# Skill Ontogeny Among Tsimane Forager-Horticulturalists

Eric Schniter,<sup>1</sup> Michael Gurven,<sup>2</sup> Hillard S. Kaplan,<sup>3</sup> Nathaniel T. Wilcox,<sup>1</sup> and Paul L. Hooper<sup>4</sup>

<sup>1</sup>Economic Science Institute, Chapman University, One University Drive, Orange, CA 92866

<sup>2</sup>Integrative Anthropological Sciences Unit, Department of Anthropology, University of California-Santa Barbara, Santa Barbara, CA 93106

<sup>3</sup>Department of Anthropology, University of New Mexico, 1 University of New Mexico, Albuquerque, NM 87131 <sup>4</sup>Department of Anthropology, Emory University, Atlanta, GA 30322

*KEY WORDS* acquisition; proficiency; expertise; development; life history theory

ABSTRACT Objectives: We investigate whether age profiles of Tsimane forager-horticulturalists' reported skill development are consistent with predictions derived from life history theory about the timing of productivity and reproduction. Previous studies of forager skill development have often focused on a few abilities (e.g. hunting), and neglected the broad range of skills and services typical of forager economies (e.g. childcare, craft production, music performance, story-telling). *Materials and Methods:* By systematically examining

*Materials and Methods:* By systematically examining age patterns in reported acquisition, proficiency, and expertise across a broad range of activities including food production, childcare, and other services, we provide the most complete skill development study of a traditional subsistence society to date.

*Results:* Our results show that: (1) most essential skills are acquired prior to first reproduction, then developed further so that their productive returns meet the

Humans are unique among primates due to their encephalized brain, complex feeding strategies, extensive multi-generational cooperation, and slow life history (Bogin and Smith, 1996; Hawkes et al., 1989; Kaplan et al., 2000). The Embodied Capital Model (ECM) of human life history evolution hypothesizes that this Human Adaptive Complex may be an evolved response to the skills-intensive, socio-ecological niche occupied by humans (Kaplan and Robson, 2002; Robson and Kaplan, 2003; Kaplan et al., 2010). It proposes that the coevolution of slow growth with reduced mortality has facilitated the unique characteristics of the evolved human life history: the long prereproductive life-stage during which critical skills are learned by juveniles and adolescents, the reproductive life-stage during which large surpluses are produced and transferred to dependent kin, and a postreproductive life-stage during which older adults continue to make downward transfers while also complementing the contributions of others in their extended networks. To extend our understanding of the evolved human life history, we systematically study the development of a broad range of skills looking at retrospective self-reports, nominations of experts, and estimates of individuals' daily production and consumption of food, among a group of forager-horticulturalists from the Bolivian Amazon. The results illustrate how changes in embodied capital and the needs of dependent offspring predict the development of complementary skills and services.

General approaches to modelling mammalian lifehistories (e.g., Charnov 1991, 1993) presume that fitness is maximized when the energy put into foraging is increasing demands of dependent offspring during adulthood; (2) as postreproductive adults age beyond earlier years of peak performance, they report developing additional conceptual and procedural proficiency, and despite greater physical frailty than younger adults, are consensually regarded as the most expert (especially in music and storytelling), consistent with their roles as providers and educators. We find that adults have accurate understandings of their skillsets and skill levels –an important awareness for social exchange, comparison, learning, and pedagogy.

Discussion: These findings extend our understanding of the evolved human life history by illustrating how changes in embodied capital and the needs of dependent offspring predict the development of complementary skills and services in a forager-horticulturalist economy. Am J Phys Anthropol 158:3–18, 2015. © 2015 Wiley Periodicals, Inc.

allocated according to body size – suggesting that foraging effort should increase up until physical maturation and plateau for the remainder of the life course (e.g., see discussion in Kramer and Ellison, 2010). While these general life history models have performed well in comparative studies of primate foraging (Schuppli et al. 2012), research on human foragers suggest that peaks in their daily caloric production more typically occur well after their physical maturation (e.g., see Bliege Bird and Bird, 2002; Bock, 2002; Blurton Jones and Marlowe, 2002; Gurven and Kaplan, 2006; Crittenden et al., 2013).

ECM expects that foraging effort not only reflects body size, but also the accumulation of embodied capital

\*Correspondence to: Eric Schniter. E-mail eschniter@gmail.com

Received 6 October 2014; revised 6 April 2015; accepted 8 April 2015

DOI: 10.1002/ajpa.22757

Published online 29 April 2015 in Wiley Online Library (wileyonlinelibrary.com).

Additional Supporting Information may be found in the online version of this article.

Grant sponsor: National Science Foundation; Grant numbers: DDIG #0612908 (E.S.), BCS-0136274 (M.G.), and BCS-0422690 (H.K.); Grant sponsor: NIH/NIA (M.G. and H.K.); Grant number: R01AG024119.

such as skill and knowledge in relation to task difficulty and changing needs of the family budget (Bock, 2002; Gurven and Kaplan 2006; Crittenden et al., 2013). Along with other evolutionary models of the human life course, such as the Grandmother Hypothesis (GH; Hawkes et al., 1998; Hawkes, 2003), and the model proposed by Lee (2003), ECM has highlighted the fundamental role of net downward energetic transfers from older to younger kin in fostering the evolution of long lifespan. We extend the scope of ECM to not only focus on skills immediately impacting energy budgets but also to focus on skills affecting individuals' information capital. Knowledge related to difficult skills is typically transferred from older to younger (Ruddle and Chesterfield, 1977; Hewlett and Cavalli-Sforza, 1986; Ohmagari and Berkes, 1997; Lozada et al., 2006).

Contributions that donors of different ages make to kin can have impacts on fitness and thereby affect the value of survival at those ages. This perspective extends the standard Hamiltonian formulation of the "force of selection" that is exclusively determined by the age schedule of reproduction (Baudisch, 2005; Bourke, 2007). While Fisher's reproductive value declines to zero by the age of menopause, one's "productive value" (a net measure of inclusive fitness contributions) has the potential to decline more slowly (for data on Ache huntergatherers see Kaplan and Robson, 2002). For the Tsimane, Gurven et al. (2012) show that adults remain in a positive net caloric production phase (where mean daily consumption < production) for up to three decades past the age of menopause, enabling the support of remaining dependent offspring until age of self-sufficiency. These formal studies of skill development, production, and transfers greatly contribute to our understanding of the human life course.

In spite of their strengths, many studies of life history strategy largely ignore the skills involved in non-caloric transfers and services. For example, raw material processing, domestic tasks, and caregiving are tasks that both children and adults can contribute to (e.g. see Kramer, 2002; Kramer and Ellison, 2010; Stieglitz et al., 2013). Most studies to date instead focus on one skill set or limited sets of subsistence skills (e.g., Bock, 2002; Walker et al., 2002; Gurven et al., 2006; Reyes-Garcia et al., 2009; Henrich and Broesch, 2011; Demps et al., 2012; Crittenden et al., 2013). To fill this gap, we examine the acquisition, proficiency, and expertise of a broad range of skills among Tsimane foragerhorticulturalists of the Bolivian Amazon. In addition to skills essential for food production (e.g., gardening, fishing, hunting), we examine childrearing, craft production, household chores, social activity, music, and story-telling.

For each skill they possessed, informants reported ages of "acquisition" (i.e., when they achieved the basic ability to self-sufficiently perform the skill without necessary delegation, supervision, or guidance) and "proficiency" (i.e., a high level of conceptual and procedural knowledge needed to perform the skill well). Informants also nominated others whom they judged to be "expert" at the skill. We test whether age profiles of skill are consistent with predictions derived from ECM about the timing of actual food production (based on net daily caloric production measures), and the timing of reported skill levels (i.e., proficiency and expertise) in food production (e.g., with hunting, fishing, and gardening), information production (e.g., with social activity, music, and storytelling) and reproduction (e.g., with childcare).

### HYPOTHESES AND PREDICTIONS

Our overarching hypothesis is that the time-path of skill development corresponds with functional "life goals" specific to each of three stages of the human life course. In the *prereproductive life stage* the goals are to: (1) acquire basic competence with a skillset to support one's self; and (2) attract and secure a mate, which often involves demonstrating the first goal. In a natural fertility ecology, the goals of the *reproductive life stage* are to (3) reproduce and produce, optimally developing and using skills to support reproduction, such that (4) offspring are successfully raised to be able to accomplish prereproductive and reproductive goals 1, 2, 3, and 4. After reproduction ceases with menopause, an additional 10-20 years of life are needed for the last-born offspring to fully achieve goals 1, 2, 3, and 4. During transition to the postreproductive life stage, adults (5) continue making contributions towards fulfilling kin's goals 1, 2, 3, and 4, despite age-related senescence. Below we derive several predictions concerning skill development across the life course.

### Prereproductive life stage

The prereproductive life stage includes gestation, infancy, childhood, adolescence, and ends at first reproduction. The mean female age of first reproduction is 19.11 (SD 2.15) years across a sample of 17 small-scale subsistence societies (Walker et al., 2006). During this period, young adults are generally protected, remain relatively free of responsibilities that require great exertion or risk, and are supported by the surplus food production of older adults (Kaplan, 1994; Kaplan et al., 2000; Lee and Kramer, 2002; Lee, 2013).

