

Robert Walker, Kim Hill, Hillard Kaplan and Garnett McMillan

Department of Anthropology,  
University of New Mexico,  
Albuquerque, New Mexico  
87131, U.S.A. E-mail:  
robwal@unm.edu?

Received 23 March 2001  
Revision received 15  
October 2001 and accepted  
19 December 2001

**Keywords:** Ache hunters,  
strength and skill, human  
life history evolution.

## Age-dependency in hunting ability among the Ache of Eastern Paraguay

This paper examines changes in hunting ability across the lifespan for the Ache of eastern Paraguay. Hunting ability is decomposed into two components—finding prey and probability of kill upon encounter—and analyzed for important prey species. Results support the argument that skill acquisition is an important aspect of the human foraging niche with hunting outcome variables reaching peaks surprisingly late in life, significantly after peaks in strength. The implications of this study are important for modeling the role of the human foraging niche in the co-evolution of various outstanding human life history characteristics such as large brains, long lifespans, and extended juvenile periods.

© 2001 Academic Press

*Journal of Human Evolution* (2002) 42, 000–000

doi:10.1006/jhev.2001.0541

Available online at <http://www.idealibrary.com> on IDEAL®

### Introduction

The human foraging niche, and hunting in particular, is often interpreted as playing a central role in the evolution of human behavior and life history (e.g., Dart, 1953; White, 1959; Washburn & Lancaster, 1968; Isaac, 1978; Hill, 1982; Lancaster & Lancaster, 1983; Foley & Lee, 1991; Foley, 1992). Several studies have quantitatively examined age-dependent food production ability in traditional societies. These include Gijjigali foragers (Meehan, 1982; Altman, 1987), mixed economies in Botswana (Bock, 1995), children's subsistence activities on Mer, Torres Strait (Bleige Bird *et al.*, 1995), Gidra (Kawabe, 1983; Ohtsuka, 1983, 1989) and Etolo (Dwyer, 1983) hunters in Papua New Guinea, Hadza foragers (Blurton Jones *et al.*, 1989, 1997; Hawkes *et al.*, 1989, 1995; Marlowe, 2000; Blurton Jones & Marlowe, 2001), Ache and Hiwi foragers (Kaplan *et al.*, 2000), and Machiguenga and Piro horticultural-foragers (Kaplan, 1994; Gurven & Kaplan, n.d.). While these studies are useful in understanding some of the diversity in age-dependent foraging ability, none explicitly

models strength and skill as determinants of hunting ability. This paper contrasts age schedules of Ache hunting ability with those of physical performance, models strength and skill effects on ability, and decomposes hunting ability into some of its constituent parts—e.g., finding game, killing game upon encounter, and archery ability.

While many foraging activities may be complicated, hunting is potentially the most skill- and strength-intensive foraging activity. This is indicated by the fact that hunting return rates peak later in life than most other food acquisition activities. Hunting return rate curves peak in the early 30s for the Hiwi (Kaplan *et al.*, 2000), 40 for the Machiguenga and Piro (Gurven & Kaplan, n.d.), early or mid-40s to mid-50s for the Etolo (Dwyer, 1983), 35–45 for the Gidra (Ohtsuka, 1989), 45–50 for the Hadza (Marlowe, 2000) and 37–42 for the Ache (this study). Some extractive gathering activities, such as mongongo nut processing (Bock, 1995, 2001), Gijjigali shellfish collecting (Meehan, 1982), and Hadza (Blurton Jones & Marlowe, 2001) and Hiwi root digging (Kaplan *et al.*, 2000), have return rate schedules with similar shapes as

hunting curves probably indicates that success is based on learned skills rather than strength.

Many ethnographers have noted the age-dependence of hunting ability. For example, Lee (1979) states that the Ju/'hoansi are superb trackers who are able to identify the name of a person based on their footprint alone, yet "tracking is a skill cultivated over a lifetime, that builds on literally tens of thousands of observations" (Lee, 1979:47). Liebenberg (1990), who worked with the !Xo, concludes that a hunter's career peaks between the ages of 30 and 45 with "an optimum combination of physical fitness, skill, wisdom, and experience" (Liebenberg, 1990:70). No anthropologist has reported being able to hunt at the same ability level as their study group members, and most ethnographers usually only make kills if a native hunter brings them to the game (Kaplan *et al.*, 2000). In contrast, anthropologists and acculturated natives appear to gather fruits and plant resources with a rate of return similar to more experienced individuals (see Blurton Jones *et al.*, 1994 for data on acculturated !Kung).

Understanding the causes of this age profile of food acquisition has implications for the evolution of large brains, extended juvenile periods, and long lifespans in humans. If proficiency in the human foraging niche requires extended periods of time in skill acquisition, then large brains, extended juvenile periods and a long lifespan may be co-evolutionary responses to a dietary shift (Kaplan *et al.*, 2000). However, a debate currently exists among human behavioral ecologists concerning the importance of skill *vs.* strength components in hunting and gathering and the implications for human life history evolution. Some argue that foraging activities do not require long learning periods and have demonstrated that forager children can produce a significant percentage of their daily caloric allowance (Bleige Bird *et al.*, 1995; Blurton Jones *et al.*, 1997).

Experimental studies with the Hadza have demonstrated that activities like Baobab tree climbing, digging tubers, and archery either show no increases with age or that the increases are better explained by augmented strength as opposed to skill and that lost practice time does not adversely affect performance (Blurton Jones & Marlowe, 2001). Results from these studies have been used to infer that the complexity of human foraging does not explain the selection for large brains or delayed maturity during the course of human evolution. The juvenile "waiting" period is then seen as a result of slow growth due to low levels of adult mortality and the extension of this period is therefore epiphenomenal with respect to increased learning (Hawkes *et al.*, 1998, 2000; Blurton Jones *et al.*, 1999).

On the other hand, Kaplan *et al.* (2000) present evidence showing that rates of return on difficult foraging tasks, such as hunting and extractive foraging, among the Ache, Hiwi and Hadza, peak at older ages than would be expected by strength and endurance effects. It is interesting that children's activities respond to environmental variation and that they can produce a significant percentage of their food in certain environments where foraging is relatively safe, for example Hadza (Blurton Jones *et al.*, 1997) and Mer (Bleige Bird *et al.*, 1995) *vs.* !Kung (Blurton Jones *et al.*, 1994) and Ache (Hurtado *et al.*, 1985) ecologies and in seasons of the year when easily-accessible foods such as fruits are available (Blurton Jones *et al.*, 1989; Kaplan, 1997). However, in terms of total calories and macronutrients provided to a hunter-gatherer diet, difficult-to-acquire extracted resources appear to be much more important than easily acquired foods (Kaplan *et al.*, 2000).

While some foraging activities may depend more on strength than skill, this does not vitiate the argument that subsistence task learning is an integral part of the

juvenile and early adult behavior. For example, young Hadza boys “entertain themselves by trying to shoot birds and small animals” (Blurton Jones *et al.*, 1989:379). This activity probably results in a sacrifice of short-term foraging returns that Hadza girls accrue in the harvest of plant products. The boys then are potentially investing in skill acquisition in order to develop adult proficiency (though the authors conclude otherwise. Blurton Jones *et al.*, 1997). Indeed, Marlow (2000) sees experience as being important for the observed age pattern of Hadza hunting because the peak in hunting performance and reputation occurs after peak physical performance, as we also conclude for the Ache data presented here. We hypothesize that some important foraging activities do require extended periods of skill acquisition in order to reach proficiency and that a skill-intensive human foraging niche has potentially important implications for the evolution of the human life history.

In this paper we attempt to disaggregate the effects of strength and skill on Ache hunting success. We conceptualize skill as specific motor performance that includes cognitive and memory functions. This is distinguished from strength and endurance, conceptualized as general motor performance and as the energetic capacity to perform work. Strength is considered a growth-based form of organized somatic tissue or embodied capital (*sensu* Kaplan, 1996), whereas skill is considered an experience-based form of embodied capital (Kaplan, 1996; Bock, 2001). Both strength and skill are expected to have positive functional impacts on resource harvesting rates. Skill acquisition is likely to comprise both physical and cognitive abilities that may require appropriate exposure and practice during developmental windows (Bock, 2001) as well as long periods of adult experiential learning.

