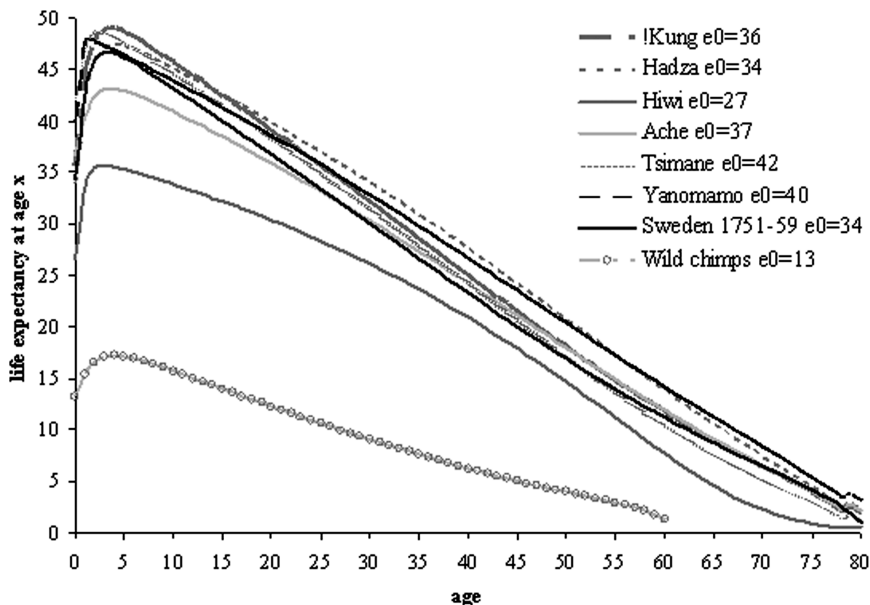## CHAPTER 3

Beyond the Grandmother Hypothesis: Evolutionary Models of Human Longevity

Michael Gurven and Hillard Kaplan

The maximum life expectancy has risen steadily by more than two years every decade over the past two centuries, 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; Oeppen and Vaupel 2003). Although much of the increase in life expectancy in the nineteenth century can be attributed to better sanitation, modern medicine, and improved diets (Riley 2001), there is strong evidence that the general pattern of a long life span is not unique to the past century, and that current increases in life span may be a consequence of plasticity in our evolved human life history. Converging evidence shows that living into "old age" is not unique to modern populations or to even agriculturalists (cf. Lovejoy 1981; Washburn 1981). Data from extant foragers with little to no access to medical attention or modern foods, including the Ju/'hoansi (Rosenberg this volume), Ache, and Hadza, show that women who survive to age forty-five can expect to live an additional twenty to twenty-two years, even though at birth mean life expectancies in these populations range from thirty to thirty-seven years of life (Blurton Jones K. Hawkes and J. O'Connell 2002; Gurven and Kaplan 2007). Extrapolations based on comparative analyses of brain weights and body sizes among nonhuman primates suggest a maximum life span between sixty-six and seventy-eight years for early *Homo sapiens*(-Hammer and Foley 1996).[1] Existing paleontological evidence suggests that a postreproductive life span existed anywhere from 150,000–1.6 million years ago (Bogin and Smith 1996; Caspari and Lee 2004). A recent cross-cultural exploration of mortality patterns across the life course among hunter-gatherers and forager-horticulturalists shows survival into the sixth and seventh decades of life and depicts a unique life history characteristic of our species that cannot be explained as an artifact of modern conditions (Figure 3.1).

1

54   A Global Vision of Aging, Culture and Context

Figure 3.1
Age-Specific Life Expectancy: Expected Number of Years Remaining for Six Sample Human Populations, Sweden, 1751–1759, and Wild Chimps.

Note: All groups show roughly the same trajectory, with most differences concentrated in the first few years of life. The much shorter life expectancy for wild chimpanzees is given as a comparison. All curves are based on life-table estimates using the Siler model. Life expectancies at birth (e_0) are given in the legend. Figure adapted from Gurven and Kaplan (2007).