While the prereproductive stage is cross-culturally characterized by net caloric dependency on older reproductive and postreproductive adults (see Lee, 2000), several studies also call attention to how patterns of bidirectional transfers (both products and services) can vary widely among subsistence groups, reflecting socioecological constraints, opportunities, and tradeoffs (e.g., Kramer, 2005, 2011, 2014; Kramer and Ellison, 2010; Hooper et al., 2014). In environments where children can safely work at easy tasks or with foods requiring little strength or knowledge to process or acquire, they may contribute more to the household economy (Cain, 1977; Draper and Cashdan, 1988; Blurton Jones et al., 1989; Bliege Bird and Bird 2002; Bock 2002; Kramer, 2002, 2005). For example, by working in the milpas, Maya children make substantial contributions in the maize economy (Kramer, 2005); whereas among Tsimane, safety and strength considerations preclude children from making substantial contributions to swidden horticulture or hunting. Tsimane horticulture is skill and strength intensive: choosing an ideal garden location requires knowledge and the cultivation of gardens requires strength and stamina for strenuous tree falling, clearing of thick underbrush, controlling fires, and awareness of poisonous snakes when planting, weeding, or harvesting. Tsimane hunting similarly entails dangers from predators, snakes, stinging insects, thorny and toxic plants, and requires strength, coordination, and knowledge of animals and ecology (see Online Supporting Information 1 for details).

Classic life history theory relies on Charnov's (1991, 1993) "production function" to model the transition from physical growth to reproduction. At the transition to age of first reproduction, the organism reallocates energy away from growth and towards reproduction. We extend this model, recognizing that in humans, the ability to be economically self-sufficient and fully support dependents is often achieved later than sexual maturity (e.g., see Hill and Hurtado, 2009; Howell, 2010; Marlowe, 2010; Lee, 2013; Gurven et al., 2012; for exceptions see Cain, 1977; Blurton Jones et al., 1989; Lee and Kramer, 2002). ECM proposes that the extensive provisioning of material and informational resources to prereproductive dependents supports their learning and on-the-job training in areas of food production, craft production, and childrearing. In fact, by providing assistance to younger siblings, children will offset parent's childcare burden and benefit parental fitness (e.g., see citations in Kramer, 2011). Parental costs of provisioning and caring for young are also offset by offspring's increasing surplus returns over the long reproductive and postreproductive life span (Kaplan et al., 2000; Robson and Kaplan, 2003). Social learning of conceptual elements and procedures is well underway during childhood when safe and simple tasks are often delegated or supervised (Ruddle and Chesterfield, 1977; Hewlett et al., 2011; Kline et al., 2013; Stieglitz et al., 2013). However, the necessary strength and size needed for coping with dangers, independent performance, and dedicated practice are often undeveloped until after the adolescent growth spurt, approximately age 10 for females and 12 for males (Bogin and Smith, 1996), when adult stature is nearly attained and most skills are finally mastered (e.g., see Draper, 1976; Ruddle and Chesterfield, 1977; Cain, 1977; Hewlett and Cavalli-Sforza, 1986; Ohmagari and Berkes, 1997).

**Prediction 1.** Age of acquisition for food production, child-rearing, and craft production skills will occur during adolescence and prior to adulthood.

To evaluate our first prediction about the timing of skill acquisition, we investigated 31 food production skills (including three tool use skills, 11 hunting skills, six fishing skills, five gardening and husbandry skills, and six food processing skills), 10 childrearing skills (including healthcare, childcare, birth, and family planning skills), 28 household chore and craft production skills, nine social skills, and 13 cultural skills (music, stories, and dreams).

### **Reproductive life stage**

The reproductive stage for females is defined by fertility, spanning from the onset of reproduction to its cessation prior to menopause (approximately age 37–45 for foragers, Kaplan et al., 2010). The postfertility period, as discussed below, is an extension of the reproductive career. During the reproductive stage, a primary goal is maintaining sufficient food production to track the waxing and waning demands of a family of dependents accumulated under a natural fertility schedule. This means parenting and grand parenting roles will often blend together towards the end of this stage, with adults becoming grandparents as early as 36, close to a decade prior to cessation of the reproductive stage. On average, Tsimane women become mothers by age 18 and men become fathers by the age of 20, with an interbirth interval of 2.6 years (Winking, 2005; Winking et al., 2007). Their offspring consume more than they produce until about age 20, and a last-born will remain dependent until its mother is in her sixties (Gurven et al., 2012). The average fertility schedule of a Tsimane man is tied to that of his wife, normally a few years younger (Kaplan et al., 2010).

As the number and net caloric demands of dependents increase in a family, parents and grandparents are faced with greater provisioning and caregiving demands. In general, we expect that performance with child rearing and food production skills is most needed and thus reported at highest levels by the time of greatest offspring demands. It is reasonable to expect that informants would recognize their own childrearing performance only after having reared (to adulthood) one or more offspring with success. Recognition of food production performance should more directly reflect actual daily net production. When the net caloric demand of dependents is highest, forager adults relying primarily on hunting and gathering are producing the most food (Gurven and Walker, 2006). Physical strength that contributes to food production is highest earlier in adulthood, while returns from "cognitive capital" (e.g., via applied and communicated knowledge and experience) may increase or show stability with age until the final decade of life (Salthouse, 1993; Schaie, 1994; Park et al., 2002). Thus, even after the expected age of peak food production (timed to meet dependents' needs), conceptual and procedural learning continues. Knowledge accumulated with experience should contribute to greater confidence over one's proficiency and pedagogical capability.

**Prediction 2.** While performance for childrearing and food production should be highest around the time of greatest offspring dependency, informants' self-ratings of proficiency with these skills (reflecting self-recognition of accumulated conceptual and procedural knowledge and confidence) will be highest concurrently or later.

During the reproductive life stage, an adult's reputation for expertise with a childrearing skill may continually improve over time, as competent demonstrations to others garner recognition, and as greater skill proficiency is achieved. However, as physical senescence limits mobility, the ability to demonstrate skills requiring strength may be increasingly compromised affecting the likelihood of being publicly identified for food production expertise.

**Prediction 3.** During the reproductive life stage, the likelihood of being nominated expert for food production skills requiring strength will be higher than for those with minimal strength requirements (P3.1). During this time, the frequency of expert nominations received for food production skills requiring minimal strength will increase at a faster rate than for those requiring strength (P3.2).

#### Postreproductive life stage

Strength declines in adulthood with the onset of sarcopenia (the monotonic loss of skeletal muscle with age

contributing to increasing disability and frailty: Roubenhoff, 2000), with an average 11% decrease in muscle performance every decade after age 45 among Tsimane (Kaplan et al., 2010). By the seventh decade of life when all one's children are economically self-sufficient, caloric production among Tsimane and other foragers declines (Amoss and Harrell, 1981; Walker and Hill, 2003; Gurven and Kaplan, 2006; Gurven et al., 2012), functional disability increases (Kaplan et al., 2010; Stieglitz et al., 2014) and food transfers to kin declines (Kaplan et al., 2000; Hooper, 2011). Despite their functional deficits, older adults are often consulted and respected for their reliable knowledge of traditional stories and myths, ethics for living in accordance with (and not angering) the spirit-world, animal and plant knowledge, locations of hunting grounds and sacred locations, and superior knowledge of family lineage histories and past events (Iamele, 2001). In fact, kin and non-kin alike will publicly refer to older Tsimane with honorary titles like jayej (grandmother) or via' (grandfather).

Important socioecological factors affecting different opportunities for older adult contributions can be highlighted by drawing comparisons between other subsistence societies and Tsimane. Among energy limited foragers who relocate camp frequently, elders may be intentionally neglected, abandoned, or even killed if they become too difficult to care for, cannot keep up with the band, or cannot cope with the masticatory stresses of their diet (e.g., Simmons, 1945; Hill and Hurtado, 1996); whereas among the semi-sedentary Tsimane who supplement their diet with more easily consumed cultivated foods, older adults can be supported and are given respect, allowing opportunities to provide their juniors services including food processing, childcare, craft production and other domestic tasks, and knowledge transfer such as by storytelling and performing music (Schniter, 2014).

As the opportunity costs of developing pedagogical, oratory, and musical skills may be high during childrearing years (due to the heavy burden of provisioning multiple children), reproductive-aged adults benefit when co-resident older parents and other kin assist with these contributions. Under these conditions there is increased utility for older kin, and older non-kin neighbors to specialize in activities that are low-strength, and in some cases most-difficult. As heterogeneity in physical (Maddox and Clark, 1992; Nelson and Dannefer, 1992) and mental abilities (Christensen et al., 1999; Ardila, 2007) increases at late ages, it reinforces greater specialization in the postreproductive life stage, with older adults increasingly focusing on skills best suited to their abilities and contribution opportunities.

**Prediction 4.** The highest levels of "very proficient" self-evaluations (P4.1) and received expert nominations (P4.2) in low-strength skills unrelated to food production, will be delayed until after offspring provisioning demand is greatest (after  $\sim$ age 40).

**Prediction 5.** With age, postreproductive adults' reported skill sets will increasingly be composed of most-difficult skills and skills requiring only minimal strength.

Despite physical aging and compromised skill performance at later ages, younger kin can acquire skill "knowhow" by accessing older adults' conceptual and procedural knowledge of how to proficiently perform a skill. As older adults increasingly take advantage of opportunities to transfer accumulated knowledge to younger kin, reputational information about their expertise spreads across social networks, leading to a growth in consensual recognition of their expertise over time. Dispersed networks may cause time lags in reputational information flow leading to a "delayed" public recognition of expertise. Additionally, informants' psychology may be biased towards nominating older targets as experts, independent of demonstrated skill (Henrich and Gil-White, 2001).

