Grandparenting and the evolution of post-reproductive lifespan PI: Gurven

Project Summary

The proposed research will investigate the biodemography of longevity and the behavioral contributions of post-reproductive individuals among the Tsimane, a traditional population subsisting on a combination of foraging and simple horticulture. It seeks to explain why the human lifespan is extended in comparison to other primates and mammals of similar body size. Although the expected adult lifespan has increased over the past century, due in part to improved diets, medicines, and public health, data among foragers and horticulturalists without access to modern healthcare illustrate that the pattern of a long, post-reproductive lifespan is not novel, and that recent increases in longevity are just extreme manifestations of a general human pattern.

Intellectual Merit: The proposed research is designed to test the empirical adequacy of several alternative explanations for the extension of the human lifespan. The "grandmother hypothesis" [**GMH**] (Hawkes et al. 1998), 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 "embodied capital" [**ECM**] model (Kaplan et al. 2000) proposes that human economic and childrearing niche is skill- and knowledge- intensive, shifting productivity from younger to older ages and that this shift in productivity selected for increased investments in survival and longevity. The patriarch hypothesis [**PH**] (Marlowe 2000) proposes that an extended lifespan provides direct reproductive benefits to men, who do not experience reproductive cessation. Finally, the mother hypothesis [**MH**] (Peccei 2001) argues that most direct care of offspring will come from mothers, rather than grandmothers. A core component in most of these models is that older individuals can increase their inclusive fitness through non-reproductive, kin-directed behavior. Our approach is to investigate the direct and indirect benefits that older individuals may provide their genetic descendents, and to address the question of "Why longevity?" from two complementary perspectives. First, we will examine the *behavioral pathways* by which individuals may affect their descendants' well-being. The research is designed to determine if and how men and women adjust their behavior as they age to provide childcare, protection, and other services for grandchildren and other descendant kin. We will examine how older individuals negotiate residence patterns, time budgets, and resource production in ways that benefit children and grandchildren. We will also examine how absolute levels of resource production and investment in descendants change with the increasing age, and dependency, of grandparents. The second approach is to measure proximate and ultimate *effects of older individuals on descendant kin*. At a proximate level, we will examine whether grandparental presence positively impacts physical growth and negatively impacts rates of morbidity and illness of grandchildren. At an ultimate level, we will examine whether the presence of grandparents is associated with an increase in children's completed fertility and grandchildren's survivorship. Finally, it is our goal to contextualize the effects of grandparents with a careful study of cultural perceptions of aging and of "being old" (*isho*) among group members of all ages. We will explore expectations of roles for older individuals, and collect case histories of past and present experiences with grandparents.

Broader impacts: The proposed study advances research in several ways. To date, there have been no extensive tests of the different approaches by examining the overall fitness effects among kin, and the proximate means by which such effects are realized, in a traditional population with a sufficiently large sample size. The proposed research will contribute to student training, and the participation of traditionally underrepresented groups by involving community members in data collection, and by training Tsimane' in primary health care. The research will also develop new partnerships in the host country. Our data will also be used for the planning of health initiatives and to provide an empirical basis for requests of financial support from the national government. While not living replicas of our ancestors, people in societies such as the Tsimane are living under conditions similar to those characteristic of the long history of selection during which the human life course evolved. Our strategy is not to treat the Tsimane as a prototype of the past, but to determine the universal and variable features of the human life history under relatively traditional conditions. This research is urgent in that this next decade will probably be the last during which research with

relatively intact and isolated groups will be possible. The data collected by this research program will be an archive for future scientists who will no longer be able to obtain the information directly.

Project Description

Results from previous NSF research

Gurven and **Kaplan** received NSF funding in 2001-2003 (#BCS-0136274, $150,709) for the first phase of a research agenda which examines the behavioral, economic and social dimensions of development and aging among the Tsimane' of Bolivia. Our current sample includes baseline census, medical, and demographic information on over 2,000 Tsimane Amerindians living in 17 villages. Preliminary analysis of medical and anthropometric information shows high rates of morbidity due to gastrointestinal (~30%), respiratory (20-40%), and other illnesses (30-60%), and high rates of growth stunting (30-60%) A preliminary analysis of 635 living and dead individuals contributing 15,725 person-years shows a mean age of death at 48. Roughly 22% of Tsimane die before age 15, and 17% die before age 5. Preliminary analyses of a pilot time allocation study show a slow, steady increase of time investment in more difficult production tasks with age, with juveniles spending a substantial portion of their time in play and leisure activities. Grandparents spend substantial time in both food production and direct care of grandchildren. Data entry and management is almost complete and a series of papers are in preparation.

I. Research Objectives

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, whereas chimpanzees in the wild have an expected adult lifespan of 14 additional years upon reaching reproductive maturity at age 13, human foragers and forager-horticulturalists without access to modern medicine have an expected adult lifespan of some 40 additional years upon reaching reproductive maturity at age 19, and are expected to live an additional two decades if they reach age 45 (Kaplan et al. 2000; Blurton Jones et al. 1999; 2002).

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 (1952), 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**] (Hill & Hurtado 1991). A specific version of the GMH has been proposed by Hawkes, Blurton-Jones and O'Connell (1998) and explained more fully by Hawkes (2003) and O'Connell et al. (1999). 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 (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**].

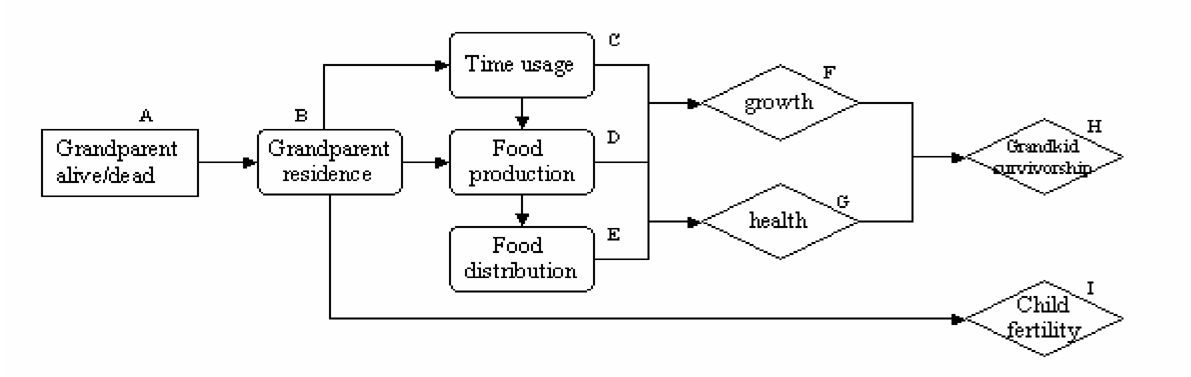
An alternative view focuses on men. Marlowe (2000) argues that the extension of the lifespan is driven by selection on men, stressing the fact that men do not experience menopause and can have children into the 7th and 8th decades of life. His argument, called the *patriarch hypothesis* (hereafter **PH)**, 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 & Robson 2002) 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, men often experience 'effective menopause', because their last reproductive event is often tied to their wife's last reproduction (Gurven & Hill 1997).

