the regional effects are stronger at younger ages, whereas the period effects are stronger in adulthood and old age.

Causes of death over the lifespan reflect the importance of infectious disease at all ages, but also reveal some important differences across the life course. Beginning with pregnancy, an analysis of reported ('emic') causes of miscarriages shows that over a third (36.5%) were induced by an abrupt and rough traumatic fall, 16% from over-working and carrying too much weight (usually firewood, agricultural produce or large bundles of palm thatch), and 15% from

maternal sickness. An additional 7% were self-induced as a means of spacing births or because of doubts concerning paternity.

Almost half of all infant deaths in our sample are due to infectious disease, for a total rate of 39.3 deaths per thousand infant risk years (Table 8). Respiratory infections, such as whooping cough, pneumonia, measles and tuberculosis account for half of these diseases of infectious origin. The largest community, Fatima, had the highest rate of respiratory infectious disease (25.4/1,000). There is also a six-fold difference in measles rates across regions, confirming our suspicion that certain disease outbreaks were likely localized in space and time in the Tsimane region. Diarrhea, extreme parasitism, other gastrointestinal disease and perinatal complications together account for about a third of infant deaths. Complications at birth or perinatal infection accounted for about a fifth of infant deaths with a total rate of 18.7/1,000, but the forest communities showed a much higher rate, 33.8/1000. Perhaps some of those cases were cryptic forms of infanticide. Of the 10% of deaths reported to be due to accidents or violence, one third of these are from infanticide, and one-fourth from falls out of hammocks or baby slings. Infanticide was most frequent in the forest region (4.8% of infant deaths). The rate of infanticide is low, compared with reported estimates for other Amerindian populations (see Hill and Hurtado: Table 14.1; Early and Peters 2001: Table 19.9).

Over three-fourths of all early childhood deaths are due to infectious disease (79%), with forest and riverine regions showing the highest rates due mainly to respiratory disease (8.5 and 8.3/1,000, respectively - Table 4). While infectious disease accounts for a greater percentage of deaths during early childhood than in infancy, the actual rate of death due to infectious disease is only about a quarter (10.4/1000) as high as in infancy. The lower percentage in infancy is due to the greater relative importance of perinatal birth complications and accidents and violence in

infancy. The large drop in death rates due to infectious disease during early childhood reflects the increase in immunocompetence as children grow.

A similar percentage (72%) of late childhood deaths are due to infectious disease, but the death rate (3.3/1000) is only about one third as high as in early childhood and less than one tenth the rate of infancy. One-fourth of deaths are due to measles and 14% due to accidents or violence. The riverine sample shows the highest infectious disease rate (4.6/1,000), twice that in the acculturated region where infectious disease is the lowest (2.3/1,000).

By early adulthood, infectious disease drops to less than one-half of all causes of death, although death rates, especially for respiratory illnesses, remain at a similar level as in late childhood (2.9/1,000). Overall, tuberculosis is responsible for 13% of deaths, with higher incidence evident in forest and riverine regions. The forest region shows an over eight-fold higher incidence of violent and accidental deaths compared with that in other regions (17/1,000), due mainly to higher rates of homicide. Violence and accidents account for 28% of all early adulthood deaths (Table 8). Common accidental deaths are due to trees falling in fields during clearing activities, drowning in rivers, snake bites and suicide. For women, death in childbirth accounts for a large fraction of deaths, especially during the prime reproductive years.

Over half of deaths in middle adulthood are due to infectious disease (59.8%) and this life stage witnessed a doubling of the incidence of death from infectious disease (7.0/1,000). The incidence of death from infectious respiratory disease and digestive illnesses (e.g. appendicitis, obstructed gut, gallbladder disease) also doubled. Accidents and violence continue to explain almost a fourth of all middle aged adult deaths and show an increase in the death rate (2.7/1,000, Table 4). Over one third of these deaths (total of 9%) are due to homicide (incidence 1.1/1,000).

Tuberculosis is a cause of 14% of late age deaths with a four-fold increase in death rate compared with that in middle adulthood (7.7/1,000). This four-fold increase is also observed for pneumonia (1.9/1,000) and respiratory infectious disease in general (18.7/1,000). The riverine sample shows the highest incidence of respiratory infectious disease (23.8/1,000), double that of Fatima where the death rate is lowest (12.0/1,000). Immune function appears to be increasingly compromised in old age. Accidents and violence are the next largest macro-cause of death, accounting for 17% of deaths and with prevalence of 9.6/1,000. The acculturated sample shows the highest rates of deaths due to intestinal disease and accidents and violence, particularly homicide (4.1/1,000). The death rates from cancer and cardiovascular deaths are not trivial (3.3 and 1.9/1,000, respectively), even if these two categories only explain 6% and 3% of late age deaths, respectively. It is relevant to note that 26% of the 58 older adults dying of unknown causes were said to have died of “old age”. Old age is said to occur when there are no obvious symptoms and the person is usually reported to have been feeble, blind and/or unable to walk. It is possible that a large percentage of deaths in old age are actually the sequelae of cancer, given the frequent occurrence of intestinal disease and respiratory diseases, and this large unknown category.

Summary of results

1. Prior to 1990, 14% of Tsimane died in their first year of life, 26% before age 15 and 44% before age 45. Life expectancy at birth was 43 years. Upon reaching age 15, Tsimane could expect to live until age 58. Those reaching age 45 could expect to live until age 66. Those reaching age 65 live an average of 9 additional years.

2. Sex differences in mortality are evident during reproductive adult years and late adulthood. Women show 35% higher mortality from 16-39 and men show 50% higher mortality after age 60.
3. Villages in the remote forest and riverine regions show highest overall mortality, with 2-4 times higher mortality until middle adulthood.
4. There was little change in mortality over most of the life course throughout the period 1950-89. Overall life expectancy at birth improved by 8 years from 45 to 53 after 1990. There was a larger period effect on death rates during middle and late adulthood than during infancy and childhood. In the remote villages, infant death rates changed little, whereas death rates among older adults decreased sharply.
5. Over half of all deaths are due to infectious disease, especially respiratory and gastrointestinal infections. Accidents and violence account for a quarter of all deaths. Cancer and cardiovascular disease are relatively rare causes of death, but in old age, it is possible that their rates may be as high as those in developed countries.

DISCUSSION

There is substantial regional and temporal variability among mortality profiles in Tsimane communities. Overall, those living closest to town suffered lower mortality, and all regions witnessed improvements in survivorship during the 1990's. However, the pattern of change and regional variation is complex, and differentially distributed across the life course. Regional effects were strongest at younger ages, and period effects were stronger at older ages.

This pattern is partially consistent with the overall framework of epidemiologic transition, but also in some ways, highly inconsistent with the historical transitions in developed countries upon which the theory was built (Omran 1971). Even the accelerated, delayed and transitional models of epidemiologic change (Olshansky and Ault 1986) do not adequately capture the Tsimane experience. The patterns presented here are consistent in the sense that diseases of infectious origin are, in large part, responsible for the high mortality rates of the Tsimane, and because modernization has had a substantial effect on lowering the risk of death due to infectious disease. They are inconsistent in the sense that although our data show an overall decrease in mortality in the past decade, we have observed a modest or no effect of period on infant mortality rates in remote Tsimane communities. When western countries historically underwent epidemiologic transitions, reductions in infant and child mortality rates showed the greatest improvements (Omran 1971).

We would like to offer briefly an elaboration of epidemiologic transition theory to help explain this pattern of results, and to provide a broader framework for examining mortality transitions worldwide. Our basic proposal is that mortality transitions can be decomposed into changes in three factors that may operate somewhat independently: 1) host vitality and immune defenses; 2) exposure to morbidity and mortality risks; and 3) modalities for treatment and prevention of morbidity and mortality risks. Host vitality refers to phenotypic condition and the ability of the host to combat assaults of infectious diseases and other forms of morbidity through biological defenses. Presumably, host vitality is improved with better nutrition and sufficient antibody responses due to prior disease history. Exposure to morbidity and mortality risks can change in response to a) public investments, such as in the water supply and sewage treatment; b) population movements, density and distribution, which affect the introduction and rate of

spread of new and old diseases (Ewald 1994); c) host behavior, such as handwashing, risk taking, diet and exercise and d) a variety of other factors, including the emergence of new diseases, and incomplete antibiotic treatment. Treatment modalities can change in response to a) public investments and technological change, such as the availability of vaccinations, antibiotics, clinics and hospital services, b) cultural change, such as loss or gain in knowledge of traditional or modern healing practices, and c) host behavior, including the knowledge, capability and choice to utilize different treatment options ranging from traditional healers, public and private clinics, to purchased or collected natural and commercial pharmacopeias.

