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ARTICLE

The Tsimane Health and Life History Project: Integrating anthropology and biomedicine

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Abstract

The Tsimane Health and Life History Project, an integrated bio-behavioral study of the human life course, is designed to test competing hypotheses of human life-history evolution. One aim is to understand the bidirectional connections between life history and social behavior in a high-fertility, kin-based context lacking amenities of modern urban life (e.g. sanitation, banks, electricity). Another aim is to understand how a high pathogen burden influences health and well-being during development and adulthood. A third aim addresses how modernization shapes human life histories and sociality. Here we outline the project's goals, history, and main findings since its inception in 2002. We reflect on the implications of current findings and highlight the need for more coordinated ethnographic and biomedical study of contemporary nonindustrial populations to address broad questions that can situate evolutionary anthropology in a key position within the social and life sciences.

KEYWORDS

evolutionary anthropology, behavioral ecology, evolutionary medicine, aging, cooperation

1 | INTRODUCTION

Pioneering research among the Ju/'hoansi (Dobe! Kung) of Botswana and Namibia (Howell, 1979, 2010; Lee & DeVore, 1976), the Ache of Paraguay (Hill & Hurtado, 1996) and Hadza of Tanzania (Blurton Jones, 2016; Marlowe, 2010) helped pave the path toward long-term prospective study of the demography, socio-ecology and life history of contemporary foraging populations. These and other vital empirical studies of nonindustrial populations identified universal features of the evolved human life history: an encephalized brain, extended

postreproductive life span, delayed juvenile growth, high fertility with multiple dependents, extensive intra- and intergenerational resource transfers and cumulative culture (Hill, Barton, & Hurtado, 2009; Kaplan, Hill, Lancaster, & Hurtado, 2000; Kaplan, 1997). This adaptive complex of traits helped humans colonize nearly all of earth's terrestrial and coastal ecosystems, with rapid demographic and geographic expansion beginning ~45,000-60,000 years ago (Henn, Cavalli-Sforza, & Feldman, 2012). Although the exact timing and context of the evolution of these traits remain difficult to ascertain, a valuable approach for learning about this human adaptive complex is the holistic study of

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FIGURE 1 The Tsimane. Extensive sociality, a central feature enabling delayed childhood, high fertility, and long life span, is manifest in cooperative production, distribution, and child care. Photo credits: Michael Gurven

contemporary nonindustrial populations with limited access to modern amenities such as sanitation, health care, and labor-saving technology.

In designing the Tsimane Health and Life History Project (THLHP), our goal was to integrate traditional ethnography with advances in methods and concepts from demography, economics, psychology, epidemiology, gerontology, and biomedicine. To test competing models of human life history evolution (Hawkes, 2003; Kaplan et al., 2000), we seek to relate changes in economic productivity, resource transfers, and social networks to changes in physical growth, development, and aging. A classic expectation from life-history theory is that low exogenous mortality is a prime driver shaping a slower life history — that is, one involving prolonged maturation, greater investments in mainte-

nance, and longer life (Stearns, 1992). A more sophisticated approach treats mortality as endogenous and co-evolving with other life history traits, such as the role of learning in development (Kaplan & Robson, 2002). The learning-intensive foraging niche shifted an already slow life history further in this direction, but questions remain: How did increased investments in learning and mortality reduction co-evolve and how are they related to mortality-reducing effects of human sociality, risk buffering, and cumulative culture? How did this ecological shift affect food production and sharing, risk reduction, and mating patterns? How do different sources of morbidity, such as exposure to a diverse array of pathogens and co-morbidities, affect growth rates, maintenance costs, and aging? To what extent are human-specific traits

a coordinated and coevolved bundle versus a mix of adaptations and byproducts? To address these and other questions, we need to better understand: causes of morbidity and mortality in the absence of health care and other modern amenities; how different organ systems function by age in nonindustrial settings; and the social structure that may have been both a cause and effect of reducing morbidity and mortality. Joint behavioral and biomedical inquiry among contemporary nonindustrial societies like the Tsimane thus forms a core element of reconstructing patterns of human aging, health, life history, and sociality among ancestral humans.

We also aim to study how “modernization,” defined here as a trend toward greater participation in the market or cash economy, affects health and reshapes aspects of social ecology. Contemporary nonindustrial populations like the Tsimane are experiencing rapid social, economic, and cultural change. Socioeconomic transformation caused by increasing access to cash economies, wage labor, schooling, sanitation, and access to both modern medicine and amenities adds layers of complexity to defining how changing conditions alter health, risk management, and life history. Careful study is necessary for evaluating whether chronic diseases, such as cardiovascular disease (CVD) and diabetes, were common during human evolutionary history or are novel, resulting from an “evolutionary mismatch” as a consequence of the faster pace of lifestyle and environmental change as compared to genetic change.

These guiding research questions and themes about the human life course motivated inception of the THLHP. Over the last two decades, new research questions and directions grounded in life-history theory have arisen, building on existing findings and contributing to important debates across multiple disciplines.

2 | BEYOND HUNTER-GATHERERS

Hunter-gatherers would be ideal case study populations, given that humans lived as hunter-gatherers for most of our evolutionary history. However, most extant foraging populations are too small to adequately test causal models, especially among older adults. A broader range of societies is also required to understand evolved human reaction norms across different environments during recent millennia. Subsistence horticulturalists who also hunt, gather, and fish share many similarities with existing full-time hunter-gatherers, including natural fertility, minimal access to modern sanitation or medicine, and limited group size. Differences between foragers and horticulturalists can shed light on the impacts of plant and animal domestication on health and life-history-relevant traits, including parasite burden, nutritional status, fertility, mobility, residence patterns, and social structure. Bottlenecks and expansions of human populations during the advent of agriculture also had profound effects on human population genetics (Fumagalli, Sironi, Pozzoli, Ferrer-Admetlla, Pattini, & Nielsen, 2011; Hawks, Wang, Cochran, Harpending, & Moyzis, 2007), further highlighting the importance of nonforagers when considering health and disease in contemporary populations.

3 | THE TSIMANE OF BOLIVIA

Bolivia is home to 36 indigenous groups that together constitute over 60% of the population (INE, 2012). Of the 30 groups inhabiting the tropical lowlands, the Tsimane are among the most isolated (along with the Yuqui and Siriono) (Figure 1). The Tsimane are forager-horticulturalists of the Bolivian Amazon who subsist on slash-and-burn horticulture (mainly plantains, rice, sweet manioc, and corn); fishing in rivers, streams and lagoons; hunting a large array of neotropical mammals; and seasonal gathering of fruits and other foods, such as honey and nuts. They inhabit more than 90 villages numbering from 50 to 500 individuals along the Maniqui, Quiquibey, and Mato Rivers and interfluvial *terra firme* (Figure 2). While early censuses in the late 1990s estimated a population size of 6,000 Tsimane, the most recent THLHP census in 2015 suggested a number closer to 16,000 (also see INE (2012)) and a population growth rate of over 3.5%. Unlike most extant foragers, the relatively large Tsimane population provides the opportunity for study of all stages of the human life course, including late adulthood, which is essential to study competing models of human life-history evolution.

Throughout the first half of the twentieth century, Tsimane maintained a traditional lifestyle because of the relative absence of navigable roads in their territory. Road and river access has been improved by logging, development projects and new technologies such as the recent boom of *pequi* outboard boat motors in the last five years, but access remains somewhat limited for many villages, especially during certain periods of the year when heavy rains wash out bridges and dirt roads and make river travel dangerous. This variable access to the market and associated nontraditional cultural influences act as a quasi-experimental opportunity for examining effects of socioeconomic change on decision-making (McAllister, Gurven, Kaplan, & Stieglitz, 2012), economic production (Schniter, Gurven, Kaplan, Wilcox, & Hooper, 2015), social networks (Rucas, Gurven, Winking, & Kaplan, 2012), sharing and risk management strategies (Gurven, 2004b; Gurven, Jaeggi, von Rueden, Hooper, & Kaplan, 2015), and health (Gurven, 2012b; Gurven, Blackwell, Rodríguez, Stieglitz, & Kaplan, 2012; Gurven, Jaeggi, Kaplan, & Cummings, 2013; Trumble, Stieglitz, Rodríguez, Linares, Kaplan, & Gurven, 2015). Many of these outcomes also affect the pace of socioeconomic change, thus providing additional opportunities to examine the relative importance of the determinants underlying market participation.