Elsewhere we have argued that sixty-five to seventy-five years is the closest equivalent of an adaptive human life span as this is the modal age range of many later adult deaths for hunter-gatherers (Gurven and Kaplan 2007). Figure 3.1 shows that much of the variation in age-specific life expectancies among preindustrial populations occurs in the first few years of life, and the subsequent age trajectories of mortality show a similar profile across the life course. The longevity of these societies is noteworthy, as an individual that survives to age fifteen can expect to live an additional thirty to forty-four years, and a survivor to age forty can expect to live an additional twenty to twenty-eight years. Departures from these patterns in the ethnographic and paleodemographic literature are likely due to high rates of contact-related infectious disease and violence, and methodological problems such as poor age estimates of older individuals, biased preservation of the skeletons of infants and older individuals, and improper usage of model life tables (Blurton Jones et al. 2002; Gurven and Kaplan 2007).[2] However, recent reestimation of several common paleo-mortality curves based on improved methods shows a life course pattern similar to that of the ethnographic sample (Konigsberg and Herrmann 2006).

Chimpanzees in both the wild and under favorable conditions in captivity show much higher rates of adult mortality and significantly shorter life spans.

A fundamental feature of the human life course of evolutionary significance is the substantial postreproductive period for women. Even men, while physiologically capable of producing viable offspring well until their eighties, show a similar age-specific decline in fertility, but the decline appears five to ten years later than for females, among the Ju/'hoansi, Ache, and Yanomamo (Hill and Hurtado 1996). Initial enthusiasm for a theory that could explain menopause and more generally reproductive cessation (Hawkes, O'Connell and Blurton Jones 1989; Hill and Hurtado 1991; Rogers 1993) was met with some obstacles after theoretical modeling and early empirical tests showed little support for the notion that reproduction should terminate early in the life span. Moreover, there is little evidence for any upward secular trend in the age at menopause over the past century, despite increases in life span, changes in the age at menarche, and an estimated heritability in the age of menopause of 40 to 60 percent. Reproductive cessation exists in other closely related primate species, especially in captivity, although there is no evidence for a lengthy postreproductive life span among our primate cousins. It is now thought that menopause is the conserved ancestral condition, which thereby shifts the focus of explanation to the long life span after the termination of reproduction (Kaplan 1997; Hawkes et al. 1998; Judge and Carey 2000).

From the perspective of natural selection, the significant period of human life spent in a postreproductive state is a conundrum, because sterility is the evolutionary equivalent of death. Its occurrence in humans (and absence in most other mammals) is one of the most challenging puzzles of evolutionary biology today. As described previously, 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); rather it is the extended lifespan of humans after reproduction has ceased that is rare (Gould, Flint and Graham 1981; Treolar 1981).

EVOLUTION AND LONGEVITY

Several theories have been proposed to explain this remarkable extension of the human life span. The classic theory of senescence in evolutionary biology was first proposed by Medawar (1952), developed further by Williams (1957), and then formalized by Hamilton (1966). It proposes that as individuals age, they contribute less to biological fitness, or the future proliferation of their DNA in the gene pool, because less of their expected lifetime fertility remains. Consequently, natural selection acts more weakly to reduce mortality at older ages. The existence of substantial postreproductive life among humans therefore suggests that older individuals have "reproductive value" by increasing fitness through nonreproductive means.

George Williams was first to propose that beginning at ages forty-five to fifty, mothers may benefit more from investing their energy and resources in

56   A Global Vision of Aging, Culture and Context

existing children rather than from producing new ones (1957). This idea became known thirty years later as the "Grandmother Hypothesis." A specific version of the Grandmother Hypothesis has been proposed by Hawkes, Blurton-Jones, and O'Connell (1998) and explained more fully by Hawkes (2003). Their model focuses on intergenerational transfers among women and proposes that older women can increase their future genetic representation (i.e., inclusive fitness) by enhancing offspring fertility and survivorship of grandchildren through provisioning or providing support to younger generations. Among foragers, the resources acquired by women are strength-intensive, disadvantaging young children and thereby increasing the value of older women's labor contributions. According to this view, extensions in the human life span are driven by selection on women, and the value of resource transfers from grandmothers to grandchildren. Some of the initial inspiration for the Grandmother Hypothesis came from fieldwork done with Hadza foragers in Tanzania, where "hardworking" older women were observed to produce substantial quantities of food.