In the case of western countries in the late nineteenth and early twentieth centuries, most of the change in mortality appears to be due to the second factor, exposure to morbidity risks, and perhaps some smaller contributions of the first and third factors (Barrett and others 1998). At the turn of the century, most major cities had cleaned up their water supply and developed more adequate systems of sewage. There were also changes made in crowding and housing. These changes greatly reduced exposure to infectious disease. Since infants and children under age 5 are most susceptible to dying from such infections, these changes in public health had major effects on the mortality rates of young children (Schofield and others 1991). While there were continual improvements in treatment modalities, the major gains in treatment and prevention due to the advent of antibiotics and effective vaccines did not come until later in the century (McKeown 1976).

The Tsimane case is quite different. Disease exposure probably has not decreased at all, and may even have increased. Although there have been a few attempts to provide clean water in Tsimane villages near San Borja, these attempts have been largely unsuccessful and the vast majority of Tsimane people obtain their water from untreated surface water sources. Attempts to

create ground wells in more distant communities have also been largely unsuccessful. Due to increasing population in the region as a whole, increased livestock near San Borja, and increased use of motorized transport and toxic detergents, water quality may perhaps be substantially worse now than in the past few centuries. Based on the results of fecal analyses, we have found that members of all of communities in our sample present high rates of parasitism, with prevalences near 100% in many communities, and frequent gastrointestinal infections. Common parasites include *Uncinaria* (hookworm), *Ascaris lumbricoides* (roundworm), *Strongyloides stercoralis*, *Giardia lamblia* and *E. histolytica*. Moreover, behavioral practices that increase disease exposure remain intact. Very little handwashing is practiced, and soap is frequently unavailable or not used regularly. Infection and re-infection is possible through several routes. Unwashed hands prepare and handle foods that are only rinsed with potentially contaminated water. Children's waste products are wiped cleaned with rags or leaves, and such cleaning is not usually followed by washing. Finally, communal drinking of homemade beer (*chicha* or *shocdye*), generally not prepared using hygienic practices, is an important component of daily social life in every Tsimane community.

On the other hand, there have been significant changes in the third factor, treatment modalities. During the 1990's, there was an increase in immunization campaigns that even sporadically entered remote regions. In 1990 the mission-organized health clinic, Horeb, was established outside of San Borja to provide medical assistance for Tsimane. An evangelical mission-affiliated nurse also helped with numerous cases of hospital care of gravely sick individuals during this time, in coordination with personnel at Horeb. Analysis of inpatient records for the year 2000 shows a large number of people receiving treatment, primarily for infant and child diarrhea, fevers, pneumonia, influenza, skin and eye infections. The majority of

patients came from nearby communities due to excessive travel time for members of distant communities and lack of sufficient food for patients and family members while awaiting recovery. There is also a municipal hospital in San Borja to which Tsimane sometimes travel when they are gravely ill. Some have received surgeries there. Moreover, there are itinerant merchants that travel to Tsimane communities, both distant and far, to trade forest products and food for clothes, cooking utensils, alcohol, and, importantly, antibiotics and treatments for Leishmaniasis.

With these factors in mind, we offer the following set of hypotheses to explain the pattern of mortality change among the Tsimane. The life expectancy of the Tsimane had already begun to change by 1950, and this is why we find a life expectancy of about 44, instead of the usual 35 for other pre-modern populations. The first set of changes was due largely to host factors, as a result of nutritional improvements with the introduction of rice horticulture, citrus fruits and some market exchange. From 1950 to 1990, large regional differences in mortality rates developed, because members of the closer villages could travel to receive medical treatment. Members of close villages were also more likely to be involved in patron-client relations with Bolivian *patrones*, who sometimes helped provide medical assistance. In communities with missionaries, people also received direct help and were also assisted in traveling to receive medical treatment in San Borja. Communities closer to San Borja also experienced greater nutritional and health status, because of increased participation in wage labor and market exchange, enabling them to buy shoes, clothes, soap and food. Even though villages near San Borja tend to be large and residents may therefore be at a greater risk of exposure to disease vectors requiring sufficient host density, the longer history of interaction with outsiders, and easier access to money and medicines seem to outweigh any potential cost of increased

morbidity. Access to the market and domesticated animals also seems to outweigh any potential change in diet quality due to reduced access to meat and fish in these acculturated villages.

Preliminary analysis of children's heights and weights from the 18 study communities shows a higher prevalence of stunting in forest and riverine villages than in acculturated villages and Fatima. Among adults, we found higher weights-for-age for those living in the acculturated communities and Fatima, and lowest for adults living in remote interior forest and riverine communities, suggesting caloric shortage, greater energy expenditure or greater complications due to infections. We found no differences in adult height by region. Godoy et al. (2006) also show no evidence for any secular change in adult heights from 1920-1980 birth cohorts, in contrast to other reported increases in height among other indigenous populations with increasing market exposure and healthcare access (Barrett and Brown 1971; Laure 1991; Leonard and others 1996). Investments in human capital (i.e. schooling, literacy, Spanish speaking ability) showed no relationship with differences in men's height, and only slight positive impact on women's height during this time period. They explain the lack of any secular trend by the lack of any substantial intensification of market integration, and the continual presence of infectious disease. To the extent that increases in adult height tend to track improvements in nutrition, parasitism and infectious disease and mortality (Crimmins and Finch 2006; Eveleth and Tanner 1990), these data are consistent with our argument that the sources of morbidity and mortality have remained roughly the same in recent history.

The period improvements in health due to greater access to medical care did not benefit all age groups equally. One hypothesis is that infants and young children in remote villages often die before they receive treatment. Because of their increased vulnerability, infants and toddlers frequently die within days of becoming sick. The travel time of two or more days from remote

communities to San Borja can be long and difficult, especially for sick young children. Moreover, it frequently rains torrentially, and no travel is possible during those times. One tragic case recently occurred. We received an emergency message from a remote, forest community for whom we provided a radio. The log bridges along the dirt road leading to their community had been washed away by recent rain storms. They asked if we could send a motorcycle out to retrieve the sick infant. As we were preparing the emergency evacuation that same day, the villagers called again to say that it was too late and the baby had died. In addition, because infant death is so frequent, there appears to be some resignation to its occurrence. As is commonly the case in Amazonian societies, newborns are often not given names until they are over one year old, and have passed the high mortality period. Additionally, sicknesses are rarely viewed as caused by microscopic pathogens that respond to medical treatment, especially in more remote villages. Instead, sickness and disease is due to sorcery by forest or river guardians, or by suspicious, jealous or angry individuals. Attitudes of resignation and the native understanding of causes of sickness often result in delays for receiving proper treatment, with death as an unfortunate result. In our experience, we have found that it is not uncommon for Tsimane to seek out medical attention when it is too late. While these same problems sometimes occur in the communities nearby San Borja, they are less frequent because of the reduced travel time, greater access to money and increased familiarity with medical treatments and personnel. This may perhaps explain the very large differences in infant and child mortality across regions.

In contrast, in the case of adults and older people, there is more time and motivation to travel and obtain treatment. We hypothesize that the large period effects on adult mortality in the remote communities is due largely to increased access to the clinic and hospital, and the purchase of antibiotics. Prior to 1990, the access was much more limited. The reduction in mortality

among adults over age 40 is due to fewer tuberculosis and respiratory-related deaths. Increased resistance to tuberculosis and other infectious illness may also have contributed to reductions in adult deaths. Digestive illnesses such as appendicitis and intestinal infections, and accidents are also greatly reduced in the 1990's among older adults. Emergency medical attention for older adults may be partly responsible for lower mortality at Fatima. Greater mobilization of effort to treat older adults with chronic and acute illnesses, rather than any decrease in the incidence of illnesses, may be responsible for improvements in adult survivorship over the last decade.