Physical strength is primarily a function of body size, which should peak around adulthood. Cross-sectional analyses of physical performance measures across the lifespan for Ache hunters demonstrate that individuals tend to be the strongest around age 24 and senesce thereafter (Walker & Hill, n.d.). This pattern is seen in body size, grip strength, push-ups, pull-ups and chin-ups. Individuals in their early 20s also show the highest absolute  $VO_2$  max estimates, considered a valid measure of the functional capacity of the cardiorespiratory system, and they are also the fastest in the 50 m dash (see methods and graphs in Walker & Hill, n.d.). Studies of modern populations find peaks in cardiorespiratory (Shvartz & Reibold, 1990) and muscular performance (Bäckman *et al.*, 1995) in the late teens. Performance peaks in the 20s have been found for cardiorespiratory and muscular performance in an Inuit population (Rode & Shephard, 1971) and in grip strength for the Gidra (Ohtsuka *et al.*, 1987) and a Zapotec-speaking community in Mexico (Malina *et al.*, 1982). Based on numerous studies of muscle function in modern societies, Aoyagi & Shepherd (1992) conclude that physical strength remains rather constant from maturity to around age 45 and then declines at an accelerating rate. Bäckman and associates (1995) study in Sweden of eight different muscle groups found both men and women to be strongest at the age of about 17–18, a strength that remains nearly constant until 40 and then declines. However, while isometric muscle strength in these studies may remain relatively constant for some time after maturity, this does not appear to hold for either the traditional studies listed above or for more general performance measures like  $VO_2$  max or running speed in either modern or traditional populations. Dynamic and cardiorespiratory measures are likely to be better overall indicators of physical activity that is applicable to most hunting activities.

This paper examines age-dependent trends in archery and hunting data among the Ache to test the hypothesis that reaching proficiency in hunting ability necessitates long periods of learning prior to and after physical maturity. Hunting data are decomposed into the two important components of hunting return rate—finding game and the probability of a successful pursuit when game is encountered. Multivariate statistical models separate strength effects from skill effects on ability. Hunting outcome variables are examined across the lifespan to compare differences between age of peak strength and age of peak hunting ability. We present preliminary results from a project designed to measure the effects of experience on the hunting success of naive hunters. In addition, patterns of human hunting are contrasted to documented patterns of chimpanzee hunting.

#### *Study group*

Food acquisition data have been collected since the early 1980s among the Northern Ache of eastern Paraguay, shortly after peaceful contact. All ethnographic evidence suggests that the Northern Ache were hunter-gatherers without horticulture before contact in the 1970s (Hill & Hurtado, 1996; Clastres, 1998). Since then the Ache frequently trek into the forest with family groups and return to a permanent reservation settlement after several days to a month. The Ache have exclusive use rights to the Mbaracayu Reserve where they are allowed to hunt with hands, machetes, and bows and arrows but not using firearms or dogs. In 1998, the Ache at the Arroyo Bandera settlement, where most of the data in this study were collected, spent 14% of all person days (range 0–50% for individuals) on trek (McMillan, 2001).

Ache men harvest on average 4 kg of undressed meat per foraging day. There are, however, real and consistent differences in ability between adult men (Kaplan & Hill,

1985; Hill & Hurtado, 1996), on the order of a ten-fold difference (Hill & Hawkes, 1983). Moreover, controlling for age, hunting ability is correlated with both increased fertility and survivorship of offspring (Hill & Hurtado, 1996) making it an important aspect of biological fitness.

Game animals comprise up to 80% of the Ache diet in the forest (see Kaplan *et al.*, 2000). In order of decreasing importance (in terms of biomass harvested) these include the nine-banded armadillo (*Dasyopus novemcinctus*), paca (*Agouti paca*), brown capuchin monkey (*Cebus apella*), tapir (*Tapirus terrestris*), white-lipped peccary (*Tayassu pecari*), coati (*Nasua nasua*), red and grey brocket deer (*Mazama* sp.), collared peccary (*Tayassu tajacu*), and tegu lizard (*Tupinambis marianae*) (Hill *et al.*, 1997; Hill & Padwe, 2000). The majority of these prey animals weigh less than 10 kg with the exception of the white-lipped peccary (mean adult weight 24.9 kg) collared peccary (16.3 kg), deer (25.8 kg), and tapir (177.0 kg) (Hill & Padwe, 2000). Many hunts are cooperative ventures between several men, and the Ache utilize a dynamic set of often dangerous techniques to harvest these prey species (see Hill & Hawkes, 1983 for descriptions).

## Methods

#### *Arrow shooting contests*

Fifteen arrow shooting contests at two colonies were conducted with the format chosen by the Ache—two with women including several teenagers, one with women and both sex youths 10–16 years of age, and the other 12 with men 17 years of age or older. During the course of a contest, each individual shot ten times at a wad of straw wrapped in a burlap sack (target diameter 25.0 cm) propped above the top of a tree with a 4 m pole. The average straight-line distance from the shooter to the target was 8.8 m for women and youths and 14.3 m for

men. The contests simulate an extremely difficult monkey shot because of the shallowness of the angle (33–34°). The contestants chose whether or not to participate in any one event creating a participant bias with those deciding to shoot also being the more confident shooters. Nonetheless, young men who often do not own bows were encouraged to participate by the authors and by other Ache. The contestants split into two teams for each event with the winning team receiving the equivalent of US\$15 to split among 6–10 people.

#### *Young hunter's notebook data*

During the pre-contact period (i.e., prior to the mid 1970s), hunters spent almost every healthy day of their lives hunting with the exception of bad weather days. On the reservation today, school and then horticultural activities and wage labor compete with hunting for a young man's time. Thus, by the year 2000, most young men had very little hunting experience. In May 2000, a selected group of 11 men, ages 14–37, who were relatively inexperienced at hunting, agreed to participate in a hunting experiment. They are paid the equivalent of US\$3 per day for their efforts, slightly less than expected from wage labor but with the added benefit of obtaining meat that is otherwise expensive to buy. They keep a daily log in a notebook of their hunting activities. This log includes foraging time start and end and a description of every resource encounter, i.e., who found the resource, who participates in the pursuit, and if the resource is harvested and by whom. After running the experiment for several weeks, their notebooks were inspected for completeness, and after several clarifications their recording has become remarkably detailed.

The 11 young hunters have documented 571 hunting days (3624 hours) between May 2000 and June 2001. This methodology supplements time-consuming focal

follow data, avoids confounding factors caused by an anthropologist's presence (see McMillan, 2001), allows cross-validation between hunters' records, and will eventually allow us to analytically track their improvement over time starting from a measured base return rate. The 11 young men's notebooks have thus far proved to be internally consistent. That is, because cooperative hunting is the norm, all involved in a pursuit generally report the same finder, caller, and killer, though they occasionally fill out their notebooks cooperatively. There are 64 man-days of overlap between focal follow and interview data collected by a researcher and data collected by the young men in their notebooks. This overlap allows for a reliability test. The number of finds per day for nine prey species (no tegu lizards were found) recorded in the notebooks matches up closely with those documented by the researcher over the 64 days (555 matches, 21 mismatches, Cronbach's reliability alpha 0.8915). Information regarding who kills what is 100% reliable over the sample.

#### *The hunting sample*

Hunting data are taken from nine forest treks in 1981–82, 12 in 1997–98, and five in 2000 and are combined with the younger hunter's notebook data. Trekking data include information gained from a combination of both focal follows of individual hunters, end-of-day interviews of the day's activities, and game weights of all animals killed on a particular day. The 10 most important prey species in the Ache diet (the above list plus the agouti, a small rodent) are the focus of finding rates and probabilities of kill upon encounter in this study. In order to make a kill, a hunter must first find or be called to game and then, if the decision to pursue is made, attempt a kill. We analyze outcomes of the search and pursuit modes separately as two integral components of hunting ability.

**Table 1 Sample population sizes (*n*) for three age groups separated by decade of data collection**

Age group	Decade	<i>n</i>
<25	80s	23
	90s/00	6 (0)
25-40	80s	21
	90s/00	16 (11)
>40	80s	13
	90s/00	18 (8)

Numbers in parentheses represents the number of individuals represented in both decades.

The sample composition broken down by age groups and decade of data collection are presented in Table 1. The age distribution of hunters has shifted over the last two decades. In the trekking data from 1981–82, 40% of the hunters in the sample were under the age of 25 (lower bound age 12). In recent years, 1997–98 and 2000, this number has fallen to 16%, though this age group currently constitutes 36% of the male population of hunting age (i.e., 12 or older) at Arroyo Bandera.