**Prediction 6.** Consensually recognized expertise will be highest at ages that coincide with or are older than ages of greatest conceptual and procedural knowledge proficiency.

Older adults often co-reside in extended family clusters with many less experienced dependent kin in close proximity, thereby facilitating information transmission from one-to-many. Among Tsimane, traditional pedagogy with respect to learning the behavior of animals and fish, and of morality and proper social behavior, is accomplished through oral broadcast of a rich repertoire of songs and stories (Huanca, 2006). This form of delayed productivity, extending beyond peak ages of caloric production and of importance to youngsters, is consistent with ECM expectations.

**Prediction 7.** In the postreproductive life stage, expertise in traditional pedagogy (music and story-telling skills) will be increasingly recognized with age.

## METHODS

### Study population

The Tsimane (population  $\sim$  15,000) are foragerhorticulturalists inhabiting the lowland forests and savannas east of the Andes in the Beni department of Bolivia. The Tsimane reside in multigenerational households across 90+ small kin-based villages (mean population = 124, SD = 98) with no modern sanitation, water purification, or electricity. Their environment is characterized by high pathogen burden and by high fertility (total fertility rate = 9). There is strong sexual division of labor with men and women spending about equal amounts of time in complementary but specialized activities: low strength low skill production activities compatible with childcare for women, and high strength high skill acquisition activities such as hunting, fishing, and wage labor for men (Gurven et al., 2009). Men spend around 50% of their working time outside of house in pursuit of wild foods, roughly double the amount of time spent gardening for males aged 18-45.

The Tsimane diet is mostly derived from nonmarket sources: hunted game (17%), wild caught fresh water fish (7%), collected fruits and nuts – both wild and cultivated (6%), domesticated free-range poultry and livestock (2%), swidden horticulture –primarily rice, manioc, and corn (66%), and only minimally supplemented with market goods such as purchased crackers, salt, sugar, pasta, and cooking oil (2%) (Martin et al., 2012). Tsimane lack significant material wealth and use natural materials to produce many of the items they rely on daily including baskets, textiles, houses, canoes, hunting and fishing tools, gardening tools, food processing tools, and musical instruments. Other goods are bartered for with merchants or purchased at market centers with the occasional proceeds of jatata palmpanel sales, garden produce sales, or wages earned with loggers and ranchers. Details about markets, diets, hunting, fishing, gardening, associated material culture, and gender specific roles are found in Online Supporting Information 1. Tsimane are semisedentary: regardless of village of residence, men and women tend to move throughout their lives and regularly travel to distant villages for extended stays with kin (Miner et al., 2014). Although exposed to Jesuit missionaries in the late 17th century, Tsimane have lived and continue to live autonomously and remain relatively isolated from Bolivian society at large (see Iamele, 2001; Huanca, 2006 for general ethnography). Although most villages now have schools, few children or adults regularly attend. Tsimane are very sociable, and it is normal to visit (sóbaqui) daily with neighbors in small groups or in larger groups at parties (Ellis, 1997). When available, people gather to drink vats of shocdye', a home-brewed manioc beer, and to listen to the musical performances and traditional stories that older adults broadcast (Iamele, 2001; Schniter, 2014).

### Tsimane skills survey

We developed a *Skills Survey* to investigate Tsimane self-evaluations of skill proficiency, and to identify consensus judgments about others' expertise in a variety of skills. These skills were identified from twenty-two semi-structured interviews with Tsimane men and women aged 20–72 years (mean age 35 years). These resulted in 101 specific skills from across 12 skill categories, which were then reviewed by a panel of six Tsimane researchers and their spouses who unanimously agreed on a refined list of 92 skills to use in the *Skills Survey* (see Online Supporting Information 2 for complete list of skills). They also categorized skills and rated them on their strength requirements.

Many Tsimane skills are gender specific, but most (n = 51) are unisex. Of the skills we study, both femalespecific skills (n = 11), and male-specific skills (n = 30)are considered equally important to both genders, as the end products of these skills are usually of mutual benefit. Skills were assigned to five categories: food production, childcare and reproduction, household chores and craft production, social and market, and music and stories. The list of specific skills comprising these categories is detailed in Online Supporting Information 3. Extensive ethnographic information about skill sets is given in Online Supporting Information 1. Fifteen skills (i.e., skills #1, 3, 7, 10, 39, 41, 44, 45, 61, 68, 72, 73, 80, 85, and 92 in Online Supporting Information 2) were omitted from analysis because these only rarely received expert nominations, very few informants claimed to possess these skills, or they were deemed subject to strong cohort effects, making interpretation of age effects particularly unreliable. The final skill set consists of 77 skills (48 for females, 69 for males, and 40 for either gender).

In 2006, a panel of six Tsimane researchers and the lead author interviewed 421 Tsimane (51% male) aged 15–86 from a sample of eight villages using the *Skills* 

Survey (complete coverage of all adults present during the study period, 71% of the censused population for those villages); we index these informants by  $i \in$ {1,2,.,421}. Descriptions of the eight villages are included in Online Supporting Information 4, and residential mapping described below. We find significant village and residential cluster effects on expert nominations (see Online Supporting Information 5 for details), and control for them below. We also find interviewer effects on reports of having skills and proficiency with skills, and parameterize our multivariate statistical models so that results discussed below are for "the average interviewer."

Our sample is composed of nine individuals in the prereproductive life stage (ages < 18), 319 in the reproductive life stage (ages 18 to 44), and 93 in the postreproductive life stage (ages 45+). The relative proportions of reproductive and postreproductive aged individuals sampled do not differ significantly from those in the census population. Combining the 421 informants (who could be and frequently were nominated experts) with 176 others they nominated experts, we have a set of 597 potential expert nominees for unisex skills (i.e., "targets"); we index them by  $e \in \{1, 2, .., 597\}$ . All experts nominated in this study were from the same eight villages that the judges were from. Furthermore, of the 22,170 nominations made, 99% were of adults (mean age 44, SD 14) living within the same village as the judge. For each appropriate skill, indexed by s, the following questions were asked:

- 1. "Are you able to and in the habit of ...?" If informant i answered "yes" for skill s, then  $H_i^s = 1$ ; otherwise  $H_i^s = 0$ . Older adults who had lost the ability to perform a skill often reported not having the skill and were recorded as not having the skill  $(H_i^s = 0)$ . Those who answered yes  $(H_i^s = 1)$  to this first question about skill s were also asked the following five questions about that skill (questions 2–6):
- 2. "Is ... difficult (to do)?" Informants chose one of three ordered responses to this "performance difficulty" question: We let  $PD_i^s = 1$ , 2, or 3 if informant *i* responded "very easy," "not so difficult/not so easy" or "very difficult," respectively, for each skill *s* they possessed. As explained to informants, this measure covers a variety of factors that affect difficulty, including level of detailed complexity, number of sub-tasks involved, muscular and hand-eye coordination, and memory or performance requirements.
- 3. "Does it take a long time to learn ...?" Informants chose one of three ordered responses to this "learning difficulty" question: We let  $LD_i^s = 1$ , 2, or 3 if informant *i* responded "quickly learned (minutes/hours)," "takes some time (days/weeks)" or "takes a long time (years)," respectively, for each skill *s* they had.
- 4. "At what age did you acquire basic competence with  $\dots$ ?" The variable  $AA_i^s$  codes this "acquisition age" in years (i.e., when one first acquired capability for basic performance and practical application). In an attempt to anchor ages, we sometimes used a set of standardized photographs of known-age Tsimane from outside of the immediate sample. Informants who responded with Tsimane terms for age-grades were asked to further refine their answers by choosing a photograph that was most likely representative of the age they had in mind within that age-grade.
- 5. "Do you know how to ... well?" Informants chose one of three ordered responses to this "proficiency"

question: "not so well," "more or less" or "very well." The response "not so well" was rare (<1%), so we let  $P_i^s = 1$  when informant *i* responds "very well,"  $P_i^s = 0$  otherwise, for each skill *s* possessed. We hereafter refer to  $P_i^s = 1$  as "very proficient".

6. "Who do you know to be most expert at ...?" We recorded a maximum of three expert nominations for each skill s. We let  $N_{ie}^s = 1$  if informant *i* nominated potential expert *e* as expert for skill s; otherwise  $N_{ie}^s = 0$ .

The Skills Survey combined with census and demographic information enable us to assign ages for all informants  $i(A_i)$  and potential experts  $e(A_e)$ . For each skill s, we compute a measure of skill difficulty,  $D^s$ , as the weighted average (based on the first principal component of informants' ratings across skills, scaled to have unit variance) of performance difficulty  $PD_i^s$  and learning difficulty  $LD_i^s$  (average values given in Online Supporting Information 2). The median value of  $D^s$ across all skills divides the set of skills into two halves, referred to below as the "most difficult" and "least difficult" skill subsets. The Tsimane researchers partitioned skills into categories requiring high or low "strength", defined as muscular strength, endurance, agility, and cardiorespiratory fitness (see Online Supporting Information 3). We let  $M^s = 1$  for skills s requiring high strength,  $M^s = 0$  otherwise.

### Demography, census, residential geolocation, food production and consumption

Between 2002 and 2006, census data were recorded by researchers of the THLHP, documenting age, sex, kinship, and community membership using methods described in Gurven et al. (2007). Geo-referenced location of occupied residential structures (n = 250) was surveyed by the first author using a handheld GPS receiver. We queried about and noted the occupants associated with each residence. Adult parents and their co-resident dependents (i.e. offspring and adopted dependents) were classified together as nuclear families. For each village, the first author categorized GPS locations of structures into mutually exclusive and exhaustive "residential clusters" of spatially proximate structures.