Some of these hypotheses may prove incorrect. We are currently collecting data to test them. However, we hope that this framework will prove useful for analyzing epidemiologic transitions in traditional aboriginal groups and in developing societies. It has already been recognized that standard epidemiologic transition theory, as developed by focusing on trends among nations, may require revision when focused more narrowly on distinctions based on ethnicity, sex, socioeconomic status and ecology (Gaylin and Kates 1997). Lack of a clean water supply and sanitation hurt many people throughout the developing world, especially in rural areas but sometimes in urban areas as well (Gribble and Preston 1993). Differential access to medical attention is likely to affect the character of mortality transitions by age and sex. Host factors are also likely to play a role in areas of high food insecurity.

There are clear applied implications here. Programs that assess host factors, exposure and treatment modalities as separate factors may be able to more efficiently direct personnel, resources and funds to areas of greatest potential impact. In the case of the Tsimane, it is clear that improved water supply and sanitation could make a large difference in disease exposure and transmission. In the more remote communities, it will be necessary to train community health workers and provide them with the materials for primary care treatment. At the present, almost

all of the medical resources are provided to the more acculturated communities nearby San Borja, because of their greater political influence and because of logistical ease. Our data clearly show that infants and young children are dying at higher rates in remote communities.

Compared with other documented Amazonian groups, Tsimane survivorship ranks as moderately favorable. Mortality among Amazonian Indians varies widely over space and time, ranging from the initial Neel and Weiss Yanomamo study reporting an average life expectancy at birth of 21 years to a recent Ache life expectancy in 1996 of 51 years. Infant mortality among a sample of small-scale populations varies from 10% to 34% (Salzano and Callegari-Jacques 1988). Survivorship to age 15 ranges from 38% among Xingu to 86% among Kaxuyana, with a mean of 69%, based on a survey of forager-horticulturalists reported in Salzano and Callegari-Jacques (1988). Very low survivorship is likely due to contact-related epidemics (Coimbra Jr. and others 2002). Tsimane child survivorship and life expectancy at birth are higher than those for South American hunter-gatherers such as the Ache (Hill and Hurtado 1996), Hiwi (Hill and others n.d.) and Warao (Layrisse and others 1977). However, as found among most indigenous groups with respect to the national standard, Tsimane life expectancy still lags far behind that of Bolivia ($e_0=64$ in 2000), which already carries the lowest life expectancy in South America.

Despite living in a similar tropical macro-environment and engaging in a similar set of subsistence activities, Amazonian populations differ in terms of endemic parasitism, experience with infectious disease, tuberculosis and measles (Black 1975; Hurtado and others 2005). Increasing integration of Amazonian populations into national society is likely to improve health and increase survivorship, although outcomes will vary depending on the combination of prior history of infectious disease exposure, public health infrastructure, shifting diets and access to medical treatments. The census of indigenous Amazonia is estimated to be only a tiny fraction of

pre-contact estimates (e.g. 4-6 million in pre-contact Brazil vs. 100,000 in 1950 – Ribero (1967)). The future livelihood of indigenous Amazonian populations, especially in regards to decision-making about resource use, fertility and family planning depends critically on recent mortality patterns and expected mortality in current and future generations.

CONCLUSION

We conclude with some remarks about the human life course and its evolution. As we have shown elsewhere for other groups (Gurven and Kaplan 2006; Kaplan and Robson 2002), adult mortality among the Tsimane does not conform to expectations of the Gompertz model that assumes mortality rates increase at a constant exponential rate after its nadir at the end of childhood. Instead, mortality rates increase very slowly during prime adulthood, and even in middle age. The proportional rate of mortality increase grows sharply after age 60. Immunocompetence drops dramatically, and death rates from infectious disease increase sharply as a result. A range of chronic illnesses, including heart disease, cancer and gastrointestinal illnesses also occur at relatively high frequencies. It is possible that chronic disease actually occurs at higher frequencies among people who have been exposed to infection throughout their lives, as hypothesized by Costa (2000) and Finch and Crimmins (2004). Preliminary analysis of our economic data shows that very few people remain productive after age 70. Our hypothesis is that natural selection in the context of the traditional human lifestyle resulted in an effective lifespan of about 65-70 years (Gurven and Kaplan 2006). The data presented in this paper show that medical interventions can greatly reduce mortality rates in old age, but we do not see

evidence of significant increases in the productive lifespan upon which natural selection acts. We have shown elsewhere, as have others (e.g. Lee 2003), that intergenerational transfers, rather than direct reproduction, are a good candidate for the extension of human longevity. However, after about 15 years of post-reproductive investment in children and grandchildren, there may have been little evolutionary advantage to living longer. A quantitative understanding of the human life course remains a challenge, but we may now be closer to an adequate understanding of its determinants.

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TABLE 1. Tsimane demographic sample characteristics

Village	# of interviews	# of repro histories	# of complete repro histories	# of deaths	census 2003	Location	Dates sampled
Anachere	17	67	38	52	37	Upper Maniqui	May/2003
Aperecito	41	116	82	108	71	Forest	Oct/2002, Feb/2003
Boreyo	24	59	45	41	48	Upper Maniqui	May/2003
Cachuela	17	44	33	27	34	Upper Maniqui	Dec/2003
Campana	19	40	34	39	45	Forest	Feb/2003
Catumare	5	27	18	20	29	Upper Maniqui	May/2003
Cosincho	76	198	161	178	219	Upper Maniqui	Oct-Dec/2003
Cuverene	47	165	114	116	80	Forest	Sept-Oct/2002, Jan-Feb/2003
Donoy	9	46	25	49	19	Upper Maniqui	May/2003
Emeya	20	95	60	96	50	Upper Maniqui	May/2003
Jamanchi 1	39	132	79	87	111	Forest	Jul/2005
La Cruz	116	382	298		307	Near San Borja	Jul-Sept/2003
Mision Fatima	161	405	286	279	460	Upper Maniqui	June/2003, Aug/2004
Moseruna	30	67	52	61	91	Forest	Mar/2003
Munday	26	73	63	54	66	Upper Maniqui	Nov/2002
Nuevo Mundo	12	33	25	50	35	Forest	Feb/2003
San Miguel	118	348	188	129	325	Near San Borja	Mar-May, Sept/2003
Tacuaral del Mato	91	229	143	160	313	Near San Borja	Sept-Oct/2003
Uishiricansi	15	33	25	26	38	Forest	Feb/2003
	883	2,559	1,769	1,572	2,378		

Deaths only include people with known years of birth and known or estimated ages at death

TABLE 2. Mortality Rates (per 1,000 individuals) by abridged age groups, geographical region and time period

	Fatima	Forest	Riverine	Near San Borja	Overall	Mortality Ratio
Time Frame	Age <1					
1950-1989	173	179	202	118	169	1.23
1990-2002	120	194	161	89	137	
	Ages 1-4					
1950-1989	20	23	26	9	20	1.60
1990-2002	8	17	18	8	12	
	Ages 5-14					
1950-1989	6	7	8	6	7	1.89
1990-2002	5	4	5	1	4	
	Ages 15-39					
1950-1989	7	8	12	5	8	1.79
1990-2002	4	7	6	2	5	
	Ages 40-59					
1950-1989	12	17	19	25	19	2.59
1990-2002	4	7	8	10	7	
	Age 60+					
1950-1989	94	80	87	34	77	2.25
1990-2002	42	33	30	36	34	