BEYOND THE GRANDMOTHER HYPOTHESIS

Peccei proposes an amendment to this view (2001). She points out that long-term juvenile dependence among humans implies that adults who cease reproducing in their forties will not finish parenting until they are sixty or older (see also Lancaster and King 1985). The notion that most of the benefits to longevity derive from helping offspring rather than grandchildren has been called the "Mother Hypothesis."

An alternative view focuses on men. Marlowe argues that the extension of the life span is driven by selection on men, stressing the fact that men do not experience menopause and can have children into the seventh and eighth decades of life (2000). His argument, called the "Patriarch Hypothesis," is that men accrue status and power as they age, which they use to obtain reproductive benefits. These benefits and the lack of a physiological menopause selects for their greater longevity. Formal demographic models of life history evolution typically focus only on females, but two-sex demographic models where men tend to be older than their spouses may also lead to a pattern of delayed senescence after the age of fifty (Tuljapurkar, Puleston and Gurven 2007).

A fourth view, the "Embodied Capital Model" proposes that timing of life events is best understood as an "embodied capital" investment process (Kaplan et al. 2000; Kaplan and Robson 2002; Gurven, Kaplan and Gutierrez 2006). Embodied capital is organized somatic tissue such as muscles, immune system components, and brains. 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 human foragers consume (Walker et al. 2002; Gurven, Kaplan and Gutierrez 2006). 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

Beyond the Grandmother Hypothesis   57

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 life-span coevolved with the lengthening of the juvenile period, increased brain capacities for information processing and storage, and intergenerational resource flows.

Embodied capital theory also proposes that meat acquisition and extractive foraging generate complementary roles for men and women in a sexual division of labor, where both invest directly in offspring and grandoffspring in long-term unions. Contributions from older men, in addition to that of women, are therefore expected, rather than the solitary pursuit of alternative mating opportunities as men's partners age. In fact, men often experience "effective menopause," because their last reproductive event is often tied to their wife's last reproduction (Gurven and Hill 1997).

EMPIRICAL STUDIES OF BENEFITS TO OLD AGE

The starting point for most evolutionary theories is the realization that successful reproduction is not only a matter of producing offspring (i.e., maximizing fertility). Among humans, it requires many years of assistance and nurturing. This includes common tasks like acquiring food and sharing it with offspring, protecting children from environmental dangers and other hazards, and fostering education of productive and social skills necessary for successful adulthood. This perspective places the acquisition and distribution of food at the center of reproductive fitness, rather than fertility. These hypotheses have broad implications for understanding the evolution of distinct human life history traits, the organization of social communities, and intergenerational social dynamics. Nonetheless, there have been few empirical investigations, 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 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 (1989). These same researchers later showed that grandmothers who worked longer hours had grandchildren who experienced positive weight gain (Hawkes et al. 1998). 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 one to two years old, whereas only paternal grandparents had a positive effect on a daughter's fertility (Sear et al. 2003). Several historical studies reveal significant grandparental effects. Jamison et al. showed that maternal grandmother presence was associated with substantially higher grandoffspring survivorship in a Japanese village from 1671–1871 (2002). Voland and Beise

58   A Global Vision of Aging, Culture and Context

(2002) found significant positive effects of maternal grandmothers on grandchild survival, negative effects of paternal grandmothers, and no effects of grandfathers (Beise and Voland 2002). Some evidence suggests that variation in child mortality may affect reproductive success more than variation in fertility in populations not using modern birth control, and so grandparental effects may be concentrated on reducing child mortality (Strassmann and Gillespie 2003). 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 and Weitzel 1996).[3]

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 postmenopausal women, often consume more food than they produce (Kaplan and Gurven 2005). Despite the hard work of Hadza grandmothers, even these women supply only a small proportion of the total calories in the diet. Contrary to stereotypes that situate the Ju/'hoansi as the "typical forager," the majority of food in forager diets comes from hunting and fishing activities, and these are largely the domain of men (Cordain et al. 2000; Kaplan et al. 2000). Moreover, limited macronutrients such as proteins and lipids are widely acquired almost exclusively by men in many forager groups. Thus, the 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.

