

A Theory of Human Life History Evolution: Diet, Intelligence, and Longevity

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Human life histories, as compared to those of other primates and mammals, have at least four distinctive characteristics: an exceptionally long lifespan, an extended period of juvenile dependence, support of reproduction by older post-reproductive individuals, and male support of reproduction through the provisioning of females and their offspring. Another distinctive feature of our species is a large brain, with its associated psychological attributes: increased capacities for learning, cognition, and insight. In this paper, we propose a theory that unites and organizes these observations and generates many theoretical and empirical predictions. We present some tests of those predictions and outline new predictions that can be tested in future research by comparative biologists, archeologists, paleontologists, biological anthropologists, demographers, geneticists, and cultural anthropologists.

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Our theory is that those four life history characteristics and extreme intelligence are co-evolved responses to a dietary shift toward high-quality, nutrient-dense, and difficult-to-acquire food resources.

The following logic underlies our proposal. First, high levels of knowledge, skill, coordination, and strength are required to exploit the suite of high-quality, difficult-to-acquire resources humans consume. The attainment of those abilities requires time and a significant commitment to development. This extended learning phase, during which productivity is low, is compensated for by higher productivity during the adult period and an intergenerational flow of food from old to young. Because productivity increases with age, the investment of time in acquiring skill and knowledge leads to selection for lowered mortality rates and greater longevity. The returns on investments in development occur at older ages. This, in turn, favors a longer juvenile period if there are important gains in productive ability with body size and growth ceases at sexual maturity.

Second, we believe that the feeding

niche that involves specializing on large, valuable food packages promotes food sharing, provisioning of juveniles, and increased grouping, all of which act to lower mortality during the juvenile and early adult periods. Food sharing and provisioning assist recovery in times of illness and reduce risk by limiting juvenile time allocation to foraging. Grouping also lowers predation risks. These buffers against mortality also favor a longer juvenile period and higher investment in other mechanisms to increase the life span.

Thus, we propose that the long human life span co-evolved with lengthening of the juvenile period, increased brain capacities for information processing and storage, and intergenerational resource flows, all as a result of an important dietary shift. Humans are specialists in that they consume only the highest-quality plant and animal resources in their local ecology and rely on creative, skill-intensive techniques to exploit them. Yet the capacity to develop new techniques for extractive foraging and hunting allows them to exploit a wide variety of different foods and to colonize all of earth's terrestrial and coastal ecosystems.

We begin with an overview of the data on which the theory is based: a comparative examination of hunter-gatherer and chimpanzee life-history traits and age profiles of energy acquisition and consumption. The data show that hunter-gatherers have a longer juvenile period, a longer adult lifespan, and higher fertility than chimpanzees do. Hunter-gatherer children are energetically dependent on older individuals until they reach sexual maturity. Energy acquisition rates increase dramatically, especially for