TABLE 3. Logistic regression of infant and child mortality

Variable	Comparison	estimate	Sig	odds ratio	95% C.I.		n	Model Fit		
					lower	upper		- 2LogL	Chi ² Wald	p- value
<i>(A) Infant Mortality Rate, <1</i>										
SEX	female vs. male	-0.008	.914	0.985	0.743	1.305	1,938	1361	10.2	0.0687
REGION	Forest vs. Near San Borja	0.113	.354	1.474	1.005	2.161				
	River vs. Near San Borja	0.229	.051	1.712	1.181	2.482				
	Fatima vs. Near San Borja	-0.030	.815	1.335	0.894	1.993				
PERIOD	Pre-1990 vs. 1990+	0.114	.124	<i>1.255</i>	0.940	1.675				
<i>(B) Early child mortality, ages 1-4</i>										
AGE	1 year	-0.310	.001	0.733	0.607	0.887	6,018	966	32.4	0.0001
SEX	female vs. male	0.252	.016	1.393	1.099	2.490				
REGION	Forest vs. Near San Borja	0.266	.116	<i>2.445</i>	1.271	4.703				
	River vs. Near San Borja	0.389	.018	2.765	1.451	5.267				
	Fatima vs. Near San Borja	-0.028	.887	1.823	0.902	3.685				
PERIOD	Pre-1990 vs. 1990+	0.243	.025	1.627	1.064	2.486				
<i>(C) Child mortality, ages 5-15</i>										
AGE	1 year	-0.091	.001	0.913	0.866	0.963	26,818	1830	23.9	0.0005
SEX	female vs. male	-0.028	.735	0.946	0.686	1.305				
REGION	Forest vs. Near San Borja	0.037	.792	1.434	0.885	2.323				
	River vs. Near San Borja	0.225	.081	<i>1.730</i>	1.098	2.725				
	Fatima vs. Near San Borja	0.061	.699	1.467	0.876	2.459				
PERIOD	Pre-1990 vs. 1990+	0.244	.011	1.629	1.118	2.373				

TABLE 4. Cause-specific death rates (per 1,000 individuals), n=1,418 deaths with known causes

Category of illness	Geographical Region				Age group						TOTAL
	Forest	River	Fatima	San Borja	<1	1-5	6-15	16-39	40-55	60+	
I. Infectious and parasitic disease	8.7	10.0	7.5	6.8	39.3	10.4	3.3	2.9	7.0	30.1	8.3
A. Gastrointestinal	3.7	2.2	1.5	1.5	13.3	3.2	0.8	0.2	0.4	1.4	2.0
B. Respiratory	10.0	6.3	4.1	3.9	19.5	6.3	2.0	2.0	4.4	18.7	4.8
1. Whooping cough	0.6	0.5	0.5	0.5	3.9	0.7	0.1	0.0	0.1	1.0	0.5
2. Pneumonia	1.0	1.0	1.2	0.8	7.2	1.5	0.1	0.1	0.5	1.9	1.0
3. Measles	4.5	1.6	0.3	1.2	2.7	2.2	1.2	0.5	1.1	2.4	1.2
4. Tuberculosis	1.1	1.3	0.6	0.6	0.4	0.2	0.1	0.8	1.7	7.7	0.8
C. Cutaneous	2.2	0.8	1.0	0.6	4.9	0.3	0.3	0.3	1.0	4.3	0.9
D. Nervous system	0.1	0.3	0.1	0.0	0.4	0.2	0.0	0.1	0.5	0.0	0.1
E. Sepsis	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.1	0.5	0.0
II. Malignant neoplasms	1.7	0.0	0.2	0.2	0.0	0.0	0.0	0.2	0.2	3.3	0.2
III. Blood disorders / immune system	0.2	0.0	0.1	0.2	0.2	0.2	0.1	0.0	0.3	0.0	0.1
IV. Endocrine system	0.2	0.4	0.2	0.1	2.2	0.1	0.0	0.0	0.0	1.0	0.2
VI. Nervous system	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
VIII. Cardiovascular	0.1	0.3	0.1	0.1	0.2	0.0	0.1	0.1	0.4	1.9	0.2
IX. Respiratory	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.5	0.0
X. Digestive	2.2	0.7	0.5	0.4	0.7	0.0	0.4	0.4	0.9	5.3	0.5
A. Stomach	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.0	0.0
B. Appendix	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.1	1.4	0.1
C. Intestinal	1.2	0.4	0.3	0.2	0.2	0.0	0.2	0.3	0.2	2.9	0.3
D. Hepatic	0.5	0.1	0.1	0.0	0.2	0.0	0.1	0.1	0.2	0.5	0.1
E. Gallbladder and pancreas	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
XI. Skin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
XIII. Genitourinary	0.8	0.1	0.3	0.2	0.1	0.2	0.0	0.1	0.1	2.9	0.2
XIV. Pregnancy and childbirth	5.3	1.9	0.9	1.5	18.7	0.1	0.0	0.6	0.0	1.0	1.9
XV. Perinatal	1.5	1.2	1.0	0.4	10.6	0.0	0.0	0.1	0.0	0.0	1.0
XVI. Congenital	0.0	0.2	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.1
XVII. Accidents/violence	8.3	2.5	2.0	2.2	8.3	2.2	0.7	1.7	2.7	9.6	2.4
A. Homicide	3.2	0.7	0.2	0.6	0.5	0.0	0.1	0.8	1.1	1.4	0.5
B. Suicide	0.9	0.0	0.2	0.1	0.0	0.0	0.0	0.1	0.4	1.9	0.1
C. Infanticide	0.4	0.3	0.1	0.2	2.7	0.1	0.0	0.0	0.0	0.0	0.3
D. Abuse/neglect	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
E. Fall	0.1	0.3	0.3	0.4	2.1	0.2	0.1	0.0	0.0	1.0	0.3
F. Drowning	1.1	0.5	0.3	0.2	1.0	0.7	0.2	0.2	0.0	1.9	0.4
G. Animal attack	0.7	0.0	0.2	0.1	0.1	0.1	0.0	0.1	0.4	0.5	0.1
H. Tree fall	0.8	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.1	0.5	0.1
I. Lost	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
J. Other Accidental	1.1	0.3	0.6	0.4	1.5	0.7	0.2	0.2	0.4	0.5	0.4

TABLE 5. Logistic regression of adult mortality

Variable	Comparison	Estimate	Sig	odds ratio	95% C.I.		N	Model Fit		
					lower	upper		- 2LogL	Chi ² Wald	p-value
<i>(A) Early adult mortality, ages 16-39</i>										
AGE	1 year	0.027	.009	1.028	1.007	1.049	30,027	2476	41.6	<.0001
SEX	female vs. male	0.146	.035	1.340	1.021	1.759				
REGION	Forest vs. Near San Borja	0.257	.024	2.399	1.538	3.741				
	River vs. Near San Borja	0.335	.002	2.593	1.673	4.018				
	Fatima vs. Near San Borja	0.026	.855	1.904	1.151	3.150				
DECADE	Pre-1990 vs. 1990+	0.244	.002	1.629	1.197	2.218				
<i>(B) Middle Adult mortality, ages 40-59</i>										
AGE	1 year	0.057	.0002	1.058	1.027	1.090	9,477	1381	40.3	<.0001
SEX	female vs. male	-0.130	.142	0.772	0.546	1.091				
REGION	Forest vs. Near San Borja	0.005	.972	0.704	0.453	1.094				
	River vs. Near San Borja	0.055	.707	0.740	0.475	1.153				
	Fatima vs. Near San Borja	-0.417	.044	0.461	0.254	0.839				
DECADE	Pre-1990 vs. 1990+	0.459	.0001	2.506	1.680	3.738				
<i>(C) Late adult mortality, ages 60+</i>										
AGE	1 year	0.080	.0001	1.083	1.043	1.125	1,878	750	40.5	<.0001
SEX	Female vs. male	-0.189	.075	0.685	0.451	1.039				
REGION	Forest vs. Near San Borja	-0.076	.657	1.454	0.754	2.804				
	River vs. Near San Borja	0.061	.723	1.668	0.861	3.231				
	Fatima vs. Near San Borja	0.465	.010	2.498	1.271	4.910				
DECADE	Pre-1990 vs. 1990+	0.451	.0001	2.467	1.599	3.805				

