

How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span

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Abstract

Human hunting is arguably one of the most difficult activities common to foraging peoples now and in the past. Children and teenagers have usually been described as incompetent hunters in ethnographies of hunter-gatherers. This paper explores the extent to which adult-level competence is limited more by the constraints of physical capital, or body size, and brain-based capital, or skills and learning. The grandmother hypothesis requires that production is an increasing function of size alone, while the embodied capital model stipulates that production is a function of both size and delayed learning. Tests based on observational, interview, and experimental data collected among Tsimane Amerindians of the Bolivian Amazon suggest that size alone cannot explain the long delay until peak hunting productivity. Indirect encounters (e.g., smells, sounds, tracks, and scat) and shooting of stationary targets are two components of hunting ability limited primarily by physical size alone, but the more difficult components of hunting—direct encounters with important prey items and successful capture—require substantial skill. Those skills can take an additional ten to twenty years to develop after achieving adult body size.

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Introduction

Human children spend a longer time growing than any other primate, an exaggeration of an already exaggerated feature of the primate order—an extended period of juvenile development and delayed onset of sexual maturation (Schultz, 1956; Clark, 1971; Leigh and Park, 1998). The observation that humans and other primates spend about a quarter of their lives in a juvenile phase has sparked considerable debate about the functional significance of delayed adulthood, especially when combined with radiations towards increased encephalization and extended life span (Jerison, 1973). The extension of childhood and insertion of adolescence are seen as prominent, recent features of

human life history (Bogin and Smith, 1996; Bogin, 1997; Dean et al., 2001; Bock and Sellen, 2002).

To date, four alternative explanations for delayed maturation have been proposed, based on social competition, risk-aversion, trade-offs between growth and reproduction, and learning- and skill-based food acquisition strategies (Pagel and Harvey, 1993; Leigh, 2001; Pereira and Fairbanks, 2002). Social explanations focus on intragroup competition, where extra time is necessary to develop social competency (Dunbar, 1998; Barton, 1999). The risk-aversion hypothesis, proposed by Janson and van Schaik (1993), argues that growth is slow among social primates in order to avoid resource competition and thereby serves to reduce the risk of dying due to fluctuations in food supply.

The third hypothesis views optimal age at reproductive maturation as a trade-off between increased production from the benefits of growing longer (and hence larger) and the decreased probability of reaching reproductive maturity because

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with each additional unit of time invested in growth there is some risk of dying (Charnov, 1993). This model has been extended and applied to humans in the form of the grandmother hypothesis (GH). The grandmother hypothesis applies Charnov's (1993) model of optimal age at reproduction to explain the juvenile period as an artifact of selection on longer life span due to the indirect fitness benefits that accrue to magnanimous grandmothers (Hawkes et al., 1998; Alvarez, 2000; Hawkes, 2003).

Finally, learning- and skills-based models focus on the difficult adult foraging niche of many primates, especially humans, where much time early in life is devoted to acquiring the critical coordination, skills, and knowledge necessary for proficient adult foraging (Bogin, 1997; Ross and Jones, 1999). The embodied capital (EC) approach extends this approach to explain delayed maturation, extended life span, and increased encephalization as a coevolutionary response to the demands of the difficult human foraging niche (Hill and Kaplan, 1999; Kaplan et al., 2000; Kaplan and Robson, 2002). According to this view, natural selection acts to extend life span when early learning yields high production payoffs over the duration of a longer adult life span. Similarly, longer life span puts selection pressure to grow more slowly early in life and to spend this time learning when such investments lead to higher production payoffs later in life. The EC approach also indirectly incorporates the risk-reduction hypothesis. Mathematical modeling (Kaplan and Robson, 2002; Robson and Kaplan, 2003) has shown that the gains from learning act to increase the optimal level of investment in mortality reduction at all ages. As a result, human children should have the lowest mortality of any primate. It is frequently observed that children in hunter-gatherer societies do not engage in activities that place them at risk (Draper, 1976; Blurton Jones et al., 1989). Thus, EC links foraging and ultimately reproductive success to brain-based "embodied" capital, which includes the suite of skills, knowledge, and abilities that impact future performance, as well as the maintenance and repair mechanisms that act to reduce mortality so that later gains can be realized.

This paper tests the competing predictions of the grandmother and embodied capital models. These differ primarily with respect to the importance of learning and the attendant brain-based mental faculties in selection for an extended prereproductive period. While GH and EC both argue that intergenerational resource transfers from older to young individuals are critical aspects of human life history that allow low-producing preadults to grow slowly (see also Lee, 2003), only EC links the development of the brain with a functional extension of early life. According to GH, the juvenile period is a waiting time to maturation; the advantage of big brains, if any, is that humans can quickly learn the skills required for being a successful forager after reaching adult size (Blurton Jones and Marlowe, 2002). Any benefits to extended childhood are not necessary for explaining the long juvenile period, but are instead by-products of a long life span. It is the gain from physical growth in the context of adult mortality rates that determines the length of the juvenile period. A recent comparison of competing

hypotheses with respect to specific patterns of prematurational growth showed strongest support for the EC model (Leigh, 2001: 235). Nevertheless, more data are necessary for a definitive test.

This paper examines age trajectories of hunting ability and physical growth among a group of forager-agriculturalists, the Tsimane of Bolivia, in order to test several key differences between EC and GH with respect to limitations on adult productivity. The GH predicts that foraging success should be limited primarily by physical body size. Therefore, once mature adult size is reached, individuals are expected to quickly learn the necessary skills to become proficient adult foragers (Blurton Jones and Marlowe, 2002; Bird and Bliege Bird, 2005; Tucker and Young, 2005). Foraging success is thus limited by what Bock (2002) referred to as "growth-based" rather than "experience-based" capital. Alternatively, the EC predicts that because the human foraging niche is focused on nutrient-dense and difficult-to-acquire resources, long periods of learning and experience combined with physical growth are required to achieve foraging success (Kaplan et al., 2000; Walker et al., 2002; Bock, 2005; Gurven and Kaplan, 2006). Individuals should allocate time to activities based on the strength and skill requirements of those activities, the potential effects of on-the-job learning ("experience") on later productivity, the danger of different tasks, and labor substitution within the context of a division of labor within and among a set of households (Bock, 2002; Bock and Johnson, 2004; Gurven and Kaplan, 2006). More difficult tasks in terms of strength and skill should witness a later onset of peak productivity.

Previous research on the difficulty of human and nonhuman foraging strategies

Interspecific analyses of nonhuman primate diets show that the overall complexity of the foraging niche correlates positively with larger brains, longer juvenile periods, and longer life spans in comparisons of primate species using multivariate analyses that control for social group size and body size (Kaplan et al., 2003). Juvenile chimpanzees take several years to achieve adult levels of termite fishing (Goodall, 1986). Brown, white-faced, and weeper capuchin monkeys all show significant increases in invertebrate foraging success during the first several years of life (Janson and van Schaik, 1993).

Similar associations between brain size and developmental periods have been found among birds (Wunderle, 1991; Iwaniuk and Nelson, 2003). Foraging skills improve significantly for four years among cooperatively breeding white-winged choughs (Heinsohn et al., 1988), and the time it takes to reach adult levels is longer when help during development is rare (Heinsohn, 1991). It has been argued, however, that much of the juvenile deficiencies in nonhuman animals are due to physical constraints or risk aversion, rather than cognitive or experience-based limitations (Heinsohn, 1991).

With respect to humans, quantitative data based on intensive behavioral sampling (summarized by Kaplan et al., 2000) and a broad survey of 229 groups show that animal foods constitute over 60% of the diet among modern hunter-gatherers

(Cordain et al., 2000; Cordain et al., 2002). Data from a number of different foraging societies suggest that meat acquisition generally requires a high level of skill and coordination, as hunters must navigate over relatively large ranges and incorporate extensive cues, signs, and context-specific knowledge concerning animal behavior and ecology (see Blurton Jones and Konner, 1976; Leibenberg, 1990). Apart from hunting, certain nonmeat items, which also form an important component of hunter-gatherer diets, such as roots, tubers, nuts, and palm hearts, must first be located, then extracted from a solid substrate. These foods have already been identified as difficult to acquire and process, with EC emphasizing both strength and skill and GH emphasizing strength alone. In comparison with nonhuman-primate diets, nutrient-dense, calorically rich resources constitute the vast majority of human hunter-gatherer diets (Kaplan et al., 2000).

Changes in foraging proficiency with age have been examined among the Ache (Walker et al., 2002), Gidra (Ohtsuka, 1989), Hadza (Blurton Jones and Marlowe, 2002), Hiwi (Kaplan et al., 2000), Mardu (Bird and Bliege Bird, 2005), Machiguenga and Piro (Gurven and Kaplan, 2006), Meriam (Bird and Bliege Bird, 2002; Bliege Bird and Bird, 2002), and Mikea (Tucker and Young, 2005). The Ache, Gidra, Hadza, Hiwi, and Machiguenga and Piro studies show that men's hunting success peaks in the age range of 35–50, while other foraging and fishing activities peak by about age 20. Several cases of extraction activities show similar delayed productivity (albeit not as extreme), such as shellfish collecting among Gidjingali (Meehan, 1982) and mongongo-nut processing among Okavango Delta peoples (Bock, 2002). Conversely, the Meriam research team (Bird and Bliege Bird, 2002, 2005; Bliege Bird and Bird, 2002) found that increases in children's productivity in several fishing and hunting activities closely tracked changes in physical growth. Tucker and Young (2005) found few differences in productivity rates between children and adults in tuber extraction.