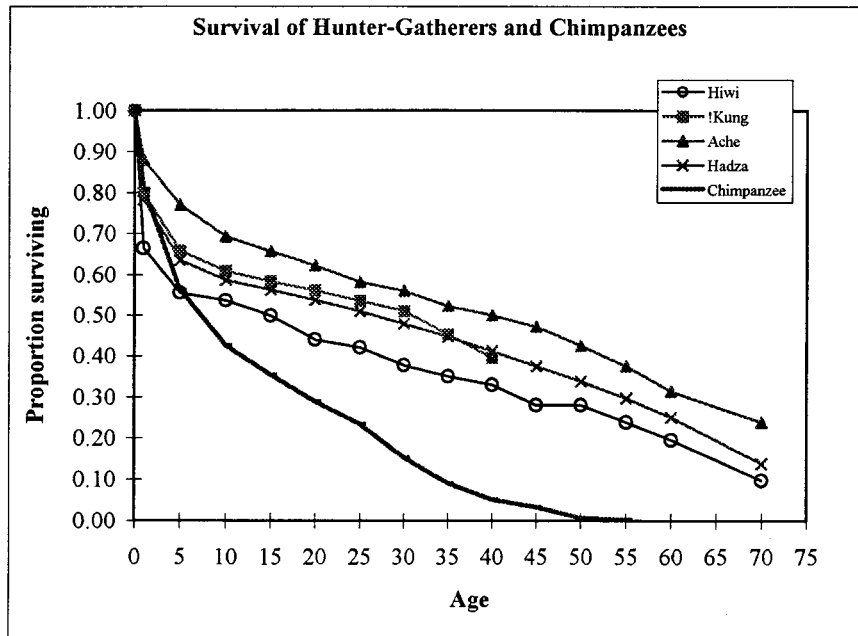


Figure 1. Survival curves for forager populations were derived from sources listed in notes for table 1. Chimpanzee mortality is from a synthetic life table combining all mortality data from Bossou, Gombe, Kibale, Mahale and Tai.⁸

males, until mid-adulthood and stay high until late in life.

We then present both theoretical and empirical tests of our theory. For the theory to be correct, a model of natural selection must show that mortality rates, the length of the juvenile period, and investments in learning co-evolve in the ways predicted by the theory. Building on existing models of life-history evolution,¹⁻⁵ we develop such a model. The results of our analysis confirm the theory's predictions. Those theoretical tests are followed by empirical tests. In order for our theory to be correct, we must demonstrate that: Humans do, in fact, consume more skill-intensive, difficult-to-acquire, high-quality foods than do chimpanzees and other nonhuman primates; Difficulty of acquisition explains the age profile of production for both humans and chimpanzees; Men play a large role in supporting human reproduction; The foraging niche occupied by humans lowers mortality rates among juveniles and adults relative to corresponding rates among chimpanzees and other nonhuman primates. We present strong evidence in support of the first three propositions and suggestive evidence in support of the fourth.

We then examine the evolution of the primate order to determine whether the same principles invoked in our theory of hominid evolution explain the major primate radiations. We then consider the fundamental differences between our theory and the "grandmother hypothesis" recently proposed by Hawkes, Blurton Jones and O'Connell.^{6,7} We conclude with a listing of the new and unique predictions derived from our theory.

Our theory is not the first to propose that high-quality foods, extractive foraging, and hunting are fundamental to human evolution. However, it is the first to do so with a specific model of natural selection that unifies the evolution of life history, brain and intelligence, diet, and age profiles of food production and consumption. As a result, it organizes existing data in a new way and leads to a novel set of predictions.

DIFFERENCES BETWEEN THE LIFE-HISTORY TRAITS OF HUNTER-GATHERERS AND CHIMPANZEES

Mortality, Fertility, and Growth

Figure 1 shows the differences between the life spans of traditional hu-

man foragers and chimpanzees; Table 1 compares a variety of life-history traits of the two species. The hunter-gatherer data come from studies on populations during periods when they were almost completely dependent on wild foods, having little modern technology and no firearms, no significant outside interference in interpersonal violence or fertility rates, and no significant access to modern medicine. The chimpanzee data are compiled from all published and unpublished sources that we are aware of. Because of small sample sizes at individual sites, mortality data were combined to create a single synthetic life table and survival function that combines all data for wild chimpanzees.⁸

Despite the fact that the human juvenile and adult periods are longer than those of chimpanzees and that human infants are larger than chimpanzee infants at birth (about 3 kg versus 2 kg), hunter-gatherer women characteristically have higher fertility than do chimpanzee females.

The data suggest that hunter-gatherer children have a higher rate of survival to age 15 (60% versus 35%) and higher growth rates during the first 5 years of life (2.6 kg/yr versus 1.6 kg/yr) than do juvenile chimpanzees. Chimpanzees, however, grow faster between ages 5 and 10, both in absolute weight gain (2.5 kg/yr for chimps versus 2.1 kg/yr for humans) and proportional weight gain (16% per year for chimps versus 10% per year for humans) (Table 1). The early higher weight gain for humans may be due to an earlier weaning age (approximately 2.5 years for hunter-gatherers versus 5 years for chimpanzees) and parental provisioning of