TABLE 6. Period life table, 1950-1989, 648 deaths, 47,854 person-years

Age	Female					Male				
	d_x	P_x	q_x	l_x	e_x	d_x	P_x	q_x	l_x	e_x
0	73	491	0.148	1.000	42.8	68	498	0.137	1.000	44.2
1	14	442	0.032	0.852	49.2	11	461	0.024	0.863	50.2
2	11	411	0.027	0.825	49.8	10	433	0.023	0.842	50.4
3	8	373	0.021	0.803	50.1	5	401	0.012	0.823	50.5
4	4	349	0.011	0.786	50.2	2	378	0.005	0.812	50.1
5	3	327	0.009	0.777	49.8	4	350	0.011	0.808	49.4
6	8	907	0.009	0.769	49.2	6	954	0.006	0.799	49.0
7	5	874	0.006	0.763	48.6	6	925	0.006	0.794	48.3
8	8	848	0.009	0.758	47.9	7	889	0.008	0.789	47.6
9	6	816	0.007	0.751	47.4	5	857	0.006	0.782	46.9
10	6	793	0.008	0.746	46.7	5	825	0.006	0.778	46.2
11	2	760	0.003	0.740	46.1	6	806	0.007	0.773	45.5
12	2	722	0.003	0.738	45.2	10	780	0.013	0.767	44.8
13	3	694	0.004	0.736	44.3	2	741	0.003	0.758	44.4
14	2	664	0.003	0.733	43.5	3	706	0.004	0.755	43.5
15	3	644	0.005	0.731	42.6	0	682	0.000	0.752	42.7
16	5	622	0.008	0.727	41.8	6	666	0.009	0.752	41.7
17	4	606	0.007	0.721	41.1	3	647	0.005	0.745	41.1
18	3	588	0.005	0.717	40.4	5	621	0.008	0.742	40.2
19	2	569	0.004	0.713	39.6	3	601	0.005	0.736	39.6
20	4	551	0.007	0.710	38.7	5	580	0.009	0.732	38.8
21	5	539	0.009	0.705	38.0	1	556	0.002	0.726	38.1
22	6	523	0.011	0.699	37.4	3	538	0.006	0.725	37.2
23	6	485	0.012	0.691	36.8	2	521	0.004	0.721	36.4
24	4	461	0.009	0.682	36.2	7	502	0.014	0.718	35.5
25	5	430	0.012	0.676	35.5	4	481	0.008	0.708	35.0
26	3	410	0.007	0.668	35.0	3	455	0.007	0.702	34.3
27	4	396	0.010	0.663	34.2	1	434	0.002	0.697	33.5
28	3	384	0.008	0.657	33.5	2	421	0.005	0.696	32.6
29	4	377	0.011	0.652	32.8	0	408	0.000	0.693	31.7
30	2	355	0.006	0.645	32.1	6	395	0.015	0.693	30.7
31	3	343	0.009	0.641	31.3	0	377	0.000	0.682	30.2
32	3	332	0.009	0.635	30.6	3	358	0.008	0.682	29.2
33	3	313	0.010	0.630	29.9	3	342	0.009	0.676	28.4
34	5	297	0.017	0.624	29.1	4	333	0.012	0.670	27.7
35	3	282	0.011	0.613	28.6	1	321	0.003	0.662	27.0
36	3	268	0.011	0.607	27.9	1	311	0.003	0.660	26.1
37	4	257	0.016	0.600	27.2	5	301	0.017	0.658	25.1
38	5	240	0.021	0.591	26.6	4	292	0.014	0.647	24.5
39	4	229	0.017	0.578	26.2	3	277	0.011	0.638	23.9
40	2	221	0.009	0.568	25.6	8	266	0.030	0.631	23.1
41	1	207	0.005	0.563	24.8	3	247	0.012	0.612	22.8
42	5	197	0.025	0.560	24.0	4	233	0.017	0.605	22.1
43	0	187	0.000	0.546	23.6	2	222	0.009	0.595	21.4
44	2	172	0.012	0.546	22.6	5	207	0.024	0.589	20.6
45	4	159	0.025	0.540	21.8	2	187	0.011	0.575	20.1
46	2	147	0.014	0.526	21.4	3	174	0.017	0.569	19.3
47	3	138	0.022	0.519	20.6	3	161	0.019	0.559	18.6
48	1	132	0.008	0.508	20.1	5	153	0.033	0.549	18.0

49	1	122	0.008	0.504	19.2	1	141	0.007	0.531	17.6	
50	4	116	0.034	0.500	18.4	3	138	0.022	0.527	16.7	
51	2	106	0.019	0.482	18.0	3	128	0.023	0.515	16.0	
52	3	103	0.029	0.473	17.3	2	120	0.017	0.503	15.4	
53	1	97	0.010	0.460	16.8	2	114	0.018	0.495	14.6	
54	4	95	0.042	0.455	16.0	5	106	0.047	0.486	13.9	
55	4	88	0.045	0.436	15.6	3	95	0.032	0.463	13.5	
56	2	79	0.025	0.416	15.3	0	85	0.000	0.449	12.9	
57	0	72	0.000	0.405	14.7	2	81	0.025	0.449	11.9	
58	0	66	0.000	0.405	13.7	4	74	0.054	0.438	11.2	
59	3	62	0.048	0.405	12.7	1	68	0.015	0.414	10.8	
60	5	55	0.091	0.386	12.3	5	64	0.078	0.408	9.9	
61	1	45	0.022	0.351	12.4	7	60	0.117	0.376	9.7	
62	0	39	0.000	0.343	11.7	4	49	0.082	0.332	9.8	
63	0	37	0.000	0.343	10.7	2	45	0.044	0.305	9.6	
64	1	35	0.029	0.343	9.7	2	41	0.049	0.292	9.0	
65	2	32	0.063	0.333	8.9	1	37	0.027	0.277	8.4	
66	3	26	0.115	0.312	8.5	3	35	0.086	0.270	7.6	
67	0	21	0.000	0.276	8.4	3	32	0.094	0.247	7.2	
68	2	20	0.100	0.276	7.4	4	27	0.148	0.224	6.9	
69	3	17	0.176	0.249	7.1	0	22	0.000	0.190	6.9	
70	0	14	0.000	0.205	7.5	1	19	0.053	0.190	5.9	
71	0	11	0.000	0.205	6.5	4	18	0.222	0.180	5.2	
72	0	9	0.000	0.205	5.5	1	13	0.077	0.140	5.4	
73	1	8	0.125	0.205	4.5	0	9	0.000	0.130	4.8	
74	2	7	0.286	0.179	4.0	0	9	0.000	0.130	3.8	
75	0	5	0.000	0.128	4.1	4	8	0.500	0.130	2.8	
76	1	5	0.200	0.128	3.1	0	3	0.000	0.065	3.5	
77	0	3	0.000	0.102	2.7	0	2	0.000	0.065	2.5	
78	1	3	0.333	0.102	1.7	1	2	0.500	0.065	1.5	
79	1	2	0.500	0.068	1.0	0	1	0.000	0.032	1.0	
80	1	1	1.000	0.034	0.0	1	1	1.000	0.032	0.0	
		318.8	22933.2					329.4	24920.8		

TABLE 7. Abridged Period life table, 1990-2000, 361 deaths, 31,589 person-years

Age group	Female					Male				
	d_x	P_x	q_x	l_x	e_x	d_x	P_x	q_x	l_x	e_x
<1	65.4	639	0.102	1.000	54.0	73.2	699	0.105	1.000	54.3
1-5	32	2149	0.057	0.898	59.1	27	2377	0.044	0.895	59.6
5-10	10	2179	0.023	0.846	58.6	13	2301	0.028	0.856	58.3
10-15	7	1964	0.018	0.827	54.9	7	1949	0.018	0.832	54.9
15-20	8	1662	0.024	0.812	50.8	7	1782	0.019	0.817	50.8
20-25	6	1381	0.021	0.793	47.0	8	1509	0.026	0.801	46.8
25-30	7	1200	0.029	0.776	43.0	7	1216	0.028	0.780	42.9
30-35	5	994	0.025	0.754	39.2	2	1065	0.009	0.758	39.1
35-40	7	742	0.046	0.735	35.1	6	848	0.035	0.751	34.5
40-45	1	641	0.008	0.701	31.7	0	667	0.000	0.725	30.6
45-50	3	544	0.027	0.696	26.9	10	608	0.079	0.725	25.6
50-55	3	422	0.035	0.677	22.6	5	465	0.052	0.668	22.6
55-60	4	273	0.071	0.653	18.3	5	333	0.072	0.633	18.7
60-65	8	204	0.179	0.607	14.5	5	229	0.104	0.587	15.0
65-70	2	170	0.057	0.499	12.2	3	134	0.106	0.526	11.4
70-75	4	85	0.211	0.470	7.7	4	67	0.260	0.470	7.5
75+	3	36	0.345	0.371	4.1	4	55	0.308	0.348	4.2
	175.4	15285				186.2	16304			

FIGURE LEGENDS

FIGURE 1. Map of Tsimane study area and sample communities.