4 | RESEARCH DESIGN AND SAMPLE

The THLHP, codirected by HK and MG, officially began in 2002 after initial excursions by MG to Tsimane territory in 1999. From its inception, the research design has included a mobile biomedical team composed of Bolivian physicians, biochemists, and Tsimane research assistants. This team visits each village roughly once a year to provide broad snapshots of physical condition and health, demography, and socioeconomic life (Figure 3). A reduced “core team” of a few anthropologists and Tsimane research assistants complements this mobile

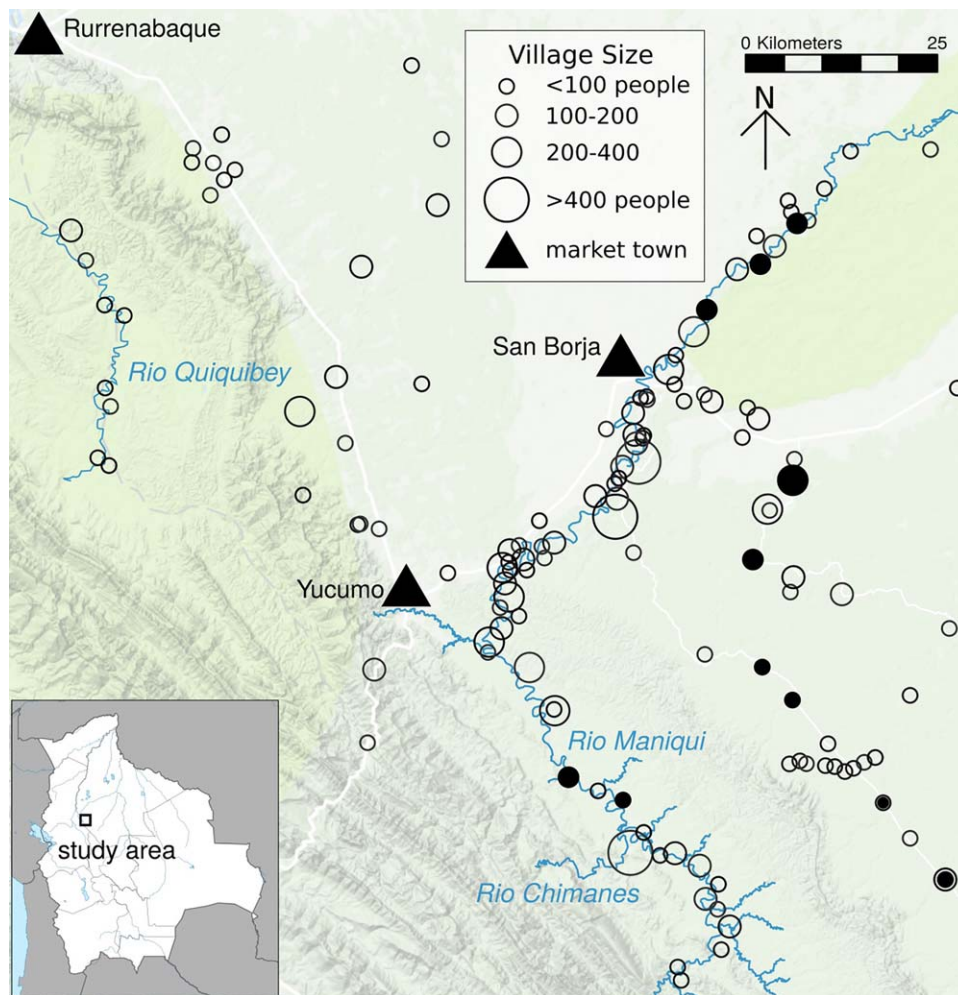


FIGURE 2 Map of Tsimane territory and study villages. Solid circles signify “core” villages where relatively long-term study has occurred; empty circles are other villages visited by the biomedical team; triangles reflect towns. Sizes of circles are proportional to village census size

team through more focused, longer-term sampling and more intensive economic data collection in core villages (Figure 4). These extended field sessions in core villages provide rich ethnographic study of economic and social behavior and health.

Funding was initially provided by the National Science Foundation in 2001 and 2004, and then, beginning in 2004, continuously by the National Institutes of Health/National Institute on Aging. NIH/NIA support permitted expansion of project scope and content. Thus, not only sampling, but the breadth and depth of data collection have expanded considerably over the project’s duration (Figures 3 and 4). Our initial sample included 18 villages, which then expanded to 23 by 2005, 85 by 2009, and 90 by 2015. In addition to employing Bolivian biomedical and administrative project personnel, the THLHP has collaborated with an international and interdisciplinary team of cardiologists, gerontologists, demographers, economists, biologists, psychologists, and epidemiologists (Box 1). To date, 17 Ph.D. dissertations and 8 undergraduate honors theses have been written in collaboration with the THLHP. Numerous graduate students and postdoctoral scholars have assisted in many aspects of project operations (see www.unm.edu/~tsimane).

Our holistic bio-behavioral approach has the advantage that we can link information on multiple phenotypes for the same individual over time to better understand factors influencing aging, health, and sociality. Our team has collected systematic baseline data at the individual level on many phenotypic traits: demographic, behavioral, morbidity, and biomarkers related to health and aging, infectious exposure, inflammation, and other indicators of immune function, as well as measures of physical and functional status (Figure 4). The span of measures is derived from surveys, physical exams, and biospecimens (blood, feces, urine, saliva). Several THLHP protocols were modified from prior life-course epidemiological studies in high income countries (e.g., NHANES), permitting direct cross-cultural comparisons (Box 1).

Since 2007, the THLHP has focused on aging, particularly the examination of associations among atherosclerosis, cardiovascular health, and immune function. While Tsimane experience high levels of inflammation, which is implicated in nearly all stages of atherosclerosis and is a strong risk factor for heart disease (Gurven, Kaplan, Winking, Eid, Vasunilashorn, Kim, Finch, & Crimmins, 2009), Tsimane also engage in demanding physical activity throughout life, show minimal obesity, and have limited

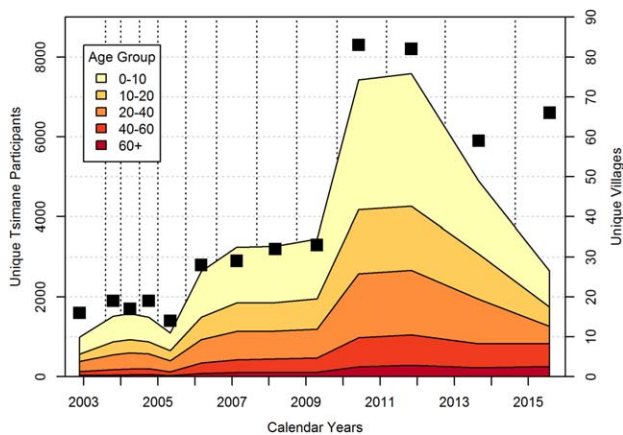


FIGURE 3 Age structure of biomedical surveillance by calendar year (2002-2015). Colored polygons show the number of unique individuals sampled in each age group, while black boxes indicate the number of unique villages sampled. Over the sample period, there were 13 rounds (indicated by vertical dotted lines) of varying length (mean \pm SD = 0.99 ± 0.40 yrs, range 0.42-1.80 yrs). In 2013-2015, THLHP sampled all adults age 40+ each round, but partitioned the <40 age group sampling into two or three rounds [Color figure can be viewed at wileyonlinelibrary.com]

food intake, which are protective against heart disease. Given the opposing effects that these factors may have on chronic disease risk, understanding the impact of inflammation in an infectious context is an important goal. To this end, we have started investigating relationships between cardiovascular and metabolic outcomes, infectious load, inflammatory and anti-inflammatory immune activation, genetic susceptibility variants, functional status, VO_2 max, physical activity and diet, economic productivity and social roles, and psychosocial factors. Collection of diverse bio-behavioral and demographic data enables a comprehensive analysis of the effects of modernization and social processes on these health outcomes. Thus, our research program attempts to advance a

“whole organism” understanding of the aging process in environmental conditions similar to those in which humans evolved, while also studying reaction norms and potential health-related mismatches as those environmental conditions change.

5 | WHAT HAVE WE LEARNED SO FAR?

New THLHP findings replicate those from earlier studies of foragers and forager-horticulturalists, demonstrating a skill-intensive economic niche with a long learning period, biparental investment, socially mediated risk-buffering, multigenerational resource transfers by parents and grandparents to dependent young, high productivity of postreproductive adults until the eighth decade of life, and a long adult life span. In fact, none of the patterns found in early studies have been contradicted by Tsimane research. However, this new research has enriched our understanding of: (1) life span and the aging process; (2) the role of infectious disease in shaping different life history components, including growth and senescence; (3) chronic disease and lifestyle change; (4) the life history of production, consumption and cooperation; (5) marriage, parental investment, and conflicts of interest between spouses; (6) status striving, personality, and determinants of reproductive success; and (7) how modernization affects traditional lifeways (see Table 1). In what follows, we discuss each theme in turn.

5.1 | Life span, aging and well-being

From the period 1950-1989, life expectancy at birth among Tsimane was 43 years; by 2002, life expectancy increased to about 53 years (Gurven, Kaplan, & Zelada Supa, 2007). Despite recent improvement, Tsimane death rates at all ages are similar to those in Europe in the 1800s (Gurven, Kaplan, Crimmins, Finch, & Winking, 2008). Unlike the typical pattern observed historically, in which initial increases in life span are largely caused by reductions in infant and child mortality, the improvement from 1990-2002 was more a result of reduced death

Box 1. THLHP in Comparative Context

The THLHP uses cross-sectional and longitudinal biomedical, epidemiological, demographic, and anthropological methodologies that are directly comparable to methods used in the U.S., other developed countries, and the developing world (Figure 4). Those comparisons illuminate the evolved aging process manifested in demographic, epidemiological, functional, and behavioral outcomes, as well as how changes in current environments interact with this evolved system to produce modern outcomes. Although the THLHP involves comprehensive study of many topics in a single population (Table 1), a broader perspective requires comparative study with a wider range of variation in key predictors. To this end, Tsimane data have been applied to comparative studies of mortality (Gurven & Kaplan, 2007), fairness (Henrich et al., 2005; Henrich et al., 2006), morality (Barrett et al., 2016; Fessler et al., 2015), wealth inheritance and inequality (Borgerhoff Mulder et al., 2009), postmarital residence (Walker et al., 2013), physical growth rates (Walker et al., 2006), sleep (Yetish et al., 2015), and sexual division of labor (Stieglitz, Gurven, Kaplan, & Hopfensitz, 2016). Ongoing comparative studies involving Tsimane include cardiovascular disease, bone strength, diabetes, epigenetics and aging, personality structure, breast milk composition, cooperation, and jealousy. The THLHP has also influenced the design of other projects, such as the Shuar Health and Life History Project, and recent studies among Agta and Pygmies.