The proposed research is designed to test the empirical adequacy of these alternative explanations for the extension of the human lifespan. Three of those theories are sex-specific. Implicit in each of the GMH, PH, MH proposals is that selection for extended lifespan in one sex has secondary, epiphenomenal effects on the other sex, or that lifespan is extended in each sex for different reasons. MH and GMH propose that selection on females is responsible for lifespan extension, and is driven by 1st and 2nd generation kin-benefits, respectively, whereas PH proposes that it is driven by selection on males through direct effects on own fertility. In contrast, ECM proposes that the shift in productivity to older ages occurs among both men and women and that selection on both sexes for longer lifespan operated through effects on descendant kin. We will examine the direct and indirect benefits that older individuals may provide their genetic descendents and investigate their causes. This requires two complementary sets of research objectives. The first objective is to study the *behavioral pathways* by which individuals may affect their descendants' well-being. The goal is to determine if and how men and women adjust their behavior as they age in order to provide food, childcare, and other services for children, grandchildren and other descendant kin: The second objective is to measure the *effects of older individuals on descendant kin*. We will measure three classes of effects: demographic, health, and physical growth. These two objectives generate 15 inter-related research questions (*RQ*). The alternative theories predict different answers to many of these research questions, especially with respect to sex differences in both behavior and fitness effects. Therefore, for each of these questions, we will examine sex differences and determine how sex interacts with the aging process and impacts on descendant kin.

Behavioral Pathways – Figure 1 shows the behavioral pathways through which older individuals may affect the fitness of descendant kin. Older individuals can only exhibit effects on kin if they are alive (A). If alive they may adjust their behavior in several ways to increase positive impacts. The first set of questions therefore concerns behavioral adjustments in terms of residence (B), activity budgets (C), food production (D), and food consumption (E). Rather than taking the observed residence patterns for granted, we will examine whether residence patterns of older individuals are consistent with the availability of kin descendants who can benefit from grandparental attention, focusing on offspring and grand-offspring. The next step is to investigate activity budgets (C), particularly time allocated to productive labor and childcare, and how they change during the post-reproductive portion of life. We will measure short-term behavioral adjustments in time allocation, such as how parents and grandparents respond to child illness. We will also measure age-specific patterns of food production (D) and food consumption (E) to uncover the magnitude of surplus or deficit production, and the direction and magnitude of food transfers from older individuals to other group members.

FIGURE 1. Diagram of grandparental influence

Behavior *Proximate effects* *Fitness effects*



RESIDENCE PATTERNS
RQ1) Do older individuals choose to reside in villages with the greatest possible number of kin descendants, controlling for the number of alternative caretakers? **RQ1b)** Do residence changes by older individuals result in the possibility for greater investment in offspring and grandoffspring?

The four models generate alternative predictions with respect to residence. GMH predicts that older females, but not males, will reside where they can make the most difference to grandchildren, whereas MH predicts residence in terms of help for children. PH and GMH predict that men will make residence choices in terms of increasing own fertility, showing a bias towards communities with better mating prospects and not towards aid for descendant kin. ECM predicts that both men and women will make residence choices that maximize benefits to descendant kin.

Current residence of living grandparents will be assessed as to whether it presents the best possibility for descendant kin investment. For each grandparent, we will examine the number and ages of sons, daughters, and grandoffspring living in all appropriate villages, while controlling for the number of alternative caretakers (e.g. in-laws and other grandparents) living in those villages. We will then be able to rank the choice of residence for each grandparent and examine the extent to which rank predicts current residence. In this analysis, we will consider all 280 individuals over the age of 45 in our sample (see Village Sample). Census updates of our study villages over the five years will provide information on changes in residence as well.

ACTIVITY BUDGETS
RQ2) As men and women age, what proportion of time is spent in activities that may directly or indirectly benefit descendants? **RQ3)** Do older individuals increase their work effort or care activities when grandoffspring are sick or injured, or when daughters and sons' wives are pregnant or breastfeeding small children? **RQ4)** Do age and physical condition predict relative proportions of time spent in strength- and skill-intensive activities, respectively?

Understanding how grandparents exhibit positive impacts on grandoffspring health, growth, and survivorship requires an exploration of how grandparents use their time in ways that can affect kin welfare. These include childcare, instruction, play, babysitting, protection, manufacture of goods that affect others, and healing, as well as food acquisition activities. When children are sick or injured, we should also expect to see an increase in time spent in care and babysitting activities. Again, the alternative models generate different predictions. We should expect grandmothers to be the ones primarily engaging in these beneficial activities according to GMH, greater investment in children than grandchildren according to MH, and little investment in grandchildren by grandfathers according to PH. ECM generates two unique predictions: one is that men, even as they age, will adjust their behavior, especially food production and tool manufacture, to maximize benefits to descendants; the other is that both sexes will evidence a shift from strength- to skill- intensive activities as they age.

During years 1, 3, and 5 of the project when intensive behavioral observations will be made, activity budgets will be monitored, using community-wide scan sampling techniques.

FOOD PRODUCTION AND DISTRIBUTION
RQ5) To what extent are older individuals net consumers or net producers, and how does the level of their production change as they age? **RQ6)** What is the direction and intensity of resource transfers by older individuals to specific kin? **RQ7)** What percentage of children's care and food come from parents, grandparents and others? **RQ8)** To what extent do older individuals bias food to kin with greatest 'need', including net caloric dependency of offspring and grandoffspring, and the presence or absence of other older helpers?

An important avenue by which older individuals can impact grandoffspring growth, health, and survivorship, or offspring fertility is to provide crucial resources to descendant kin, delivered during important periods. If food is an important pathway for increasing inclusive fitness, it must be shown that grandparents produce large quantities of food, and that significant portions of these foods are directed towards descendant kin. Additionally, kin with greatest need, as measured by greater net dependency (a combination of age and number of offspring), should receive more food from older individuals than those with less need. We also predict that older individuals will direct more food to grandchildren, whose other grandparents are dead or absent. Hill and Hurtado (1996) hypothesize that such behavioral adjustments may result in underestimates of grandparental effects in analyses that regress the survival of grandchildren on whether grandparents are alive. Food acquisition may be more important during periods of reduced work effort by mothers when pregnant or lactating dependent offspring, and so we further predict that grandparental time investments in food production should be greatest when their daughters or sons' wives are pregnant or are breastfeeding.

GMH predicts that women are the ones who should produce abundant quantities of food and should distribute these to grandoffspring, whereas MH predicts a greater proportion of food transfers to offspring. GMH and PH predict that men will adjust behavior to increase fertility at older ages, although PH recognizes a greater role of male parental investment, predicting that older men will be provisioning offspring, rather than grandoffspring. The data used to answer these questions will be derived from a combination of behavioral observations and interviews regarding food production and food consumption (see Methods).