FIGURE 2. Tsimane age-sex pyramid based on censuses in 18 study village censuses during 2002-2003 ($n=2,291$ individuals).

FIGURE 3. Infant mortality rate (IMR), per 1,000 births, from 1950-2000 in five year intervals ($n=2,119$ births).

FIGURE 4. Probability of survival to age x (l_x) and age-specific mortality rates (h_x) for males and females under age 15, 1950-1989.

FIGURE 5. Siler-estimated survival curves (l_x) and age-specific mortality rates (h_x) for males and females across the lifecourse, 1950-1989. Dashed bold line shows raw male l_x curve.

FIGURE 6. Siler-estimated mortality rates (h_x) for 1950-1989 and 1990-2002 time periods.

Triangles indicate the ratio of mortality hazards from 1950-89 to 1990-2002.

FIGURE 7. Infant mortality rate (IMR) and probability of dying before age 5 (q_5) as a function of village distance to market town San Borja (in km).

FIGURE 8. Infant mortality rate (IMR) and probability of dying before age 5 (q_5) as a function of village population size.

FIGURE 1.

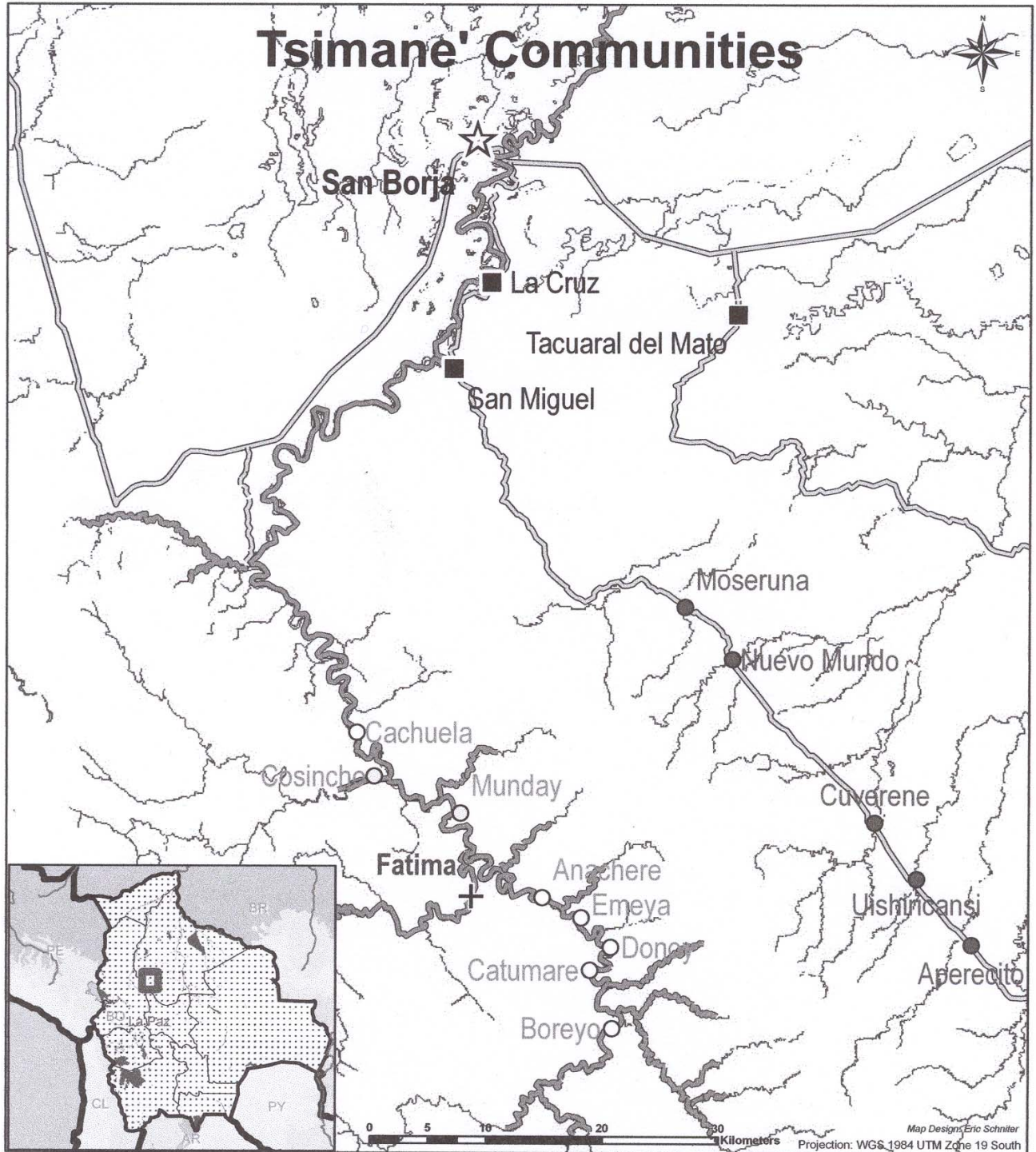


FIGURE 2.

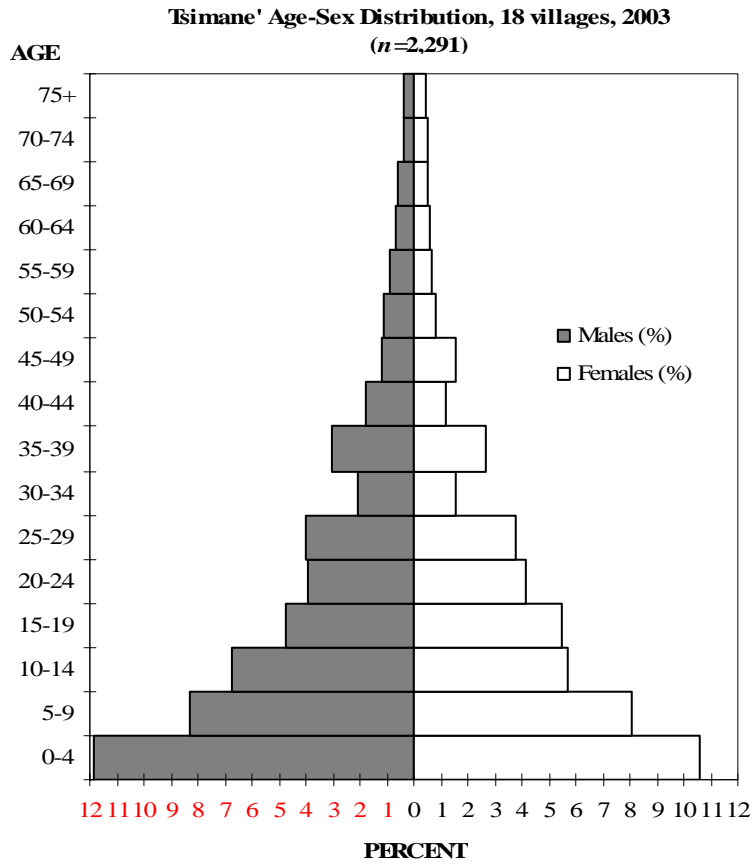


FIGURE 3.