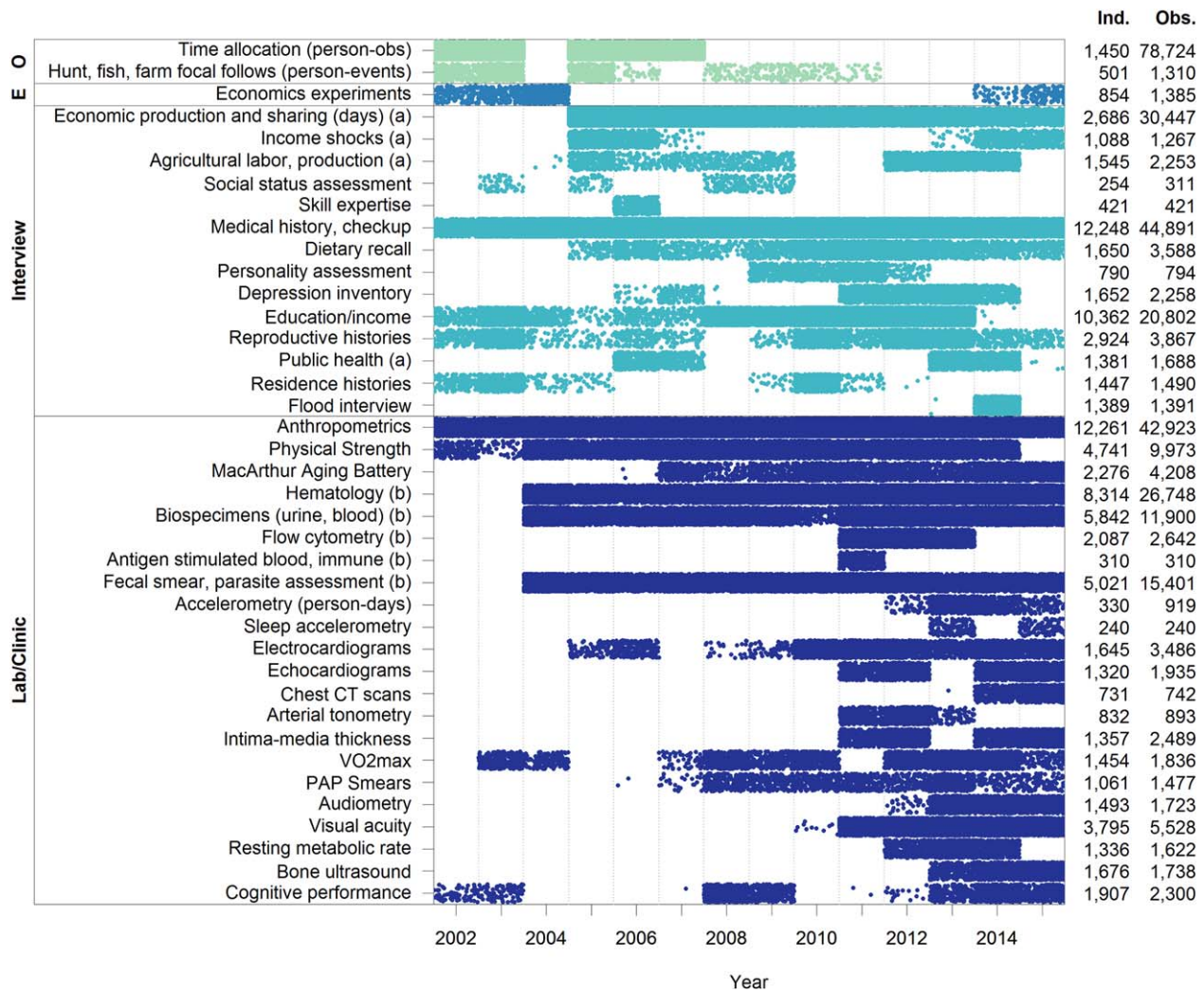


FIGURE 4 Summary of data types and sample sizes. Color of bars refers to data type. From top to bottom: behavioral observations (O), experiments (E), interview, laboratory/clinical. Data points are distributed along the x-axis according to the year of their collection^a reflects household-level data; otherwise data are at the individual level.^bThe following measures are obtained from biospecimens: FECES - presence or absence of 17 parasites, helminth egg burden; SALIVA, URINE - reproductive hormones; URINE - C-peptide, oxidative stress; BLOOD - Leukocyte count and subsets, cytokines, immunoglobulins, ESR, DNA, blood lipids [Color figure can be viewed at wileyonlinelibrary.com]

rates in adulthood than during infancy or childhood. We suspect that this is due to differences in access to medical interventions for adults and older children, since they have a greater ability than do infants or young children to seek and survive treatment. Despite recent improvement in access to health care facilities, Tsimane cultural beliefs about sickness and death, coupled with some ethnic discrimination in town, may still deter people from seeking treatment. The modal age of adult death is 70 years ($SD = 6.3$), similar to that among hunter-gatherers and other horticulturalists and 1.5 decades earlier than that in high-income countries (Gurven & Kaplan, 2007).

By the age of 60 years, Tsimane show evidence of significant physical disability. Physical strength declines continuously by the fourth decade of life (Gurven, Kaplan, & Gutierrez, 2006) (Figure 5). At the age of 60 years, more than 60% of Tsimane complain about hearing loss, more than 80% have trouble seeing close distances, and more than 70% can no longer chop large trees in their fields. About 50% of men and 70% of women over age 70 can no longer

walk long distances and frequently complain about painful arthritis in their legs, back, and hips. Over 70% of men no longer hunt by age 70; these men complain about weakness, lethargy, and having poor eyesight and hearing. Functional disability is a strong predictor of Tsimane depression: adults aged 50+ years in the top decile of a composite disability measure score 14% higher on a depression scale than those in the bottom decile after controlling for multiple potential confounders (Stieglitz, Schniter, Von Rueden, Kaplan, & Gurven, 2014). Depression increases with age, as disability increases and limits production and sharing ability, which runs counter to the common claim that human depression universally peaks in mid-adulthood (i.e., mid-life crisis) (Weiss, King, Inoue-Murayama, Matsuzawa, & Oswald, 2012).

Alongside late life declines in strength, coordination, and functional status, several components of adaptive immune function show evidence of rapid senescence. Naïve CD4+ helper T-cells, essential for mobilizing immune defenses against unfamiliar pathogens, are

Box 2. Research Ethics and Community-Based Participatory Research

Given the high morbidity, mortality, and lack of public health infrastructure in the Tsimane region, our code of ethics for conducting long-term fieldwork in Bolivia is to provide aid and assistance where possible, from specialized medical care on a case-by-case basis to humanitarian efforts following environmental disasters. To facilitate these efforts, formal agreements have been established and maintained with several Bolivian institutions, including universities; medical schools; national, regional and local governments; hospitals; national laboratories; and nongovernmental aid institutions. In conjunction with epidemiological data collection efforts of the mobile biomedical team, project physicians treat Tsimane in their villages for various bacterial and fungal infections, abscesses, minor trauma, diarrhea, parasites, and other primary care needs. Since the project's inception, over 45,000 person-visits with a physician providing clinical care have been conducted, with an average of 3,400 individual patient-visits per study year. Core team members residing in villages for longer periods than the mobile team offer further primary care as needed by villagers. For Tsimane with more urgent needs requiring specialized medical care, we have facilitated their transport and treatment in San Borja or, when necessary, in Trinidad, Cochabamba, San Ignacio, or La Paz, while ensuring their proper recovery and follow-up treatment if necessary. Since 2007, 456 Tsimane have received such specialized care. Examples of cases include hernia surgeries; osteomyelitis and fractured bones; cystocele, ovarian and abdominal tumors; congenital diseases; head trauma; brain tumors; severe burns; cataract and pterygion surgeries; and treatment for severe trauma (e.g., snakebite, machete lacerations). Aside from providing or facilitating medical care, the THLHP has also trained over 45 Tsimane as project personnel, many of whom have contributed critical advice on identifying problems, managing logistics, and navigating politics. The THLHP also has provided educational workshops on different aspects of disease detection and prevention and donated shortwave two-way radios for intervillage and village-to-town communication. THLHP collaborators have also donated medical equipment to local hospitals (e.g., surgical supplies, endoscopes, EKG machine) and provided further clinical training to Bolivian medical professionals. Biannual reports (in Spanish) including results of Tsimane epidemiological surveillance are provided to the Tsimane political council (*Gran Consejo Tsimane*) and local authorities to help solicit government resources to meet the health care needs of the Tsimane.

Box 3. Strengths and Limitations

Longitudinal studies are the gold standard for studying life-course processes (e.g., development, aging) and linkages across life stages, but they are rare in anthropology. The ability to prospectively link behavioral, psychological, health, and other data from the same individuals is a major strength of the THLHP design. Yet the broad range of topics covered by THLHP is both its main strength and weakness. Given limited personnel, some topics are given more attention and studied in greater depth than others. The duration of longitudinal data varies by data type and longitudinal data do not exist for some protocols. However, most data, even if preliminary, have helped motivate further study with existing and new collaborators. For example, initial data on age profiles of cognitive performance using a simple battery of psychometric tests has led to more focused studies of cognitive aging and dementia.