It is important to note that these studies used observed caloric return rates or time spent per day as the only measures of productivity. Only the Ache study examined age-specific trends in components of hunting activities and demonstrated that finding and pursuing prey require significantly more time to master than marksmanship. Because most of these studies measured age trends in productivity as caloric return rates from a cross section of individuals based on actual events, strong inferences about age trends suffer from a self-selection bias. The most common of these biases stems from secular decreases in time spent hunting due to increased market access and formal education among children and younger adults in these societies. It is therefore unclear whether large increases in performance in the cross-sectional sample are due to actual age-related increases in ability, or due to the fact that adults may have spent more time foraging (and little to no time in school) than today's children and adolescents when they were young. Self-selection can also introduce biases in the opposite direction. Children may only participate in foraging activities when conditions are favorable (such as when shellfish are abundant), whereas adults may forage under

both favorable and unfavorable conditions. This would introduce a bias, reducing the difference between adult and juvenile return rates from foraging. Similarly, if adults make key decisions about patch choice and when children should forage, children's rates of return of foraging may depend on the inputs of adults.

New data and analyses

In this study, we disaggregate the components of hunting ability across the life span among the Tsimane of Bolivia in greater detail than in previous studies, using a combination of observation, interview, and experiment. Our goal is to determine if strength—or some other measure of body size—alone predicts each of these components, or whether there is also evidence for learning and skill development. In addition, we estimate the relative impact of strength and skill on the growth of hunting ability from age 10 to 40, and its subsequent decline in old age. The following components of hunting success are analyzed: encountering animals both indirectly and directly, pursuing animals, and successfully capturing animals. The relative importance of body size versus skill in explaining age profiles for each component is then evaluated. The EC hypothesis predicts a particular age ordering in those components. If skill and learning are determinants of hunting return rates, we should find that indirect encounters with signs of animals should reach peak levels at earlier ages than direct encounters with animals because it is often easier to see signs of animals than it is to directly encounter them. The EC also predicts that kill rates peak at even older ages because a successful pursuit requires not only marksmanship but making the animal vulnerable to being killed without scaring it. Finally, caloric return rates should peak at the oldest ages since greater skill should translate into acquiring more total meat per hour through efficient selection of prey items. Any other ordering of these age profiles would provide evidence against EC. In addition to those data, experiments with target-shooting and identification of animal tracks were also conducted to measure additional components of skill and knowledge. While most research to date has used body size as a proxy for strength, this study utilizes multiple direct measures of strength to conduct more rigorous tests of the two hypotheses.

A particular advantage of this study is that none of the Tsimane participants in the sample received prior schooling, so there is no confound of secular age trends in hunting ability due to formal education.

Methods

Study group

The Tsimane are forager-agriculturalists living in lowland Bolivia. Most Tsimane live in small villages composed of a number of extended family clusters, totaling roughly 50–150 individuals. Most of the food that the Tsimane consume derives from horticulture, fishing, hunting, and gathering. They cultivate plantains, rice, corn, and sweet manioc in small

swiddens and regularly fish and hunt for meat. Villages are usually located along major and minor rivers; however, all hunting data were collected in two remote communities located within prime forest area where hunting is a common activity. Strength and growth data were collected from a larger sample of seventeen villages. More detailed background information on the Tsimane is provided by Chicchón (1992), Reyes-García (2001), Godoy et al. (2004), and Gurven (2004).

Tsimane in the study communities engage in more hunting than fishing due to the close proximity of primary and secondary forest. Most men hunt about twice a week, although some men hunt more and others less. Tsimane regularly hunt using shotguns and with the tracking assistance of dogs. Dogs are particularly useful for finding certain game animals, such as agouti paca, although they are viewed as a hindrance to locating and capturing monkeys. Dogs were present on 54% of the sampled hunts. While the use of dogs certainly enhances hunting success, proper training and communication with hunting dogs are necessary to ensure success. The weapons of choice are usually 12-gauge shotguns, although these and ammunition for them are often not available. In our sample shotguns were used on 56% of the hunts, while bows and arrows were carried on 47% of the hunts (showing that sometimes both are used for their differential advantages).

In terms of biomass harvested, the most abundant resources were collared peccary (1,033 kg, 84 kills), Brazilian tapir (884 kg, 10 kills), gray brocket deer (467 kg, 28 kills), howler monkey (452 kg, 102 kills), agouti paca (410 kg, 67 kills), white-faced capuchin monkey (250 kg, 73 kills), and coatimundi (247 kg, 71 kills). Together, these seven species constituted 82% of the biomass, or 70% of the kills, and were the main focus of the analyses presented in this paper. Other prey animals included turtles, squirrel monkeys, seven-banded and nine-banded armadillos, and cracid birds. Less common prey animals were white-lipped peccaries, spider monkeys, and collared and giant anteater.

Hunting sample

Hunting data were collected from interviews with 59 male residents in two study communities from October 2002 through July 2003. The sample included 420 foraging trips with a total of 654 kills. Each resident was interviewed every other day regarding hunting activities that occurred on the previous two days. A trained bilingual Tsimane (Maguin Guitierrez) conducted all of the interviews. He identified all animals killed on the trip by the interviewee and others on the trip. Homs spring scales were used to weigh animal kills to the nearest 0.1 kg upon a hunter's return to the village after a foray. Only 64% of kills were directly weighed. Estimates for unweighed or partially weighed animals were made using average weights from previously measured kills, and from data in Eisenberg (1989) and Redford and Eisenberg (1992), using information collected on species, sex, and age of kills. Animal weights were then converted to calories using conversion ratios for similar species given in Hill and Hawkes (1983).

Hunters were asked about all *direct encounters* with animals, whether each of these animals was pursued, whether pursuits resulted in kills, and reasons for not engaging in a pursuit. Hunters were also asked about *indirect encounters* with animals. These are grouped into four categories: (a) *smell*, which usually referred to scents of animals, excrement, and urine; (b) *sound*, which includes animal calls and shuffling and scrambling of animals in brush or trees; (c) *spoor*, which includes tracks, trails, disturbed underbrush, or other indicators of the recent path of potential prey; and (d) *scat*, or animal urine and feces. Other indicators, such as salt licks, water holes, and partially eaten fruits and other foods were also recorded, but not systematically enough to warrant inclusion here. While the quantity and content of indirect and direct encounters elicited by interview may be subject to recall error and elaborate storytelling, the senior author cross-checked several stories with multiple participants to independently verify the reliability of the interviews. Hunters have good memories regarding recent hunting events, and there was no suggestion of deliberate fabrication. For all trips, the number of dogs, bows and arrows, shotguns, and other technology were also recorded. Hours of departure and arrival were also recorded for most single-day trips.

Arrow-shoot competitions

Arrow-shoot competitions were held in the two study communities, and an additional community along the Maniqui River. One contest placed a small target (plantain heart) at a horizontal distance of 16 m, and a vertical distance of 10 m. This was meant to imitate a monkey hunt (*sensu* Blurton Jones and Marlowe, 2002; Walker et al., 2002), though the target was further away than a typical shot during a real monkey hunt. In the other contest, the target was placed at ground level at a distance of 16 m from the hunter. Each person was given five attempts, and hits were scored in two ways. The first (score1) gave one point for each solid hit, and the second (score2) added to this a half point for skims, where the arrow may have grazed the target, but did not lodge in or slice through it. The sample of men was 81 and 73 for high- and low-target contests, respectively. The winner of each contest for each age group was awarded a prize worth about \$10 (wristwatches) to further motivate the shooters.

Print identification

Laminated flashcards of animal prints for 16 common and rare animals from the Bolivian Amazon were made from enlarged photocopies of drawings presented in Emmons (1990). These were chosen as a way of distinguishing the knowledge of children, adolescents, and young and older adults. It was carefully explained to each participant that the cards were representations of real prints. Participants were asked to name the animal whose prints most resembled that diagrammed on the card. Each participant scored a point for each correctly identified set of prints. Five individuals were

excluded from analysis because it was clear that they did not understand the task. The final sample included 42 males.

Physical growth

Physical growth was measured using cross-sectional measures of height (in centimeters), weight (in kilograms), and body strength (in kilograms times meters per second squared). Height was measured using a portable Seca Model 214 stadiometer. Weight was measured using a digital Tanita BF-572 scale. No shoes or sandals were worn during height and weight measurement. Total strength was measured as the sum of five separate measures using a Lafayette manual muscle tester and a Smedley III grip-strength tester. Together, these were used to examine upper-body, leg, and hand strength. Chest strength was measured as the participant pressed the instrument between the palms of each hand, with the elbows perpendicular to the body at midchest height. Shoulder strength involved placing the instrument on the subject's wrist, where the subject's arm was outstretched to the side of the body at a right angle. The subject raised his arm against the investigator's resistance. Leg strength was measured in two ways. The first was a leg lift against resistance on the ankle with the subject lying on his/her side, and the second was a leg lift against resistance on the thigh just above the knee in a seated position with legs bent. The samples for these measures included more males than those in the sample communities ($n = 399$ for height and weight; $n = 99$ for strength).