The number of days spent hunting for Arroyo Bandera men from 1995–1999 was recorded by a native Ache informant (Hill *et al.*, 1997; McMillan, 2001). The percent of days spent hunting for the young data-collecting men before the experiment (August 1995–December 1999) is only 2%, but during the experiment (15 May–30 June 2001) has risen to 13%. Several of the men did not reside at Arroyo Bandera for sample period before the experiment started, but they are unlikely to have done any hunting elsewhere as other Ache settlements rely less on foraging. Two young men each spent a year in military service.

Because of the secular trend of decreasing time allocations to traditional hunting, the effects of age on hunting ability (with body size controlled) presented in this paper are likely results of both acculturation-driven cohort effects and true age effects. Both support the hypothesis that hunting requires

skill investment, but it is possible that the role of experience becomes much more important as the range of skill variation in the population increases with acculturation.

#### *Data analysis*

Data analyses are conducted in SAS using the GLIMMIX (general linear mixed models) macro. This macro allows both fixed and random effects. A random effect variable representing an individual is used throughout this paper. A random effect parameter estimate is constructed for each individual that accounts for individual variation that may exist independently of strength and skill measures (i.e., unmeasured heterogeneity) and is thus preferable to using each individual as a single data point, especially since most individuals enter the sample at various ages and body sizes. The individual random effect also controls for the lack of independence inherent in using various numbers of multiple measurements on any one individual without making the assumption of a homogenous population and biasing the results towards those individuals who are over-represented in the data set (Verbeke & Molenberghs, 1997).

The general equation for the models is  $Y_{ji} = \beta_0 + \beta_1 \text{AGE}_{ji} + \beta_2 \text{AGE}_{ji}^2 + \beta_3 \text{BODY SIZE}_{ji} + \mu_i$  where  $Y_{ji}$  is the outcome variable for event  $j$  (e.g., prey encounter or day of hunting) for individual  $i$ .  $\beta_1$ – $\beta_3$  are fixed effect parameters that relate age and body size (kg) to  $Y_{ji}$ .  $\mu_i$  is a random effect estimated for each individual  $i$  in the sample. Finding rate models include an additional term that adjusts for methodological differences (focal follow, interview and notebook), and the pursuit models include an additional term for differences in decade and another random effect that accounts for various prey types. Finding rates with game are expected to follow a Poisson distribution (Stephens & Krebs, 1986) so counts of prey found per day are statistically modeled assuming Poisson errors. The link function

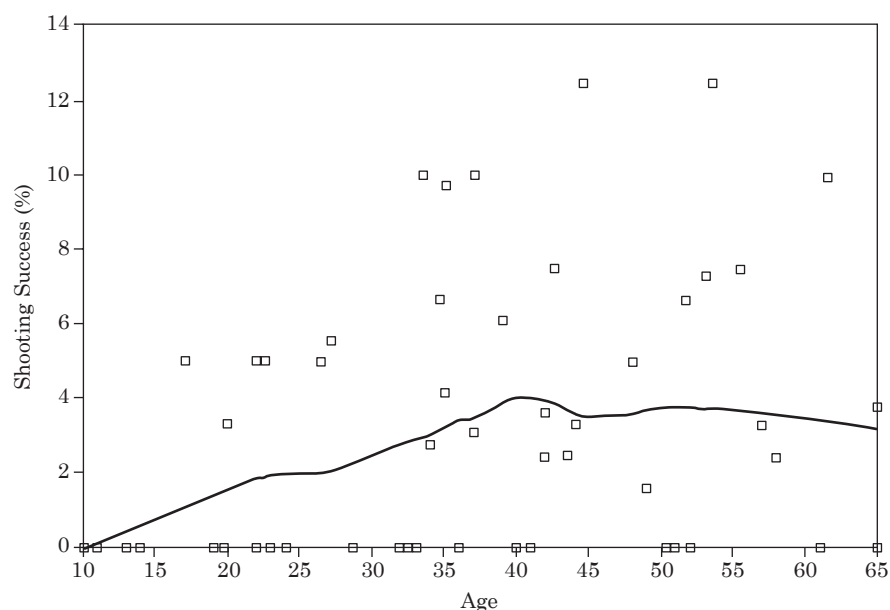


Figure 1. Percentage of shots individual men stuck into the target by age with a LOWESS fit using SPSS software. The sample is 2004 shots by 57 different men.

is adjusted by total foraging time to make each day comparable. Probability of kill upon encounter and probability of shooting a successful arrow are modeled as a probability using logistic regression. Unfortunately there are no accepted global goodness of fit test for GLIMMIX models. However, each model fit can be compared to non-parametric curve fits (e.g., LOWESS) in plots of dependent variable by age. Those comparisons suggest that the models produce curves that very closely approximate the nonparametric fits.

## Results

### *Arrow shooting*

The overall success, or arrows stuck into the target, was 2 in 344 (0.6%) for all women, 0 out of 70 for the male youths, and 81 out of 1934 (4.2%) for the men. Assuming a straight line shot with constant velocity, an arrow more than about one degree off target is a miss. Considering the additional

adjustments necessary to account for gravitational force and wind speed, it is remarkable that the target was ever hit.

We analyze all arrow shoots for adult men and male youths because the target was of similar size, angle, and distance (though adjusted closer for the youths) for each of the ten contests (2004 shots by 57 different men). We use a logistic regression model with hit (=1) or miss (=0) as the dependent variable and individual as a random effect. Both age and grip strength (or body size) are significant predictors of success with similar magnitudes up to age 40 (AGE parameter estimate=0.1142,  $P=0.0170$ ; GRIP parameter estimate=0.1198,  $P=0.0269$ ) with no significant effect thereafter (AGE  $P=0.3352$ , GRIP  $P=0.1757$ ). The age effect is illustrated in Figure 1 where success rate increases to around age 40 and then levels off. There are large differences between men as seen both in the graph and in the significant individual random effect in the model ( $P=0.0266$  for all ages). Because

the archery data are cross-sectional, we cannot separate the true age effects from a potential cohort effect on these results, but we tentatively conclude that strength and skill are important determinants of shooting ability.

#### *Rates of finding and killing prey*

Ache hunting follows an ordered sequence. First, hunters generally enter search mode spread apart from other hunters, out of sight but within carshot. If a resource is found, a hunter can decide to ignore it, to call others, or to pursue it alone. If the resource is not ignored, the hunter spends some time in pursuit and then goes back to searching, thereby repeating the sequence. In order to make a kill, a hunter must first find or be called to game and then, if the decision to pursue is made, attempt a kill. We analyze outcomes of the search and pursuit modes separately as two integral components of hunting ability.

Figures 2(a) and (b) shows the age profile of hunting return rate (kilograms of prey killed per hour) and demonstrates that killing rates continue to increase well after full-adult strength is obtained. Overall hunting ability peaks at approximately age 37 in the 1980s but has shifted slightly to around age 42 in the 1990s, probably due to less practice time in the later sample. Note how some good hunters are successful into their 60s, though the sample size at older ages is very small. Figure 2(b) demonstrates rates of increase of individual hunters sampled in both decades. These longitudinal data suggest that the age profile of hunting ability is real, as opposed to an artifact of acculturation. Of the eight men first sampled in their late teens or early 20s and then again in their 30s or 40s, four hunters increased in their ability at an average rate approximate to that of the LOWESS curves in Figure 2(a), two hunters had exceptional increases, and two hunters had small increases. Patterns of senescence in Figure 2(b) are

much more variable as the end points tend to be for only a few individuals with lower amounts of hunting time, yet some hunters do remain quite productive into their 50s.

Counts of prey found per day are statistically modeled in Table 2. To make different man-days comparable, time spent out of camp is entered in the model as an offset. Table 2 analyzes rates of finding the ten important prey items. Direct independent effects in the model include age, age-squared and body size (in kg). Data are analyzed separately for the 1980s and the 1990s/2000 sample.

The analyses indicate that finding rates increase with age and then decrease. The age effect on finding game is positive and the age-squared term is negative. Both are significant and models of each decade have parameter estimates of similar magnitude. Given the parameter estimates from Table 2, prey finding rates peak at age 39 and 38 for the first and second study periods, respectively. Figure 3 graphs rates of finding prey across the lifespan for the 1990s only (because of better methodological homogeneity) for armadillos (finding rate peaks at age 38), pacas (age 36), and monkeys (age 49). These performance peaks are surprisingly late in life, significantly later than age when physical strength peaks.