For biomedical surveillance, coverage and acceptance rates are very high (>85%), helping to ensure representativeness and minimize selection bias. High participation rates are possible because we have developed long-term trusting relationships in the villages and close ties with relevant institutions such as the *Gran Consejo Tsimane* and other local political groups. Providing medical care and training Tsimane in health promotion has greatly improved our reception in the area, helping avoid loss to follow-up and contributing to Tsimane human capital development. Another strength has been to develop the local Bolivian infrastructure to permit field-friendly methodologies comparable to those used in more traditional laboratory or clinical settings, including echocardiograms, ultrasounds, CT scans, flow cytometry (Blackwell et al., 2016), tissue doppler, and in-vitro antigen stimulation (Stieglitz, Trumble, et al., 2015; Trumble, Blackwell, et al., 2016). This capacity building and advanced training has been an important part of our continued success in working with local hospitals and other institutions.

TABLE 1 Research Domains and Foci of the THLHP. To date, 109 peer-reviewed publications in 42 scientific journals or as book chapters spanning 14 disciplines have used THLHP data. In addition to anthropology, these publications have addressed important areas in gerontology, genetics, demography, physiology, epidemiology, economics, psychology, general medicine, cardiology, immunology, osteology, and biology.

DOMAIN	FOCI	RELEVANT CITATIONS	
Aging, maintenance and mortality	Immune function	Blackwell et al., 2011; Blackwell et al., 2013; Blackwell et al., 2015; Blackwell et al., 2016; Gurven et al., 2016; Vasunilashorn et al., 2011	
	Hormone-behavior interactions	Jaeggi, Trumble, Kaplan, & Gurven, 2015; Trumble et al., 2012; Trumble et al., 2013; Trumble, Smith, O'Connor, Kaplan, & Gurven, 2014; von Rueden, Trumble, et al., 2014	
	Physical senescence	Kaplan et al., 2010; Pisor et al., 2013; Trumble, et al., 2015	
	Infection	Blackwell et al., 2011; Blackwell et al., 2013; Blackwell et al., 2015; Gurven, et al., 2008; Gurven, et al., 2009; Gurven, Trumble, Stieglitz, Rodríguez, Linares, Kaplan, & Gurven, 2016; Martin, Blackwell, Gurven, & Kaplan, 2013; Stieglitz, Blackwell, et al., 2012; Stieglitz, et al., 2015; Vasunilashorn et al., 2010; von Rueden, Trumble, et al., 2014	
	Cardiovascular disease	Gurven, Blackwell, et al., 2012; Gurven, Kaplan, et al., 2009; Gurven, Trumble, Stieglitz, et al., 2016a; Horvath et al., 2016; Vasunilashorn et al., 2010	
	Genetics	Horvath et al., 2016; Vasunilashorn et al., 2011	
	Life history theory	Blackwell et al., 2015; Gurven, 2012a; Gurven, Costa, et al., 2016; Gurven & Kaplan, 2008; Gurven et al., 2006; Gurven, Stieglitz, et al., 2012; Hooper, Gurven, & Kaplan, 2014; Hooper, Gurven, et al., 2015; Kaplan, Gurven, & Winking, 2009; Kaplan et al., 2010; Kaplan et al., 2015; McAllister et al., 2012; Schniter et al., 2015; Walker et al., 2006; Walker, Gurven, Burger, & Hamilton, 2008	
	Bone strength	Stieglitz, Beheim, et al., 2015; Stieglitz, Madimenos, Kaplan, & Gurven, 2016	
	Bio-demography	Gurven, 2012b; Gurven & Fenelon, 2009; Gurven & Kaplan, 2007; Gurven & Kaplan, 2008; Gurven et al., 2007; Hooper et al., 2014; Kaplan & Gurven, 2008; Kaplan, Gurven, et al., 2009; Kaplan et al., 2010; Tuljapurkar, Puleston, & Gurven, 2007	
	Psychological well-being	Stieglitz, Jaeggi, et al., 2014; Stieglitz, Schniter, et al., 2014; Stieglitz, Trumble, et al., 2015	
Physical activity and performance	Cognition	Gurven, Fuerstenberg, et al., 2016; Trumble, Gaulin, Dunbar, Kaplan, & Gurven, 2016; Trumble, Stieglitz, Thompson, et al., 2015	
	Sleep	Yetish et al., 2015	
	Metabolism	Gurven, Trumble, Stieglitz, Yetish, et al., 2016	
	Functional ability	Pisor et al., 2013; Stieglitz, Jaeggi, et al., 2014; Stieglitz, Schniter, et al., 2014	
	Mobility and migration	Gurven, Jaeggi, et al., 2013; Jaeggi et al., 2015; Miner, Gurven, Kaplan, & Gaulin, 2014; Trumble et al., 2014	
	Cooperation and fairness	Social preferences	Gurven, 2004a; Gurven, 2004b,a; Gurven, Stieglitz, et al., 2012; Gurven & Winking, 2008; Gurven, Zanolini, & Schniter, 2008; Gurven, 2014; Henrich et al., 2005; Henrich et al., 2010; Henrich et al., 2006; Kaplan, Hooper, & Gurven, 2009; Marlowe et al., 2008; Marlowe et al., 2010; Straub et al., 2010; Walker et al., 2013
		Food sharing	Gurven & Von Rueden, 2006; Hooper et al., 2014; Hooper, DeDeo, Caldwell Hooper, Gurven, & Kaplan, 2013; Hooper, Gurven, et al., 2015; Jaeggi & Gurven, 2013; Jaeggi et al., 2016; Stieglitz, et al., 2016
Social networks		Gurven et al., 2015; Hooper et al., 2014; Hooper et al., 2013; Hooper, Demps, Gurven, Gerkey, & Kaplan, 2015; Hooper, Gurven, et al., 2015; Jaeggi et al., 2016; Pisor & Gurven, 2016; Rucas et al., 2006a; Rucas et al., 2012; Rucas, Gurven, Kaplan, & Winking, 2010; Stieglitz, Schniter, Von Rueden, Kaplan, & Gurven, 2014	
Inequality		Borgerhoff Mulder et al., 2009; Gurven et al., 2015; Gurven et al., 2010; Stieglitz, Gurven, Kaplan, & Hooper, 2016; von Rueden, et al., 2014	
Leadership		Glowacki & von Rueden, 2015; von Rueden, Gurven, Kaplan, & Stieglitz, 2014	
Morality		Barrett et al., 2016; Fessler et al., 2015; Gurven, 2014; Henrich et al., 2010; Henrich et al., 2006; Marlowe et al., 2008	
Conflict and aggression		Rucas et al., 2006a; Rucas et al., 2012; Rucas et al., 2010; Trumble et al., 2012; Trumble et al., 2013	

(continued)

TABLE 1 (continued)

DOMAIN	FOCI	RELEVANT CITATIONS
	Domestic violence	Stieglitz, et al., 2012; Stieglitz et al., 2011
	Formidability	Sell et al., 2010; Sell et al., 2009
Ontogeny	Somatic growth	Blackwell et al., in press; Stieglitz, et al., 2015; Veile, Winking, Gurven, Greaves, & Kramer, 2012; Walker et al., 2006
	Task delegation	Stieglitz, Gurven, Kaplan, & Hooper, 2013
	Skills acquisition and learning	Gurven et al., 2016; Kaplan, Gurven, & Winking, 2009; Kaplan et al., 2010; Schniter et al., 2015
	Intergenerational transmission	Borgerhoff Mulder et al., 2009; Gurven et al., 2010; Gurven, et al., 2012; Schniter et al., 2015
	Breastfeeding or complementary feeding	Han et al., 2016; Martin et al., 2012; Veile et al., 2014
	Puberty and adolescence	Hodges-Simeon, Gurven, Cárdenas, & Gaulin, 2013; Hodges-Simeon, Gurven, & Gaulin, 2015; Hodges-Simeon, Gurven, Puts, & Gaulin, 2014; Hodges-Simeon, Sobraske, Samore, Gurven, & Gaulin, 2016
	Personality	Gurven, von Rueden, Massenkoff, Kaplan, & Lero Vie, 2013; Gurven et al., 2014; von Rueden et al., 2015
Food production and livelihood	Foraging	Gurven, 2012a; Gurven et al., 2006; Hooper, Demps, Gurven, M., Gerkey, D., & Kaplan, 2015; Jaeggi et al., 2015; Schniter et al., 2015; Trumble et al., 2014
	Horticulture	Gurven et al., 2010; Trumble et al., 2013
	Division of labor	Gurven, 2012a; Gurven, et al., 2009; Hooper, et al., 2015; Jaeggi et al., 2016; Kaplan, Hooper, & Gurven, 2009; Stieglitz et al., 2013
	Social status	Glowacki & von Rueden, 2015; Gurven & Von Rueden, 2006; Von Rueden, Gurven, & Kaplan, 2008; von Rueden et al., 2011; von Rueden, Gurven, et al., 2014; von Rueden, et al., 2014
Mating and reproduction	Mate acquisition	Stieglitz, Blackwell, et al., 2012; Winking et al., 2013
	Marriage	Gurven, 2012a; Gurven, et al., 2009; Stieglitz, et al., 2012; Stieglitz, et al., 2016; Stieglitz, et al., 2012; Stieglitz et al., 2011; Winking, 2006; Winking, Gurven, Kaplan, & Stieglitz, 2009; Winking et al., 2007; Winking et al., 2013
	Fertility	Blackwell et al., 2015; Gurven et al., 2014; Kaplan et al., 2010; Tuljapurkar et al., 2007; von Rueden et al., 2011; Winking et al., 2013
	Parental investment	Gurven, et al., 2009; Hooper et al., 2014; Hooper, et al., 2015; Hooper, et al., 2015; Winking, 2006; Winking & Gurven, 2011; Winking, Gurven, & Kaplan, 2011a,b; Winking et al., 2009; Winking et al., 2007
	Fertility transition	Kaplan et al., 2015; McAllister et al., 2012
	Costs of reproduction	Gurven, et al., 2016; Stieglitz, et al., 2015

considerably depleted by age 50, while natural killer cell counts are substantially elevated (Blackwell, Trumble, Maldonado Suarez, Stieglitz, Beheim, Snodgrass, Kaplan, & Gurven, 2016). Consistent with these patterns, a measure of epigenetic age acceleration, based in part on the estimation of immune cell counts, is higher among Tsimane than among other populations (Horvath, Gurven, Levine, Trumble, Kaplan, Allayee, Ritz, Chen, Lu, Rickbaugh, Jamieson, Sun, Li, Chen, Quintana-Murci, Fagny, Kobor, Tsao, Reiner, Edlefsen, Absher, & Assimes, 2016).