Effects on descendant kin – For this second objective, our goal is to measure the fitness contributions of older individuals by comparing individuals who are alive with those who are dead (A), comparing individuals who are co-resident with individuals who reside in other villages (B), and by comparing individuals who vary in their behavior with respect to time investment (C), food production (D), and food sharing (E). We will test for direct effects of grandparental presence, food, and time inputs on physical growth (F), and health and morbidity (G). Finally, we will assess the direct and indirect impacts of grandparents on grandoffspring mortality (H) and offspring fertility (I). Analysis of demographic outcomes will utilize both retrospective and prospective data on births, deaths and residence patterns. Our main focus will be on demographic outcomes for descendants, but because PH and ECM make alternative predictions about male and female fertility during the aging process, we will also measure the impacts of survival on own fertility for men. Assessment of health and growth effects will be done prospectively over a five year period, to examine both cross-sectional and longitudinal effects on infants, toddlers, and small children age ten and younger. Linking behavioral measures of grandparental inputs, such as time and food, to growth, morbidity, and mortality outcomes help avoid the typical phenotypic correlation problems that often plague life history analyses (see Significance section below; and Hill and Hurtado 1996; Stearns 1992).

EFFECTS ON CHILD GROWTH
RQ9) To what extent does parental and grandparental survival, co-residence and behavior affect the physical growth rates of children, in terms of weight, height, body density, and fat mass? **RQ10)** To what extent do growth rates correspond to positive food and time inputs of grandparents?

GMH and PH predict that only grandmothers should show a significant positive impact on grandoffspring growth patterns. ECM predicts positive effects of both sexes. MH predicts that only mother presence should determine child growth, and that the effects of grandparents should be small or nil. Child weights, heights, body density, and fat mass (see Methods, Part D) will be recorded prospectively every other year during the five year study.

EFFECTS ON HEALTH AND MORBIDITY
RQ11) To what extent does parental and grandparental co-residence and survival behavior affect rates of illness and morbidity among children, and recovery times from morbid events? **RQ12)** To what extent does parental and grandparental food production and time inputs affect rates of illness and morbidity, and recovery times from morbid events?

Similar predictions obtain for health and morbidity as for growth. Prospectively over the five year duration of the study, we will examine health and morbidity of the 1,035 children aged 10 and under. Durational information about sicknesses will be ascertained from one- and two-week retrospective interviews of parents during family visits by the physicians. A sub-sample of children for which behavioral information regarding time and food inputs exist will be used to address RQ12.

EFFECTS ON SURVIVORSHIP AND FERTILITY
RQ13) To what extent do grandparental survival and co-residence affect grandoffspring survival (prospectively and retrospectively), and offspring age-specific and completed fertility? **RQ14)** To what extent does parental survival and co-residence affect offspring survival and fertility? **RQ15)** What are age-specific fertility rates and the expected post-reproductive lifespan (expected time from last reproduction to death) for men and women respectively?

GMH predicts positive effects for grandmothers, while ECM predicts positive effects for grandparents of both sexes. MH predicts little effect for any grandparents, and greatest effect for parental presence. Controls regarding father and mother presence will therefore be included to test MH. PH predicts little or no effect of grandfathers on grandoffspring survivorship or offspring fertility. Rather, PH predicts that age-specific fertility in men will decrease more slowly than in women and that fitness benefits to men should accrue primarily through direct reproduction rather than through inter-generational effects.

In testing the many predictions, we define four dummy variables for the presence or absence of maternal and paternal grandmother and grandfather. 'Presence' will be measured in two ways for the retrospective analyses: alive or dead, and co-residence or non co-resident. Prospective analyses will also utilize grandparental time allocation to feeding and caring for the child. In prospective analyses of survivorship, we will also control for child growth to examine grandparental effects, independent of food inputs. These quantitative analyses will be complemented by an attempt to gain a more qualitative understanding of the aging process. It is our goal to contextualize this investigation with a careful study of cultural perceptions of aging and of "being old" (*isho*) among group members of all ages. We will explore expectations of roles for older individuals, and collect case histories of past and present experiences with grandparents.

II. Scientific Significance

Worldwide life expectancies have more than doubled over the past two hundred years, from an estimated 25, to 65 in men and 70 in women (Riley 2001). The maximum life expectancy has risen steadily by more than two years every decade (Oeppen and Vaupel, 2002), a dramatic improvement that suggests new answers to old questions about programmed senescence and the existence of biologically determined maximal life-spans (Wachter and Finch 1997; Austad 1999). Although much of the increase in life expectancy in the 19th century can be attributed to better sanitation, modern medicine, and improved diets (ibid), there is strong evidence that the general pattern of a long lifespan is not unique to the past century, and that current increases in lifespan may be a consequence of plasticity in our evolved human life history. There is converging evidence that living into "old age" is not unique to modern populations, or to even those with agriculture (cf. Washburn 1981). Data among extant foragers with little to no access to medical attention nor modern foods, including the !Kung, Ache, and Hadza, show that women who survive to age 45 can expect to live an additional 20-22 years, even though mean life expectancies at birth range from 30-37 (Blurton Jones et al. 2002). Extrapolations based on comparative analyses of brain weights and body sizes among non-human primates suggest a maximum lifespan between 66-78 for *Homo sapiens* (Hammer and Foley 1996), and the possibility that a post-menopausal lifespan existed anywhere from 0.15-1.6 mya (Bogin & Smith 1996; Peccei 2001). There is strong evidence that estimates of lifespan among extant foragers depict a unique life history characteristic that cannot be explained as an artifact of modern conditions (see Blurton Jones et al. 2002 and refs therein).

These results imply that a significant post-reproductive period is a fundamental feature of the human life course for women. Even men, while physiologically capable of producing viable offspring well until their 80's, show a similar age-specific decline in fertility, but delayed by 5-10 years among the !Kung, Ache, and Yanomamo (Hill and Hurtado, 1996). These results generated initial enthusiasm for a theory that could explain menopause, and more generally reproductive cessation (Hawkes et al., 1989; Hurtado & Hill, 1991; Rogers 1993). However, theoretical modeling and empirical tests showed little support for the notion that reproduction should terminate early in the lifespan (Hurtado & Hill, 1991; 1996; Rogers, 1993). Moreover, there is little evidence for any upward secular trend in the age at menopause over the past century (Peccei, 1999), despite increases in life-span, changes in the age at menarche, and estimated heritabilities in age of menopause of 40-60%. Given the existence of menopause in other closely-related species but a much shorter post-reproductive lifespan, it is now thought that menopause is the conserved ancestral trait. This shifts the focus of explanation to the long lifespan after the termination of reproduction (Hawkes et al. 1998; Kaplan 1997; Judge & Carey 2000).

Even if effects on descendant kin cannot explain menopause, they might explain lifespan. The starting point for these theories is the observation that successful reproduction is not mainly a matter of producing offspring, but rather is a matter of acquiring food and allocating it to offspring so as to maximize the number of surviving, sexually mature adults. This perspective places the acquisition and distribution of food at the center of reproductive fitness, rather than fertility. Despite the generality of these hypotheses, and their implications for understanding the evolution of distinct human life history traits, the organization of social communities, and intergenerational social dynamics, there have been few explicit empirical tests, and no studies where data were collected for the primary purpose of comparing the different hypotheses.