Both GH and EC predict that more physical capital should correlate with higher productive performance. While each of the measures describes “body size” or physical capital, it is important to recognize that weight and height are monotonically increasing functions of age, while strength is expected to increase until adulthood and decrease thereafter. If production performance is limited only by weight or height, then we should not expect to find any declines in performance at later ages. We view total strength as the best approximation of available physical capital that can be utilized to engage in subsistence tasks. We give precedence to analyses contrasting the effects of age versus strength, but report analyses involving weight and height for comparison with previous studies (e.g., Bliege Bird and Bird, 2002).

Data analysis

Age trends were assessed using a combination of loess, logistic, linear, and nonlinear regression analyses (LOESS, GENMOD, GLM, MIXED, and NLIN procedures in SAS v9.1; SAS Institute, 2003). Loess regression was used to present smooth nonparametric age-curves for arrow-shoot, track-identification, and physical-growth data. Logistic regression was used to estimate the probability of animal pursuits and kills using the general estimating equations procedure, GENMOD. This and the MIXED procedure control for the correlated structure of data when the same people contributed different numbers of trip-days or events to the sample throughout the year. Linear regression was used to examine direct and

indirect encounter rates, as well as overall rate of caloric acquisition. Encounter rates were defined as the number observed animals per hour spent on trek. Second-order and third-order age terms were included in these analyses of indirect encounters because these are not expected to decrease at older ages, but also not expected to increase linearly over the entire life span. Nonlinear regression was used to estimate rates of encountering different animal types, using the formula, $Y = age^a \cdot e^{b \cdot age}$ (Gurven and Kaplan, 2006). Nonlinear regression was used to check the results of loess smoothing.

The probability of pursuing a prey animal after directly encountering it was modeled using general estimating equations with a logistic link function. The model is equivalent to a logistic regression with the individual's identification number (PID) treated as a repeated measure. The number of other men present on the trip, presence of dogs, and whether guns were brought on the trip were added as controls in the model because each may independently impact any decision to pursue an animal.

In modeling the probability of a successful kill (upon pursuit and upon encounter), we also used general estimating equations that allow for repeated occurrences of the same men in the data and control for the animal species, number of other men present, and use of dogs and shotguns. We report p -values from two sets of analyses. The first set includes controls for repeated occurrence of the same hunters in the data and the second set ignores the identity of the hunter. Both are reported because the small effective sample size after the covariates and hunter identities were considered complicates interpretation because age, weight, and height are linked tightly to the hunters' identities, and hence these variables are more likely to drop out of the model.

The caloric return rate measures the overall efficiency of hunting in terms of the output (calories) in relation to the input (time). We estimated return rate in two ways. First, we summed all of the calories acquired by each hunter from all animals and divided the sum by the total hours that the hunter spent foraging over the sample period. This yielded a database in which each data point corresponds to one person. Second, we estimated daily return rate, which allowed additional covariates, such as the presence of other men, dogs, or the use of guns, to be included in the analysis. For the first approach, we used a weighted ordinary least squares (OLS) regression to estimate the single and joint effects of age and strength on return rate. For the second, we used a linear mixed model, which controls for the fact that some of the men contributed more hunting events than others.

Arrow-shoot performance was analyzed with OLS regression using age, age², and body-size measures. Instead of total strength, we used upper-body strength because shooting requires strength only in arms, grip, shoulders, chest, and back. Regression analyses controlled for village, since arrow-shoot contests were done in three study villages.

To examine the relative importance of strength and skill on hunting ability, we proceeded in two steps. The first step was to conduct multiple-regression analyses controlling for other covariates—prey species, the presence of dogs, weapons

used, and other hunters present. The next step compared the values for a 10- and 40-year-old hunters, respectively, so that the results were not confounded by senescence. We determined the amount of change in the predicted values for the two ages due to strength (or other measures of body size) and skill, respectively. The estimates were calculated for age and each body-size measure separately by substituting the appropriate age or average strength, height, and weight for 10- or 40-year-old males and using the appropriate partial-regression estimates.

Results

We first present age-specific trends of physical growth. These will be used for comparison with age trends in hunting performance. Performance will then be described by examination of encounter rates, kill rates, and rates of energy gain per hour spent hunting. Changes in ability will also be described by arrow-shoot and track-identification experiments. We assess the relative importance of physical size versus skill by a combination of visual inspection of age trends and by multivariate analysis.

Physical growth

Figure 1 displays three measures of physical growth for Tsimane males, standardized to maximum adult values. Height approaches peak level most rapidly, followed by weight and strength (Table 1). By age 20, at least 90% of adult height, weight, and total strength are achieved. From ages 9 to 30, there is little difference in the age trajectories of weight and strength gain. Unlike weight and height, strength declines from age 30, with a 43-year-old as strong as a 20-year-old, and a 55-year-old as strong as a 16-year-old. This strength

Table 1

Body size by age

Body-size measure	Peak level	Age at peak	Age at 75% of peak	Age at 90% of peak
Height	163 cm	31	9	14
Weight	63 kg	35	16	20
Strength	122 kg×m/s ²	29	16	20

trajectory peaks later than among the Ache (Walker et al., 2002), Bugakwe and Hambukushu (Bock, 2002), and Hadza (Blurton Jones and Marlowe, 2002) because these studies examined only upper body strength. Tsimane upper body strength peaks at age 26, but nonetheless shows a trajectory that is very similar to that of total strength (Pearson correlation $r = 0.98, p < 0.0001$).

Encounters

Indirect encounters. Indirect encounters, grouped as smells, sounds, spoor, and scat, often preceded direct encounters, although often they did not lead to any direct interaction with prey. These variables are graphed by age using loess regression in Figure 2. Overall, indirect encounter rates peak in the mid-20s. Smells, sounds, spoor, and scat all reveal significant age and body-size effects when examined separately. Table 2 shows that, when analyzed together in the same model, body size and strength are significant predictors of sounds, spoor, and scat. Age is a significant predictor only of smells when paired with strength—but not when paired with weight or height. Summing all encounters reemphasizes the general result that age is an insignificant predictor of increases in indirect encounters when analyzed simultaneously with body size or strength. Adding a second-order age term does not change the qualitative results, which suggests that until early adulthood, physical development is more important than chronological age in determining indirect encounters.

Direct encounters. We first estimate the average rate that hunters encounter each of the seven major prey species per hour spent on a trek. Figure 3a shows the encounter rate for paca, coati, tapir, howler and capuchin monkeys, brocket

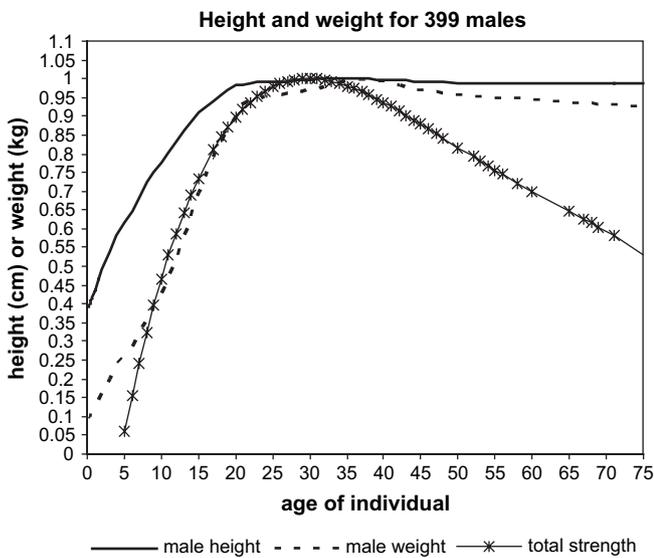


Fig. 1. Physical growth of Tsimane males by height, weight, and body strength. All measures are standardized relative to their maximal values. Strength is sum of five measures comprising chest, arm, hand, thigh, and leg strength components (see text).

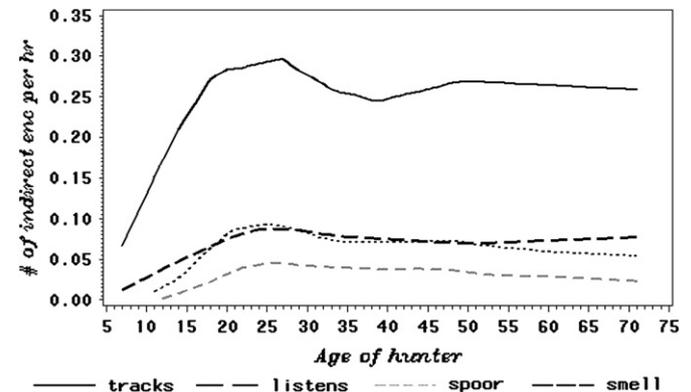


Fig. 2. Number of animal tracks, sounds, smells, and scat encountered per hour spent foraging (by age of hunter). Curves generated using loess regression.