In late life, fluid cognitive abilities related to reasoning and processing speed also appear to decline from their peak in early adulthood, whereas crystallized abilities based on cumulative experience and knowledge increase throughout the life span (Gurven, Fuerstenberg, Trumble, Stieglitz, Beheim, Davis, & Kaplan, 2016; Trumble, Stieglitz, Thompson, Fuerstenberg, Kaplan, & Gurven, 2015). While this pattern

has been widely documented in Western contexts, it had never before been systematically assessed in a nonliterate or nonindustrial population. While the decline in fluid abilities seems to mirror changes in physical abilities with age, nondeclining crystallized abilities are consistent with the functional role of middle-aged and older adults as mentors, instructors, and caregivers in Tsimane society. Resource production is positively associated with psychological well-being for older adults (Stieglitz, et al., 2014), which is consistent with a human life-history perspective emphasizing the importance of adult economic production surplus and downward net transfers.

In summary, mortality rate increases in late adulthood are linked to changes in phenotypic condition due to aging and associated declines in muscularity and physical strength, aerobic fitness, sensory acuity, and immune function. Those changes, in turn, are linked to changes in

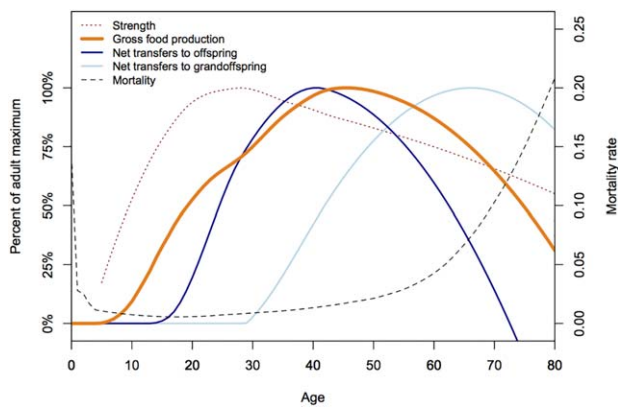


FIGURE 5 Age profiles of caloric production, net food transfers to children and grandchildren, physical strength, and mortality. Though physical growth and strength peak in early adulthood, food production ability peaks in the fifth decade of life. Transfers to children peak by around age 40, while those to grandchildren peak in the 60s. Horticulture increases the productivity of older adults more than would be expected among hunter-gatherers. By the age of 70 years, productivity and transfers decline while mortality increases rapidly [Color figure can be viewed at wileyonlinelibrary.com]

economic productivity and psychological well-being. The productivity of Tsimane adults supports net economic transfers to descendants until the eighth decade, coinciding with the modal age of adult death among Tsimane and other subsistence populations (Gurven & Kaplan, 2007). These findings demonstrating declining fitness-related utility at late ages are compatible with the “disposable soma” theory of aging, which views aging as the result of compromised energy allocation favoring investments providing fitness benefits earlier in life (e.g., reproduction) in light of somatic maintenance costs that increase with age. However, despite speculation, it still has not been clearly determined why humans live as long as they do but not longer. Our working hypothesis is that the fitness benefits of costly investments in grandchildren outweigh the fitness costs of slowing down the aging process, but that these benefits diminish once grandchildren are past the high-mortality period early in life. Given dispersal, migration, and the dilution of genetic relatedness with each successive generation, the sum of fitness effects over all descendants may be too small to favor further delays in aging.

5.2 | Pathogens and life history

Tsimane exhibit high rates of diverse infections. Over 66% of Tsimane have at least one intestinal parasite, the most common being hookworm (*Ancylostoma duodenale* or *Necator americanus*, prevalence 56%), roundworm (*Ascaris lumbricoides*, 15%) and whipworm (*Trichuris* sp., 4%) (Blackwell, Gurven, Sugiyama, Matemeros, Lieber, Martin, Kaplan, & Snodgrass, 2011). Protozoan infections are also common, including *Giardia lamblia* (30%) and *E. histolytica* (5%). About half of men and women have anemia, with children and adolescents showing the highest risk (56% for girls, 63% for boys). Polyparasitic co-infection is not uncommon. Several helminth species co-occur, whereas helminths such

as hookworm and roundworm seem to have protective effects against giardia infection (Blackwell, Martin, Kaplan, & Gurven, 2013). Helminths also affect Tsimane fertility. Hookworm reduces fertility, while roundworm may shorten interbirth intervals, perhaps by increasing maternal immunological tolerance of a fetus (Blackwell Tamayo, Beheim, Trumble, Stieglitz, Hooper, Martin, Kaplan, & Gurven, 2015). Given the high transmission rate of multiple pathogens in the Tsimane environment, the prevalence of several parasites and investments in immune defenses against them (e.g. immunoglobulin-E, IgE) peak earlier in childhood than in populations with lower transmission rates (Blackwell, Gurven, Sugiyama, Madimenos, Liebert, Martin, Kaplan, & Snodgrass et al., 2011). This finding is consistent with the “peak shift” hypothesis, which suggests that peak incidence rates occur at younger ages as immune defenses develop earlier in more infectious environments.

Infections are the main source of Tsimane morbidity and mortality over the life course (Gurven, Kaplan, & Zelada Supa, 2007). Gastrointestinal illness and respiratory infections are frequent: 30%-40% of infants and young children suffer from each; 30%-40% of adults suffer from gastrointestinal illness; and 20%-30% of adults suffer from respiratory infections. Living in a pathogenic environment likely favors pro-inflammatory (CRP, IL-6) alleles (Vasunilashorn, Finch, Frimmins, Vikman, Stieglitz, Gurven, Kaplan, & Allaye, 2011) and higher levels of inflammation than do more hygienic environments. Levels of CRP, an indicator of inflammation, are higher than among Americans, especially in childhood (Blackwell et al., 2016). Cross-sectional estimates of life lived with high CRP indicate that by the age of 34 years, Tsimane have spent an average of 15 years (42% of life) with high CRP whereas, in the U. S., the corresponding number is 6.8 years (19%). Tsimane CRP levels in early life are higher than those sampled among diverse populations, including Italians, Mexicans, Filipinos, and Native Americans (Gurven, et al., 2008). CRP levels vary between and within individuals, with half of the total variation being between individuals; thus, elevations likely do not represent only acute infections, which instead are moderately stable within individuals over time (Blackwell et al., 2016). Trichomoniasis is more prevalent among Tsimane living near town than among those living farther from town (Stieglitz, Blackwell, Gutierrez, Linares, Gurven, & Kaplan, 2012). In contrast, Tsimane living farther from town have higher CRP than those living near town, suggesting higher exposure to other infectious diseases in remote villages. Other biomarkers also suggest high levels of immune activity throughout life: Tsimane have higher levels of leukocytes, erythrocyte sedimentation rate, B cells, and natural killer cells than do Americans at all ages (Blackwell et al., 2016). Tsimane adults also show a higher rate of decline in naïve CD4 T helper cells than occurs in other populations, which might put them at greater health risk when exposed to new infections (Blackwell et al., 2016). On average, 20% of Tsimane white blood cells (WBCs) are eosinophils, consistent with high levels of parasitic infection, as compared with a U.S. reference range of <5%. Antibodies related to infection are also high among Tsimane: immunoglobulin-G (IgG) levels are about twice as high and IgE, which is most relevant for helminthic infection, is about 100 times higher than typical U.S. levels (Blackwell et al., 2011).

Perhaps as a consequence of high levels of infection and immune activation, Tsimane have elevated resting metabolic rates and 10%–15% of metabolism is associated with immune activation (Gurven, Trumble, Stieglitz, Yetish, Cummings, Blackwell, Beheim, Kaplan, & Pontzer, 2016). The high prevalence of infection and the shunting of requisite energy toward immune defense may help explain the slow somatic growth and stunting common among Tsimane, as well as similarly energy limited populations experiencing high pathogen burden (Blackwell, Urlacher, Beheim, von Rueden, Jaeggi, Stieglitz, Trumble, Gurven, & Kaplan, 2016). Population differences in growth trajectories during childhood may reflect patterns of pathogen exposure and immune investment, since Tsimane show slower growth during periods of their early peak IgE production (Blackwell et al., 2011). The higher energetic cost of tolerating and/or defending oneself from parasites may be further offset by other shifts in energy use. Possibilities in the Tsimane context include lower physical activity, sickness behavior (Stieglitz, et al., 2015), cachexia and osteopenia (Stieglitz, Beheim, Trumble, Madimenos, Kaplan, & Gurven, 2015), dyslipidemia and anemia (Gurven, Trumble, Stieglitz, Yetish, Cummings, Blackwell, Beheim, Kaplan, & Pontzer, 2016; Straub, Cutolo, Buttgerit, & Pongratz, 2010).