Because strength peaks at the age when peak body size is attained, body size is used as a proxy for overall physical strength in the model; the positive linear age effect can then be interpreted as a measure of skill. The negative parameters for the age-squared term (Table 2) probably reflects both diminishing returns to knowledge and decreased stamina resulting in the eventual decline in finding rates. Body size is significant for the finding rate model for the 1980s in Table 2, but not for the 1990s/2000 sample. Interestingly, Ohtsuka (1989) found this similar pattern to be true for the Gidra Papuans—a higher and significant correlation between hunting return rate and grip

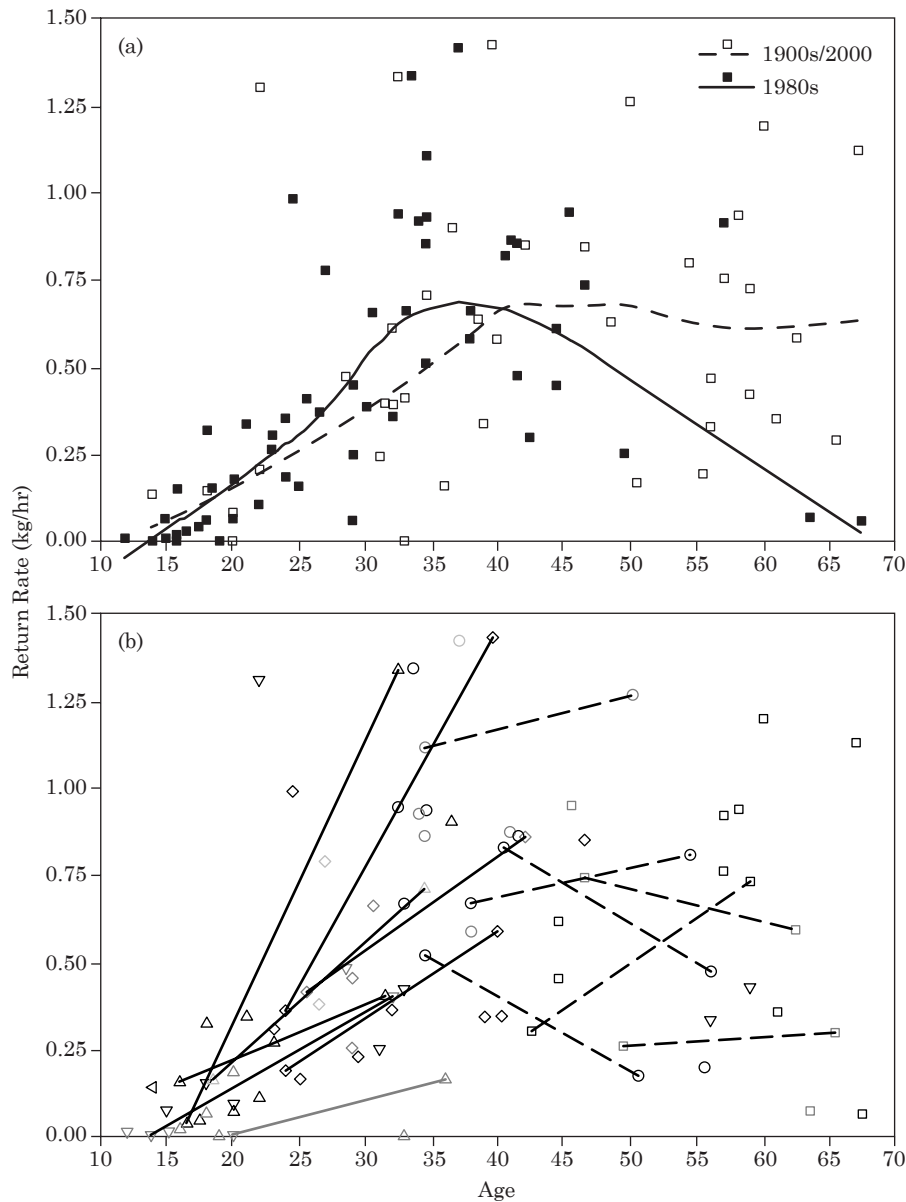


Figure 2. (a) LOWESS curves fitted to return rates for 78 individual hunters (1392 hunter-days) across the lifespan separated by decade. The denominator for return rates is total time out of camp. The return rate data use focal follow and interview data for 1981–82 and notebook, focal follow, and interview data for 1997–98 and 2000. (b) Graph is the same as (a) except hunters that were sampled in both decades have their data points connected with a line to show longitudinal trends.

strength in 1971–72 than in 1981 where there was a nonsignificant correlation. Perhaps strength becomes less of an important determinant of hunting ability as a population undergoes acculturation and the range of variation in skill within the

**Table 2** GLIMMIX models of rates of finding all ten prey per hour separated by decade

Dependent	Intercept	Age	Age $\times$ age	Body size	Individual	Interview	Notebook
1981–82 finding rate model (824 hunter-days; 57 hunters)							
All 10 prey	- 6.4899 ( $<0.0001$ )	0.0931 (0.0155)	- 0.0011 (0.0204)	0.0555 (0.0004)	0.1215 (0.0149)	- 1.0605 ( $<0.0001$ )	
1997–98/2000 finding rate model (512 hunter-days; 40 hunters)							
All 10 prey	- 3.0949 ( $<0.0001$ )	0.0874 (0.0010)	- 0.0011 (0.0020)	0.0056 (0.4307)	0.0121 (0.3097)	- 0.1706 0.1813	- 0.7346 ( $<0.0001$ )

Estimates are given with their associated  $P$ -values in parentheses. Individual ID is entered as a random effect with the cumulative individual effect given. Interview and Notebook represent methodology as compared to the baseline of focal follow data.

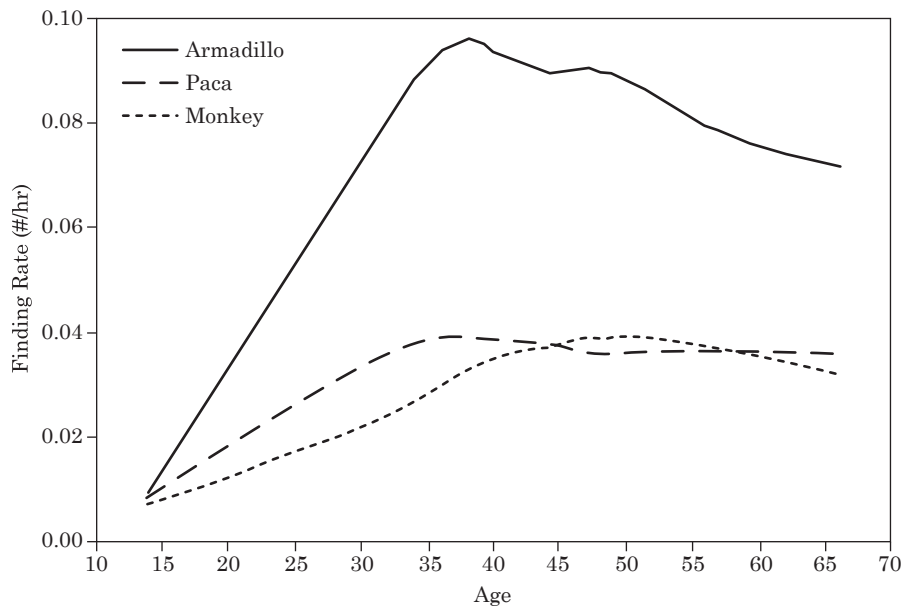


Figure 3. LOWESS curves of finding rates per hour with armadillos, pacas, and monkeys across the lifespan (other prey too rare to display) for the 1990s/2000 sample.

population increases. Nonetheless, our measure of skill (age with body size controlled) is strong and significant for both decades.

Methodological differences are captured by comparing interview against the baseline of focal data in Table 2. The strong negative effect of interview methodology in the 1980s results from the end-of-day interviews being much less rigorous than those used more recently. Interview data in the 1990s/2000

are more comparable with focal data due to more rigorous interview techniques. The striking difference in the latter decade is between the young hunter's notebook data and the focal follow data. Controlling for age and grip strength, these young hunters find all ten prey at only 48% of the focal follow rate ( $P < 0.0001$ ; Table 2). This strong effect is due to inexperience as opposed to methodological differences because interview, focal and notebook data

**Table 3** GLIMMIX logistic models of the probability of kill upon encounter

Model	Effect	Estimate	Pr> t
Pursuits with all ten prey ( $n=2642$ )	Intercept	-4.0300	0.0003
	Age	0.0853	0.0010
	Age $\times$ age	-0.0010	0.0019
	Body size	0.0077	0.4515
	Decade 80	1.0398	<0.0001
	Individual ( $n=91$ )	0.0577	0.0536
	Coati	1.1859	0.0025
	Armadillo	1.1226	0.0015
	Tegu lizard	1.0365	0.0226
	Monkey	0.7543	0.0328
	Paca	-0.0005	0.9988
	C peccary	-0.0878	0.8498
	Agouti	-0.3140	0.4939
	Deer	-0.9235	0.0310
	W-L Peccary	-1.1562	0.0036
	Tapir	-1.6192	0.0038
Monkey pursuits ( $n=588$ )	Intercept	-4.4932	0.0068
	Age	0.2071	0.0015
	Age $\times$ age	-0.0023	0.0034
	Body size	-0.0214	0.4517
	Individual ( $n=71$ )	0.4446	0.0132
	Decade 80	1.3929	<0.0001

The all-ten-pursuits model has prey type as a random effect with prey listed in descending order of kill probability. Decade80 is a dummy variable indicating if the pursuit occurred in the 1990s/2000 (=0) or in the 1980s (=1).

in the sample from the latter decade all show high validity as demonstrated above.