To date, most studies of grandparental effects have suffered from limited data, insufficient sample size, or specific statistical problems.[4] More importantly, 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 throughout early childhood. Behavioral studies of older women in preindustrial contexts also consist of small samples and usually focus only on absolute food production rather than food transfers to kin or other noncaloric contributions. In an attempt to address these problems and advance the ecological study of longevity, we initiated the Tsimane Health and Life History Project in 2002.

TSIMANE HEALTH AND LIFE HISTORY PROJECT

Since 1999, we have conducted fieldwork with Tsimane Amerindians living in the Bolivian Amazon. In 2002, we began focusing on household economics, demography, growth, development, and aging with a large-scale project conducted in eighteen villages.[5] The underlying goal of our project has been to understand different physical and cultural dimensions of the aging process in a

3

4

5

Beyond the Grandmother Hypothesis   59

fairly remote, traditional population of forager-horticulturalists who live in a world without supermarkets, refrigerators, plumbing, health care, and formalized social security benefits. Tsimane inhabit a highly infectious environment, with prevalence and incidence rates of respiratory and gastrointestinal disease and parasitic infection much higher than those experienced in the developed world. Mortality rates among Tsimane resemble those of Sweden and other European countries in the mid-nineteenth century and are indicative of a population in the beginning stages of an epidemiologic transition (Gurven, Kaplan and Zelada Supa 2007), where the causes of deaths shift from those due to infectious disease to chronic conditions such as heart disease and cancers (Omran 1971). Given the relatively large population of Tsimane (roughly 8,000 individuals), we have been fortunate to learn about the lives of a large sample (by anthropological standards) of older adults.

It is very rare for Tsimane to live beyond the age of eighty, and there is no reliable evidence that Tsimane have ever lived beyond the age of ninety. However, it must be remembered that even if mortality was low among older adults, there is still likely to be only a small percentage of older individuals present in small, high-fertility populations. Among high-fertility national populations in the year 2000, such as Botswana or Bolivia, only 0.3–0.9 percent were older than eighty years. If the Tsimane population pyramid were representative of these national patterns, the study sample of 2,500 individuals would show at most seven to twenty-three individuals older than eighty. Problems with age estimates aside, there have been few studies of the very elderly in foraging and small-scale horticultural societies for the simple reason that small foraging populations of (say) 150 individuals are unlikely to have even one individual over eighty, and perhaps only four people over the age of sixty-five (see Rosenberg in this volume).

Among the Tsimane, older adults are referred to as *isho' muntyi* (old people). No specific language terms connote different stages of older life (*furdye'*), although certain physical descriptions such as *fucruij jam mi'i aty jam ca've'* (white-haired, cannot walk, and can no longer see well) have been used to describe very old adults in their seventh decade. Old age is often defined by the Tsimane themselves as severe physical decline such as frequent aches and pains over most of the body, an inability to walk far distances, and when overall ability to perform common tasks is compromised.