In summary, infectious disease has multiple phenotypic consequences. Not surprisingly, it appears to upregulate immune activity, resulting in greater energy expenditures throughout life and more rapid senescence of some immune cell populations. Variation in pathogen burden across human environments and over time within individuals seems to be associated with adaptive and plastic immune responses. The Tsimane, living in a warm, humid, tropical environment in relatively settled communities, may experience greater pathogen burden than other contemporary and ancestral human populations. Yet their modal age at death is similar to that of subsistence-level populations living in drier environments (Gurven & Kaplan, 2007). Perhaps natural selection on human aging has resulted in a species-typical life span despite differing sources of morbidity and death across populations.

5.3 | Chronic disease, mismatch, and lifestyle change

The THLHP provides an opportunity to test ideas about the role of environmental and socioeconomic change on health concerns believed to be either universal aspects of human aging or consequences of an evolutionary mismatch between longstanding genetic adaptations and novel environments. We have found that several conditions common in urban areas of both high and low-income countries are rare or absent among Tsimane. As noted elsewhere (Rook, 2012; Yazdanbakhsh, Kreamsner, & van Ree, 2002), allergies, atopy, and other auto-immune diseases are rare among Tsimane. This is to be expected, according to the “hygiene” and “old friends” hypotheses, which propose that early pathogenic exposures, especially to helminths, help promote improved immune regulation in ways that temper pro-inflammatory conditions (Rook, 2012; Yazdanbakhsh, 2002). Benign prostate hyperplasia is also rare, presumably due in large part to lower testosterone levels in early adulthood than those in Western populations (Trumble, Stieglitz, et al., 2015). Reproductive cancers, such as endometrial, ovarian, breast and prostate cancers, are often associated with high levels of cumulative exposure to repro-

ductive hormones, and appear to be rare among Tsimane as suggested by our clinical data. However other cancers of more infectious etiology, such as cervical cancer, are more common among Tsimane than in other populations (Stieglitz, et al., 2012).

Atherosclerosis, the main cause of cardiovascular disease (CVD), also appears to be largely absent among Tsimane for several reasons. First, obesity, high cholesterol, and hypertension are all associated with greater heart disease and stroke risk in Western countries. But the prevalences of adult obesity and hypercholesterolemia are much greater in the U.S. than among Tsimane (Gurven, et al., 2012). Even after adjusting for their lower body mass, rates of blood pressure increase in adulthood are lower among Tsimane than in 52 other populations from the INTERSALT study (Gurven, et al., 2012). Second, despite living in semi-permanent villages with limited residential mobility, Tsimane are not sedentary. They engage in high levels of moderate physical activity (Gurven, Jaeggi, Kaplan, & Cummings, 2013) and show both strong cardiorespiratory fitness, as measured by $VO_2\text{max}$ (Pisor, Gurven, Blackwell, Kaplan, & Yetish, 2013), and a high prevalence of bradycardia (resting pulse <60). Third, Tsimane diet is lean and rich in fiber and omega-3 fatty acids (Martin et al., 2012); also, it is uncommon for them to smoke cigarettes (Gurven, Kaplan, et al., 2009).

On the other hand, CRP and IL-6, two inflammatory biomarkers that independently predict CVD morbidity and mortality, are elevated among Tsimane, likely as a result of pathogenic exposure (Blackwell et al., 2016; Gurven, et al., 2008). Tsimane high-density lipoproteins (HDL) or “good cholesterol” levels are also low (Vasunilashorn et al., 2010). However, peripheral arterial disease (PAD), a precursor to fully developed atherosclerosis, as assessed by ankle brachial blood pressure index, is not observed among adults, although PAD increases with age in every other population studied to date (Gurven, Kaplan, et al., 2009). Several hundred “verbal autopsy” reports of recent and past deaths also reveal few cases of obvious cardiac or cerebrovascular events. Thus, mortality selection does not appear to be culling younger individuals with CVD. An ongoing collaboration with the *Horus* team (Thompson, Allam, Lombard, Wann, Sutherland, Sutherland, Al-Tohamy Soliman, Frohlich, Mininberg, Monge, Vallodolid, Cox, Abd el-Maksoud, Badr, Miyamoto, el-Halim Nur el-din, Narula, Finch, & Thomas, 2013) is quantifying levels of calcification in the coronary and thoracic aortic arteries based on high-resolution computed tomography (CT) scans of older adults. Ongoing cranial CTs will assess changes in cerebral morphology to help understand cognitive aging, dementia, and the link between CVD and dementia. Given the relative absence of overt atherosclerosis and vascular disease, we expect to find lower rates of cognitive impairment and several types of cerebral atrophy in late adulthood among Tsimane than observed elsewhere. Alternatively, greater infection, inflammation, and limited schooling may accelerate cerebral atrophy, cognitive decline, and dementia.

One novel investigation currently underway is to explore the role of pathogenic exposure, particularly helminths, in risk of atherosclerosis and type 2 diabetes. Helminths, as part of their strategies to ensure their survival and reproduction, have multiple effects on their hosts. They consume blood lipids and glucose, alter lipid metabolism, and

modulate immune function toward greater T_H2 polarization. In combination, these conditions can lower blood cholesterol, reduce obesity, increase insulin sensitivity, decrease atheroma progression, and reduce the likelihood of atherosclerotic plaque rupture (Gurven, Trumble, Stieglitz, Blackwell, Michalik, Finch, & Kaplan, 2016; Wiria, Sartono, Supali, & Yazdanbakhsh, 2014). Consistent with these expectations, we have found that biomarkers of helminthic infection (e.g., IgE, eosinophils) are inversely associated with total cholesterol, LDL, HDL, and obesity (Vasunilashorn et al., 2010). Total cholesterol is almost 10 points lower among those with elevated CRP and IL-6 and 19 points lower among those with elevated IgE controlling for potential confounders (Vasunilashorn et al., 2010).

In summary, Tsimane have a very low frequency of chronic diseases typically found in Western populations. The relative roles of energetic expenditure, diet, and pathogen burden in explaining differences in chronic disease risk among populations are still poorly understood due to the scarcity of detailed, longitudinal studies of appropriate populations in epidemiological transition, but each appears to play a contributory role. THLHP research shows that a more nuanced understanding of the role of infection-induced inflammation in the etiology of chronic diseases is needed. Perhaps high levels of inflammation are atherogenic and diabetogenic only in the context of high adiposity and minimal exercise. Alternatively, different sources of inflammation may have different effects on chronic disease, with infection in some cases actually lowering chronic disease risk.

5.4 | Production, cooperation, and sharing

The Tsimane production and sharing network is multigenerational. Total fertility rate is high (nine births per woman). Also, until late adolescence, Tsimane produce less food than they consume (Gurven, Stieglitz, Hooper, Gomes, & Kaplan, 2012; Hooper, Gurven, Winking, & Kaplan, 2015). Thus, the caloric burden on families can be substantial, especially for younger parents with multiple highly dependent offspring. Efficient food production peaks when Tsimane are in their 40s, especially for hunting and other difficult, skill-intensive activities (Gurven, Winking, Kaplan, von Rueden, & McAllister, 2009) (Figure 5). Peak productivity extends long beyond peak strength (Gurven et al., 2006), suggesting the importance of skills-based practice and learning. Although delayed productivity is clear for hunting (Gurven et al., 2006; Walker, Hill, Kaplan, & McMillan, 2002), expertise in a wide range of production, manufacturing, and other tasks (e.g., childcare, conflict mediation) is reported most frequently among middle-aged or older adults (Schniter et al., 2015). Nuclear families provide much of the daily calories, with older adults, including parents, grandparents, and siblings providing substantial amounts of food to younger kin (Hooper, et al., 2015). As strength and functional ability decline in later adulthood, Tsimane shift emphasis toward low-strength and high-skill subsistence and political activities, including hook-and-line fishing and horticulture, conflict mediation, village leadership roles, and storytelling (Schniter et al., 2015). Food sharing is widespread within extended families, but more limited in scope than typically is described among foragers. Kinship and relative need, as determined by recipient age, productivity,

family size, and health status largely determine the magnitude and direction of resource flows (Gurven, Stieglitz, et al., 2012; Hooper, et al., 2015).

Similar associations among food production, sharing behavior, and intergenerational transfers of calories to facilitate reproduction have been noted across human populations (Kaplan et al., 2000). These associations support two-sex theoretical models of human longevity, emphasizing that postreproductive adults may “indirectly” reproduce by improving the survival and fertility of younger relatives (i.e., embodied capital model). Whereas among chimpanzees, our nearest primate relatives, reproductive decline is strongly linked to somatic decline and increasing risks of mortality, human reproductive senescence precedes somatic senescence by roughly 20–25 years (Kaplan, Gurven, Winking, Hooper, & Stieglitz, 2010). After ceasing to reproduce, both men and women provide net economic transfers to children and grandchildren. On average, by the time they reach age 70, Tsimane rarely give food away to others outside of the household and so contribute less to sharing networks. The time delay between unproductivity due to physical deterioration and death appears to be short (Figure 5). Given this pattern of productivity and transfers, further delays in the age at menopause would produce net economic deficits within families because older adults would not be able to produce enough food for their own offspring (Kaplan et al., 2010).