The problem of self-selection makes it difficult to determine whether some hunters are better than others because they have more experience or if better hunters are simply spending more time hunting. To avoid this problem we can examine the notebook data for improvements from a baseline and enter number of days hunted into the regression. No increase in hunting ability among the 11 young men is detectable over the 13.5 months since the beginning of the experiment despite the fact that the mean number of hunting days per individual is 52. The 95% confidence interval of the parameter estimate of days spent hunting on return rate with is unfortunately quite wide (-0.00299, 0.000817) due to high day-to-day variance in hunting returns. The upper 95% level would translate into an

increase of 0.3 kg/hr/year, an order of magnitude *above* the rate of increase seen in Figure 2(a). Nonetheless, the lack of improvements of the 11 individuals each with an average of 52 days of experience is consistent with the fact that it takes over two decades for hunting return rates to peak at around age 40, though more data are clearly needed to refine our estimate of the rate of increase with experience.

#### *Probabilities of successful pursuits*

The probability of killing prey upon encounter is modeled in Table 3 using logistic regression (failed attempt=0 or kill=1). Each data entry used in the probability of kill-upon encounter analysis consists of a man-pursuit, so each pursuit recorded has an entry for each person involved. Direct effects in the models include age, age-squared, body size and

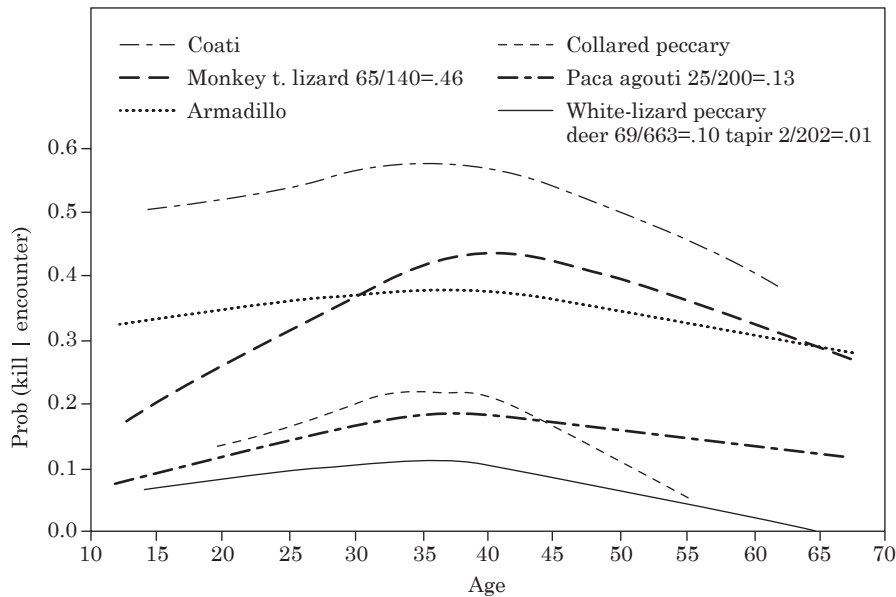


Figure 4. LOWESS curves of the probability of kill upon encounter across the lifespan for all ten prey species. Those with no discernible age effect are given an average success rate in the legend.

decade (1980s *vs.* 1990s/2000). The first model in Table 3 controls for individual skill differences and different numbers of pursuits with the ten main prey items by entering individual and prey type as random effects.

Probability of a kill after an encounter increases and then decreases with age. The age effect on the probability of making a kill is positive, and the age-squared term is negative. Both are significant. Figure 4 gives the probability of kill upon encounter for each of the ten important prey species across the lifespan. Most prey demonstrate shallow ability peaks in the mid to late 30s with the exception of monkeys. Monkey pursuit success demonstrates a sharp rise in ability into the 40s. This is due to complex maneuvering amidst dense undergrowth necessary to make a clear shot at mobile monkeys in the forest canopy without shooting or being shot by other hunters. The strong age effect on the probability of a kill upon a monkey encounter is also due to young men who

may not even carry a bow but, nonetheless, often assist in monkey hunts by climbing trees to flush out monkeys. This is one example of the allocation of hunting tasks on the basis of differential skill. Better monkey hunters also scored better in the arrow shooting contests as demonstrated by the correlation between individual random effect coefficients (measures of intrinsic ability) for monkey pursuit success and arrow shooting contests ( $r=0.46$ ,  $P=0.006$ ,  $n=31$ ).

We could find no significant effect of body size on probability of kill upon encounter and conclude that strength is relatively unimportant in comparison to skill. This is surprising because strength was found to be an important determinant of archery ability. However, approximately 60% of harvest animal biomass comes from hand hunted animals, and once an animal is grabbed or subdued most Ache of hunting age are probably capable of making a kill. It is likely a subtle combination of pursuit stealth and

know-how learned through many repetitions that make the difference between a kill and a failed opportunity.

The probability of kill upon a monkey encounter is modeled separately in Table 3 as Ache hunters inform us that monkeys are a very difficult prey to kill. Indeed, the age, decade, and individual random effect are stronger for monkeys than in the all-ten prey model. Using the logistic regression results in Table 3, we can solve for the probability of kill upon encounter for all ten prey and monkeys at each age. At the peak age in ability (age 45), men in the 1980s made a kill on 24% of encounters but men in the 1990s/2000 only made kills on 10% of encounters. The probability of a successful kill upon a monkey encounter in the 1980s is about 50% higher than in 1990s/2000. Perhaps this decade effect results from lost practice. No significant age by decade interaction could be found on the probability of a successful kill; thus it appears that men of all ages are less efficient from lack of practice.

### Discussion

Ache informants provide anecdotal evidence suggesting that successful hunting requires intelligence and a period of learning. For example, informants state that teenage boys learn hunting by first specializing on armadillos and pacas, which are burrowing animals that require only a little practice to kill. Later, boys begin using bows and arrows (that are made for them by older men) and start to hunt terrestrial game, deer, peccaries, tapir, etc. But if they wound these animals, older hunters are usually called to help track them. Only in their late 20s do hunters begin to make their own tools and participate in monkey hunts as archers. This is partially because predicting where monkeys will flee, and getting into position for a good shot through thick forest undergrowth is complicated. In addition,

hunters surround monkeys and shoot from all angles and older hunters are afraid the younger inexperienced hunters will either shoot somebody by accident (not correctly calculating the trajectory of their arrow) or get shot themselves. Such accidents are common (KH was shot in the back in 1982 during one of these events). Finally, calculating where an arrow will fall requires integrating information about angles, velocity, wind speed and intervening vegetation. Young hunters frequently lose several arrows in each hunt, while older hunters usually find most of the arrows they shoot.

Consistent with this description of the ontogeny of hunting skills are the observations of two men, who suffer from mental disabilities. The first, who was most afflicted, was able to kill armadillos, pacas, tegu lizards and coatis, but no other game. The first three of these species are found in burrows and killed by hand, and coatis are found in trees, and caught by hand and slammed to death when they jump to escape. The other concentrated primarily on the same hand-killed animals although he sometimes killed monkeys as well. Between 1994 and 2000 his total game harvest consisted of 79% armadillos and only 7% monkeys whereas the average for all other hunters was only 60% armadillos and 14% monkeys.

We have found significant age effects on important measures of hunting ability (with body size controlled). Most notable of these are total number of prey found per hour and the probability of kill upon encounter with important prey species, especially monkeys. Peaks in these measures occur much later in life than age of peak physical performance. We could find no significant effect of body size on the probability of a successful pursuit. While strength is certainly an important factor in some foraging activities such as bow-and-arrow shooting, our results indicate that skill is more important in attaining proficiency in finding and killing prey.