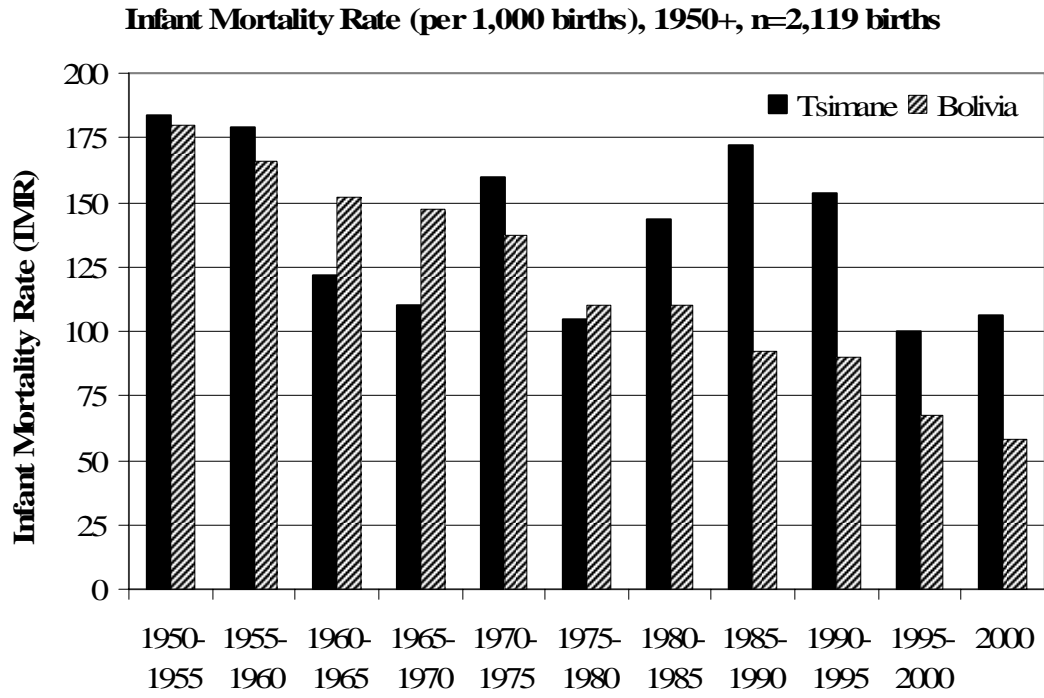


FIGURE 4.

Infant and child mortality by sex, 1950-89

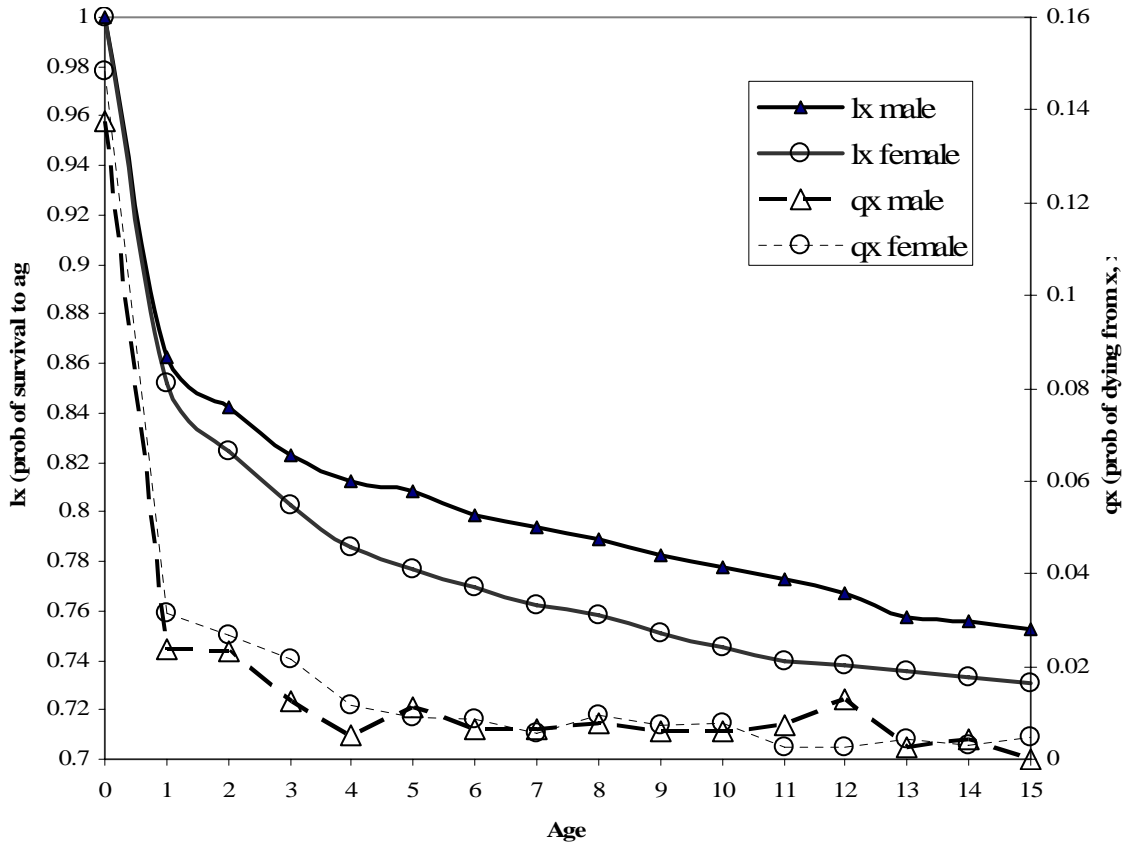


FIGURE 5.

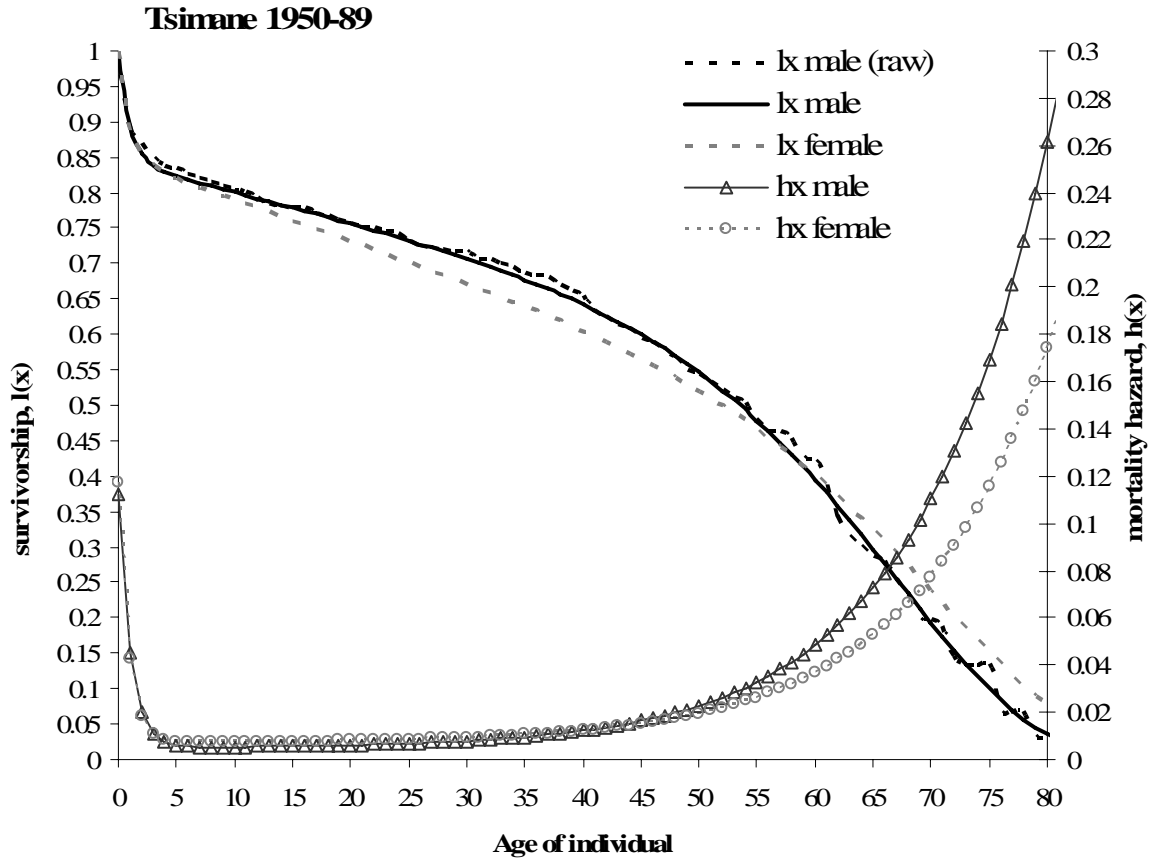


FIGURE 6.