Informal exchange networks help Tsimane manage multiple risks like sickness and injury, in addition to those from daily food shortfalls (Gurven, et al., 2012; Jaeggi, Hooper, Beheim, Kaplan, & Gurven, 2016). The “prices” implicitly negotiated in these informal exchange networks partly reflect individual differences in supply and demand, which itself relates to household needs and abilities (Jaeggi et al., 2016). Since the 1970s, increasing exposure to markets and state-sponsored economic development initiatives have offered new ways for Tsimane to buffer against risks or shocks. Do greater market interactions substitute or supplement more traditional sharing networks? Somewhat surprisingly, those with greater wealth give a greater proportion of their food to others and have more sharing partners (Gurven et al., 2015). While villages with higher mean income do show less reciprocity, overall, our findings suggest that traditional sharing patterns are not eroded due to incipient market integration, a pattern that is at odds with reports from other populations (see Gurven et al., 2015, for discussion). Instead, sharing can be used for display and networking, in addition to buffering against risk. How Tsimane recuperate losses with aggregate shocks like the massive flood that affected over 40 villages in February 2014 is a subject of ongoing research.

In summary, the THLHP helps bridge theory with empirical data that establishes vital links between kin-selected altruism, exchange networks, age profiles of productivity, and human life history traits. Food transfers are motivated by the interaction of genetic relatedness with need (Hooper, Gurven, et al., 2015). The needs of young children and families characterized by high dependency ratios predict downward transfers from older individuals, but only in proportion to shared genetic relatedness. These findings provide insights into how intergenerational transfers and increased longevity may have co-evolved in a ratchet-like process (Lee, 2008).

5.6 | Marriage and reproductive decision-making

The natural fertility regime of Tsimane provides opportunities to better understand costs of reproduction, as well as both determinants and consequences of reproductive decision-making. A high fertility rate has existed at least since the 1950s in all areas of Tsimane territory, though menarche is earlier and interbirth intervals shorter closer to town (McAllister et al., 2012). Exclusive breastfeeding on demand occurs for at least four months, followed by mixed complementary feeding and breastfeeding for an additional year or until the next pregnancy (Martin, Garcia, Kaplan, & Gurven, 2016; Veile, Martin, McAllister, & Gurven, 2014). Such early complementary feeding of infants (earlier than World Health Organization recommendations of six months) seems to favor earlier resumption of ovulation at little or no cost to infant growth (Martin et al., 2016). These types of infant feeding decisions permit tests of parent-offspring conflict given trade-offs between child benefits and maternal residual reproduction. Indeed, ongoing research is addressing the extent to which birth order and birth spacing compromise children's health and nutritional status. An important tradeoff we have sought to understand is whether the direct energetic costs to mothers of high reproductive effort affect other life-history allocations. Disposable soma theory proposes that investments in reproduction trade off against investments in maintenance and survival (Kirkwood, 1990). Maternal mortality due to pregnancy and childbirth complications is higher than that in most countries (Gurven et al., 2007). However, among survivors, evidence that cumulative costs of repeated pregnancies diminish women's health and nutritional status is mixed (Gurven, Costa, Trumble, Stieglitz, Beheim, Eid Rodriguez, Hooper, & Kaplan, 2016). Although weight loss and anemia are common shortly after birth, there is minimal evidence of compromised health and nutritional status over cumulative births. Repeated births seem only to be associated with a greater likelihood of cystocele (bladder prolapse) and osteopenia (Stieglitz, Beheim, et al., 2015). Ongoing research is addressing potential short- and long-term costs to reproduction among both parents, given substantial contributions to the energetics of reproduction and linked fertility schedules of men and women.

The "ideal" family size reported by Tsimane women and men is lower than their actual fertility. Spouses' ideal fertility preferences converge among more educated couples living near town, who generally report ideal family sizes of three or four children (McAllister et al., 2012). However, individuals reporting the smallest ideal family sizes actually have the highest observed fertility. One potential explanation is that schooling in the absence of viable wage opportunities hinders the incentives to reduce fertility that typically accompany greater human capital investment. Instead, status still derives largely from one's traditional social networks and, by extension, larger families. Consistent with this view, female role models are reported to be those with the largest families (McAllister et al., 2012). The current cohort of young adult women, however, is delaying their first births more than previous generations did (Kaplan, Hooper, Stieglitz, & Gurven, 2015). It appears that a nascent fertility transition in some areas of the Tsimane territory is underway. Understanding the social, economic, and psycho-

logical determinants of fertility change is critical given Tsimane concerns over limited land, low meat supplies, and growing demand for market goods.

Tsimane marriages are largely monogamous; <5% of marriages are polygynous. Polygynous marriages mostly involve sisters, but their dynamics and implications are relatively unexplored. While polygyny generates higher fertility for husbands, it is associated with lower fertility for second wives (Winking, Stieglitz, Kurten, Kaplan, & Gurven, 2013). In general, marriages are relatively stable, with divorce uncommon after the birth of children. Extramarital sexual relationships by husbands are most likely to occur early in marriage rather than later, when wives' reproductive value is low and offspring dependency is high (Winking, Kaplan, Gurven, & Rucas, 2007). This is consistent with the view of pair bonds functioning to provision children. Men's and women's fertility schedules are strongly linked in marriage: 90% of men whose wives reached menopause did not reproduce again after their wife's last birth, consistent with an "effective menopause" or male reproductive cessation (Kaplan et al., 2010). Of the 10% who did reproduce, half (5.2%) were polygynously married and had a child with a younger co-wife.

Market integration brings new social risks and costs. Men's wage labor offers opportunities and benefits but, as observed elsewhere, is also associated with men's absenteeism, extramarital affairs, domestic violence, and sexually transmitted infection (Stieglitz, et al., 2012; Stieglitz, Kaplan, Gurven, Winking, & Tayo, 2011). Current evidence shows that spousal conflict over the use of fungible and liquid cash results from men's attempts to increase personal benefits at a cost to the family (e.g., through pursuit of extramarital affairs, often in town or other villages) (Stieglitz, Gurven, Kaplan, & Winking, 2012; Stieglitz et al., 2011). Over 85% of Tsimane women report experiencing some form of physical abuse in marriage. Men may use physical violence i.e., to quell women's objections to male disinvestment, maintain women's parental investment, and dissuade women from pursuing sexual relationships with other men. The likelihood of reporting physical wife abuse is greatest in marriages when the husband has recently had an extramarital affair (Stieglitz, et al., 2012). Greater market integration and access to perfectly fungible and liquid resources can therefore disrupt patterns of reciprocity within and across households.

In summary, the importance of resource transfers and cooperation in Tsimane life history is revealed by the conflicts of interests that arise within and among families. Male economic transfers to women and children are important, but can also be a source of tension between husbands and wives when expectations of paternal investment are unmet. The majority of verbal conflict between spouses and men's violence against women stems from complaints about lack of paternal investment, especially the diversion of resources to women other than the man's wife. These findings suggest a revision of current debates about the significance of male parental investment within marriage. In the Tsimane context, men provide the majority of calories that families consume, but men's interests are not aligned only with those of their families. Men often invest in extramarital sexual relationships, especially as young adults; this is a source of great conflict within marriages.

As children are produced in the marriage and both partners age, these conflicts subside, perhaps because as the family grows there are more mouths to feed, increasing the value of male investment and the costs of disinvestment.

5.7 | Social status, personality, and determinants of reproductive success

The THLHP has also advanced the study of social status, an immaterial positional good of psychological importance in all social primates, by focusing on its determinants and benefits. Among men, dominance, or the ability to win dyadic physical confrontations, is associated with higher intramarital fertility for age, while prestige, the gaining of respect and influence from expertise or character, provides both higher intramarital fertility and lower offspring mortality; both are associated with a greater number of extramarital affairs (von Rueden, Gurven, & Kaplan, 2011). Both types of status elicit support from allies and deference from competitors, but high-status men are not provisioned more than their peers. Prestigious but not dominant men marry wives who first give birth at earlier ages, which multivariate analysis suggests is the strongest pathway between status and fitness among Tsimane. Men's prestige derives from leadership abilities, oratory skill, traditional productive skills like hunting, and novel skills that are crucial for obtaining market resources and navigating town life. High-status men have lower levels of the stress hormone cortisol and are less likely to suffer from respiratory illness (von Rueden, Trumble, Thompson, Stieglitz, Hooper, Blackwell, Kaplan, & Gurven, 2014).

Women's status competition is less overt but equally important. The domains of conflict shift across the life course (Rucas, Gurven, Winking, & Kaplan, 2012). Although physical attractiveness is a key factor in studies of women's status in Western populations, other characteristics, such as work ethic, trustworthiness, communication abilities, and childcare abilities, can trump its importance in evaluations of Tsimane women's status (Rucas, Gurven, Kaplan, Winking, Gangestad, & Crespo, 2006b). Subjects of ongoing research include the costs and benefits of women's status investments, changes in their status with greater schooling and market integration, and how men's and women's status interrelate and affect pair-bond dynamics (e.g., bargaining) and child wellbeing.