As in many cultures, older adults are held in esteem in popular Tsimane ideology. Older adults are sometimes respectfully addressed as *jayej* (grandmother) or *via'* (grandfather) by nonrelatives and treated with respect. They are revered for their specialized knowledge of medicinal plants, animals, and navigation in the tropical rain forest that surrounds their thatch homes. They also possess greater knowledge about navigating the world of forest spirits that provoke sickness and bad luck if certain transgressions are made. It is widely recognized that older adults are often fearless speakers unafraid to voice their opinion, and they often resolve conflicts or reprimand the wayward. This is often expressed as literally "knowing how to speak" (*chij peyaqui*). Even

60   A Global Vision of Aging, Culture and Context

One of the oldest Tsimane women alive today, Francisca Temba, age 76, and her daughter Demecia, age 48, prepare the fermented beverage *shucdye* made from masticated manioc and mixed with maize.

with the institution of formal chiefs and bilingual Tsimane teachers over the past thirty years, older adults (who are mostly monolingual in Tsimane) still voice their opinion through the younger chiefs and teachers. Grandparents also sometimes help set up marriages for their grandchildren and are often used as babysitters and as foster parents, especially when parents undertake extended visits to other villages or the local market town. Older adults are frequently noted as experts in common manufacturing activities, such as handbag weaving and bow and arrow making, and named as skilled hunters and fishers. When queried, many people name their parents or other older adult relatives as key people who through example or close proximity have helped "train" them in a variety of important activities. These observations suggest that older people are motivated to help younger generations often and in critical ways that are not captured by solely focusing on daily caloric contribution to the diet.

Despite an ideology that highlights some strengths of older people and the sentiment often voiced that "it's good to have them around," the lives of older people are not carefree or without considerable difficulty. During informal conversations, we heard stories of siblings conflicting over who should care for their aged parents and complaints by older people that they are too frequently neglected by their kin.[6] It is our impression that with physical decline past age

Beyond the Grandmother Hypothesis   61

Tsimane economic life is inherently social. Here members of an extended family composed of three generations from the remote riverine village of Catumare eat fish stew (*jo'na*) with plantains.

sixty, older Tsimane seem to be viewed more as net burdens, and especially so by the time they reach their seventies. Based on conversations and demographic interviews, parental abandonment, neglect, and suicide (especially upon the death of a spouse) were probably not uncommon occurrences in the past. Living alone without kin support and visits by children is a haunting prospect for many older people and characterizes the essential fear of growing old among many Tsimane. It is a fear that should not be permitted to consume one's thoughts. As a forty-three-year-old man from a remote community on the upper Maniqui river remarked, "I am not afraid [of getting old]. It's dangerous to be afraid. Filled with fear we die."

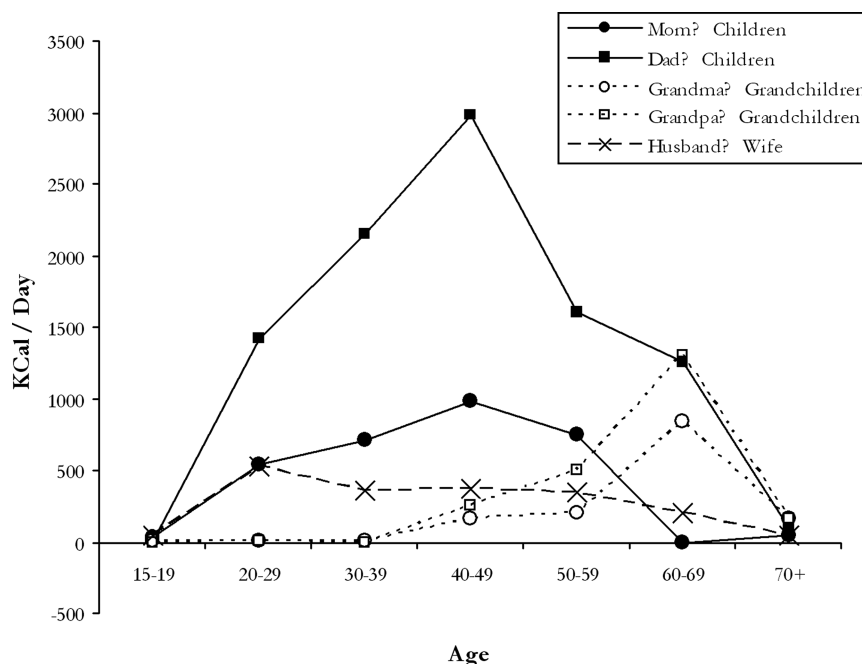## IMPLICATIONS FOR NEW RESEARCH DIRECTIONS