Table 2
Multiple regression of indirect encounters on age, strength, height, and weight

Variable	Total indirect encounters		Smells		Sounds		Spoor		Scat	
	Estimate	<i>p</i>	Estimate	<i>p</i>	Estimate	<i>p</i>	Estimate	<i>p</i>	Estimate	<i>p</i>
Age	0.0012	0.30	0.0007	0.016	0.0004	0.20	-0.0009	0.62	0.0002	0.53
Strength	0.0013	0.08	0.0005	0.007	0.0006	0.003	0.0001	0.95	0.0002	0.26
<i>r</i> ²	0.09		0.26		0.21		0.01		0.04	
Age	-0.0006	0.59	0.0002	0.42	0.0000	0.94	-0.0008	0.71	-0.0002	0.56
Height	0.0059	0.0001	0.0010	0.0001	0.0012	0.0001	0.0024	0.16	0.0007	0.006
<i>r</i> ²	0.33		0.46		0.42		0.05		0.18	
Age	-0.0006	0.56	0.0001	0.66	-0.0003	0.34	-0.0008	0.71	-0.0003	0.42
Weight	0.0066	0.0001	0.0014	0.0001	0.0018	0.0001	0.0031	0.19	0.0010	0.001
<i>r</i> ²	0.35		0.47		0.30		0.04		0.18	

deer, and collared peccary using nonlinear regression. Encounters tend to approach peak levels by about 20 years of age for paca and coati, 35 years of age for howler and capuchin monkeys and deer, and 45–50 years of age for collared peccary. The sum of encounters for the seven animals by age is shown in Fig. 3b. Overall, summed encounter rates peak by age 37, about a decade later than indirect encounter rates, as predicted by EC.

Table 3 presents the results of multiple-regression analyses of direct encounter rates on strength and age, both for each major prey item separately and for the summed encounter rate. Simple OLS regression (not shown) of summed encounter rate on age and strength, respectively, show that both are highly significant. Similar results of regressions of age on encounter rate were found for five of the seven major prey species. Only paca and coati show no statistically significant effect of age; these are the two prey items for which dogs have a large effect on encounters.

Multivariate regression of age and strength eliminates the effect of strength, leaving only the age effect on overall encounter rate. This same result occurs in the analysis of daily encounter rates when controlling for presence of dogs and other hunters. Among specific prey types, only peccary and deer show significant impacts of age, and not of strength, on encounter rates. Using height or weight instead of strength as the measure of body size reduces the effect of age, and both height and weight become highly significant independent predictors of encounter rate.

Pursuits

The average probability of engaging in a pursuit after an encounter is 89% (*n* = 809 pursuits). The probability of a pursuit is above 70% for all seven animals, and above 90% for most, with little age-specific variation. In fact, age, strength, and weight are mostly insignificant in all regression analyses (not shown). Only capuchin monkey and collared peccary show statistically significant age effects, where younger and older men are more likely to pursue. Strength has no predictive power of pursuit probability, and weight only negatively predicts collared peccary pursuits [$\exp(\text{estimate}) = 0.91$, *p* = 0.02]. Analyzing age and body size together eliminates all age effects, while

the negative effect of weight on collared peccary pursuits remains. These results show that age and body size have a minimal influence on whether hunters actively pursue the majority of prey animals in their diet, suggesting that changing

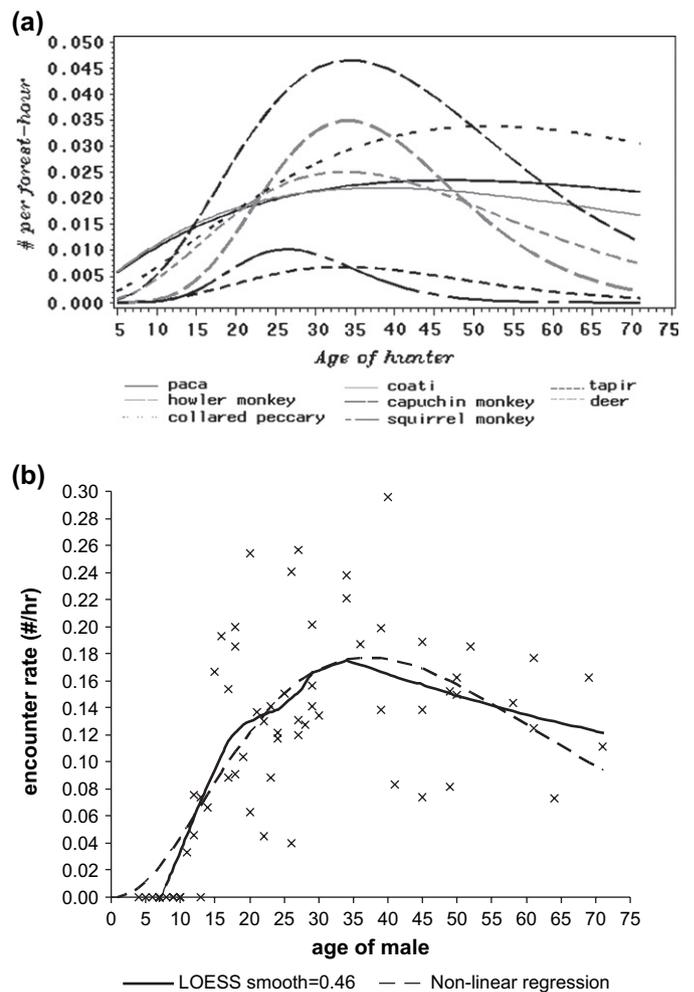


Fig. 3. (a) Encounter rate (number per hour spent foraging) with seven most common animal species by age. Curves are generated by nonlinear regression, according to the formula $Y = age^a \cdot e^{b \cdot age}$. (b) Overall encounter rate with any of seven common species. Curves generated using nonlinear and loess regression.

Table 3
Multiple regression of direct prey-encounter rate on age, age², and strength for summed encounters and for each of seven prey items

Animal	Age		Age ²		Strength		r ²	F	p
	Estimate	p	Estimate	p	Estimate	p			
All seven	7.52E−03	0.02	−8.42E−05	0.05	4.35E−04	0.37	0.36	8.4	0.0001
Howler monkey	9.86E−04	0.55	−1.16E−05	0.56	2.72E−04	0.16	0.20	3.4	0.02
Coati	7.56E−04	0.67	−7.20E−06	0.76	−1.31E−04	0.61	0.02	0.3	0.83
Paca	4.41E−05	0.98	7.49E−07	0.97	−4.03E−05	0.85	0.01	0.1	0.96
Collared peccary	2.68E−03	0.02	−3.05E−05	0.04	−1.33E−04	0.42	0.21	4.0	0.01
Tapir	2.62E−04	0.54	−3.54E−06	0.52	3.18E−05	0.61	0.06	0.9	0.45
Capuchin monkey	1.16E−03	0.33	−1.25E−05	0.43	2.78E−04	0.05	0.30	6.4	0.001
Deer	1.46E−03	0.05	−1.74E−05	0.09	5.90E−05	0.60	0.24	4.5	0.008

motivation with age does not mediate the relationship between encounter rates and kill rates.

Kills and caloric return rate

We next examine the probability of a successful kill. Table 4 shows that over half of all kills were made with shotgun and rifle combined, 16% with bow and arrow, and the remainder by machete, sticks, dogs, and other techniques. Figure 4 illustrates the probability of a successful kill upon pursuit for the same seven prey species. Most prey items, with the exception of paca, show an increase and then a decrease with age, reflecting development and senescence. The overall probability of a successful kill is 61% ($n = 716$). The overall probability of a kill upon encounter is 55%. It is 58% when dogs are present, 52% without dogs, 57% with guns, and 48% without guns. The differences among prey items are also revealing. For example, howler monkeys, once they are heard, are relatively easy targets with the highest kill rate. Kill rates during adulthood do not change significantly until they begin to decline as hunters reach late middle age. The more difficult animals to kill are peccary, tapir, deer, and capuchin monkey since they are more likely to escape. Kill rates of these animals show a much steeper age trend, with a later peak. Overall kill rate for the seven prey species shows a peak at age 39 (Fig. 5).

Age, weight, and height are highly significant when examined separately in analyses of kill probability upon encounter or upon pursuit that include the covariates of animal species, other men present, and use of dogs and shotguns (Table 5). Strength has no significant effect. When examining age and body size simultaneously, both measures lose statistical significance at the 0.05 level when controlling for repeated representation of hunters in the data, probably because of collinearity. In more standard logistic regression, age is statistically significant (Table 5, column 3). Regardless of the statistical significance, the magnitude of the age effect, as measured here by the odds ratio from 10 to 40 years of age, is comparable to or greater than the effect of body size. Results are similar for encounter-contingent and pursuit-contingent probabilities of animal kills. Thus, age and body size both contribute to the likelihood of making successful kills after encountering or pursuing animals.

In these multivariate analyses, the dummy variable for every animal species is statistically significant at the 0.01 level. In decreasing order of capture success, the most likely to be

killed upon pursuit is howler monkey (88% probability), followed by coati (76%), paca (66%), collared peccary (59%), tapir (52%), capuchin monkey (49%), and brocket deer (37%). The effects of dogs and guns are also statistically significant in the models. Guns more than doubled the probability of a kill (odds ratio = 2.17–2.29), while dogs have a smaller overall effect (odds ratio = 1.33–1.69). Guns consistently increased the probability of a kill for all animal species, while dogs did not increase the likelihood of a kill for capuchin and howler monkeys, tapir, or deer.

Caloric return rate

Figure 6a and b show the results of summing these kills and converting them into calories, where each data point is an individual hunter average or a daily hunting event, respectively. Caloric return rates peak at about age 45 in both analyses. When analyzed separately, age and the three body-size measures are mostly significant in all regression analyses (first four rows of Table 6). Univariate regression estimates in Table 6 show that age and strength both contribute to return rates. The strength term captures the increase and decrease of physical performance with age, while the age term captures the effect of the increasing knowledge and skill by age.