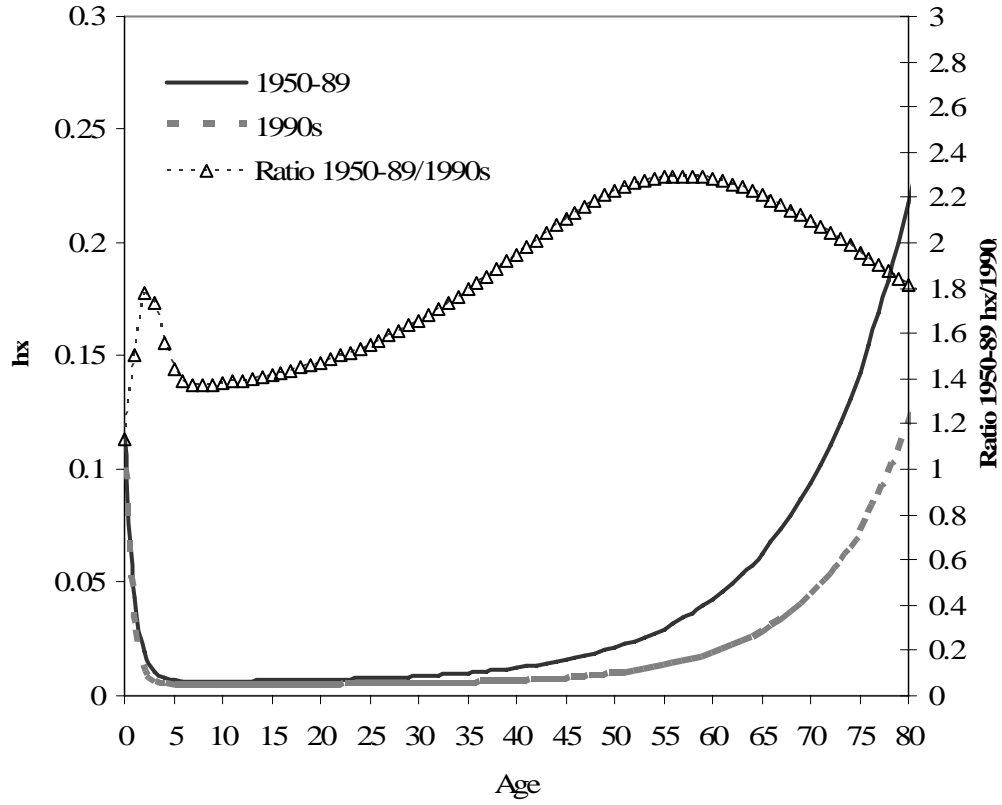


FIGURE 7.

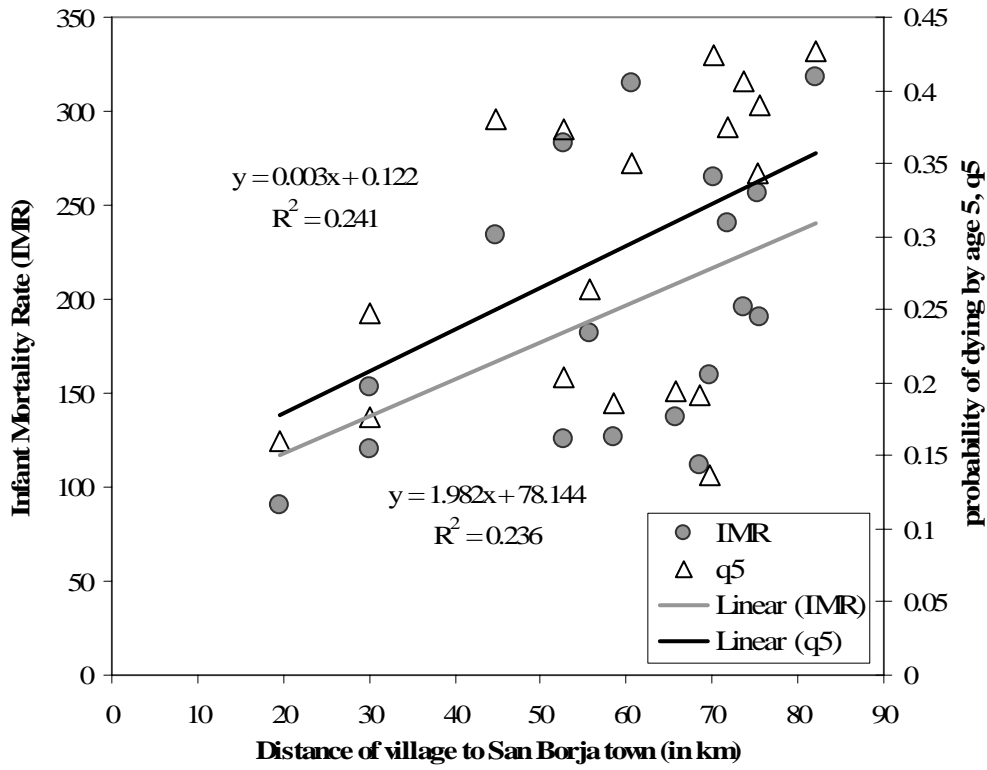
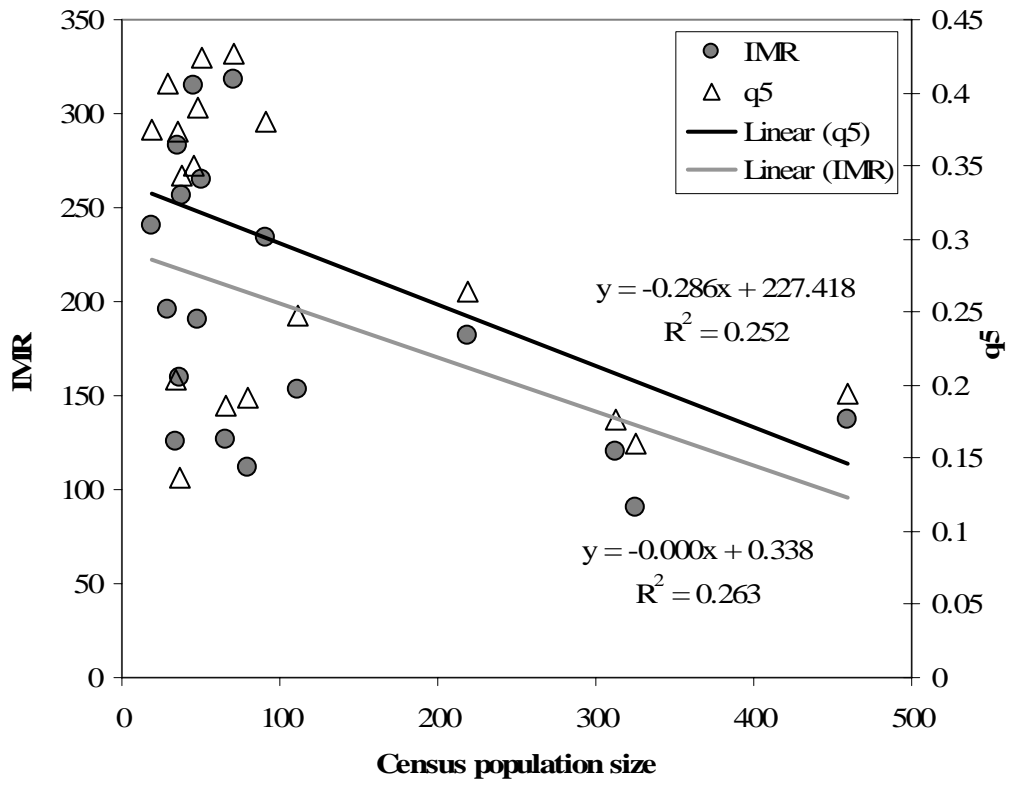


FIGURE 8.



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¹ There are no significant differences in overall mortality by decade from 1950 to 1989 (Chi-square=0.92, $p < 0.82$, poisson regression).

² Including reproductive histories of siblings who were not directly interviewed reduces this estimate to 112/1,000, revealing the tendency for relatives to forget infants who died shortly after birth.