Existing attempts to measure the effects of older individuals on descendant kin have produced mixed results. Among foragers, Hawkes et al.'s (1989) initial report of 'hardworking grandmothers' who produce more calories than younger women, was an impetus for the growing interest in grandparental effects on life history. Hawkes et al. (1998) later showed that grandmothers who worked longer hours had grandchildren who experienced positive weight gain. In a rural farming population in the Gambia, Sear and colleagues (2000; 2002) showed that maternal, but not paternal, grandmothers had a positive effect on grandchild nutrition and on survivorship among children 1-2 years old, whereas only paternal grandparents had a positive effect on fertility (Sear et al. 2003). In urban societies, there is evidence that grandmothers positively impact cognitive and health outcomes (Pope et al. 1993), and psychological and sociological well being (Alawad & Sonugabarke 1992; Wilson 1986). Several historical studies reveal significant grandparental effects. Jamison et al. (2002) showed that maternal grandmother presence was associated with substantially higher grandoffspring survivorship in a Japanese village from 1671-1871. Voland and Beise (2002) found significant positive effects of maternal grandmothers on grandchild survival, negative effects of paternal grandmothers, and no effects of grandfathers (Beise & Voland 2002). There is suggestive evidence that variation in child mortality may affect reproductive success more than variation in fertility in natural fertility populations (Strassmann & Gillespie, 2002), and so grandparental effects may be concentrated on reducing child mortality. Several survey studies also suggest that maternal grandmothers and grandfathers are more emotionally close, spend more time with, and invest more resources in grandchildren than paternal grandparents (DeKay 1995; Euler & Weitzel 1996).

However, among the Ache of Paraguay, grandparents had little to no effect on offspring fertility and grandoffspring survivorship (Hill and Hurtado, 1996). Additionally, analyses of forager food production where substantial quantitative data exist suggest that adult women, including post-menopausal women, often consume more food than they produce (Kaplan et al. 2000; Kaplan & Gurven in press). Proteins and lipids are widely acquired almost exclusively by men in many forager groups (Kaplan et al. 2000). Even older Hadza women supply only a small proportion of the total calories in the diet. Thus, strong evidence in support of male subsidization of female reproduction is inconsistent with the notion that older individuals, particularly females, are important breadwinners who can significantly influence nutrition. However, the extent of grandmaternal or grandpaternal effects on fitness through non-caloric means is still relatively unexplored. It has been suggested that grandparents may provide protection, direct childcare, useful skills and knowledge, and political leverage (Guttman 1994), but no study has systematically examined this possibility.

To date, most studies of grandparental effects have suffered from limited data, insufficient sample size, or inadequate controls to counter problems of phenotypic correlations and unobserved heterogeneity. *No study has yet measured and linked the proximate ways in which grandparents exhibit the positive, negative, or neutral effects found in analyses of survival and fertility.* Grandparental helping behavior is usually measured with proxies, such as the state of being alive or dead at the time of a grandchild's birth, during the study, or as a time-varying state during each year of early life of the grandchild (e.g. Hurtado & Hill 1996; Beise & Voland 2002). Behavioral studies of older women also consist of small samples (cf. Beise & Voland 2002), and usually focus on absolute food production rather than food transfers to kin (e.g. Hawkes et al. 1989; 1998). For example, no direct evidence has been published that older Hadza women direct food shares to grandchildren. Studies that examine direct fitness effects of grandparental presence are also vulnerable to problems of selection bias. Any study of grandparental effects may underestimate the true effects of grandparents if a loss of grandparents leads to shifts in allocation of support by other kin members. Additionally, phenotypic correlations often mask evidence of true trade-offs when individuals with a greater access to resources, or those in better condition, are able to invest sufficient resources to two functions, such as fertility and survivorship, so that a positive correlation is seen between the two traits, rather than the negative correlation predicted from life history theory. For example, children and grandchildren may exhibit higher fertility or survivorship because their grandmothers are more robust, or because their kin have more resources, and not as a result of direct kin investment (Pennington & Harpending, 1993; Hill & Hurtado 1996; Beise & Voland 2002).

Our research design will allow us to overcome problems of phenotypic correlation and unobserved heterogeneity, to the extent possible, by controlling for differences in resource access, and by linking proximate modes of helping with fitness-related effects on survival and fertility. This will be the first study to examine the causal pathways illustrated in Figure 1, and will do so for a much larger sample of individuals (see Village Sample).

We recognize that no one society can taken as a prototype of the past, given the range of historical and ecological conditions in which our ancestors lived. Moreover, all traditional subsistence societies are undergoing dramatic change, and global and national forces affect each of them (see Methods). While not living replicas of our ancestors, people in small-scale, kin-based, subsistence societies, such as the Tsimane, are living under conditions most similar to those characteristic of the long history of selection during which the human life course evolved. To obtain an adequate understanding of the latter portion of the human lifespan, we will require cross-cultural and historical data to understand the relationships between social and ecological conditions and behavioral outcomes. Our strategy is not to treat the Tsimane as a prototype of the past. It is our goal that the Tsimane research and the methods we develop will stimulate cross-cultural comparative research on the latter portion of the human life course, so that we can determine the universal and variable features of the human life history under relatively traditional conditions. This research is urgent in that this next decade will probably be the last during which research with relatively intact and isolated groups will be possible. The data collected by this research program will be an archive for future scientists who will no longer be able to obtain the information directly.

III. Broader Significance, Training and Research Collaborations

In addition to the scientific and applied goals, the proposed research will contribute to student training and the participation of traditionally underrepresented groups in research. Five graduate and undergraduate students have participated in prior data collection and will continue to do so in the future. Graduate students, Stacey Rucas, Jeff Winking, and another to be named, will conduct dissertation research, and an undergraduate, Amanda Veile, will assist in the project and write an honors thesis. Two Bolivian students, Robin Mamani and Maria Crespo, will also participate in the research. All these students have undergone thorough training in the data collection methodologies and the theoretical and methodological logic of the research design. Advanced methods classes at

UNM and UCSB will use the data to train students in data analysis and publication.

The research is also designed to involve the community members themselves in data collection, and to train Tsimane' in primary health care. The project will employ six Tsimane' research assistants—Alfredo Zelada, Feliciano Cayuba, Ernesto Pache, Luciano and Pascual Durvani and Maguin Gutierrez—who have already worked as translators for the team physicians, conducting anthropometry and strength testing, and collecting census data. They are also being trained in health promotion by the doctors and in the collection of economic data. The project will also train health promoters from Tsimane' communities in the research sample. The project maintains a strong collaborative relationship with the *Gran Consejo Tsimane'*, the overarching political organization for the Tsimane'. In fact, the *Consejo* and its president, Jorge Añez, are actively involved in the project, providing personnel, logistical support, and ideas. The project also supports active involvement of Native Americans in research, helps build capacity among local indigenous organizations with information and training so that they can participate in governance and policy development, and improves the health and well-being of the Tsimane' people. To this end, we have also conducted a series of radio programs and educational public presentations in San Borja to raise awareness about health issues affecting Tsimane, and will continue to do so. These programs have helped to improve the strained relations between Bolivian nationals and Tsimane.