Demographic interviews, described at length in Gurven et al. (2007), were conducted from 2002 to 2005 with 1,702 individuals in order to identify consanguineal and affinal kinship relations, ascribe ages, and to estimate age profiles of mortality and fertility. Production and sharing interviews were conducted between 2005 and 2009 roughly twice per week among 245 nuclear families covering 1,198 individuals, to estimate daily caloric production (of food) and food transfers by age and sex (see Hooper, 2011; Hooper et al., 2015 for details).

Daily caloric consumption was estimated by distributing total caloric production among individuals according to their basal metabolic rates, as estimated using FAO formulae (Schofield, 1985; FAO, 2001) according to age, sex and body mass estimates from Gurven et al. (2006). An individual's daily net caloric production was calculated by subtracting their estimated daily caloric consumption from measured daily gross caloric production. The net caloric consumption demand of children specific to parental age was calculated by summing the net caloric production of all children an average parent would have at that age, based on age-specific fertility and mortality schedules.

### Data analysis: age-specific response likelihoods

We examine the likelihood that informants report high (vs. low) skill proficiency (the response  $P_i^s = 1$ ) and the likelihood that informants nominate any particular person as expert (the response  $N_{ie}^s = 1$ ). Binary response variables like these can be analyzed by means of a "generalized linear model" (McCullagh and Nelder, 1989). The proficiency reports  $P_i^s$  are the simpler case so we describe that approach here (see Online Supporting Information 5 for discussion of the expert nominations model). Our primary interest lies with the dependence of the response likelihood on the age of informants. The purpose of the model is to statistically remove the influence of other factors that could be correlated with age, or are likely sources of appreciable variance, and to smoothly characterize the response likelihood with an age polynomial. We view the probability  $\Pi_i^s$  of a "very proficient" response from informant i on skill s as  $Prob(P_i^s = 1 | A_i, AA_i^s, X_i, Z^s)$ . As indicated by the four symbols in the conditioning list, we view this probability as depending on four factors:

- 1. informant *i*'s current age  $A_i$ ;
- informant i's age AA<sup>s</sup><sub>i</sub> when she initially acquired the skill;
- 3. other characteristics of informant i, captured by a vector of informant characteristics  $X_i$  (informants' sex, village and interviewer); and
- 4. other characteristics of skill s, captured by a vector of skill characteristics  $Z^s$  (skill category, skill difficulty  $D^s$  and strength requirement  $M^s$ ).

Generalized linear models write the probability  $\Pi$  of a response such as  $P_i^s = 1$  as a function of a "linear predictor"  $\eta$ , a real-valued variable linearly composed of the conditioning variables, each weighted by estimable parameters in a vector  $\theta$ . The linear predictor is then transformed into a probability by means of a suitable function such as the logistic response function  $\Pi = [1 + \exp(-\eta)]^{-1}$  we use in our models.

The essence of our linear predictor of "very proficient"  $(P_i^s = 1)$  responses is *linear predictor = polynomial in age*  $A_i$  + other factors governing the proficiency response, or

$$\begin{split} & \eta_i^s = a_1(A_i - 35) + a_2(A_i - 35)^2 + a_3(A_i - 35)^3 + a_4(A_i - 35)^4 \\ & + g(AA_i^s, X_i, Z^s, \theta). \end{split}$$

The function g is the expected value of the linear predictor for an informant of age  $A_i = 35$  (the mean age of the informants in our sample), given the acquisition age  $AA_i^s$  and other characteristics  $X_i$  of informant i and characteristics  $Z^s$  of skill s; and  $\Pi = \left[1 + \exp\left(-g\left(AA_i^s, X_i, Z^s, \theta\right)\right)\right]^{-1}$  is the model probability that informant i says she is very proficient at skill s if she happens to be the average age 35 of all informants. The inverse of the logistic response function is the "log odds ratio"  $\ln[\Pi/(1-\Pi)] = \eta$ . Therefore, we have

$$\begin{split} &\ln\left[\Pi_{i}^{\rm s}/(1-\Pi_{i}^{\rm s})\right] = a_{1}(A_{i}-35) + a_{2}(A_{i}-35)^{2} + a_{3}(A_{i}-35)^{3} \\ &+ a_{4}(A_{i}-35)^{4} + g\left(AA_{i}^{s}, X_{i}, Z^{s}, \theta\right). \end{split}$$

Many of the figures in our results below are graphs of the age polynomial portion of this expression for the log



**Fig. 1.** Cumulative distribution functions (CDFs) of self-reported acquisition age for skills in five categories: food production, household chores and craft production, social and market activity, childcare and reproduction, music and stories. Few skills are acquired before adolescence (approximately 6% for females and 13% for males), most skills are acquired during adolescence (approximately 84% for females and 78% for males) and the remaining skills (approximately 10% for females and 9% for males) are acquired during early adulthood. During adolescence females acquired 78% of childcare and reproduction, 71% of food production, 78% of household chore and craft production, 74% of social and market, and 70% of music and story-telling skills. During adolescence, males acquired 74% of childcare and reproduction, 64% of food production, 71% of household chore and craft production, 64% of food production, 71% of household chore and craft production, 70% of social and market activity, and 75% of music and story-telling skills.

odds ratio favoring some response by our informants, given our estimates of the parameters in this expression (the polynomial coefficients a and other coefficients and effects  $\theta$ ). The estimated value of the function *g* is removed, so that these graphs are to be interpreted as changes in the log odds ratio with age, relative to an age 35 informant with otherwise identical characteristics  $AA_i^s$  and  $X_i$ . Statistical analysis of the estimated polynomial coefficients  $a_i$  allows us to derive confidence intervals for ages at which skill proficiency reports reach their "peak", as well as allowing statistical comparisons of these "age-proficiency profiles" across different skill sets (see Online Supporting Information 5). Most of the maxima we evaluate as peaks are interior maxima with interior confidence intervals derived from tests on the slope of the polynomial. However, some age profiles increase or decrease over the entire age range, so maxima are observed at corners: In this case, confidence intervals are derived from a test on the level of the polynomial.

### RESULTS

### Prereproductive life stage

# **P1:** Are food, craft production, and childrearing skills acquired before adulthood? Yes.

Figure 1 shows cumulative distribution functions (CDFs) for self-reported ages of skill acquisition in five categories of skills for men and women. Table 1 reports distributions of gender-specific mean acquisition ages for each skill category.

Almost everyone we sampled possesses one or more skills in each of the categories, except for music and storytelling in which about only half possess them (228 of the 421 subjects have one or more of these latter skills). Median ages of skill acquisition range from 13 to 16 for females, and 14–17 for males (Table 1). Food production skills are generally acquired earliest, followed by chores and craft skills, social and market skills, childcare and reproductive skills, and music and storytelling skills as the final skill set (Fig. 1). The differences between the within-informant median timing of food production skill and music & storytelling skill acquisition is around three years (39 months for males, n = 152, and 32 months for females, n = 71, both p < 0.0001). For both males and females, eight of the ten possible pairwise comparisons of skill categories reject a zero median difference in mean acquisition age at p < 0.01. Males acquire skills later than females (11 months for food production and 22 months for chores and crafts; p < 0.01 in all five categories by a Satterthwaite *t*-test with unequal variances). Male acquisition ages are also significantly more variable than those of females (p < 0.01 in all five categories by a folded *F*-test).

By age 20, the CDFs of all skills are above 95 and 90% in women and men, respectively. Thus, any differences in the proportion of skills held by adult age cohorts should be due mostly to secular changes over the past several decades, such as integration into the cash economy and greater schooling, rather than delayed learning. We examine the relative size of skill portfolios held by informants across age cohorts, finding that younger age cohorts reported fewer skills than older cohorts, and a difference in size of male and female skill portfolios for the 21-30 year old age cohort (Fig. 2). There is no significant main effect of gender  $(F_{1,361} =$ 0.07, p = 0.79) but there is a strongly significant interaction between gender and age cohort ( $F_{3,361}$ = 5.39, p = 0.001) as suggested by Figure 2's disjoint confidence intervals for male and female proportions in age cohort 21-30. Only the age effect remains significant when comparing the two age cohorts aged > 40 years ( $F_{1,120}$ = 4.22, p = 0.042): the most convincing demonstration of a cohort difference since none of the informants reported any skill acquisition after age 40. A two-way unbalanced ANOVA (with gender and age categories as factors),

Centile	Repro and rearing			Food production			Chores and crafts			Social and market			Music and stories		
	90	75	50	90	75	50	90	75	50	90	75	50	90	75	50
Females															
Point estimate	17.4	15.8	14.6	15.0	14.0	13.2	15.8	14.5	13.6	18.3	16.0	14.0	20.0	18.0	16.0
Upper C.I. 95%	18.3	16.3	15.0	15.7	14.3	13.5	16.6	14.8	13.7	19.8	16.5	14.5	21.0	19.0	17.0
Males															
Point estimate	20.0	18.0	16.0	16.4	15.1	14.1	18.3	16.8	15.6	21.0	17.0	15.0	22.5	19.5	17.0
Upper C.I. 95%	20.6	18.2	16.5	17.2	15.4	14.5	19.2	17.0	16.0	24.0	18.0	15.3	25.5	20.3	17.3

TABLE 1. Percentiles for mean acquisition ages reported by informants by categories

Percentile: For example, "75" means "75% of informants" mean acquisition ages are less than or equal to the value shown in the "point estimate" row. The unit of observation reported in the point estimate row is mean acquisition age in a category for all skills reported by each informant. Upper C.I. 95%: This is a distribution-free, rank-based upper confidence limit (at 5% significance, one-tailed) for the point estimated age at each centile.