In the multivariate analyses of return rate that consider age and body size simultaneously, both parameters lose statistical significance in all cases except when age is analyzed with strength, again probably as a result of collinearity (see below). In this case, age is highly significant, representing all of the increase in return rate from 10 to 40 years of age. Further

Table 4
Method of kill for prey animals in sample

Method	Apercито		Cuverene		Total	
	n	%	n	%	n	%
Shotgun	120	33.9	111	37.0	231	35.3
Rifle	133	37.6	10	3.3	143	21.9
Bow and arrow	24	6.8	79	26.3	103	15.7
Machete	13	3.7	56	18.7	69	10.6
Stick	24	6.8	22	7.3	46	7.0
Dogs	13	3.7	9	3.0	22	3.4
Other	27	7.6	13	4.3	40	6.1
Total	354		300		654	

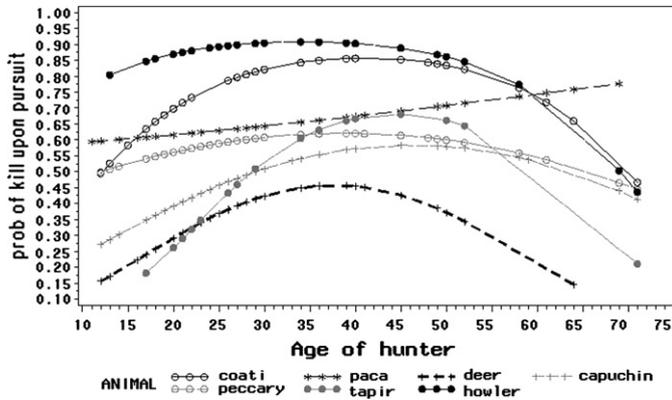


Fig. 4. Probability that a hunter kills an animal after pursuit for seven common prey species. Curves generated by logistic regression with second-order age terms and animal \times age interaction.

exploration of strength and return rate reveals that the weakest and strongest individuals both exhibit lower return rates than those of intermediate strength. There is no a priori justification for including a second-order strength term in the model even though its inclusion would improve the fit of the model. The lack of significance for age and weight or height may be due to the high correlation between these variables (age and weight: Pearson's $r = 0.73$, $p < 0.0001$; age and height: $r = 0.69$, $p < 0.0001$).

The relative importance of strength and skill on components of hunting ability

Age accounts for 33% of the increase in total indirect encounters over the 30-year span from age 10 to 40, with strength accounting for the remaining 67%. Age does not add any meaningful contribution to predict the increase in indirect encounter rates when compared with weight or height.

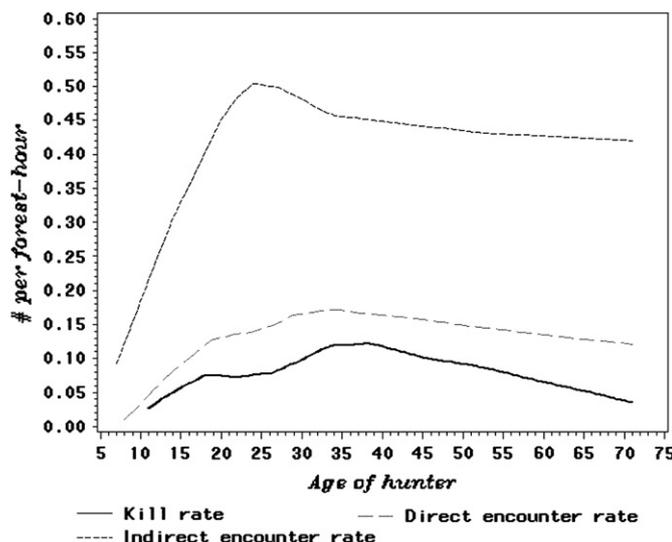


Fig. 5. Total direct and indirect encounter rate and kill rate as a function of age.

With respect to direct encounter rates, age accounts for 78% of the overall increase when compared to strength, 64% when compared to height, and 17% when compared to weight. These results show that both age and weight are important predictors but that height is a poor predictor of encounter rates.

With respect to kill rates, a 40-year-old by age alone is 3.1 times more likely to kill an animal upon pursuit than a 10-year-old. By strength, weight, and height alone, the effects are 1.4, 3.8, and 3.8 times greater for a 40-year-old than for a 10-year-old. Based on the logistic-regression estimates in Table 5, the magnitude of the age effect on the probability of a kill, as measured here by the odds ratio from 10 to 40 years of age, is comparable to or greater than the effect of body size (Table 5; age vs. strength: 2.3 vs. 1.2; age vs. height: 3.0 vs. 1.8; age vs. weight: 2.2 vs. 2.4).

With respect to caloric return rates over the 30-year time span, there appears to be a 1250-calorie-per-hour difference in performance (Table 6; Fig. 6). This difference constitutes about 75% of the total growth in hunting efficiency over the life course. Using the partial estimates in Table 6 allows us to calculate the separate effects of age and body size on hunting efficiency. Columns 4 and 7 of Table 6 show that 45–55% of the increase in efficiency is due to age. Weight is a better predictor of performance than height, but it is clear that both age and body size (but not strength) predict return rates across the life span.

Figure 7 shows the age profiles for strength, indirect encounters, direct encounters, kills upon encounter, and caloric return rates normalized to their maximum values. It is clear that indirect encounters and strength peak earliest, followed by direct encounter rates, kill rates, and finally return rates. More importantly, a multiple regression analysis of return rates on direct encounters, age, and strength when restricted over the age range of increasing performance from 15 to 45 years of age reveals a significant independent effect of age (estimate = 28.7, $p = 0.05$), and not strength (estimate = -5.09 , $p = 0.46$). Similar results obtain by replacing strength with weight or height. Thus, the delay in peak return-rate performance is largely due to delayed effects of learning and experience.

As expected under EC, age (as an index for skill after controlling for strength) plays an increasingly important role in determining performance as each component of hunting ability is added together.

Arrow-shoot performance

Total performance is calculated as the sum of the two score1 or score2 measures from high and low target events. Minimum total score is 0 and maximum is 10. These are graphed by age in Figure 8 using loess smoothing. Inspection of the graph shows that the curves track the age patterning of weight growth over the life course. Multivariate regression shows that only weight is a significant predictor of overall target shooting performance (weight: $p = 0.04$ and 0.06 for sum of score1 and sum of score2, respectively). Neither upper body strength nor height significantly covary with performance after

Table 5
Univariate and multivariate regression of probability of (1) kill upon pursuit and of (2) kill upon encounter on age and body-size measures

Variable	Probability of kill upon pursuit				Probability of kill upon encounter			
	Parameter estimate	<i>p</i>	<i>p</i> *	Odds ratio age 10–40	Parameter estimate	<i>p</i>	<i>p</i> *	Odds ratio age 10–40
Univariate regressions								
Age	0.0977	0.03	0.0008	3.10	0.0771	0.07	0.006	2.62
Age ²	−0.0012	0.06	0.0009		−0.0009	0.12	0.005	
Strength	0.0063	0.11	0.04	1.43	0.0026	0.38	0.29	1.16
Weight	0.0368	0.0001	0.0005	3.76	0.0265	0.001	0.006	2.60
Height	0.0368	0.0001	0.004	3.76	0.0259	0.008	0.03	2.54
Multivariate regression of age and strength								
Age	0.0730	0.14	0.03	2.32	0.0674	0.14	0.03	1.96
Age ²	−0.0009	0.19	0.03		−0.0009	0.19	0.03	
Strength	0.0028	0.33	0.42	1.17	0.0001	0.96	0.97	1.01
Multivariate regression of age and height								
Age	0.0966	0.12	0.02	3.00	0.0838	0.14	0.03	2.37
Age ²	−0.0012	0.12	0.01		−0.0011	0.16	0.02	
Height	0.0160	0.33	0.34	1.78	0.0077	0.59	0.62	1.32
Multivariate regression of age and weight								
Age	0.0756	0.17	0.06	2.16	0.0664	0.19	0.08	1.90
Age ²	−0.0010	0.17	0.04		−0.0009	0.21	0.05	
Weight	0.0245	0.04	0.07	2.42	0.0157	0.12	0.20	1.76

* Without control of individual's identification number.

controlling for village and age effects. It appears that performance at arrow-shoot competitions is dependent mostly on size, and it peaks earlier in life than the ability to encounter and kill animals. This suggests that marksmanship is not the critical issue in determining age-related changes in hunting return rates; rather, it is the ability to find an animal and get in a position to get a good shot at it before it escapes that are the most difficult components of hunting ability.

Examining the difficult and easy targets separately, the average success rate was 10% for the “high” target ($n = 81$) and 19% for the “low” target ($n = 73$) contests. Incorporating “skimmed hits” inflates the success rate to 18% for “high” and 25% for “low” targets. These results conform to participant statements that the high target was more difficult to hit than the lower one.