The research will also develop new partnerships in the host country. UCSB has already formed an agreement with the Anthropology Department at the Universidad Mayor de San Andres (UMSA) in La Paz. Significantly, the Ministry of Health has provided team physicians with auxiliary training in sample preparation for tuberculosis. Ministry of Health officials have expressed interest in our epidemiological data, and in our training program of Tsimane health promoters. We will therefore submit copies of our data to them. In addition, the Medical School of UMSA and the University of New Mexico have begun the process of developing a formal agreement to involve students and graduates from both schools in the project over the long run. The team physicians are graduates of the UMSA Medical School. In addition, we have collaborative ties with non-governmental organizations working in the area of native health, including the Andean Rural Health Project in Bolivia. Additionally, Bolivians on our team are a cultural mix from the highlands and the lowlands, two groups whose interactions are typically marked by suspicion and distrust. Finally, the project has developed a collaborative relationship for information and data sharing with another research group, headed by Ricardo Godoy, Bill Leonard, Thomas McDade, Viki Reyes, and Vicente Vadez, who are collecting health, economic and ecological data in the Tsimane' region.

A long term goal of this project is to develop a cross-cultural data archive for interested scientists now and in the future. The results of this research will be published in journals of evolutionary and cultural anthropology, economics, biology and population studies.

IV. Research Design

The Study Population

The Tsimane are lowland forager-horticulturalists living in small villages of about 75 individuals composed of extended family clusters, located primarily in the Maniqui river system in the Beni region of Bolivia. Approximately 7,000 Tsimane inhabit 80 villages in the forest and savanna regions between the towns of San Borja and San Ignacio de Mojos (VAIPO 1998). Almost all of the food the Tsimane consume comes from horticulture, 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 activities. Although the Tsimane' were exposed to Jesuit missionaries in the late 17th century, they were never successfully settled in missions and remain relatively unacculturated. 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 Moseten, who inhabit the southern and northern stretches of Tsimane territory. New mission posts in several different villages only began in the 1950s (Chicchon 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. With support from NSF's Cultural Anthropology program, detailed behavioral observation (food production, time allocation, childcare, social relations) was conducted in two upstream villages on the Maniqui river (Cosincho and Munday) and two interior forest villages (Cuverene and Aperecito). We have met with all 22 of the study communities in the sample and have received enthusiastic support for the project. In fact, we were asked by the *Gran Consejo Tsimane'* to expand our coverage of Tsimane' communities within the Multiethnic Territory (Territorio Multi-etnico), and the Beni Biological Reserve.

The generality of the GMH, ECM, MH, and PH do not require study of strictly foraging groups. Indeed, most strictly foraging populations would not be suitable for this kind of study, because their small size precludes a sufficiently large sample to answer the research questions posed above. The Tsimane' are an ideal population for this study. First, the large population size allows for study of a significant number of older individuals. Second, they continue to invest much time and energy in foraging and other subsistence activities, and derive over 93% of their calories from non-market sources. The existence of agriculture gives older individuals another option for helping descendant kin. Third, the Tsimane are mostly endogamous and have very low rates of outmigration. Therefore there is very little loss of people during longitudinal follow-up, even if there is movement across villages. Fourth, the higher fertility of Tsimane, in comparison with many forager groups, allows for a greater number of options for kin investment, and acts as a greater source of variation in our sample. We recognize the possibility for secular trends in fertility and mortality over the past fifty years due to increased exposure to national society, formal education, wage labor opportunities, and sporadic immunization campaigns (although preliminary analyses suggest few differences in fertility, and slight differences in child mortality only in the last ten years). Secular trends may confound retrospective-based analyses and thus, we will include control dummy variables for each 10-year cohort.

The Village Sample

The complete sample will consist of 22 Tsimane' villages with a population of approximately 2,800 individuals. This sample includes approximately 40% of all Tsimane. This population yields a sample of 280 adults over age 45 (10%), and 95 over age 60 (3.3%). There are 1,035 children age 10 and under (37%). The villages vary in their proximity and ease of access to the nearest town, San Borja (pop'n: ~14,000) and their integration with the market economy. The more acculturated villages are La Cruz, Tacuaral de Matos and San Miguel, with total populations of 293, 310 and 290 individuals, respectively. The other settlements (Anachere, Aperecito, Boreyo, Cachuela, Catumare, Cochisama, Cosincho, Cuverene, Donoy, Emeya, Fatima, Moseruna, Munday, Nuevo Mundo, and Vishiricansi) are more distant, less acculturated, with little to no access to medical services. Four new communities in our sample are located downstream on the Maniqui River within the Beni Biosphere Reserve. These include Campo Bello, Chacal, Chaco Brasil, and Puerto Mendez. Intensive behavioral observations of time allocation and resource production will be focused in six villages, while indirect measures of these activities will be done in the other 16 villages (see section D).

The duration of the proposed study is five years. There are two justifications for the multi-year study design. First, the longitudinal panel design allows prospective analyses that focus on the relationships between time investment, resource production and transfers, and child growth and morbidity. Because each of these components will be measured prospectively, we will avoid the pitfalls of cross-sectional such as problems of endogeneity, self-selection, and phenotypic correlation. As described above, life history-oriented studies are particularly susceptible to these kinds of problems. Appropriate inferences require a prospective design, and five years is sufficient time to witness significant changes in early childhood. Second, the longitudinal design affords us the opportunity to examine change in aiding behavior among the oldest of our older individuals (RQ2, RQ5). Intensive field work for collecting he physical and behavioral data will be performed every other year (years 1, 3 and 5), rather than every year, to reduce the cost of the study and to insure that true age-related changes in our measures outweigh any measurement error in those measures.

Data Collection Methods

A) Demography*, *Kinship, Residence In 2002-2003, demographic interviews were conducted with 539 adults covering reproductive history, migration history, kinship, education, and marriage, in 18 of our study communities. Reproductive histories of 1,100 additional living and dead siblings and parents were also elicited during these interviews. These demographic interviews were used as a basis for age determination of the study population, and for determination of kinship relations. This project will use the same methods to complete the demography of 120 adults in the 4 study communities added to our sample, and 240 adults remaining from our previous sample. The method is described below. In each demographic interview, we also ask, in chronological order, about each of the places where the individual has lived over his or her life up to the present. Duration of stay in each place is estimated by referencing the presence or absence of specific children, siblings, and parents. At each place, interviewees are asked about the residence of each grandparent (if alive). Every adult over age 20 in our sample is interviewed about their own reproductive history, and those of their siblings and parents (alive or dead). We have employed a combination of the methodologies used by researchers with the Ache (Hill and Hurtado 1996), the !Kung (Howell 1979), and the Hadza (Blurton Jones, et al. 2002), to assign all individuals in the sample a year of birth and death, if deceased. Analysis of age at death and age-specific mortality hazards requires methods for determining dates of birth. Missionaries have recorded the dates of many births among the Tsimane' in the last 50 last years (and many of the deaths occurring in the same period). We have copies of birth records for 1,110 individuals from the Catholic Mission Fatima since 1950, as well as age estimates for another 120 individuals who were small children or young adults during the early 1950s. These records are invaluable because all of the current residents of Cachuela and Munday, and a majority of those from Cosincho, derive from Fatima, as do many other migrant individuals now dispersed in other communities. We also have birth records for another 310 individuals associated with the Evangelical Mission La Cruz. Those known dates of birth and death will be used in aging the remainder of the population.