**Fig. 2.** Proportion of all (gender-appropriate) skills held by informants in each age cohort. For each male informant *i* this is  $\bar{H}_i = \sum_s H_i^s/69$ ; for each female informant this is  $\bar{H}_i = \sum_s H_i^s/48$ .

using  $\ln[\bar{H}_i/(1-\bar{H}_i)]$  as the dependent variable, shows a highly significant main effect of age cohort ( $F_{3,361}$ = 32.21, p < 0.0001). A comparison of acquisition rates across age cohorts for each surveyed skill shows evidence of cohort effects, with younger age cohorts reporting a smaller proportion of more skills (see Online Supporting Information 6). Skills suspected to be "vanishing" traditional skills, listed in Online Supporting Information 3, show greater effects of age cohort on skill acquisition. The five skills most frequently lost among younger cohorts are woven hat production, ceramic vessel production, wheel barrow making, getting and processing bark cloth, and knowing the old stories and myths.

### **Reproductive life stage**

**P2:** Is proficiency in child rearing skills (food production, childcare and reproduction) highest during or after the time when offspring demand is greatest? Yes.

Figure 3 plots, by parental age, an average parent's gross caloric production and net caloric production, and the net caloric demand of children under 20. The peak



Fig. 3. Tsimane children's yearly net caloric demands (production minus consumption) by average parental age and an average parent's age-specific yearly production (gross) and yearly net provisioning rate (production minus consumption). Males and females make up the "average parent". Caloric demands of children accumulated under the Tsimane's natural fertility schedule are highest when parents are in their mid-30's and remain high until parents' fifth decade of life, while (gross and net) productivity peaks for adults in the mid-40's.

ages of gross and net caloric production range from 39 to 51. Figure 4 shows that the age profile of gross caloric food production overlaps substantially with the age profiles of skill proficiency ( $P_i^s = 1$ ) for food production skills alone and for food production combined with childrearing skills. Peak ages of "very proficient" self-ratings are 44–56 for combined childrearing and food production skills, and 46–62 for food production skills. Reported skill proficiency and caloric production are highest during and after (but not before) parental ages of children's peak caloric demand (ages 30–40; Fig. 3).

**P3:** Do strength requirements for food production skills affect likelihood of received expert nominations, and increased rates of received nominations with age? Yes.

We compare the relationship between consensus expertise for high-strength food production skills (e.g. hunting, clearing new fields) and for low-strength food TSIMANE SKILL ONTOGENY



**Fig. 4.** "Very proficient" self-ratings: (**a**) of food production & childrearing skills, and gross caloric production, and (**b**) of food production skills and gross caloric production. The vertical axis is log odds ratio change (relative to age 35) of "very-proficient" self-ratings for specified skills and the log caloric production change (relative to age 35 log caloric production). We found no significant difference in polynomials between males and females "very proficient" self-reports or gross production and so results are pooled by sex. A proficiency peak for skills essential to childrearing (reproduction, childcare, and food production skills) is seen from age 44 to 56 years for all food production, reproduction, and childcare skills and 46 to 62 for food production skills. The peak ages of caloric productivity are 39–51, substantially overlapping with peak ages of proficiency for specified skills.



**Fig. 5.** Consensus expertise: food production skills of (a) females and (b) males. The vertical axes are log odds ratio change (relative to age 35) of consensus expertise nominations received for food production skills. In both female (a) and male (b) figures the likelihood of being nominated expert for skills requiring strength is higher at younger ages (i.e., ages 17–34 and 36–41 for males, and between 16 and 27 for females). At younger ages the slopes of high-strength and low-strength skills are different with the likelihood of being nominated an expert in low-strength skills increasing at a faster rate (17–37 for males and 16–31 for females). At older ages (68–75 for males and 60–70 for females) the slopes are again different, creating a difference in height where the likelihood of being nominated expert for low-strength skills is higher (72–85 for males and 66–77 for females). The peak ages of consensus expertise for low-strength skills are late in the postreproductive stage (57–77 for females and 64–75 for males) whereas the peak ages for consensus expertise for high-strength food production skills are earlier (40–64 for females and 62–70 for males).

production skills (e.g. hook-and-line fishing, horticultural tasks like planting). Among both women and men of reproductive ages, the likelihood of being nominated expert for these high strength skills exceeds that for the low strength skills (Fig. 5). Expertise for high strength tasks is highest in the reproductive period for women and in the postreproductive period for men, with declines for both genders in the postreproductive period (Fig. 5). We also find that the rate of increase in received expert nominations is greater for low-strength productive tasks than for high-strength production tasks (Fig. 5). With advancing age, the likelihood of being nominated expert decreases for high-strength food production skills while it increases for food production skills requiring only minimal strength (Fig. 5).



**Fig. 6.** Consensus expertise and "very proficient" self-ratings: non-food production skills, not requiring strength. The vertical axis is log odds ratio change (relative to age 35) of consensus expertise nominations received and "very-proficient" self-ratings for non-food production skills not requiring strength. We found no significant difference in polynomials between males and females for "very proficient" self-ratings of these skills and so plot their pooled results for that measure. The peak ages of consensus expertise (51–77 for females and 45–52 for males) and for "very-proficient" self-ratings (44–61) are almost completely in the postreproductive stage.

### Postreproductive life stage

**P4:** Is consensus expertise for low-strength skills unrelated to food production highest after the parental age when offspring impose their greatest net caloric demand? Yes.

Whereas peak caloric demands of children occur from parental ages 30–40 (Fig. 3), peak ages of consensus expertise for skills unrelated to food production are almost entirely in the postreproductive period, as are peak ages for "very-proficient" self-ratings with these skills (Fig. 6).

# **P5:** Do older adults concentrate on the most difficult skills and those requiring less strength? Yes

We find that with increasing age, the skill sets of older adult women and men are increasingly composed of the more difficult skills (Fig. 7b,d) and those requiring only minimal strength (Fig. 7a,c). We also find that proficiency peaks of postreproductive adults between the ages of 41 and 62 are higher for most difficult skills (Fig. 8b) and after age 69, older adults' "very proficient" selfratings for skills requiring strength decrease at a faster rate than for skills not requiring strength (Fig. 8a)

### **P6:** Do ages of highest consensus expertise coincide with and lag behind ages of highest self-reported proficiency? Yes.

We find that peak ages of consensus expertise for skills (49–77 for females and 59–73 for males) are concurrent with or later than peak ages for "very-proficient" self-ratings (ages 45–60) (Fig. 9).

**P7:** Is expertise in traditional pedagogy more concentrated at older ages relative to other skill categories? Yes

We consider songs and storytelling as two fundamental forms of traditional pedagogy in Tsimane culture (see Online Supporting Information 1). We find that peak consensus expertise for the "music and stories" category begins at a later age than other skill categories (65 for females and 66 for males; Fig. 10). The gains in consensus expertise with age are also largest for this late maturing category of skills relative to other skill types (Fig. 10).

### DISCUSSION

We found that Tsimane not only have a keen sense of life stages and how their own skill development progresses through these, but they also make accurate assessments of others' abilities. Such knowledge may not only be required for social comparison or competition but also for social learning, pedagogy, and finding reliable partners for cooperation and exchange. Tsimane use their own terminology to describe the different phases of physical and social development: unweaned infants who cannot speak, and do not walk (approximately 0-2 years) are called *joijnó*; children (approximately 2-14 years) who speak and walk but do not seriously engage in adult production activities are called *miquity*, adolescents and young adults (approximately 14-25 years) are called nanaty; middle-aged adults (approximately 30-40 years) are called *furety*, and "older" adults (over the age of 40) are called isho' muntyi (with finer distinctions among these older people: Aty isho' refers to those "getting older", isho' refers to those who are "older", and anic isho' to the "very old"). By using emic and etic perspectives on the factors determining age-specific performance and recognition of expertise for a wide variety of essential skills, we can better understand the timing of functional and perceived adulthood and the potential fitness contributions made by adults across the lifespan.

By systematically surveying informants about their timing of skill acquisition, level of skill proficiency, and perceptions of expertise for essential food production (e.g., gardening, fishing, hunting), childrearing, and complementary skills, we have shown that: (1) most essential skills are acquired by late adolescence prior to the initiation of reproduction, then are further developed over adulthood as net caloric demand of children increase; (2) socially recognized "expertise" crucial to downward transmission of skill information occurs primarily in the postreproductive life stage; (3) gross and net caloric production peaks along with greatest offspring demand near the end of the reproductive life stage, but it is not until the postreproductive life stage that older adults reach peak self-perceived proficiency and consensus-based expertise for low-strength but high-skill activities complementary to food production; and (4) the patterns of skill development across the life course depend on their strength and knowledge requirements, and are similar in both men and women.