For the high target, age was marginally significant after controlling for village in the analysis of score1 ($p = 0.11$ for age; $p = 0.14$ for age²). Strength did not significantly predict score1, although weight did ($p < 0.05$). In analyses of the more forgiving score2, both age and weight have strong separate effects ($p = 0.04$ for age; $p = 0.04$ for age²; $p < 0.01$ for weight), but strength does not ($p = 0.84$). Multiple regressions examining age and strength or age and weight on score1 or score2 do not yield any significant results.

For the low target, age is insignificant in analyses of both score1 and score2. Upper body strength is also insignificant, while weight does significantly covary with score1 ($p = 0.04$) and score2 ($p = 0.02$). In multivariate regressions, age remains insignificant, while upper body strength marginally predicts performance ($p = 0.08$ for score1; $p = 0.14$ for score2). Replacing strength with weight yields a similar result.

Animal tracks

Figure 9 shows the total number of correctly identified animal tracks out of 16 as a function of age. A loess curve is fitted to the data, showing a peak between 35 and 40 years of age, decreasing only slightly thereafter. Separate OLS regressions on the total correctly identified (score) reveal significant effects for age ($p = 0.003$), strength ($p = 0.003$), and weight ($p < 0.001$). In multivariate analyses, age and strength show similar effects on score (standardized estimate for age: 0.40, $p = 0.01$; standardized estimate for strength: 0.38, $p = 0.02$). Both age and strength explain the delayed trajectory of animal-track knowledge. These experimental results suggest that knowledge tends to peak at later ages than marksmanship.

Summary of results

We have compared the effect of age as an index of learning and experience with strength, weight, and height as measures of body size on several components of hunting. Taken together, our results suggest that strength alone cannot account for changes in hunting ability with age, as hypothesized by proponents of GH. Both skill and strength contribute to hunting ability. As expected by EC, indirect encounters peak at earlier ages than direct encounters, which in turn, peak at earlier ages than kill and return rates. Increases in indirect encounters with age are best explained by physical growth, with peaks reached shortly after peak body size in men. However, reaching the peak number of direct animal encounters per unit time spent foraging requires about ten years beyond the age of peak body size. Decisions to pursue prey are mostly independent of age. However, making kills is not adequately

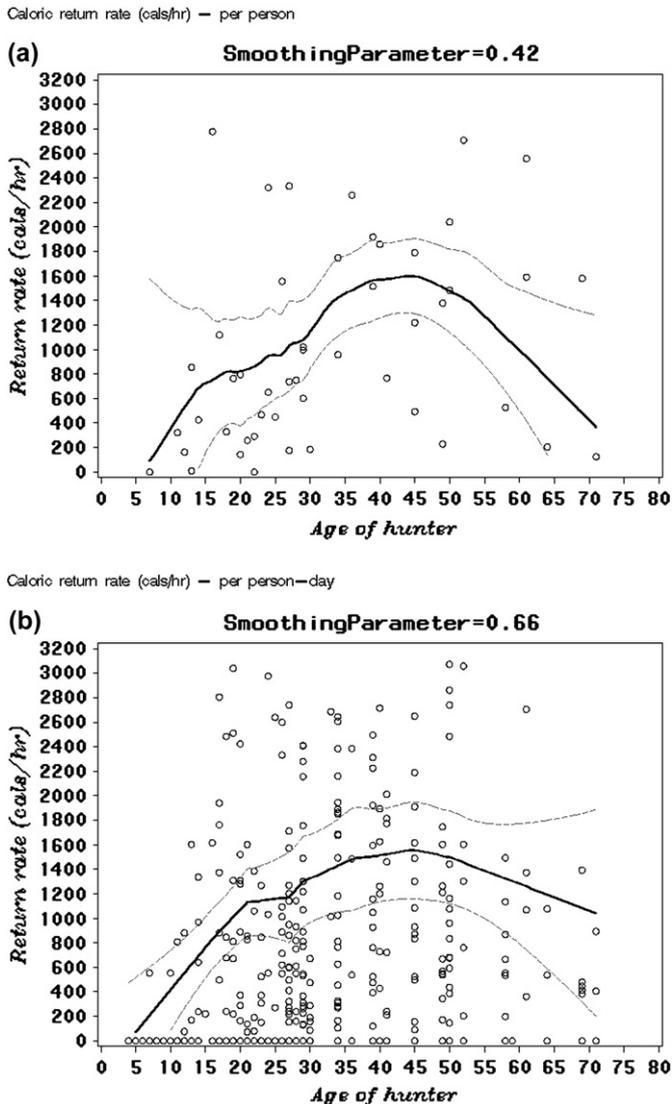


Fig. 6. Caloric return rate by age, using loess regression: (a) each data point corresponds to one person; (b) each data point corresponds to a person-day, and is weighted by number of days sampled.

explained by body size alone. We have shown that caloric return rates are more limited by age than by body size.

Discussion

The results in cross-cultural perspective

There has never been much doubt that learning is an important component of childhood and teenage years. The controversy is about whether learning is a cause or consequence of delayed growth (Bock and Sellen, 2002). In this paper, we concentrated on one activity, hunting, common among extant and many ancient foragers. Even with the use of domesticated hunting dogs and firearms, Tsimane hunting requires a significant time period to reach peak levels in performance in several key components, and this delay is not adequately explained by increases in physical capacity. While detection of clues about the presence of animals seems size-dependent, direct

encounters with animals and the subsequent killing of animals require many more years to reach peak adult levels. Similar conclusions were reached by Walker et al. (2002) based on detailed analysis of Ache hunting performance. Supporting evidence of delayed productivity based only on return rate is given by Ohtsuka (1989) among the Gidra, and by Gurven and Kaplan (2006) for Machiguenga and Piro.

Cross-cultural variation in age-profiles of hunting also provides suggestive evidence that learning has played a major role in the determination of return rates. As modern hunting techniques are introduced, especially dogs and flashlights, the effects of skill seem to diminish. Even though we see clear effects of skill on Tsimane hunting returns, those effects are smaller than among other foraging groups that depend more on traditional and difficult foraging activities. Indeed, personal experience of the authors with several South American groups that actively hunt suggests that the Ache, Machiguenga, Piro, and Tsimane show decreasing reliance on traditional and difficult foraging techniques. The proportional and absolute differences in hunting return rates between 20 and 40 year olds increases as reliance on bow and arrow and other difficult techniques increases. For example, the proportional difference between 20- and 40-year-olds is about twofold among the Tsimane and fourfold among the Ache. Machiguenga and Piro fall in between (2.5-fold).

The relative importance of learning and strength also varies across subsistence activities and their components within and among societies. Hadza and Ache arrow-shoot contests reveal a similar size-dependent pattern reported here (Walker et al., 2002), with little increases in success after early adulthood.

With respect to plant foods, large effects of skill are also found in some cases: mongongo-nut processing among Okavango Delta peoples (Bock, 2002) and tuber digging among Hadza (Blurton Jones and Marlowe, 2002). On the other hand, baobab-tree-climbing experiments among Hadza show a rapid increase in ability (Blurton Jones and Marlowe, 2002). Meriam and Mardu children engage in foraging activities, such as shellfish collecting, appropriate for their size and physical capacity, and quickly become proficient at other activities when they grow larger (Bird and Bliege Bird, 2002, 2005; Bliege Bird and Bird, 2002). The less skill involved in the activity the earlier is its peak and the more size-dependent are return rates.

While age-delays independent of body size strongly suggest that learning and practice take considerable time, there are cases when delays may not be explained by learning. For example, Tucker and Young (2005) argued that Mikea children are able root diggers and that age-related improvements are due to increased motivation (and less play) rather than increased ability. In the case of the Tsimane, however, motivation is insufficient to account for the age-related effects. Motivation to hunt efficiently may be greater for a 40-year-old hunter with five children than for a 15-year-old without a spouse or children, and such motivational differences may partly explain differences in encounter rates. However, they do not explain differences in kill rates for similar prey items, as there are no significant age effects on the decision to pursue

Table 6
Univariate and multivariate regression of overall caloric return rate and daily caloric return rate on age and body-size measures*

Variable	Caloric return rate			Caloric return rate by event		
	Parameter estimate	<i>p</i>	Difference in return rate (age 10–40)	Parameter estimate	<i>p</i>	Difference in return rate (age 10–40)
Univariate regressions						
Age	101.6571	0.002	1244	106.9	0.0004	1266
Age ²	−1.2037	0.006		−1.2942	0.001	
Strength	7.6236	0.22	435	13.1839	0.01	751
Weight	29.3807	0.0005	1058	35.5427	0.0003	1280
Height	22.2987	0.0005	803	29.87	0.0009	1075
Multivariate regression of age and strength						
Age	101.4757	0.12	1171	104.1	0.07	1171
Age ²	−1.2490	0.14		−1.3013	0.08	
Strength	−3.1296	0.74	−178	−0.8513	0.91	−49
Multivariate regression of age and height						
Age	52.8814	0.36	604	66.708	0.24	714
Age ²	−0.6547	0.34		−0.8584	0.20	
Height	12.9949	0.32	468	15.1833	0.38	547
Multivariate regression of age and weight						
Age	48.0871	0.43	527	54.9975	0.33	556
Age ²	−0.6102	0.40		−0.7294	0.28	
Weight	18.7467	0.31	675	20.9413	0.25	754

* Daily-caloric-return-rate analyses in event analyses also control for prey item, presence of dogs, guns, and number of other men on the hunt.

animals upon encounter. Motivation is also unlikely to explain the greater effects of age on the knowledge-based track-identification task than on arrow-shoot performance, for which awards were offered in a competition.