For individuals born prior to record keeping, four methods are employed. Approximate age at death and cause of death is estimated for all deceased individuals in the reproductive histories. For children, age at death will be estimated using developmental stages (just born, sitting, crawling, walking, talking, carried on the hip, able to run, fish, hunt), comparisons to known living children, and season of birth and death. For each pair of consecutive siblings, an attempt will be made to estimate the birth interval. Since this procedure yields redundant reproductive histories (e.g. if more than one sibling is interviewed), data will be checked for consistency and inconsistencies will be resolved. On the basis of those data, all living and deceased Tsimane' in the sample will be assigned estimated ages of birth and death. The second method is to rank all individuals, both living and deceased, in the sample of reproductive histories by relative age, beginning first with 5-year estimated age classes for relative age rankings. Multiple informants are used for each age class and inconsistencies are investigated and resolved. In addition, significant age-related relationships are investigated, such as 'hip-child', hunting mentor, and playgroup companions to augment the relative age lists. This procedure yields ages that can be compared to standard life tables (Howell 1979). Third, ages for as many people as possible will be estimated using historical information and known historical events. For example, a Catholic missionary, Father Marcelino, began working with the Tsimane' in 1950, and Father Martin in 1958. Both missionaries are widely known among most Tsimane in the Maniqui region. Another missionary was murdered, and many Tsimane scattered to other regions in the late 1920's. The first dirt road was cleared in the interior forest in 1970 and then refurbished in 1985. There are also dated flood years and years of large-scale epidemics. 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. A final method incorporates a sample of 70 photos of individuals with known ages. For older individuals, we have 50 photos of men and women from ages 50 through 75. We use these photos as a means of aging dead individuals at the time of their death, and for aging themselves or others during the time of death. This method works in conjunction with comparisons of dead individuals to known individuals in the community and surrounding region. These four methods will provide independent estimates of age. When all four estimates yield a date of birth within a 3-year range, the average will be used unless one or two estimates are judged to be superior to the other(s). When larger discrepancies are found, closer inspection may yield an error that can be corrected. Since a change in one individual's age produces changes in other individuals' ages (in families with reproductive histories and in similar aged individuals in the relative age lists), adjustments should lead progressively to greater consistency across the four methods.

We have already made significant progress in aging people with the first year of demographic data collection. In a preliminary test of our aging methods, we compared the age estimates we derived from a combination of the four methods mentioned above with known ages from the Fatima records for a sample of forty individuals over the age of 45. We found that 100% of the sample was within 5 years of the true, recorded age, 85% was within 3 years, 55% within 2 years, 33% within 1 year, and 25% were exactly correct. Accuracy improves consistently with decreasing age of the individual. This degree of accuracy is sufficient to answer the research questions in this proposal. Moreover, since there is a web of interconnections among families across communities and much inter-community mobility, those estimates will improve progressively as more communities are sampled and analyzed.

B) Health and Morbidity - The procedures for assessing morbidity have been piloted extensively. Team physicians have already collected complete medical histories and conducted physical exams on all individuals in four of our study communities, and with most adults over the age of 30 in fourteen of the other study communities. The same procedures will be employed with all children under age 10 in the other communities, which will add an additional 868 medical histories. This will yield a sample of approximately 1,035 medical histories and physical exams of children under age 10. Morbidity will then be monitored prospectively in years 1, 3, and 5 of the project, in household visits conducted by the physicians with the assistance of a Tsimane' translator-health promoter. Those visits will be conducted once every six months, every other year, for the entire 22 village sample. Drs. Copana will collect the medical data in the ten upstream riverine villages (Cachuela, Cosincho, Munday, Fatima, Anachere, Emeya, Donoy, Catumare, Boreyo, Cochisama), and in La Cruz. Dr. Cortez will lead a team to collect the epidemiological data in the six interior forest villages (San Miguel, Moseruna, Nuevo Mundo, Cuverene, Vishiricansi, Aperecito), and the remaining five villages (Tacuaral de Matos, Puerto Mendez, Campo Bello, Chacal, Chaco Brasil). During those visits the physicians will complete a checklist of conditions (respiratory, digestive, skin, muscular-skeletal, dental, traumatic injury) for every child aged 10 and under, and for those aged 45 and over, in every household. The physician will investigate each positive condition with standard primary care methodology, including a history and a directed physical exam. Even when there are no complaints, the physicians will conduct a brief physical to insure accurate diagnoses. In the previous first year, we found that a significant number of complaints were false positives, while a significant number of false negatives resulted in diagnoses of pathology upon further investigation. This methodology will permit virtually continuous monitoring of morbidity in the full sample. The physicians will also collect interview data regarding all serious illnesses and injuries that occurred between visits, including severity and duration of incapacitation. This will provide 6,210 'instantaneous' morbidity checks (2/yr *3 yrs*1,035 individuals) and 3,105 person-years for major morbidity episodes. The physicians will provide basic primary care services. This intervention is likely to impact morbidity and mortality in those communities. The two-tiered sampling procedure in the first year of the previous project allowed us to measure those impacts. Visits to the study villages at six month intervals, every other year, represent a minor intervention and will have a small impact on rates of mortality and morbidity.

C) Growth – Growth will be measured by a series of anthropometric measures, including height (HT), weight (WT), upper arm length (UAL), mid-upper arm circumference (MAC), and the four skinfolds (SKF): triceps (TCF), biceps (BCF), subscapular (SBF), and suprailiac (SPF). All members of our research team have been extensively trained in the collection of these measures. Following the training period, repeated measures on the same individuals were taken by different investigators to determine discrepancies in measuring techniques. These inconsistencies were progressively reduced until all members produced measures within 5mm of one another for height, and 1mm for the caliper-based body fat measures, with very high reliabilities. In order to assess nutritional status and body composition as a function of age and sex, the following indices will also be generated from these measures: 1) weight-for-age, 2) height-for-age, 3) weight-for-height, 4) Body Density, D, calculated with age- and sex- specific equations, using the sum (TSF) of the first four skin folds (TSF=TCF+BCF+SBF+SPF) from (Durnin and Womersley 1974); 5) Fat Mass, calculated as $FM = WT * 4.95/D - 4.5$ where D is body density.

D) Time allocation and resource production – We will measure time usage through direct observational and indirect interview methods in order to link variation in age-specific activities with prospective health outcomes. In a focal sub-sample of our study villages time allocation will be measured using a community-wide scan sampling methodology in which the specific activity an individual is engage in at the time of the scan is recorded. One team will be based in Fatima, another based in Chacal and Campo Bello, and another in Cosincho and Munday. Scans will be conducted three times per day at four-hour intervals from 7am-7pm, every other day. Individuals at or near the residential cluster will be observed directly and the activities of absent individuals will be obtained by informant interviews and follow-up visits. Individuals, especially children, will also be coded in terms of whether they are reported to be ill. In the smaller villages of Chacal, Campo Bello and Munday, the entire village will be scanned each time, and in the larger villages, such as Fatima, only a third of the village will be sampled in each scan. Roughly 900 people live in these villages, with 90 individuals over age 45, and 270 children under age 10. This sampling procedure will produce 200 time observations per person per sample year, and a total of 180,000 time points per year. A complete set of activity, location, and object codes already exist, so that efficient data collection is possible. Those data will be used to examine the differential usage of time spent by older individuals in productive, childcare, educational, maintenance, social and recreational activities. Time allocation for small children and adults will be recorded for use as controls when examining time use of older individuals. Interviews on time spent in productive activities will also be conducted in these and the other 17 study villages to obtain a larger sample of individuals. These interviews will be conducted during the physician visits twice a year in a panel design to investigate variation in time allocation. During each interview, household participants will be asked about the number of days spent in hunting, fishing, and in clearing, weeding, planting, or burning of fields over the previous week. These interviews were also piloted and modified during the 2002-2003 field season. While less accurate than the data produced in our subsample, preliminary analysis of these measures provide similar estimates as those derived from behavioral observation.