ECM predicts that the cost of an extended developmental period is compensated by productive surplus at later ages, and that delays in various forms of production are due to interactions between skills-based learning, on-the-job training and physical development. Net caloric production is maximized in adulthood during



Fig. 7. Scatterplots showing informants' shares of reported skills by informant age for the following: (a) females' skills requiring high strength, (b) females' most difficult skills, (c) males' skills requiring high strength, and (d) males' most difficult skills. (a) and (c) show decreases with age in the shares of skills requiring strength; (b) and (d) show increases in shares of most difficult skills from the top half of the difficulty distribution. The difficulty distribution is based on a composite measure combining perceived performance and learning difficulty, for which separate results are virtually identical when examined separately (not shown).

periods of high offspring demand, and declines into late ages as a consequence of physical senescence.

Our results show that from the reported ages, mostly under 20 years, of "acquisition" (the basic ability required for self-sufficient learning-through-doing), there are substantial delays to peak proficiency (at approximately 45-60 years) and recognized expertise (at approximately 45-70 years) for a broad range of men's and women's skills, not just high-prestige skills like hunting and leadership (Gurven et al., 2006). Due to the gains of joint investment in descendants with marriage and the sexual division of labor, ECM predicts learning-based delays in productivity for both sexes. Skills perceived as difficult to learn and perform, such as obtaining honey (#15), healing sick children (#14), making canoes (#4), houses (#17), household crafts (e.g. #5, 8, 12, 13, 16), and musical instruments (e.g., #6, 9, 11, 16), all show marked delays in proficiency and expertise that exceed the ages of peak physical condition in early adulthood by at least a decade. Even when advancing through the later-life ages of declining caloric productivity, consensus expertise increases for many household chores and forms of craft production, and for music and storytelling skills.

While the lifespan of most animals does not extend past the reproductive period (Williams, 1957; Hamilton, 1966; Levitus and Lackey, 2011), the human lifespan features a uniquely long postreproductive period of skill maturation and generativity. In numerous human societies, it is documented that postreproductive adults are not only the most proficient in a variety of skills, but they also are the most effective instructors and communicators (Simmons, 1945; Amoss and Harrell, 1981). Older adults might be revered as experts when their activities are easily observable (Davis and Wagner, 2003), if they effectively communicate their experience (Mergler et al., 1984; Adams et al., 2002; Paupathi et al., 2002), if their information is reliable and useful (Castro and Toro, 2004; Birdsell, 1979) or if they are deemed imitation-worthy due to age-based prestige (Henrich and Gil-White, 2001). Indeed, it is frequently mentioned that older Tsimane adults "know how to think (about work and what needs to be done)" (chij dyi*ji'jiyequi*). Furthermore, because they are unique in their ability to "think", they are especially skilled in planning tasks and executing them with efficiency and accuracy, and in orchestrating the schedules of other family



Fig. 8. "Very proficient" self-ratings of skills varying by: (a) strength requirements, (b) difficulty. The vertical axis is log odds ratio change (relative to age 35) of "very-proficient" self-ratings for specified skill of type. For each type of skill examined, we found no significant difference in polynomials between males and females and so plot their pooled results. "Very proficient" selfevaluations peak among older-adults with ages in the postreproductive stage. Maxima for these "very proficient" self-ratings are from ages 42 to 77 for most difficult, from ages 47 to 63 for least difficult, 45-68 for strength-requiring, and 45-57 for not requiring strength skills. Slopes of "very proficient" age profiles for skills requiring strength and skills not requiring strength are significantly different from ages 69 to 77 and slopes for most difficult and least difficult are significantly different from 65 to 77. Heights of "very proficient" age profiles for most difficult and least difficult skills significantly differ from ages 41 to 62 and at 77.



Fig. 9. Consensus expertise and "very proficient" self-ratings: all skills. The vertical axis is log odds ratio change (relative to age 35) of consensus expertise nominations received and "very-proficient" self-ratings for all skills. The horizontal axis is age of potential expert. We found no significant difference in polynomials between males and females for "very proficient" self-ratings and so plot their pooled results for that measure. The peak ages of consensus expertise (49-77 for females and 59-73 for males) and for "very-proficient" self-ratings (45-60) are in the postreproductive stage.

members -contributing to their roles as instructors, exemplars, and encouragers of skill development in vounger kin.

Our results support the notion that with advancing age, postreproductive adults accommodate their changing positions in family and society and gradually compensate for the effects of their declining physical strength by cultivating their accumulated knowledge and prestige. We find evidence for two distinct views of how skills might develop throughout adulthood before reaching the unusually late age of peak competence: (1)

the "life-long learning" account associated with the ECM suggests that the monotonic rise of procedural and declarative knowledge (Anderson, 1983) contributes to slow gradual development of more difficult knowledgeintensive skills; and (2) the "career change" and "compensation" accounts (Salthouse, 1990) where individuals compensate for declining muscle mass and productivity by cultivating and specializing in skillsets that they can perform well and which are not easily substitutable by others. Indeed, our results support the lifelong learning account, indicating that more difficult skills are increasingly represented in the skillsets of older adults and that the peaks in proficiency for the most difficult skills extend more than a decade later than for the least difficult skills. We also find support for the notion of career changes, with proficiency for food production and childrearing skills peaking around the end of the reproductive career, followed by proficiency and expertise for household chores and craft production, and for music and stories categories. These findings are also consistent with a documented shift in male time allocation within productive tasks from strengthintensive hunting to horticultural production in later middle age (Hooper, 2011). Consistent with the notion of late-life specialization, older adults specialize in the lastto-be-acquired skill set: musical and oral traditions. By capitalizing on their high prestige and the attention of co-resident novice kin, older adults may be using songs and stories to pass on knowledge.

### Limitations and future prospects

We discuss possible limitations to our study method and results. Our methods are mostly based on selfreports of skill level and third-party reports on expertise, rather than direct observation of task or skill performance. The skill profile that emerges with these data highlights the types of complementary skills that appear to be developing late in adulthood. While this suggests a



**Fig. 10.** Consensus expertise for categories of skills. The vertical axis is log odds ratio change (relative to age 35) of consensus expertise nominations received for categories of skills. The horizontal axis is age of (**a**) female, and (**b**) male potential expert. In both female and male figures the likelihood of being nominated expert for "social and market" skills is highest at the end of the reproductive life stage (from ages 36 to 43 for females and 40 to 46 for males). Likelihood of consensus expertise nomination for "Reproduction and childcare" is highest from age 45 to 57 for females and 38 to 86 for males. Expertise for "chores and crafts" peaks in the postreproductive life stage (from ages 59 to 77 for females and 55 to 86 for males) as does expertise for "food production" (from ages 36 to 77 for females and 63 to 72 for males). Finally, peak expertise for "music and stories" is first recognized at the relatively latest ages, from ages 65 to 77 for females and 66 to 86 for males. As a general pattern relative to age 35, larger gains in consensus expertise are seen for categories with maxima beginning at later ages.

complementary role for older adults in families and society, it is not necessarily consistent with a profile based on more objective measures of contributions, nor should it be interpreted as direct evidence of adult contributions. When and to whom older adults make their contributions is likely based on opportunity and circumstance, with grandparents often not supporting all grandchildren equally (Gurven and Schniter, 2010). Future studies will be needed to better evaluate conditions under which older adults' make substantial contributions to their kin's energy and information budgets via helpful services (e.g. domestic tasks, craft production, childcare) and culture transmission.

While direct observation may be most reliable, the yardstick for assessing task performance is not transparent for many skills, nor do experiments generally provide a convenient solution. Our reliance on interviews for assessing skill level is supported by a recent study showing that informant interviews may be as or more reliable than behavioral data for detecting moderate differences in individual ability in productive tasks where returns are variable or subject to noise (Hill and Kintigh, 2009). Nonetheless, several of our findings lend confidence to our interview methods. First, ages at which people report high proficiency for their own skills correspond to ages at which people are nominated experts (Figs. 6, 9). Second, the age profile of selfreported proficiency in food production skills (Fig. 5) is similar to the age profile of gross caloric production rates that derive from separate methods (Fig. 3), showing only a five year lag between point estimates of peak caloric production and of food production proficiency. Temporal self-appraisal theories (Wilson and Ross, 2001) suggest that people tend to perceive their own current abilities as "better than in the past". In light of this perceptual bias, it is reasonable that several years of downturn may

be necessary for informants to reliably detect and admit their own decline.

While the set of skills included in this study is extensive and exceeds that of any other study to date, key skills are missing (e.g., some domestic skills like cleaning, processing manioc root, making manioc beer) and several sub-categories contain only few skills (e.g., tool use, chores). While we attempted to survey skills important to males and females, our final skill set is not representative of the complete skillsets utilized by each gender. We have not accounted for how much females engage in what are classified as exclusively male skills, and how often males engage in what are classified as exclusively female skills though evidence of such performance was suggested over the course of our investigations. For example, a few females considered themselves to have skill #46 "speak in front of a group". Likewise, a few males considered themselves to have skill #34 "make small square mat". These exceptions were few and quantitatively insufficient for meaningful interpretation in terms of acquisition, proficiency, and expertise measures. Indeed, we expect that different perspectives are capable of yielding different categorizations of skills perceived to be gender appropriate, and further investigation is encouraged to address the issue of gender normativity. This should not be a major concern for our conclusions however, as the majority of investigated skills were appropriate to both genders and we see few meaningful differences between genders in our results. Where we do see interesting differences between genders is with strength-intensive skills that also contribute disproportionately to the differences between male and female skillset composition. In a separate study that quantified time spent in over 90 activities, Tsimane men overwhelmingly specialize in activities that are high strength and incompatible with childcare (Gurven et al., 2009).