Activities of Older Individuals

Most evolutionary hypotheses regarding lifespan extension focus on the benefits of living longer via the flow of resources from parents to children and from grandparents to grandchildren. On average, a Tsimane woman will be a mother by age eighteen, a grandmother by age thirty-six and a great-grandmother by age fifty-four. She therefore has many opportunities to improve the health, survivorship, fertility, economic success, and overall well-being of descendant kin. As mentioned previously, quantifying the types and magnitude of

62   A Global Vision of Aging, Culture and Context

assistance made by older adults is a necessary first step in assessing whether postreproductive lifespan is adaptive, and for evaluating whether the separate forms of aid provided by women and by men can help differentiate among evolutionary models. Among Tsimane, for example, older men shift activities away from hunting and rely more heavily on farming, whereas older women spend much of their productive time processing, rather than directly acquiring food. At their peaks, both men (in their forties) and women (in their thirties) share over half of their production with their children. After these peaks, the proportion directed towards children declines as that towards grandchildren increases. By the sixties, women are directing much more of their production to grandchildren than to children, and no longer have any subadult children to invest in. Men provide comparable amounts to children and grandchildren in their sixties. Tsimane men and women in their seventies do not contribute many calories to their descendents (Figure 3.2). Figure 3.2 shows that both men and women make contributions to younger generations, consistent with the Embodied Capital Model, and that grandparental contributions decline sharply at late ages, which is consistent with the Mother Hypothesis. The fact that husbands, fathers, and grandfathers contribute more than wives, mothers, and grandmothers, respectively, also runs counter to the sole female focus of the Grandmother Hypothesis.

Figure 3.2
Net Contributions from Parents to Children, from Grandparents to Grandchildren, and Husband to Wife by Age for the Tsimane, 2002–2005.

Beyond the Grandmother Hypothesis   63

If older age is functionally designed to improve the fitness of descendant kin, then we should expect a wide range of psychological, motivational, cognitive, emotional, and behavioral traits that focus attention on perceiving and responding to needs of particular kin. Life span psychological studies do seem to indicate that older adults acquire greater ability to integrate their knowledge and make efficient decisions as they age. This research also shows older adults to be more skilled problem solvers and negotiators, have a more positive outlook, and show less emotional distress than their younger counterparts—features that are consistent with the caretaking role of older adults (Carstensen and Lockenhoff 2003). To the extent that older adults are helpful, younger kin should be motivated to maintain proximity to them and to help ensure that they are adequately cared for. The extent of grandmaternal or grandpaternal effects on fitness through noncaloric means, while difficult to quantify, requires much additional attention. It has been suggested that grandparents may provide protection, direct child care, useful skills and knowledge, and political leverage (Gutmann 1994), but no published study has systematically examined these possibilities. As described in the previous section, preliminary investigation of nonproductive roles among older Tsimane adults has shown that they are vocal advisors, mediators, and trainers of younger adults and children in more traditional and difficult skills.

Physiological Design

If we want to understand why the human lifespan seems to be about seventy years among preindustrial peoples, and not fifty, eighty or one hundred years, the costs of remaining alive and in good condition must be considered in addition to fitness benefits. The human immune and repair systems broadly defined appear to generate a lifespan in which many cells, organs, and physiological processes show significant life-threatening changes in the seventh decade of life. Cancers, heart disease, decreased ability to work, cognitive decline, and impaired immune function greatly increase in frequency at this time, as do mortality rates (see Willcox and Willcox this volume). These outcomes are not only caused by cumulative wear and tear and novel exposure to fatty diets and a sedentary lifestyle, but instead are the result of epigenetic processes that were set in motion at the beginning of life and potentially altered throughout early and late development.(Gluckman and Hanson 2006).[7]