We will also employ a combination of observational and interview methods piloted during the 2002-2003 field season to measure food production. End-of-day hunting and fishing interviews will identify production activities performed that day, production locations, activity group composition, and quantity and type of resources acquired or harvested. These will be performed every other day for all village members living in Chacal, Campo Bello, Cosincho, and Munday, and every third day for those living in Fatima. In the other study villages, interviews (using the same twice-yearly panel design mentioned above) will be conducted to examine the frequency of different production activities for household members. Identity and quantity of game resources will be measured over the previous week, while fish will be measured over the previous two days, due to the greater abundance and shorter reliable recall periods for fish production. Agricultural fields under cultivation will be measured with GPS coordinates along the periphery of fields in the five communities mentioned above. In the other communities, household agricultural production will be elicited from interviews about the number and size of fields. Our focus will be on the number of tareas ($1/10^{th}$ of a hectare) devoted to plantains and corn, and the number of arrobas (~12 kg) of rice produced that year. These three cultigens comprise over 85% of the agricultural production. While these interview-based methods lack the precision and accuracy of direct measurement, they allow for a rough estimation of actual agricultural production. Estimation of caloric production will be achieved using a series of imputed measurements based on prior surveys, which used cross-checking of verbal reports with direct measurements from a sample of fields in four communities.

E) Resource transfers - The inter- and intra-generational flow of resources is an important aspect of human life histories, and critical to existing evolutionary models (see (Kaplan and Robson 2002; Lee 2003). During time scan samples in the five villages described in section D, researchers will also record all instances of food consumption, and ask the consumer (or nearby adult) the identity of the acquirer and donor of the food. This method should generate an additional 9,000 consumption events that can be used to determine 1) the proportion of each child's food that was acquired or produced by parents, siblings, grandparents, self and other individuals; and 2) the proportion of the food produced or acquired by older individuals that is eaten by self, children, grandchildren and other individuals. In addition, during the end-of-day food production interviews in Chacal, Campo Bello, Cosincho, Munday, and Fatima, household members will be asked to report each instance of meat, fish, other foods, and money that was either given to other households, or received from other households during the previous day. For each of these items, we will record whether the item was raw or cooked. Each household member over age 5 will be interviewed, and adults will be re-queried as to the giving and receiving of food by children under age 10. The focus on transfers given and received will allow researchers to verify informant reports, and to reduce measurement error (especially for children) on the same interview day. In the other study villages, household members will be asked these same questions by researchers during physician visits, but the time span of recall will be expanded to three days. Previous work among the Tsimane showed that a recall period of three days gave reliable and accurate information about food transfers.

F) *Interviews* – We will conduct semi-structured interviews with 30 adults between ages twenty and fifty, and with 30 adults over age fifty. We will interview both older and younger adults about their perceptions of grandparents, expectations regarding their roles as resource producers, caretakers, political actors, their contributions to family, friends, and others, and their perceptions of physiological and cognitive changes with age. We will ask how their own self-identities change with the birth of grandchildren (Fisher 1983). We will ask them to describe exemplars of 'good' grandparents, and of 'bad' grandparents. We will also ask them to describe any differences they perceive between grandmothers and grandfathers, and maternal versus paternal grandparents, in terms of social, physical, and emotional closeness to children and grandchildren. These qualitative interviews will complement and contextualize the quantitative results obtained through statistical analysis.

Data management A combination of paper forms, laptop computers and hand-held computers will be used for collection. The forms, data entry interfaces and databases have already been constructed. Each individual has been assigned a numeric personal identification number and names will be stripped from the database for confidentiality after the data are transferred. All members of the field team have been trained in data entry. Manuals for all procedures have been written and will be provided to the researchers in each village. There will be weekly communication by radio between field sites for discussing and resolving problems. This approach greatly increased data quality and consistency in our pilot work. In order to prevent data loss, databases will be regularly backed-up on Compact Disks, according to security procedures already in place. Programs written in SAS will be used to create the databases for statistical analysis. Those databases will be extensively checked for errors both by hand and with programs designed to check for inconsistencies between data sources.

Data Analysis Statistical analysis will be tailored to the specific structure of the data that will be used to answer each of the research questions outlined in the Project Description. Each individual over age 45 will contribute six data points of residence choice to answer RQ 1 and 1a (two times in each of years 1, 3 and 5). For each of the 22 communities, we will sum his/her number of children and grandchildren under age 18. For each variable, the communities will be given a rank of 1 to 5 from most to least. All communities with none (e.g., no grandchildren) will be given a rank of 5. A time series logistic regression will be performed in which the log odds of residing in a community are regressed on both the grandchildren and children rank variables, treating each rank as an indicator variable (with rank 5 as the baseline). Age, sex and community size will be introduced as control variables. A sex by rank interaction term will be use to assess whether women show greater preference than men. Age by rank for each rank variable will be used to assess whether those effects change by age. A lagged variable of residence in this village in the previous visit (yes/no) will be introduced to account for the time series nature of the data.

To answer RQ 2 and 3 on time use, we will utilize the time allocation data from the five focal communities. For each of years 1,3 and 5, we will score each individual with respect to the proportion of time spent caring for own children, grandchildren, other children, household work in a house with own minor children, in a house with grandchildren, in tool manufacture for self and for adult children, and in food production. The data on food consumption will be used to determine the proportion of times a food acquired by that individual was consumed by self, spouse, minor children, adult children, grandchildren, nieces and nephews, and others. The proportion of time spent in food production will then be multiplied by the consumption proportions to estimate the proportion of time spent provisioning each of those classes of individuals. These data will be organized in descriptive tables, disaggregating men and women and 10-year age brackets to answer RQ2. To answer RQ3, the probability of being observed in one of those activities will be regressed on number of ill children, ill grandchildren, pregnant daughters/daughter-in-laws, nursing daughter/daughters-in-law in the village, using a logistic link function. A mixed, multi-level model design will be used in this analysis (Goldstein 1997; Hougaard 2000), to take account of the hierarchical structure of the data, because communities contain multiple individuals, and each individual contributes multiple data points. Those models treat each data point, $y_{i,j,k}$, as the *k*th observation of the *j*th individual in the *i*th community. This will allow us to determine community effects and interactions between community and the effects of the other explanatory variables. Again, sex and age will be introduced as controls to test for sex biases, with sex by illness, and sex by reproductive state of daughters/daughter-in-laws interactions. A random effects term for each individual will be included in the model to account for the lack of independence among data points contributed by the same individual and to control for unobserved heterogeneity. To answer RQ4, activities will also be scored in terms of the skill and strength required to perform them, using a scoring system developed in Gurven and Kaplan (in press). A multinomial logistic regression will be performed on four activity types (low strength-low skill, high strength-low skill, etc.) to determine if men and women engage in more high skill-low strength activities as they age.