As reported in Methods, we omitted several skills from expertise analyses because they did not reliably elicit nominations from informants. We are unable to assess the confidence of our informants' judgments about expertise and consider that informants may face challenges identifying the "best" individuals at certain skills whose "product" may be difficult to observe. For this reason, residential proximity and relatedness (see Online Supporting Information 5) may be as important, or more, as predictors of expertise nominations than pure ability. Future studies on expert nominations should consider collecting measurements of informant confidence about their nominations of others. A measure of informant confidence might prove useful for calibrating consensus nomination measures.

Lastly, we acknowledge that skill development would be best captured with longitudinal data on the same individuals, but our study design instead uses a crosssection of adults in eight villages, relying on recall for estimating ages of skill acquisition. Using cross-sectional data can be problematic if age-related differences in skills are instead due to secular changes affecting Tsimane lifestyles (see Reyes-Garcia et al., 2013). We found evidence that younger cohorts (especially men aged 21-29) were less likely to acquire certain skills that were revealed in focus groups as most "vanishing" (Online Supporting Information 3, 6; Fig. 2). Young men in that age range are more involved in wage labor than older men, and women at any age (Gurven et al., 2009). Due to the evident effect of culture loss among younger generations, we focused on age-specific changes to shares of particular kinds of skills (e.g., easy versus difficult skills and skills requiring versus not requiring strength) across adult ages, rather than the absolute number of skills reported in specific categories.

### CONCLUSION

This research extends representations of "production" utilized in classical life history theory (Charnov, 1991, 1993) to now include a wider range of skill development important to noncaloric forms of production, alongside growth, reproduction, and food production trajectories. Anthropological studies of skill development and resource transfers have largely neglected the role of complementary skills and generative services in family economics, precluding a more complete understanding of the knowledge and skill development profiles of people living in a traditional subsistence society. As emphasized by cooperative breeding models (e.g., Sear and Mace, 2008; Burkart et al., 2009; Kramer and Ellison, 2010), our results highlight the development of non-caloric production skills that mature late in life among postreproductive adults and likely contribute toward downward transfers that benefit genetic descendants. The pattern of skill ontogeny described here expands upon and shows linkages between notions of cooperation in childrearing, pooled energy budgets, and knowledge accumulation while being directly consistent with the Embodied Capital Model of human life history evolution, where long life evolves in the context of a relatively difficult feeding niche and a multi-generational extended family structure with net resource flows from older to younger kin.

### ACKNOWLEDGEMENTS

Crucial assistance in the field was provided by Tsimane' anthropologists Daniel Vie Durbano, Casimiro Tayo Sanchez, Jaime Nate Cayuba, Boris Bani Cuata, Miguel Mayer Vie, and Adalid Cayuba Maito. We thank the Tsimane for their generous cooperation in this study and its pilots. We thank Jon Stieglitz for his helpful review of an earlier draft.

### LITERATURE CITED

- Adams C, Smith MC, Pasupathi M, Vitolo L. 2002. Social context effects on story recall in older and younger women: does listener make a difference? J Gerontol: Series B, 57B:P28– P40.
- Amoss PT, Harrell, S. 1981. Other ways of growing old: anthropological perspectives. Stanford: Stanford University Press.
- Anderson JR. 1983. The architecture of cognition. Cambridge, Mass.: Harvard University Press.
- Ardila A. 2007. Normal aging increases cognitive heterogeneity: analysis of dispersion in WAIS-III scores across age. Arch Clin Neuropsychol 22:1003–1011.
- Baudisch A. 2005. Hamilton's indicators of the force of selection. Proc Natl Acad Sci USA 102:8263-
- Birdsell J. 1979. Ecological influences on Australian aboriginal social organization. In Bernstein IS, Smith EO, editors. Primate ecology and human origins. New York: Garland.
- Bird RB, Bird DW. 2002. Constraints of knowing or constraints of growing? Hum Nat 13:239–267.
- Blurton Jones NG, Hawkes K, O'Connell JF. 1989. Modelling and measuring costs of children in two foraging societies. In Standen V, Foley, RA. editors. Comparative socioecology: The behavioural ecology of humans and other mammals (special publication 8 of the British ecological society). Massachusetts: Blackwell Scientific Publications.
- Blurton Jones NG, Marlowe FW. 2002. Selection for delayed maturity. Hum Nat 13:199–238.
- Bock J. 2005. "What makes a competent adult forager? " In Hewlett B, Lamb M, editors. Hunter-gatherer childhoods. Somerset: Aldine Transactions. p 109–128.
- Bogin B, Smith BH. 1996. Evolution of the human life cycle. Am J Hum Biol 8:703–716.
- Bourke AFG. 2007. Kin selection and the evolutionary theory of aging. Annu Rev Ecol Evol Systemat, 38:103–128.
- Burkart JM, Hrdy SB, Van Schaik CP. 2009. Cooperative breeding and human cognitive evolution. Evol Anthropol 18:175–186.
- Cain MT. 1977. The economic activities of children in a village in bangladesh. Popul Dev Rev 201–227.
- Castro L, Toro MA. 2004. The evolution of culture: from primate social learning to human culture. Proc Natl Acad Sci USA 101:10235–10240.
- Charnov EL. 1991. Evolution of life history variation among female mammals. Proc Natl Acad Sci USA 88:1134–1137.
- Charnov EL. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford: Oxford University Press. p 167.
- Christensen H, Mackinnon AJ, Korten AE, Jorm AF, Henderson AS, Jacomb P, Rodgers B. 1999. An analysis of diversity in the cognitive performance of elderly community dwellers: individual differences in change scores as a function of age. Psychol Aging, 14:365-
- Crittenden AN, Conklin-Brittain NL, Zes DA, Schoeninger MJ, Marlowe FW. 2013. Juvenile foraging among the hadza: implications for human life history. Evol Hum Behav 34:299–304.
- Davis A, Wagner JR. 2003. Who knows? on the importance of identifying "experts" when researching local ecological knowledge. Hum Ecol 31:463–489.
- Demps K, Zorondo-Rodriguez F, Garcia C, Reyes-Garcia V. 2012. Social learning across the life cycle: cultural knowledge acquisition for honey collection among the jenu kuruba, india. Evol Hum Behav 33:460–470.
- Draper P. 1976. Social and economic constraints on child life among the! Kung. In: Lee RB, DeVore I, editors. Kalahari hunter-gatherers: Studies of the! Kung San and their neighbors. Massachusetts: Harvard University Press.
- Draper P, Cashdan E. 1988. Technological change and child behavior among the! Kung. Ethnology 339–365.

- Ellis R. 1997 A taste of movement: an exploration of the social ethics of the Tsimanes of lowland Bolivia. PhD thesis, University of St Andrews, Unites Kingdom.
- FAO. 2001. Human Energy Requirements: Report of a Joint FAO/WHO/UNU Expert Consultation FAO Food and Nutrition Technical Report Series. Rome: FAO.
- Gurven M, Kaplan HS. 2006. Determinants of time allocation to production across the lifespan among the machiguenga and piro indians of peru. Hum Nat 17:1–49.
- Gurven M, Kaplan HS, Gutierrez M. 2006. How long does it take to become a proficient hunter? Implications for the evolution of delayed growth. J Hum Evol 51:454–470.
- Gurven M, Kaplan H, Supa AZ. 2007. Mortality experience of tsimane amerindians of bolivia: regional variation and temporal trends. Am J Hum Biol, 19:376–398.
- Gurven M, Schniter E. 2010. An evolutionary perspective can help unify disparate accounts of grandparental investment. Behav Brain Sci 33:25–26.
- Gurven M, Stieglitz J, Hooper P, Gomes C, Kaplan H. 2012. From the womb to the tomb: the role of transfers in shaping the evolved human life history. Exp Gerontol 47:807–813.
- Gurven M, Walker R. 2006. Energetic demand of multiple dependents and the evolution of slow human growth. Proc R Soc London, Series B: Biol Sci 273:835–841.
- Gurven M, Winking J, Kaplan HS, von Rueden C, McAllister L. 2009. A bioeconomic approach to marriage and the sexual division of labor. Hum Nat 20:151–183.
- Hamilton WD. 1966. The moulding of senescence by natural selection. J Theor Biol 12:12–45.
- Hawkes K. 2003. Grandmothers and the evolution of human longevity. Am J Hum Biol 15:380–400.
- Hawkes K, O'Connell JF, Blurton Jones NG. 1989. "Hardworking Hadza grandmothers." In: Standen V, Foley RA, editors. Comparative socioecology: The behavioural ecology of humans and other mammals. London: Basil Blackwell.
- Henrich J, Broesch J. 2011. On the nature of cultural transmission networks: evidence from fijian villages for adaptive learning biases. Philosophical transactions of the royal society B. Biol Sci 366:1139-1148. :
- Henrich J, Gil-White F. 2001. The evolution of prestige. Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. Evol Hum Behav 22:165–196. –
- Hewlett BS, Cavalli-Sforza LL. 1986. Cultural transmission among the aka pygmies. Am Anthropol 88:992–934.
- Hewlett BS, Fouts HN, Boyette AH, Hewlett BL. 2011. Social learning among congo basin hunter–gatherers. Phil Trans R Soc B: Biol Sci 366:1168–1178.
- Hill KR, Hurtado AM. 1996. Ache life history: The ecology and demography of a foraging people. New York: Aldine De Gruyter.
- Hill KR, Hurtado AM. 2009. Cooperative breeding in south american hunter-gatherers. Proc R Soc B: Biol Sci 276:3863– 3870.
- Hill K, Kintigh K. 2009. Can anthropologists distinguish good and poor hunters? Implications for hunting hypotheses, sharing conventions, and cultural transmission. Curr Anthropol 50:369–378.
- Hooper P. 2011. The structure of energy production and redistribution among Tsimane' forager-horticulturalists. Dissertation, University of New Mexico.
- Hooper P, Gurven M, Kaplan HS. 2014. Social and economic underpinnings of human biodemography. In: Weinstein M, Lane MA, editors. Sociality, hierarchy, health: comparative biodemography: A collection of papers. Washington, D.C.: National Academies Press.
- Hooper P, Winking J, Gurven M, Kaplan H. 2015. Inclusive fitness and differential productivity across the lifespan determine intergenerational transfers in a small-scale human society. Proc R Soc B: Biol Sci 282:20142808.
- Howell N. 2010. Life Histories of the Dobe! Kung. Oakland: University of California Press
- Huanca T. 2006. Tsimane' Oral Tradition, Landscape, and Identity in the Tropical Forest TAPS: Research: Publications: Books: Tsimane' Oral Tradition. Availabale at: http://people.