To examine changes in biological age (as opposed to chronological age), a growing number of biomarkers such as Apolipoprotein-E (ApoE) and interleukine-6 (IL-6) allelic variants, C-reactive protein (CRP), fibrinogen, telomere cap lengths, and several others are being measured in national longitudinal aging studies.[8] The markers are generally used as predictors of healthy function, morbidity, and mortality among middle-aged and elderly populations, and can be useful for making objective cross-population comparisons in health status among elderly individuals. For example, Tsimane display higher levels of the inflammation-inducing CRP than do Americans at all ages, and so a

64   A Global Vision of Aging, Culture and Context

forty-year-old Tsimane may have similar cumulative levels of inflammation as Americans do in their mid-fifties (Gurven et al. 2008). The high levels of chronic inflammation among Tsimane are likely caused by the accumulated impacts of repeated exposure to acute infections over the life course.

Although there may be broad similarities in the order in which different physiological systems decline, differences in the timing and rates of decline may be widely variable within and among populations. It will be important to examine this variation in light of differences in early life exposure to disease and malnutrition, activity profiles, stress, and social support. While life history theory has illuminated some patterns underlying physiological processes, the direct application of life history to physiology is still in its infancy, and its impact on our understanding of physiological processes is still rather limited, especially among humans.

Adaptive Aging?

Additional evidence suggests that life experiences can significantly impact rates of biological aging (see Epel et al. 2004). We propose that features of behavior, culture, and physiology may be responses to the aging process itself and that behavioral adjustment can influence the rate of aging. Analysis of time budgets among the Machiguenga, Piro, and Tsimane populations, who inhabit the Amazonian rain forests of Peru, has revealed that people adjust their activities in relation to their physical condition (Gurven and Kaplan 2006). Work effort among small-scale subsistence populations peaks at about age forty and declines thereafter. If people worked as hard in their sixties as they did in their forties, they would likely age faster and die earlier. It is likely that the advent of agriculture provides a less intensive and less dangerous set of alternatives to hunting and gathering that may reduce morbidity in older individuals among farming and forager-farming populations independently of the nutritional supplements derived from having a predictable, storable resource base. In our medical surveys, Tsimane men over age sixty, for example, complained *less* about pains in the joints, getting lost, and other problems while hunting than did men in their fifties, presumably because of the former's decreased effort and frequency in hunting activities. Older people may also differ in the size and composition of kinship and other social networks available to them, and the extent to which others in these networks act as a possible safety net or buffer during critical periods of disease or dysfunction. Research investigating characteristics of networks and their effects among Tsimane is currently underway.

As people age, deterioration in condition is likely to affect the fitness costs and benefits of alternative physiological and behavioral responses. The possibility that selection has acted on physiology in similar fashion suggests new research directions. Some age-related changes in hormone profiles, lean body mass, lipoproteins, blood hemoglobin levels, and other biomarkers may themselves be adaptive responses to aging. At present, biomarkers of aging (such as

those listed previously) are used as predictors of mortality in population research. It is often not well understood, either in terms of mechanism or functional design, why such markers correlate with biomedical risk factors and with outcomes such as morbidity and mortality. Aging and other forms of morbidity produce changes in physiological condition. Disentangling the direct deleterious effects of aging from intrinsic endogenous, and possibly adaptive, components of the aging process is a challenging task, but should lead the way to a more profound understanding of aging and its population-level manifestations.

CONCLUSION

The Grandmother Hypothesis has been historically influential for inspiring a generation of empirical and theoretical studies to better understand why longevity is a hallmark feature of the human life history. The current picture, however, is more complicated. As argued herein, grandmothers do not usually make substantial economic contributions to the diet among hunter-gatherers, while others, including fathers and grandfathers, can and do make substantial contributions. Men experience "effective" reproductive cessation and so their long period of postreproductive lifespan also merits explanation. The Grandmother Hypothesis also ignores the long, slow physical growth of children and the costly expansion of the human brain. The Embodied Capital Model instead includes these as evolved components of our life history related to the skills-intensive foraging and social niche of humans. The elongated lifespan is required to reap the gains of delayed productivity in adulthood given the sacrifices made early in life, such as slow growth, low productivity, and delayed maturation. Theoretical approaches should include contributions from both sexes, as well as any differences in fitness costs to maintaining the body. Empirical inquiries that integrate provision of calories with other fitness-relevant types of contributions from older adults, such as marriage negotiation, social transmission of knowledge, mediation during conflicts, and emotional support, will be important avenues for future research.