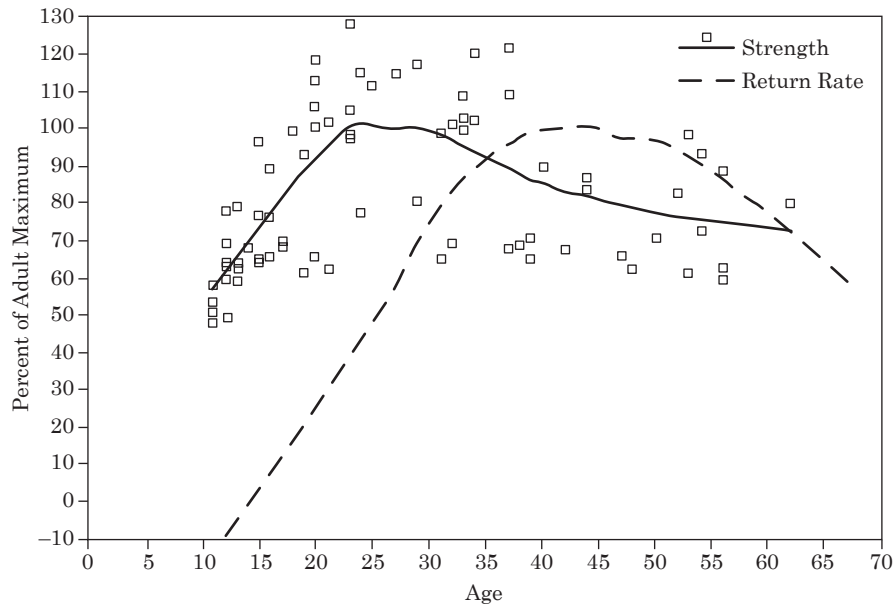


Figure 5. Comparison between hunting return rate and strength, an equally weighted composite measure of weight, grip strength, arm diameter, 50-m dash speed, push-ups, pull-ups, and chin-ups for 71 men. Both return rate and strength are on the scale of percent of adult maximum. Recall that sample sizes for hunting return rate at later ages are small.

Additionally, analysis of longitudinal notebook data from the inexperienced hunters shows no detectable improvement after 13.5 months. It remains to be seen if reservation-born Ache will ever perform at the same elevated level as their forest-born counterparts. The low rates of finding prey for the hunters collecting data in notebooks (Table 2), the lack of improvement by the young hunters over the initial 13.5 months of the study, and the strong negative effect of decade in pursuit success (Table 3) suggest not.

Interesting comparisons can be made between our results and data from Olympic athletes as peak ages in ability in various sports appear to map on to the skill-intensity of the activity. Despite the drastic improvements over the last century in Olympic training methods and equipment, Schulz & Curnow (1988) have found that the mean age of peak performers in many events has remained rather constant from 1896 to

1980. In men's short distance running, peak performance is around age 23, medium distance running age 24, long distance running age 27, and swimming age 20. Sport requiring more precise motor control takes longer to reach proficiency. For example, baseball players reach their prime at age 27 and golfers age 31 (Schulz & Curnow, 1988; Horn, 1988).

In comparison to these Olympic sports, traditional hunting takes even longer to reach proficiency. As mentioned in the introduction, hunting return rate curves peak around 35 for the Hiwi (Kaplan *et al.*, 2000), 40 for the Machiguenga and Piro (Gurven & Kaplan, n.d.), early or mid-40s to mid-50s for the Etolo (Dwyer, 1983), 45–50 for the Hadza (Marlowe, 2000), and 37–42 for the Ache [Figures 2(a) and 5]. Ohtsuka (1989) found Gidra hunters around the ages of 35–45 to have return rates four times higher than hunters in their late teens, though both age groups had equal

average grip strength. A dataset collected by an Ache informant of all game killed at Arroyo Bandera from 1995–99 that partially overlaps with the one used here, also shows an age peak at age 40 in units of game weight killed per day. Indeed, from age at highest strength (24) to age at peak returns (40), the average return rate for an Ache man more than doubles from 0.3 to 0.7 kg of raw meat per hour [Figures 2(a) and 5]. This 16-year lag between peak strength and peak hunting ability strongly implicates a significant skill component in hunting ability, a conclusion also reached by Marlow (2000) for Hadza hunters.

However, when interpreting age specific encounter and return rates, it is important to consider the use of total time spent out of camp as the denominator in these rate measures. We believe that post-peak declines in these curves with age result at least in part from older men adopting a search strategy that exploits more honey, fruits, larvae and palm products. Young men may also adopt a similar strategy, and this may then contribute to the peakedness in the return rate curve and the power of the age-squared terms in the finding rate models. This measure may underestimate the true finding rate per unit of *hunting search* time. Nonetheless, this strategy makes sense in that younger men with undeveloped hunting skills, like older men with declining strength and endurance, have lower opportunity costs per unit of hunting time foregone for time spent exploiting easier-to-acquire nongame forest products.

Given that Ache start hunting around the ages of 12–15, it takes nearly 30 years for hunters to reach their prime. Given current demographic trends, a 12-year-old Ache male on the reservation can expect to live to age 64 and would have expected to live to age 51 in the pre-contact period (Hill Hurtado, 1996). In both cases, life expectancy is beyond the age of reaching proficiency as a hunter, a requirement for

reaping the returns on investment in skill. Extant apes do not meet this requirement. For example, a 12-year-old free-living male chimpanzee expects to live to about age 25 (Hill *et al.*, 2001). Even if chimpanzees developed hunting skills at the same rate as Ache hunters, they would not reap returns on their investment because of the difference in the mortality profile (Kaplan *et al.*, 2000; Kaplan & Robson, n.d.). This suggests that the human foraging niche and the elongation of the human lifespan are linked and that selection is likely to favor concomitant increases in skill investment (e.g., brain size) with decreases in mortality (e.g., tool use and food sharing).

#### *Chimpanzee hunting*

Interesting contrasts can be drawn between the predatory behavior of modern hunter-gatherers and that of chimpanzees. Perhaps the most important difference is that humans hunt at a rate several orders of magnitude above chimpanzees (Hill, 1982; Stanford, 1999) and hunted meat constitutes only 1–3% of the calories in chimpanzee diets but an average of 59% for ten tropical hunter-gatherer societies (Kaplan *et al.*, 2000). This contrast stems from differences between the human and chimpanzees in both search and pursuit modes of hunting. Stanford (1999) states that the Gombe chimpanzees he has observed do not search for meat but rather fortuitously encounter prey on foraging forays. However, Mitani & Watts (1999), who work with the Ngogo chimpanzees, document that 41% (20/49) of hunts appear intentional in that pre-encounter hunting parties were unusually silent and walking in single file. Moreover, in a description that sounds strikingly similar to Ache hunting behavior, Mitani & Watts (1999:445) discuss how “the chimpanzees would stop, look up into the trees, scan, and change directions several times without calling” and “were extremely

attentive to any arboreal movements and would stop and search whenever motion was detected.” While chimpanzees may intentionally search for prey on occasion, Ache hunters always deliberately search for prey while moving through the forest. We attribute this behavioral difference to the enhanced ability of humans to locate prey through tracking and identifying spoor and feeding signs. This ability allows human hunters to locate and pursue prey that chimpanzees do not encounter. The ability to evaluate cryptic signs and then choose when to follow up and when to abandon the pursuit requires human levels of intelligence.

Human foragers also kill a variety of arboreal, terrestrial, aquatic, and burrowing prey with a myriad of often amazingly creative tactics (see Kaplan *et al.*, 2000). Chimpanzees focus their hunts on red colobus monkeys—82% of all hunts recorded at Gombe (Stanford *et al.*, 1994), 55% at Mahale (Uehara *et al.*, 1992), 78% at Tai (Boesch & Boesch, 1989), and 91% at Ngogo (Mitani & Watts, 1999). This pattern clearly indicates nonrandom prey selection for a smaller primate species that can be trapped or overtaken. In contrast, Ache hunters appear to harvest prey in numbers much closer to their environmental density. For eight of the major prey species, mean environmental density predicts 80% of the variation in annual harvest (Hill & Padwe, 2000). Human hunters are capable of taking the prime individuals of even the largest of species in any habitat, whereas chimpanzee hunting appears to focus on immature red colobus monkeys (84% of colobus kills at Gombe, 70% at Mahale, 78% at Tai, 66% at Ngogo (Mitani & Watts, 1999)). Piro and Machiguenga hunters focus on prime-aged individuals (Alvard & Kaplan, 1991). Moreover, cooperating Ache hunters often systematically exterminate all or most members of social groups of

brown capuchin monkeys or coatis upon encounter.