In addition, anecdotal stories of many of the hunts in the sample revealed numerous errors in judgment by younger hunters, rather than a lack of motivation. Meat is a valuable commodity that motivates males of all ages, and so it is unlikely that motivation can explain the age difference in hunting performance found among Tsimane and other groups. Indeed, why men hunt has been a controversial topic in recent treatments of men's foraging and sharing behavior, with debates over whether substantial gains are in the form of spouse and offspring provisioning (Lancaster, 1978), mating benefits through increased attention and favor (Hawkes, 1993), reputations for high phenotypic quality (Bird, 1999), or generosity (Gurven et al., 2000). It is relevant to note that, in this regard, mating-display motivation should be greater for young adult males, since many are still in search of a wife. Such effects should therefore diminish rather than augment the age effects we find.

By the time Tsimane men marry (about age 22), they are well on their way to becoming better hunters (and farmers), but they still require much experience, or on-the-job training (Bock, 2002). Thus, as pointed out by Blurton Jones and Marlowe (2002) with reference to the Hadza, learning need not be completed before maturation, marriage, or reproduction (cf. Bjorklund, 1997). Similarly, learning need not occur in constant increments throughout the entire prereproductive period in order for the long delay to be linked to later production, as stipulated by the EC model. A combination of size-dependent learning, a step-wise ratcheting up of strength and skill (or “punctuated equilibrium”; Bock, 2002) may

characterize increases in performance during certain periods of development. Furthermore, developmental milestones occur in an ordered sequence, with each building cumulatively on former achievements. Critical learning may not occur continuously but in dispersed stages, as has been found with physical growth (Lampl et al., 1992). This possibility suggests that there may be critical periods or ages when gaps in learning

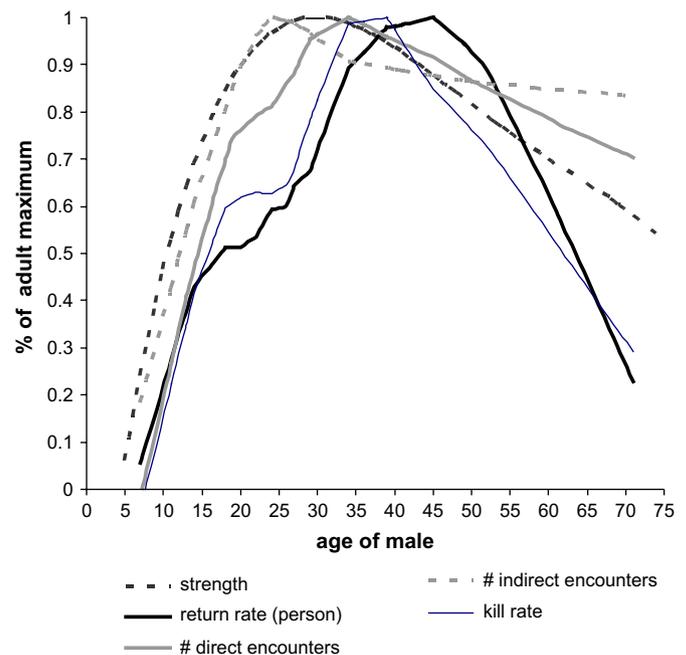


Fig. 7. Summary of age-specific trends standardized to adult maximum values. Shown are height and strength, direct and indirect encounters, track identification, arrow-shoot score, caloric return rate, and total days spent foraging during sample period.

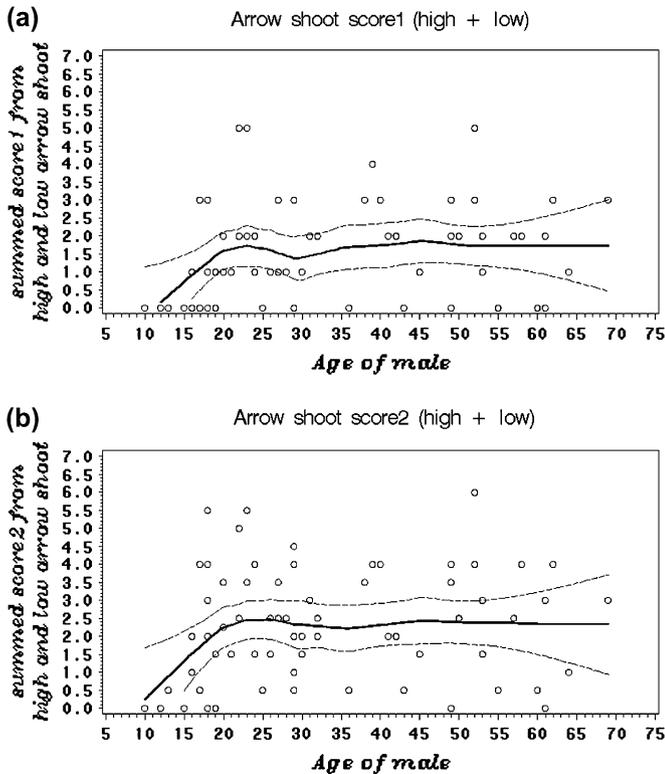


Fig. 8. Arrow-shoot performance summed for high and low targets by age: (a) score1 refers to total number of successful hits out of five tries; (b) score2 is the total number of hits and skids out of five tries.

are more detrimental to later performance (and require more catch-up time) than gaps that occur at other ages. For example, time spent in school or in other activities need not cause a decrease in performance in certain aspects of hunting if schooling occurs in late childhood or early adolescence or if time spent in school is sporadic (cf. Blurton Jones and Marlowe, 2002). On the other hand, Tsimane raised in nontraditional villages or in more urban areas who later attempt to learn hunting often must rely on dogs and hunting at night with the use of flashlights. These hunters rarely achieve the level of proficiency of hunters immersed in the traditional lifestyle. Additional evidence comes from an experiment where young

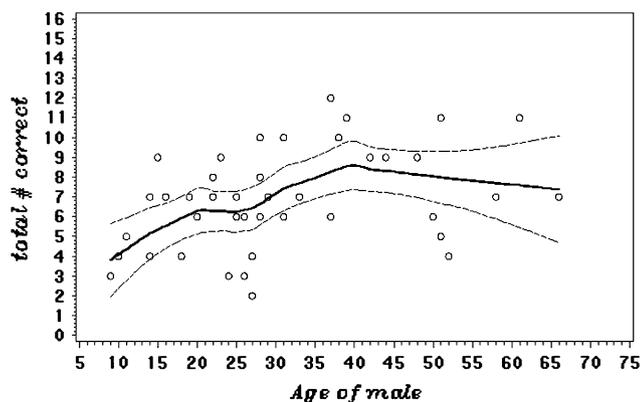


Fig. 9. Number of correctly identified animal tracks out of a possible sixteen.

Ache men were paid for each animal they killed over a thirteen-month period (Walker et al., 2002). While these men greatly increased the amount of time they spent hunting, there was no net increase in hunting return rate, encounter rates, or likelihood of a kill upon pursuit. Inexperienced adult hunters do not become highly proficient hunters even though they may benefit from the social transmission of relevant information on game behavior, locations, and successful hunting strategies from other men.

The results in historical perspective

These results have implications for improving our understanding of the life history of ancient hominids. O'Connell et al. (2002) argued that the lack of definitive evidence of large-game hunting among early *Homo* provides grounds for rejecting skill- and learning-based theories of human life-history evolution. However, it is not necessary to show that members of early *Homo* were big-game hunters to justify the links made here and elsewhere between delayed growth, encephalization, and extended life span. Many of the groups for which substantial delays in hunting performance have been reported, including the Tsimane, are primarily small-game hunters. While the source of large game is open to interpretations of hunting and scavenging (e.g., Binford, 1981; Blumenschine et al., 1994), small game is likely to have been hunted by early *Homo*. Given that chimpanzee hunting is directed towards small game (such as colobus monkeys), the first place to look for expanded hunting among early hominids is in the increased frequency and success in small-game hunting. There is evidence that small-game hunting has been an important component of human diets for at least the last 200,000 years (Stiner, 2002); we should look back further than this. We do not know if the cognitive skills required for small- vs. large-game hunting differ and if the differences depend on the prey species and ecology. It is often the case that small-game hunters rely on a greater variety of different prey items than large-game hunters. Again, such differences have yet to be studied systematically. Human hunting is nonetheless unique among primates due to the widespread sharing of spoils and the long-distance transport of kills to a home base for processing and consumption by others (Stiner, 1991).

Although still somewhat speculative, it seems that extended preadulthood in the form of novel growth stages of childhood and adolescence first appeared among late *Homo erectus*, with further extensions appearing in later species of *Homo* (Bogin and Smith, 1996). Early *Homo ergaster* shows both significant brain expansion and a lengthened developmental period (Smith, 1993), but much less so than in modern humans. Changes in early growth patterns seem to occur concurrently with increases in brain size and improvements in tools, shelter, and use of fire (Klein, 1989). Increased encephalization and longer life span are evident across grade shifts among primates, as revealed by greater intercepts of log brain size when regressed on log body size, and superior performance on most tasks reflecting higher intelligence (Byrne, 1995; Barton and Dunbar, 1997; Parker and McKinney, 1999).