An ultimate goal in the biodemography of aging is to understand the processes linking genes to phenotypes, phenotypes to mortality and fertility outcomes, and those outcomes to gene distributions over generational time. This will require both mechanistic physical models and specific theories of how natural selection acts to order those processes, both within populations of a single species and among species in evolving ecosystems. "Bottom-up" research investigates the mechanisms by which genes translate into their products, and how those products interact with environmental inputs to result in physiological and, ultimately, demographic outcomes. It is bottom-up in the sense that knowledge about how those processes work provides the empirical facts that evolutionary theories must explain. Evolutionary modeling, of which the Grandmother Hypothesis and Embodied Capital Model are one component, is "top-down" in the sense that it provides the deductive logic and the organizing principles that bring order to organismal design. Any biological understanding

66   A Global Vision of Aging, Culture and Context

of the aging process and longevity in humans—in the past, in the present, and with a keen eye focused on the future—will require innovative research initiatives that integrate both bottom-up and top-down approaches.

NOTES

1. These analyses are based on estimations of allometric equations of the form $Y = aX^b$, where Y is one of many species-typical life-history characteristics such as life span, metabolic rate, age at first reproduction, or gestation length, X is adult body size, b is the scaling exponent that describes how Y increases with changes in X, and a often adjusts for different orders or families. See Harvey, Martin and Clutton-Brock (1987).

2. Paleodemographic estimates of low child and high adult mortality for early humans does not match any modern pattern, and violates assumptions of uniformitarianism.

3. In urban societies, there is evidence that grandmothers positively impact cognitive and health outcomes and psychological and sociological well-being: Alawad and Sonugabarke (1992); Falk and Falk (2002); Hayslip and Kaminski (2005). Hayslip (this volume).

4. Of particular concern here are issues of "phenotypic correlation" and "unobserved heterogeneity." Phenotypic correlation in life history analyses refers to the situation where variation in physical condition or access to resources can lead to a spurious positive correlation between investments in two life history traits (e.g., growth and reproduction) when the true trade-off suggests a negative correlation. Only experimental manipulation or multivariate statistics can detect life history trade-offs in the face of phenotypic correlations. The problem of unobserved heterogeneity refers to the unexpected correlations between observed and omitted or unmeasured variables that can complicate the interpretation of cross-sectional analyses.

5. Research has been supported by grants from the National Science Foundation (NSF BCS-0422690, BCS-0136274) and from the National Institute of Aging (NIH/NIA 1R01AG024119-01). We are grateful to the Tsimane with whom we have worked for their generous hospitality, collaboration, and support.

6. Others such as Sokolovsky (Introduction, this volume) and Rosenberg (this volume) have commented on the interpretation of claims of neglect among older people. We believe that while many Tsimane may complain about a lack of attention merely as a way of soliciting more kin support, other older Tsimane show clear physical signs of neglect, such as an inadequate diet and poor health.

7. Epigenetic processes are characterized by heritable and potentially reversible changes in genome function that occur without altering DNA sequences. For example, paternal grandsons of Swedish men from the nineteenth century who were exposed to an abundance of food [0]during childhood in the nineteenth century were significantly more likely to die from cardiovascular disease and diabetes, which suggests epigenetic inheritance across multiple generations based perhaps on sex-linked nutritional cues (Kaati, Bygren, and Edvinsson (2002).

8. Several of these influential long-term prospective studies include the Health and Retirement Study (HRS), http://hrsonline.isr.umich.edu/, Mexican Health and Aging Study (MHAS) [http://www.mhas.pop.upenn.edu/], and English Longitudinal Study of Aging (ELSA), http://www.ifs.org.uk/elsa/index.htm.