Adult chimpanzee males make the majority of kills (Uehara, 1997). For example, adult males made 86% of the kills at Ngogo (Mitani & Watts, 1999) and some males are documented as being much better hunters (e.g., Frodo in the Gombe population who killed 10% of the colobus population in his home range, Stanford, 1995). Boesch & Boesch-Achermann (2000) show that important Tai chimpanzee hunting techniques, such as ambush and block movements and anticipation of both prey and fellow chimpanzee hunters, are progressively learned over a 20-year process, beginning at age nine or ten. The learning behavior is inferred because young chimpanzees observe hunting tactics employed by their older counterparts and adapt their movements accordingly (Boesch & Boesch-Achermann, 2000). Humans have taken skill and learning to a new level, and this is presumably reflected in increased brain size, longer juvenile dependence, and an elevated ability to harvest prey.

#### *Human life history evolution*

Results presented in this paper have important implications for understanding the evolution of the life history of our species. If hunting was an important economic activity of early hominids, the learning curve for hunting success may partially explain why humans have big brains, long learning periods, and long lifespans (Kaplan *et al.*, 2000). The same forces would apply to any type of skill intensive foraging in hominid history (*ibid.*). For example, root digging, as described for Hadza foragers, often involves difficult rock excavation and the solving of “intricate engineering problems” (Hawkes *et al.*, 1989:344).

The hominid shift into a skill-intensive foraging niche where elevated returns are realized later in life should select for increases in brain size, provided larger

brains facilitate increased capacity for learning and mortality rates are sufficiently low to allow for returns on skill investment (see Kaplan & Robson, n.d. for an theoretical model demonstrating such effects). Our results in this paper are consistent with a model that sees humans moving into a skill-intensive foraging niche after a reduction in mortality or one in which the length of the lifespan, large brain, and foraging niche are tightly bound in a co-evolutionary process. Moreover, the learning of social skills may also produce parallel selective pressures with the acquisition of goods and services coming later in life through social manipulation and coalition building, an hypothesis worthy of future tests.

Regardless of the prime mover in this evolutionary process, we suggest that current human adaptations allow post-reproductive females and adult males to produce large food surpluses in the form of hunting, fishing, tuber digging, and other forms of extractive foraging. This facilitates social systems characterized by pair-bonding, a sexual division of labor, increased food sharing, and provisioning of dependent juveniles and reproductive females (Lancaster & Lancaster, 1983). These characters, combined with mortality reduction from sociality and food sharing (Kaplan *et al.*, 2000) perhaps favor an extended juvenile period (see Stearns, 1992; Charnov, n.d.) that in turn facilitates even greater investments in skill and learning. Conceivably, this process created run-away positive feedback selection for rapid encephalization and lengthened juvenile period and adult lifespan, stabilizing at life history parameters exhibited by modern peoples.

### Conclusions

Age-specific hunting performance measures—finding rates and probabilities of kill upon encounter for important prey and

archery ability—look very different from strength schedules. Proficiency peaks in hunting ability tend to occur later in life. Hunters at the peak return rate age of 40 harvest on average 0.7 kg per hour while hunters at peak strength harvest at  $\frac{1}{2}$  that rate (Figures 2 and 5).

- Inexperienced hunters show no significant increases in hunting return rates after an average of 52 days of practice.
- Our results suggest that skill acquisition (for almost 30 years) is an important component of Ache hunting. These results have potentially significant implications for the human life history—the co-evolution of large brains, food sharing, provisioning, decreased mortality, increased fertility, increased period of juvenile dependence, sexual division of labor, and pair-bonding—in response to the occupation of a human-like foraging niche focusing on difficult-to-acquire and nutrient-dense food resources acquired in large packages.

### Acknowledgements

We want to thank the Ache for all their hospitality and to the *kbuchuvegis* for their careful effort and enthusiasm in self-data collection. Three “anonymous” *JHE* reviewers, *JHE* editor Terry Harrison, Ozzie Pearson, John Bock, Mike Gurven, and Keely Baca were very helpful for comments and criticism. Kim Hill thanks Magdalena Hurtado for insights into foraging patterns of teenage boys and older men. The following University of New Mexico sources funded this project: a Research and Allocations Grant to Kim Hill and a Lewis R. Binford Graduate Fellowship; Student Research and Allocations Committee Grant; Research, Projects, and Travel Grant; and a Latin American and Iberian Institute Research Grant to Robert Walker.

## References

- Altman, J. C. (1987). *Hunter-Gatherers Today: An Aboriginal Economy in North Australia*. Canberra: Australian Institute of Aboriginal Studies.
- Alvard, M. & Kaplan, H. (1991). Procurement technology and prey mortality among indigenous neotropical hunters. In (M. C. Stiner, Ed.) *Human Predation and Prey Mortality*, pp. 79–104. Boulder: Westview.
- Aoyagi, Y. & Shephard, R. J. (1992). Aging and muscle function. *Sports Med.* **14**, 376–396.
- Bäckman, E., Johansson, V., Hager, B., Sjoblom, P. & Henriksson, G. (1995). Isometric muscle strength and muscular endurance in normal person aged between 17 and 70 years. *Scandinavian J. Rehab. Med.* **27**, 109–117.
- Bleige Bird, R., Bird, D. W. & Beaton, J. M. (1995). Children and traditional subsistence on Mer (Murray Island), Torres Strait. *Australian Aboriginal Studies* **1**, 2–17.
- Blurton Jones, N. & Marlowe, F. (2001). Selection for delayed maturity: does it take 20 years to learn to hunt and gather? *Human Nature* **12**.
- Blurton Jones, N. G., Hawkes, K. & O'Connell, J. F. (1989). Modelling and measuring costs of children in two foraging societies. In (V. Standen & R. Foley, Eds) *Comparative Socioecology*, pp. 367–390. Oxford: Blackwell.
- Blurton Jones, N., Hawkes, K. & Draper, P. (1994). Foraging returns of !Kung adults and children: Why didn't !Kung children forage? *J. Anthropol. Res.* **50**, 217–248.
- Blurton Jones, N. G., Hawkes, K. & O'Connell, J. F. (1997). Why do Hadza children forage? In (N. L. Segal, G. E. Weisfeld & C. C. Weisfeld, Eds) *Genetic, Ethological and Evolutionary Perspective on Human Development. Essays in Honor of Dr. Daniel G. Freedman*, pp. 278–313. Washington, D.C.: American Psychological Association.
- Blurton Jones, N., Hawkes, K. & O'Connell, J. F. (1999). Some current ideas about the evolution of the human life history. In (P. C. Lee, Ed.) *Comparative Primate Socioecology*, pp. 140–166. Cambridge: Cambridge University Press.
- Bock, J. (1995). The determinants of variation in children's activities in a southern African community. Ph.D. Dissertation, University of New Mexico, Albuquerque.
- Bock, J. (2001). Learning, life history, and productivity: children's lives in the Okavango Delta, Botswana. *Human Nature* **12**.
- Boesch, C. & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *Am. J. phys. Anthropol.* **78**, 547–573.
- Boesch, C. & Boesch-Achermann, H. (2000). *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford: Oxford University Press.
- Charnov, E. L. (n.d.). Evolution of human life histories. Unpublished manuscript.
- Clastres, P. (1998). *Chronicle of the Guayaki Indians*. Cambridge: The MIT Press.
- Dart, R. A. (1953). The predatory transition from ape to man. *Int. Anthropol. Ling. Rev.* **1**, 201–217.
- Dwyer, P. D. (1983). Etolo hunting performance and energetics. *Human Ecology* **11**, 145–174.
- Foley, R. A. (1992). Evolutionary ecology of fossil hominids. In (E. A. Smith & B. Winterhalder, Eds) *Evolutionary Ecology and Human Behavior*, pp. 131–166. New York: Aldine de Gruyter.
- Foley, R. A. & Lee, P. C. (1991). Ecology and energetics of encephalization in hominid evolution. *Phil. Trans. R. Soc. London, Series B* **334**, 223–232.
- Gurven, M. & Kaplan, H. (n.d.). Determinants of time allocation to production across the lifespan among the Machiguenga and Piro Indians of Peru. Unpublished manuscript.
- Hawkes, K., O'Connell, J. F. & Blurton Jones, N. (1989). Hardworking Hadza grandmothers. In (V. Standen & R. Foley, Eds) *Comparative Socioecology*, pp. 341–366. London: Blackwell.
- Hawkes, K., O'Connell, J. F. & Blurton Jones, N. G. (1995). Hadza children's foraging: Juvenile dependency, social arrangements, and mobility among hunter-gatherers. *Curr. Anthropol.* **36**, 688–700.
- Hawkes, K., O'Connell, J. F., Blurton-Jones, N. G., Alvarez, H. & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proc. natn. Acad. Sci.* **95**, 1336–1339.
- Hawkes, K., O'Connell, J. F., Blurton Jones, N., Alvarez, H. & Charnov, E. L. (2000). The grandmother hypothesis and human evolution. In (L. Cronk, N. Chagnon & W. Irons, Eds) *Adaptation and Human Behavior*, pp. 237–258. New York: Aldine de Gruyter.
- Heyward, V. H. (1998). *Advanced Fitness Assessment and Exercise Prescription*. Champaign, Illinois: Human Kinetics.
- Hill, K. (1982). Hunting and human evolution. *J. hum. Evol.* **11**, 521–544.
- Hill, K. & Hawkes, K. (1983). Neotropical hunting among the Ache of eastern Paraguay. In (R. B. Hames & W. T. Vickers, Eds) *Adaptive Responses of Native Amazonians*, pp. 139–188. New York: Academic Press.
- Hill, K. & Hurtado, M. (1996). *Ache Life History: The Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter.
- Hill, K. & Padwe, J. (2000). Sustainability of Ache hunting in the Mbaracayu Reserve, Paraguay. In (J. Robinson & E. Bennet, Eds) *Sustainability of Hunting in Tropical Forests*, pp. 79–105. New York: Columbia University Press.
- Hill, K., Padwe, J., Bejyvagi, C., Bepurangi, A., Jakugi, F., Tykurangi, R. & Tykuarangi, T. (1997). Impact of hunting on large vertebrates in the Mbaracayu Reserve, Paraguay. *Cons. Biol.* **11**, 1339–1353.
- Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J. & Wrangham, R. (2001). Mortality rates among wild chimpanzees. *J. hum. Evol.* **39**.
- Horn, J. (1988). The peak years. *Psychology Today* **22**, 62–63.