 $brandeis.edu/{\sim}rgodoy/publications/tomasbook.pdf. \quad (Accessed on March 13, 2008).$ 

- Iamele G. 2001. Palabras Antiguas y Nuevas del Río Quiquibey, en la Amazonia Boliviana. Programa Regional de Apoyo a los Pueblos Indígenas de la Cuenca de Amazonas (PRAIA): Bolivia.
- Kaplan HS. 1994. Evolutionary and wealth flows theory of fertility: empirical tests and new models. Population Dev Rev, 20:753-791.
- Kaplan H, Gurven M, Winking J, Hooper P, Stieglitz J. 2010. Learning, menopause and the human adaptive complex. Ann N Y Acad Sci 1204:30–42.
- Kaplan HS, Hill K, Lancaster J, Hurtado AM. 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol Anthropol 9:156–185.
- Kaplan HS, Robson AJ. 2002. The emergence of humans: the coevolution of intelligence and longevity with intergenerational transfers. Proc Natl Acad Sci USA 99:10221.
- Kline MA, Boyd R, Henrich J. 2013. Teaching and the life history of cultural transmission in fijian villages. Hum Nat 24: 351–374.
- Kramer KL. 2002. Variation in juvenile dependence. Hum Nat 13:299–325.
- Kramer KL. 2005. Children's help and the pace of reproduction: cooperative breeding in humans. Evol Anthropol: Issues, News, Rev, 14:224–237.
- Kramer KL. 2011. The evolution of human parental care and recruitment of juvenile help. Trends Ecol Evol 26:533–540.
- Kramer KL. 2014. Why what juveniles do matters in the evolution of cooperative breeding. Hum Nat 25:49–65.
- Kramer KL, Ellison PT. 2010. Pooled energy budgets: resituating human energy-allocation trade-offs. Evol Anthropol: Issues, News, Rev 19:136–147.
- Lee RD. 2000. A cross-cultural perspective on intergenerational transfers and the economic life cycle. In: Mason A, Tapinos G, editors. Sharing the wealth: Demographic change and economic transfers between generations. Oxford, UK: Oxford University Press. pp 17–56.
- Lee RD. 2003. Rethinking the evolutionary theory of aging: transfers, not births, shape senescence in social species. Proc Natl Acad Sci USA 100:9637–9642.
- Lee R. 2013. Intergenerational Transfers, the Biological Life Cycle, and Human Society. Population Dev Rev 38(s1):23–35.
- Lee R, Kramer K. 2002. Children's economic roles in the maya family life cycle: cain, caldwell, and chayanov revisited. Population Dev Rev 28:475–499.
- Levitis DA, Lackey LB. 2011. A measure for describing and comparing postreproductive life span as a population trait. Methods Ecol Evol, 2:446–453.
- Lozada M, Ladio A, Weigandt. M. 2006. Cultural transmission of ethnobotanical knowledge in a rural community of northwestern patagonia, argentina. Econ Botany 60:374–385.
- Maddox GL, Clark DO. 1992. Trajectories of functional impairment in later life. J Health Soc Behav 114–125.
- Marlowe FW. 2010. The Hadza. Oakland: University of California Press.
- Martin MA, Lassek WD, Gaulin SJ, Evans RW, Woo JG, Geraghty SR, Gurven MD. 2012. Fatty acid composition in the mature milk of bolivian forager-horticulturalists: controlled comparisons with a US sample. Maternal Child Nutr 8:404-418.
- McCullagh P, Nelder JA. 1989. Generalized Linear Models, 2nd Ed., London: Chapman and Hall.
- Mergler NL, Faust M, Godstein MD. 1984. Storytelling as an age-dependent skill: Oral recall of orally presented stories. Int J Aging Hum Dev 20:205–228.
- Miner E, Gurven M, Kaplan H, Gaulin S. 1984. Sex difference in travel is concentrated in adolescence and tracks reproductive interests. Proceedings of Royal Society B 281:20141476.
- Nelson EA, Dannefer D. 1992. Aged heterogeneity: Fact or fiction? the fate of diversity in gerontological research. The Gerontologist 32:17–23.

- Ohmagari K, Berkes F. 1997. Transmission of indigenous knowledge and bush skills among the western james bay cree women of subarctic canada. Hum Ecol 25:197–222.
- Park DC, Lautenschlager G, Hedden T, Davidson NS, Smith AD, Smith PK. 2002. Models of visuospatial and verbal memory across the adult life span. Psychol Aging 17:299-
- Paupathi M, Henry M, Carstensen L. 2002. Age and ethnicity differences in storytelling to young children: Emotionality, relationality, and socialization. Psychol Aging 17:610–621.
- Reyes-Garcia VE, Broesch J, Calvet-Mir L, Fuentes-Palaez N, McDade TW, Parsa S, Tanner S, Huanca T, Leonard WR, Martinez-Rodriguez MR. 2009. Cultural transmission of ethnobotanical knowledge and skills: an empirical analysis from an Amerindian society. Evol Hum Behav 30(4), 274–285.
- Reyes-García V, Luz AC, Gueze M, Paneque-Gálvez J, Macía MJ, Orta-Martínez M, Pino J. 2013. Secular trends on traditional ecological knowledge: an analysis of changes in different domains of knowledge among tsimane' men. Learn Individual Differ 27:206–212.
- Robson AJ, Kaplan HS. 2003. The evolution of human life expectancy and intelligence in hunter-gatherer economies. Am Econ Rev 93:150–169.
- Roubenoff R. 2000. Sarcopenia: a major modifiable cause of frailty in the elderly: Sarcopenia in aging. J Nutr Health Aging 4:140–142.
- Ruddle K, Chesterfield R. 1977. Education for Traditional Food Procurement in the Orinoco Delta. Berkley: University of California Press.
- Salthouse TA. 1990. Cognitive competence and expertise in aging. In: Birren JE, Schaie KW, editors. Handbook of the psychology of aging 3rd ed. San Diego: Academic Press. pp 310–319.
- Salthouse TA. 1993. Speed and knowledge as determinants of adult age differences in verbal tasks. J Gerontol: Psychol Sci 48:29–36.
- Schaie KW. 1994. The course of adult intellectual development. Am Psychol 49:304–313.
- Schniter E. 2014. Older adults' contributions to the tsimane forager-farmer economy. Anthropol Aging 35:56–58.

- Schofield WN. 1985. Predicting basal metabolic rate, new standards and review of previous work. Hum Nutr Clin Nutr 39:5–41.
- Schuppli C, Isler K, van Schaik CP. 2012. How to explain the unusually late age at skill competence among humans. J Hum Evol 63:843-850.
- Sear R, Mace R. 2008. Who keeps children alive? a review of the effects of kin on child survival. Evol Hum Behav 29:1-18.
- Simmons L. 1945. (1970 ed.) The role of the aged in primitive society. New Haven: Yale University Press.
- Stieglitz J, Gurven M, Kaplan H, Hooper P. 2013. Household task delegation among high fertility forager-horticulturalists of Bolivia. Current Anthropology 54(2):232–241.
- Stieglitz, J, Schniter, E, Kaplan, H, von Rueden, C, Gurven, M. 2014. Functional disability and social conflict increase risk of depression in older adulthood among bolivian forager-farmers. J Gerontol: Soc Sci. doi: 10.1093/geronb/gbu080.
- Walker R, Hill K. 2003. Modeling growth and senescence in physical performance among the ache of eastern paraguay. Am J Hum Biol 15:196–208.
- Walker RS, Hill K, Kaplan HS, MacMillan G. 2002. Agedependency in hunting ability among the ache of eastern paraguay. J Hum Evol 42:639–657.
- Walker R, Gurven M, Hill K, Migliano A, Chagnon N, De Souza R, Yamauchi T. 2006. Growth rates and life histories in twenty-two small-scale societies. Am J Hum Biol 18:295–311.
- Williams GC. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398-411.
- Wilson AE, Ross M. 2001. From chump to champ: people's appraisals of their earlier and present selves. J Personal Soc Psychol 80:572-
- Winking J. 2005. Fathering among the Tsimane of Bolivia: A Test of the Proposed Goals of Paternal Care. Dissertation, University of New Mexico.
- Winking J, Kaplan HS, Gurven M, Rucas S. 2007. Why do men marry and why do they stray? Proc R Soc B 274:1634–1649.