Personality is another immaterial individual trait of profound importance in urban populations, but is rarely studied in small-scale human societies. Our exploration of the origins and implications of personality differences among Tsimane has provided novel insights. First, many personality dimensions are associated with fertility. For men, effects appear to be uniform across all areas of Tsimane territory, whereas effects for women vary by geographic proximity to town (Gurven, et al., 2014). These findings support balancing or fluctuating selection models geared to explain why heritable variation in personalities seems to be maintained over time, despite selection gradients suggesting that certain personality types have higher fitness than others. Some aspects of Tsimane personality appear to be adaptively calibrated to phenotypic condition. For both men and women, extraversion and prosocial orientation are associated with several types of embodied

capital, including body size, physical strength, schooling, and fluency in Spanish (von Rueden, Lukaszewski, & Gurven, 2015). Thus, the high ("hidden") heritability of personality may be due in part to heritability of various components of embodied capital.

In summary, status and personality differences have fitness consequences even in "egalitarian" societies. Via direct and indirect routes, dominance and prestige are different forms of male status that are linked to reproductive outcomes. One route may be through increased access to younger fecund women; another may be through increased access to hard-working women with higher fertility; and a third may be through increased resource access and generosity, also resulting in higher marital fertility. Allies and social support are both causes and effects of high status and may be critical as a form of insurance against food shortfalls, conflicts, and other risks. Understanding how social status is achieved and inherited, the types of investments that help build social capital, and trade-offs with other forms of embodied capital in both sexes is an area of ongoing research.

5.8 | Modernization and socioeconomic change

The THLHP provides insight into the complex relationships between modernization and behavior, lifestyle, and health. The transition in Tsimane lifestyle and environment is highly variable throughout Tsimane territory. Natural variation in modernizing influences creates a unique quasi-experimental condition for exploring effects of market integration and concomitant changes in diet, physical activity (Gurven, et al., 2013), reproductive strategies, and access to health care on health (Stieglitz, et al., 2012), fertility (Kaplan et al., 2015; McAllister et al., 2012), risk management strategies, social behavior (Gurven, 2004b; Gurven et al., 2015), and cognitive performance (Gurven, et al., 2016). Changes over the past decade of THLHP surveillance will provide additional opportunities for understanding how socioeconomic change occurs and why only some individuals pursue market-related opportunities. For example, extraverted adults are more likely to live near town, be fluent in Spanish, and obtain schooling, suggesting some self-selection in migration and market exposures (von Rueden et al., 2015). The low level of market involvement by Tsimane does not appear to disrupt systems of exchange and downward intergenerational transfers (Gurven et al., 2015). However, it does provide men with money and often requires their absence from family to engage in wage labor or buy and sell market goods. This can increase spousal conflict and violence through its effects on extramarital affairs, reduced subsistence efforts, and alcohol consumption (Stieglitz, et al., 2012; Stieglitz et al., 2011). Market involvement is also associated with increased access to sugar, oil, and other concentrated forms of calories. These changes are likely to affect chronic disease risk, as anecdotally shown by higher blood sugar levels among the Tsimane political leadership, who tend to live sedentary, urbanized lifestyles.

6 | CONCLUSION

The THLHP has produced exciting findings of broad relevance to evolutionary anthropology and contributed to critical debates in the social

and life sciences. Though pitched originally to improve our understanding of human life history evolution, its scope has expanded to include a broad range of topics regarding health, socioecology, and culture. This was possible only with joint directorship, engaged interdisciplinary and international colleagues, and our excellent team of postdoctoral scholars, graduate students, and THLHP personnel. Continuous funding of large-scale research is a substantial challenge, but we believe that the payoffs in terms of scholarship and direct community benefits make this a model worth emulating elsewhere. It has been our hope that the THLHP helps make evolutionary anthropology more salient within the broader social and biological sciences. An ethnographic emphasis combined with an evolutionary and ecological focus can influence multiple disciplines by highlighting aspects of human diversity typically ignored by more mainstream research traditions. For example, Tsimane findings support new ways of thinking about the role of inflammation on chronic disease, the potential benefits of helminth infection, implications of a sexual division of labor, and functional significance of relatively stable personality traits. THLHP collaborations with non-anthropologists help bring the strengths of a holistic evolutionary anthropology into other fields.

Although the Tsimane represent a single case study, an important goal is to stimulate more cross-cultural comparative research using standardized methods. For example, we recognize that a comparative approach will be needed to make broader inferences about the relative importance of infection, lifestyle factors, and genetics in chronic disease morbidity (Box 1). In this case, comparison of populations varying in parasite burden, diet, and activity profile can provide insight into the role of immune dysregulation on chronic disease progression. Coordination with established field sites and researchers can be a critical first step in this direction. We can provide methodological protocols to help standardize methods across field sites.

7 | DATA AND PROTOCOL AVAILABILITY

De-identified data have been published as supplements in many of our publications. Appropriate requests for specific data have also been honored. Plans are currently underway to clean and organize datasets for restricted public access given federal guidelines set by NIH and NSF. These will be made available via a data portal on our website: www.unm.edu/~tsimane.

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GLOSSARY

Atherosclerosis—A disease in which plaque, composed of fat, cholesterol, calcium and other substances, builds up within the arteries. Over time, plaque hardens, narrowing the arteries and limiting blood flow to organs and other body parts. Atherosclerosis can affect any artery and lead to heart attack, stroke, or death.

Benign prostate hyperplasia—A condition in men in which the prostate gland is enlarged but not cancerous. Enlargement constricts the urethra and compresses the bladder, weakening the bladder's ability to empty completely. Urethra narrowing and urinary retention in the bladder lead to a variety of health problems, including trouble urinating or frequent, painful urination.

Cumulative culture—The accumulation over time of trait modifications obtained primarily through social learning. Modifications are often ratchet-like, leading to the development and maintenance of complex technologies.

Disposable soma theory—The optimal energy allocation to growth, metabolism, reproduction, and repair that maximizes fitness often results in compromised allocation to maintenance, resulting in a physical body that deteriorates with age. Given the declining force of selection with age, the theory proposes that natural selection optimizes levels of somatic repair below that required for extensive longevity due to prioritized fitness gains of earlier investments in reproduction.

Embodied capital theory—A model that considers extension of human life span as a coordinated response to a dietary shift focused on a skill-intensive diet with food sharing. Delayed juvenility and dependency, combined with a learning-intensive cultural niche early in life, are subsidized through large economic surpluses in adulthood, multigenerational sharing, and biparental care.

Evolutionary mismatch—A state of disequilibrium whereby advantageous traits that evolved in one environment become maladaptive in new environments. Rapid, drastic changes in human environments and

lifestyles over recent millennia, especially the past 200 years, outpace the ability of genetic changes to adapt organisms to the newer environment, leading to mismatched disease and behavior.

Exogenous (extrinsic) mortality—Mortality from external causes (e.g., accidental injuries, pathogen exposure), which are distinguished from internal or intrinsic causes (e.g., degenerative disease, genetic susceptibility). Extrinsic mortality is often described as being beyond the control of an organism to alter, but organisms often exert some control to reduce mortality risks, e.g., by altering patterns of movement to avoid accidents or investing more energy in immune function.

Fluid versus crystallized cognitive abilities—Fluid intelligence is the ability to problem-solve and reason in novel situations, whereas crystallized intelligence is the ability to remember acquired knowledge and learned skills. Some related abilities such as processing speed and working memory may not neatly fit the classical “fluid” versus “crystallized” distinction.

Grandmother hypothesis—Model of extended postreproductive human life span emphasizing the inclusive fitness contributions of grandmothers, primarily through increasing survival of grandoffspring and daughter fertility.

Helminths—Multicellular eukaryotic invertebrates with tube-like or flattened bodies exhibiting bilateral symmetry. Many helminths are free-living organisms in aquatic and terrestrial environments. Most inhabit the intestines (e.g., roundworm, hookworm), but some inhabit blood vessels (e.g. schistosomes)

Horticulturalists—Use hand tools to grow domesticated plants. Horticulturalists do not use draft animals, irrigation, specially prepared fertilizers, or machinery. Horticulturalists often supplement their subsistence efforts through other means including hunting, fishing, or foraging.

Inflammation—The body's initial protective response to harmful stimuli (e.g., pathogens, irritants, damaged cells), which involves immune cells, blood vessels, and molecular mediators. Inflammation helps eliminate the initial cause of cell and tissue injury, clear out damaged cells and tissues, and initiate cell and tissue repair. Though inflammation is necessary for survival, chronic inflammation contributes to aging-related diseases such as heart disease and diabetes.

Intergenerational transfers—Flows of material (e.g., food) or non-material (e.g., information) resources across generations, e.g., from parents to offspring or grandparents to grandoffspring. Intergenerational transfers have a central role in several theories of human life history evolution. While resources are also transferred “upward” in humans, from younger to older generations, the net flow of resources in small-scale subsistence economies is from older to younger generations.

Skills-intensive foraging niche—Human forager diets consist largely of foods requiring high levels of skill and strength. Meat and other important foods (e.g., tubers, larvae, honey, nuts) require extraction from a substrate (often with technology), intensive processing, and assistance from others. Hunting return rates more than double from ages 20 to 40 years, even though strength peaks in the mid-20s. Delayed peak efficiency relative to peak strength has also been documented for other foods. Thus, large caloric deficits are incurred early in life, requiring transfers from others, and only by the mid to late teens

do individuals start producing more calories than they consume. Surplus caloric production increases with age, peaks in the 40s, then slowly declines until reaching consumption levels by the 70s.

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