- Hurtado, A. M., Hawkes, K., Hill, K. & Kaplan, H. (1985). Female subsistence strategies among Ache hunter-gatherers of Eastern Paraguay. *Human Ecology* **13**, 1–28.
- Isaac, G. (1978). The food sharing behavior of early hominids. *Sci. Amer.* **238**, 90–108.
- Kaplan, H. (1994). Evolutionary and wealth flows theories of fertility: Empirical tests and new models. *Pop. Development Rev.* **20**, 753–791.
- Kaplan, H. (1997). The evolution of the human life course. In (K. W. Wachter & C. E. Finch, Eds) *Between Zeus and the Salmon*, pp. 175–211. Washington, D.C.: National Academy Press.
- Kaplan, H. (1996). A theory of fertility and parental investment in traditional and modern human societies. *Yearb. phys. Anthropol.* **39**, 91–135.
- Kaplan, H. & Hill, K. (1985). Hunting ability and reproductive success among male Ache foragers: Preliminary results. *Curr. Anthropol.* **26**, 131–133.
- Kaplan, H. S. & Robson, A. J. (n.d.). The coevolution of intelligence and longevity and the emergence of humans. Unpublished manuscript.
- Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. (2000). The evolution of intelligence and the human life history. *Evol. Anthropol.* **9**, 156–184.
- Kawabe, T. (1983). Development of hunting and fishing skill among boys of the Gidra in lowland Papua New Guinea. *J. hum. Ergol.* **12**, 65–74.
- Lancaster, J. B. & Lancaster, C. S. (1983). Parental investment: The hominid adaptation. In (D. J. Ortner, Ed.) *How Humans Adapt: A Biocultural Odyssey*, pp. 33–66. Washington, D.C.: Smithsonian Institution Press.
- Lee, R. B. (1979). *The Dobe !Kung*. New York: Rinehart & Winston.
- Liebenberg, L. (1990). *The Art of Tracking: The Origin of Science*. Claremont, South Africa: David Philip Publishers.
- Litle, M. A. & Johnson, B. R. Jr (1986). Grip strength, muscle fatigue, and body composition in nomadic Turkana pastoralists. *Am. J. phys. Anthropol.* **69**, 335–344.
- Malina, R. M., Buschang, P. H., Aronson, W. D. & Selby, H. A. (1982). Aging in selected anthropometric dimensions in a rural Zapotec-speaking community in the valley of Oaxaca, Mexico. *Soc. Sci. Med.* **16**, 217–222.
- Marlowe, F. (2000). The patriarch hypothesis: An alternative explanation of menopause. *Human Nature* **11**, 27–42.
- McMillan, G. (2001). Ache residential grouping and social foraging. Ph.D. Dissertation, University of New Mexico, Albuquerque.
- Meehan, B. (1982). *Shell Bed to Shell Midden*. Melbourne, Australia: Globe Press.
- Mitani, J. C. & Watts, D. P. (1999). Demographic influences on the hunting behavior of chimpanzees. *Am. J. phys. Anthropol.* **109**, 439–454.
- Ohtsuka, R. (1983). *Oriomo Papuans: Ecology of Sago-Eaters in Lowland Papua*. Tokyo: University of Tokyo Press.
- Ohtsuka, R. (1989). Hunting activity and aging among the Gidra Papuans: A biobehavioral analysis. *Am. J. phys. Anthropol.* **80**, 31–39.
- Ohtsuka, R., Inaoka, T., Kawabe, T. & Suzuki, T. (1987). Grip strength and body composition of the Gidra Papuans in relation to ecological conditions. *J. Anthropol. Soc. Nippon* **95**, 457–467.
- Rode, A. & Shephard, R. J. (1971). Cardiorespiratory fitness in an Arctic community. *J. Applied Physiol.* **31**, 519–526.
- Schulz, R. & Curnow, C. (1988). Peak performance and age among superathletes: track and field, swimming, baseball, tennis, and golf. *J. Gerontol. Psychol. Sci.* **43**, 113–120.
- Shephard, R. J. (1970). Computer program for solution of the Astrand nomogram and the calculation of body surface area. *J. Sports Med. Phys. Fitness* **10**, 206–210.
- Shvartz, E. & Reibold, R. C. (1990). Aerobic fitness norms for males and females aged 6 to 75 years: A review. *Aviation, Space, Environ. Med.* **61**, 3–11.
- Stanford, C. (1995). Chimpanzee hunting behavior and human evolution. *Amer. Sci.* **83**, 256–261.
- Stanford, C. (2001). A comparison of social meat-foraging by chimpanzees and human foragers. In (C. Stanford & H. Bunn, Eds) *Meat-Eating and Human Evolution*, pp. 122–140. Oxford: Oxford University Press.
- Stanford, C., Wallis, J., Matama, H. & Goodall, J. (1994). Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982–1991. *Am. J. phys. Anthropol.* **94**, 213–228.
- Stanford, C. B. (1999). *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. Princeton: Princeton University Press.
- Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stephens, D. W. & Krebs, J. R. (1986). *Foraging Theory*. Princeton: Princeton University Press.
- Uehara, S. (1997). Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates* **38**, 193–214.
- Uehara, S., Nishida, T., Hamai, M., Hasegawa, T., Hayaki, H., Huffman, M., Kawanaka, K., Kobayashi, K., Mitani, J., Takahata, Y., Takasaki, H. & Tsukahara, T. (1992). Characteristics of predation by chimpanzees in the Mahale Mountains National Park, Tanzania. In (T. Nishida, W. McGrew, P. Marler, M. Pickford & F. DeWaal, Eds) *Topics in Primatology, Volume 1. Human Origins*, pp. 143–158. Tokyo: Tokyo University Press.
- Verbeke, G. & Molenberghs, G. (1997). *Linear Mixed Models in Practice: A SAS-Oriented Approach*. New York: Springer.
- Walker, R. & Hill, K. (n.d.). Growth and senescence in physical performance among the Ache of eastern Paraguay. Unpublished manuscript.
- Washburn, S. L. & Lancaster, C. S. (1968). The evolution of hunting. In (R. B. Lee & I. DeVore, Eds) *Man the Hunter*, pp. 293–303. Chicago: Aldine.
- White, L. (1959). *The Evolution of Culture*. New York: McGraw Hill.

## Author Queries

Page	Query
18	Hill et al., 2001. Please supply the relevant page numbers for this paper.