The divergence of the hominid line, and particularly the evolution of genus *Homo*, defines a major grade shift where brain size and life span of modern humans are very extreme values among mammals, and even primates.

Directions for future research

While our results provide strong evidence in favor of learning as a driving force in the growth of hunting ability with age, more detailed information regarding the reasons for age- or size-related changes is necessary for definitive conclusions to be reached. Most experiments and interviews to date have focused on the easiest tasks or components of foraging. No controlled systematic study of age-related changes in navigational skills, tracking, knowledge of animal behavior, stealth techniques employed, or motivation has yet been conducted in traditional populations.

In addition, we know very little about the other tasks that provide fitness-related benefits. It would be useful to have more tests of other skills, using a similar approach to that used here. These include subsistence tasks, such as gathering of fruits and other items, different kinds of fishing, processing of different foods, and tool manufacture (see Bock, 2002; Gurven and Kaplan, 2006). Little attention has been given to causes of age-related changes in nonsubsistence domains, such as child care and navigating the social world of other people. While the traditional focus of all studies in this area is hunting, due in part to its large contribution to the diet of past and extant hunter-gatherers, this study will hopefully be followed by many others that will explore ways in which delayed growth, capacities for learning, later productivity, and long life span may have coevolved in modern humans.

This paper has not considered the social dimensions of the human life course, which have received much attention (e.g., Boyd and Richerson, 1985; Dunbar, 1993). While the introduction to this paper presented four alternative hypotheses for extended maturation, there is no reason why those factors should not have acted in concert to produce the extreme intelligence and longevity of humans relative to other mammals.

Among humans, hunting is inherently social in a number of ways. First, social learning plays a critical role in the intergenerational transmission of knowledge and practices. Moreover, social learning probably increases the rate at which human children, adolescents, and adults learn how to hunt and gather efficiently (Blurton Jones and Marlowe, 2002). Tsimane children and adolescents have logged hundreds of hours of experience listening to others tell stories and anecdotes about different foraging activities before ever seriously engaging in these activities themselves. It is likely that this knowledge improves the rate of experience-based learning and of hunting performance in both children and young adults by amplifying the sample of hunting experience well beyond the capabilities of any single hunter.

The frequency of social transmission of information among nonhuman primates strongly predicts wide-ranging variation in primate brain size (Reader and Laland, 2002). Most importantly, much of this information appears to be in the context of

foraging. Inferences about animal behavior are critical for hunting success and may be precursors for making detailed inferences about human behavior.

Second, meat sharing is a fundamental feature of the human hunting adaptation. Sharing helps to reduce the high variance in acquisition of game, and would have been especially important for feeding unskilled children and juveniles. A social brain also becomes increasingly important in the context of strategic sharing of game (Stanford, 1999). For example, efficient sharing requires the monitoring of meat and other contributions made by other group members.

It would be particularly useful to extend embodied capital theory to include investments in social capital and social intelligence. The most popular alternative explanation for encephalization is the social brain hypothesis (e.g., Byrne, 1995; Dunbar, 1998). The usual justification for a “social brain” is the potential arms-race due to political maneuvering and information manipulation in large groups. An alternative view is to consider the importance of sharing in human foraging societies and how individuals utilize social relationships to maximize the gains from cooperation. While social capital has been traditionally thought of as the web of connections that one attains through family and friends (Coleman, 1988; Putnam, 2000), an individual’s social capital can also be thought of as the storehouse of perceptions held by others that affects the treatment of that person by others. There is increasing evidence that food is not shared equally to all band members in most hunting and gathering societies, except under specific circumstances (Gurven, 2004; Gurven and Kaplan, 2006). People have preferred partners, with whom reciprocal exchange is greatest. Thus, the ability to engage in profitable partnerships may require a great deal of social intelligence, and the ability to understand how one’s actions will affect future access to food and food exchange. Moreover, some proportion of food-sharing behavior is likely to be a symbolic investment in social capital that affects future cooperative interactions.

Other symbolic uses of hunting and sharing may also be important components of the hunting adaptation. As emphasized by others (Hawkes, 1990; Bird, 1999; Smith, 2004), hunting competence may play an important role in mating success. Many foraging and forager-horticulturalist societies, such as the !Kung and the Tsimane, practice bride-service, in which young men hunt to feed their future father-in-law’s family prior to having full marital rights.

Finally, it is important to take a life-history perspective on hunting and other aspects of human performance. This paper provides clear evidence that several components of hunting performance not only contain a phase of improvement with age, but also a phase in which performance declines, especially after about age 50. Strength shows a similar profile but with declines beginning to occur some 20 years earlier. Moreover, the decline in physical capacity, as measured by strength with age, and the decline in functional capacity, as measured by hunting return rates, are matched by an increasing mortality rate with age (Fig. 10). The pace of decline in caloric return rate maps the increase in mortality after age

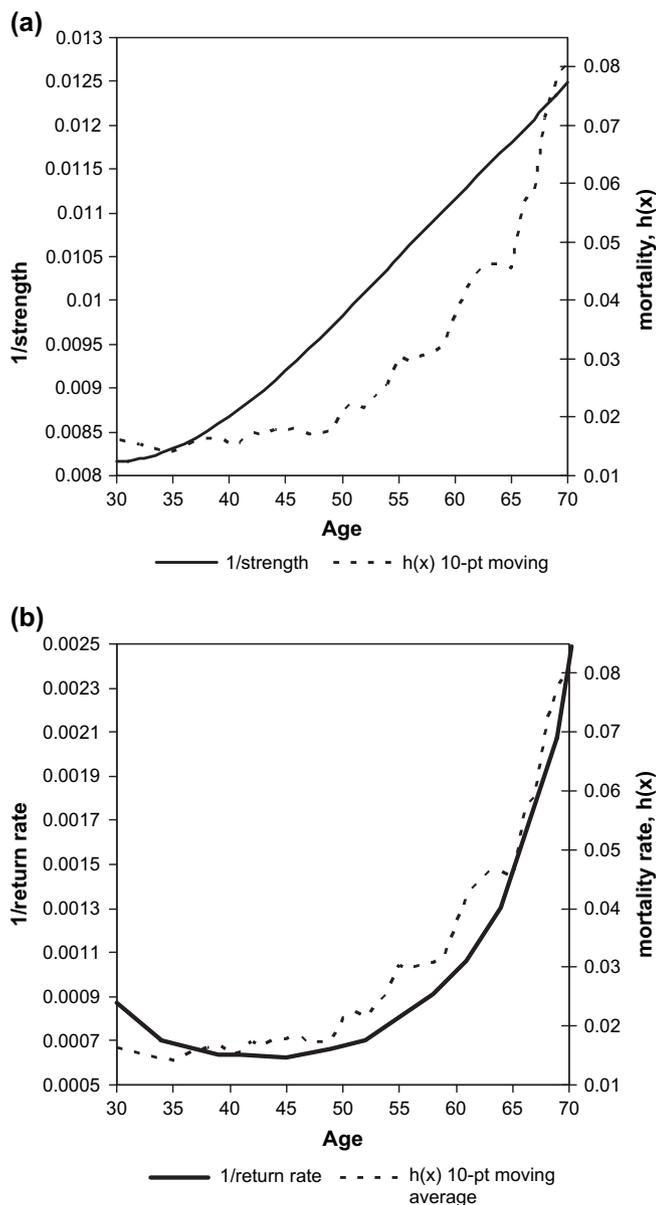


Fig. 10. Association between increases in age-specific mortality starting at age 30 and declines in (a) strength and (b) hunting performance. Increased declines in strength and return rate are operationalized as $1/\text{strength}$ and $1/\text{return rate}$, respectively. Y-axes are normalized to fill the graph. Mortality rate is estimated from unpublished demographic data covering the years 1950–1989.

30 better than the decline in strength. Unraveling these relationships and determining why the declines are not later or earlier will yield a much deeper understanding of human life history.

Conclusion

Our results support the notion that selection has acted to delay growth in order to accommodate the cognitively demanding foraging niche of humans. The learning-dependence of the human niche is bolstered by the fact that the human brain is over three times larger than expected for an anthropoid primate of our size (Falk, 1980). The embodied capital model

explicitly links brain-based capital to adult production, delayed growth, and long life span (Kaplan and Robson, 2002), whereas the grandmother hypothesis asserts that individuals can quickly learn adult foraging activities once they are physically capable. Despite the occurrence of social transmission of hunting-related information among Tsimane, this paper shows that, upon achieving adult size, 5–15 additional years of experience are required to become highly skilled in a principal domain of the hunter-gatherer lifeway. Finding animals and capturing them after pursuit are complex activities for a majority of the important prey species in the Tsimane diet. Shooting prey animals may be one of the simplest hunting tasks. Without dogs, shotguns, and a tropical forest ecology where game is relatively abundant (cf. African savanna environment of big-game hunters like the Hadza and !Kung), the age-related patterns described here would be even more delayed. Whether the emphasis is big-game or small-game hunting, analyses of the growing sample of foragers around the world suggest that hunting success comes fairly late in the life span, with significant learning both before and after men begin hunting. That some form of hunting plays an important role in most if not all ethnographic cases of hunter-gatherers suggests that such a delayed success rate is only feasible with a longer life span whereupon the early investments spent learning pay off in the form of productive surpluses, and with intergenerational transfers of resources to subsidize early growth and learning.

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