RQ 5-8 will utilize the data on food production and food consumption from the five community sub-sample as well. To answer RQ4 on net productivity, each individual's resource production per day will be summed and each individual's food consumption will be estimated, using an algorithm based on age, sex and weight developed in Kaplan (1994). Net production is then derived from subtracting consumption from production. Those data will be analyzed descriptively by sex and 5 year age cohort, as well as fit with various parametric and non-parametric models of age and sex. RQ 6 and 7 will be addressed using a similar approach. To answer RQ8 on biasing food sharing to the most needy children, each child will be scored in term of the ratio of adults to children in their household, and number of grandmothers and number of grandfathers co-resident in the village. For each grandparent-grandchild pair, the proportion of the child's consumption events derived from that grandparent will be regressed on the above explanatory variables, with community, age and sex of grandparent, and age and sex of grandchild, as controls. A household random effects term will be introduced to account for the lack of independence between children in the same household.

RQ 9-12 concerning growth and health will be examined at two levels. One level will examine the effects of grandparental co-residence on growth and will utilize the large sample of 22 communities, the panel sampling design to be employed in years 1, 3 and 5 will yield two measures per year per individual with respect to residence and morbidity, and one measure per year with respect to anthropometry and strength. This also generates a hierarchical data structure requiring mixed, multi-level models, as communities contain multiple individuals, and each individual contributing multiple data points in a time series. Weight gain and height gain between years 1 and 3 and between years 3 and 5 will be regressed on the co-residence of each of the four grandparents, as indicator variables with age, sex, community as controls. Weight at the beginning of the time interval will be included as a baseline. The second level will include grandparental time and food inputs, using the five community sub-sample. The basic structure of the analysis will be the same, except that growth will be regressed on the measures of grandparental time and food inputs as well.

A similar set of models will be used to assess morbidity, using the prospective data set. However, since each individual in the sample will be evaluated every six months in the sample, we will add a term for random effects at the individual level to control for the lack of independence among data points. The team physicians have identified 152 different diagnoses that they have encountered among the Tsimane. Those diagnoses will be treated as dependent binary variables for each evaluation. They will also be aggregated hierarchically into classes of morbidity. For example, one level will treat morbidity in different physiological systems (e.g., respiratory infections, gastro-intestinal disorders, musculo-skeletal trauma, etc). The highest level will be presence or absence of morbidity. Using those dependent variables and a logistic link function, the probability of each major class of morbidity will be regressed on age, sex, year, season, community, and vectors of individual time-invariant and time-varying co-variates (as above).

To address demographic outcomes concerning mortality and fertility (RQ 13-15), a time-varying, hazards, or event history model will be employed (Goldstein 1995; Beise & Voland 2002). The standard form for this model is: $\ln y_i(t) = b(t) + \sum_k \beta_k x_{ik} + \sum_l \lambda_l z_{il}(t)$, where ln $y_i(t)$ refers to the log-hazard of mortality, or fertility for individual *i*, *b(t)* is the base-line hazard, x_k is the *k*th time-constant covariate, and z_l is the *l*th time-varying covariate. Time-varying covariates include presence of maternal and paternal grandmother and grandfather, age of mother, age of the grandparent, and number of living siblings. Time-constant covariates include 10-year cohort and sex. Multi-level versions of these models will be used to control for non-independence and hierarchical organization of the data (Goldstein 1995; Hougaard 2000).

Statistical Power We have conducted extensive power analyses to determine whether the sample sizes we will obtain are sufficient to assess the effects of older individuals on child outcomes. Using a program developed at the Dartmouth Hitchcock Medical Center (Toteson et al. 2003), we have conducted power analyses with logistic regression for the binary variables, regarding child morbidity and mortality. Given the sample of 6,210 health checks for children under age 10, an estimated probability of being sick at .2 (a conservative estimate based on preliminary data), we should be able to detect odds-ratio effects of grandparental presence as low as 1.15 with a power of 90%, using a directed test with a p-value of 0.05 and assuming one additional covariate and a 0.2 correlation between the two predictor variables. Splitting the sample into males and females, an odds-ratio of 1.2 may be detected with 95% power. The smaller focal sample of 210 children will allow detection of odds-ratio effects of about 1.3 with 90% power. Testing for effects of grandparent presence on mortality using the complete sample of ~16,000 risk years for children under age ten (including retrospective data from reproductive histories) and assuming a 4% overall child mortality rate (estimated from preliminary data analysis), we should be able to detect odds-ratio effects of grandparental presence as low as 1.14 with a power of 90%. With the prospective analysis on the sample of 1,035 children over 5 years will allow detection of odds-ratio effects of 1.3 with 90% power.

Calendar and Responsibilities The research period is for five years between July 1, 2004 through December 31, 2008. Two Bolivian physicians, Drs. Cortez and Copana, and the six Tsimane' research assistants will work full-time on the project during years 1, 3 and 5. The assistants will aid the physicians with translation and will collect data on anthropometry and economic controls. Gurven and Kaplan will dedicate their time to project management (coordination, supervision, training and quality control), demography, focus group interviews, and data analysis. During years 1, 3, and 5, they will update the reproductive histories in all study villages. During the summers of 2005 and 2006, Gurven will complete the reproductive histories, update the relative age lists, and finalize the ages for all Tsimane in our sample. The two physicians will monitor morbidity during years 1, 3, and 5 in all 22 study villages. Graduate students will collect time allocation, resource production and distribution data during years 1, 3, and 5. Tsimane' researchers Alfredo Zelada, Ernesto Pache, and Luciano Durvani will conduct the first round of anthropometry between March and December in year 1. These researchers will repeat those measures in the same months of years 3 and 5. Gurven and Zelada will continue updating censuses during all years. Table 1 summarizes the months during which each data type will be collected, relevant personnel, and expected sample sizes.

TABLE 1.	**Months of the year**					**Personnel**	**Sample size**	**P/R**
Research method	**2004**	**2005**	**2006**	**2007**	**2008**			
Censuses and mortality	7-10	6-8	6-8	6-8	6-8	MG,HK,AZ	10,350 py	P,R
Child morbidity and health	7-12		1-12		1-12	EC,RC,TP	7,890 pp	P
Repro. hist. and kinship	7-8	6-8	6-8		6-8	MG,HK,AZ	939	P,R
Anthropometry	3-12		8-12		8-12	AZ,EP,FC,PD	3,105pp	P
Time allocation	7-12		2-12		1-12	JW, SR, RM, GS1	540,000 pp 7,980 pd	P R
Food production, transfers	7-12		2-12		1-12	JW, SR, MC, GS2	6,000 hp, 9,000 con	P
Focused interviews	7-8	2-5		6-8		MG,HK	45	P,R

MG=Gurven, HK=Kaplan, SR=Stacey Rucas, JW=Jeff Winking, EC=Dr. Edhitt Cortez, RC=Dr. Ruben Copana, MC=Maria Crespo, RM=Robin Mamani, AZ=Alfredo Zelada, EP=Ernesto Pache, FC=Feliciano Cayuba and MaG=Maguin Guitierrez, LD=Luciano Durvani, PD=Pascual Durvani. hp=household-points, pp=person-points, pd=person-days, py=person-years, con=sonsumption events. P=prospective, R=retrospective data