TABLE 1. LIFE HISTORY PARAMETERS OF HUMAN HUNTER-GATHERERS AND CHIMPANZEES

Group	Probability of Survival to Age 15	Expected Age of Death at 15 (years)	Mean Age at First Reproduction (years)	Mean Age at Last Reproduction ^b (years)	Interbirth Interval ^a (months)	Mean Weight Age 5 (kg)	Mean Weight Age 10 (kg)
Humans							
Ache female ^d	0.61	58.3	19.5	42.1	37.6	15.7	25.9
Ache male	0.71	51.8				15.5	27
Hadza female ^e	0.58	54.7				15.5	20
Hadza male	0.55	52.4				14.2	21.2
Hiwi female ^f	0.58	51.3	20.5	37.8	45.1	18	29.8
Hiwi male	0.58	51.3				16.4	33.6
!Kung female ^g	0.6	56.5	19.2	37	41.3	14	19.5
!Kung male	0.56	56.5				16	22.5
Forager mean ^c	0.60	54.1	19.7	39.0	41.3	15.7	24.9
Chimpanzees							
Bossou female ^h					51		
Bossou male							
Gombe female ⁱ	0.545	32.7	14.1		64.6	10	21
Gombe male	0.439	28.6				10	24
Kibale female ^j	0.805	35.6			68		
Kibale male	0.408	40.6					
Mahale female ^k			14.6		72		
Mahale male							
Tai female	0.193	23.8	14.3		69.1		
Tai male ^l	0.094	24					
Chimpanzee mean	0.35	29.7	14.3	27.7**	66.7	10	22.5

^a Mean interbirth interval following a surviving infant.

^b Age of last reproduction for chimpanzee females was estimated as two years prior to the mean adult life expectancy.

^c The forager mean values were calculated by weighting each forager study equally. The chimpanzee mean mortality is from a synthetic life table using data from all five sites listed.^{8,138}

^d Ache: Demographic and weight data from Hill and Hurtado.¹⁰

^e Hadza: Demographic data from Blurton Jones and colleagues.¹⁶ Weight data from Blurton Jones (personal communication).

^f Hiwi: Demographic data from Hill and Hurtado unpublished database collected on the Hiwi foragers from reproductive-history interviews conducted between 1982 and 1991 using the same methodology published in Hill and Hurtado.¹⁰

^g !Kung: Demographic and weight data from Howell.⁸³

^h Bossou: Data from Sugiyama.¹³⁹

ⁱ Gombe: Data on mortality from Hill and coworkers,⁸ and Pusey and Williams (personal communication). Gombe data on fertility from Pusey,¹⁴⁰ Tutin,¹⁴¹ and Wallis.¹⁴² Weights from Pusey.¹⁴⁰

^j Kibale: All data from Wrangham (personal communication). Mortality data in Hill and coworkers.⁸

^k Mahale: Data from Nishida, Takasaki, and Takahata.¹⁴³

^l Tai: Data from Boesch and Boesch.²⁰

highly processed foods. Among humans, the slow growth during middle childhood is intriguing. According to the allometric growth law, mammalian growth can be described by the equation $dw/dt = Aw^{0.75}$ (where change in weight per unit of time is expressed as a function of a growth constant, A , and weight, w , to the 0.75 power). Most mammals show a yearly growth constant of about 1, whereas the mean primate value for A is about 0.4.⁹ Hunter-gatherer children between the ages of 5 to 10 years are characterized by ex-

tremely slow growth, with A being approximately 0.2.

Chimpanzees spend less time as juveniles than humans do: Female chimpanzees give birth for the first time about 5 years earlier than do hunter-gatherer women. In natural habitats, chimpanzees also have a much shorter adult life span than humans do. At age 15, chimpanzee life expectancy is an additional 15 years, as compared to 39 more years for human foragers. Importantly, women spend more than a third of their adult

life in a postreproductive phase, whereas very few chimpanzee females survive to the postreproductive phase. The differences in overall survival and life span are striking (Fig. 1). Less than 10% of chimpanzees survive to age 40, but more than 15% of hunter-gatherers survive to age 70. These naturalistic observations are also consistent with data on maximum life spans. The maximum life span of humans is between 100 and 120 years, depending upon how it is calculated, which is about two times longer than the max-

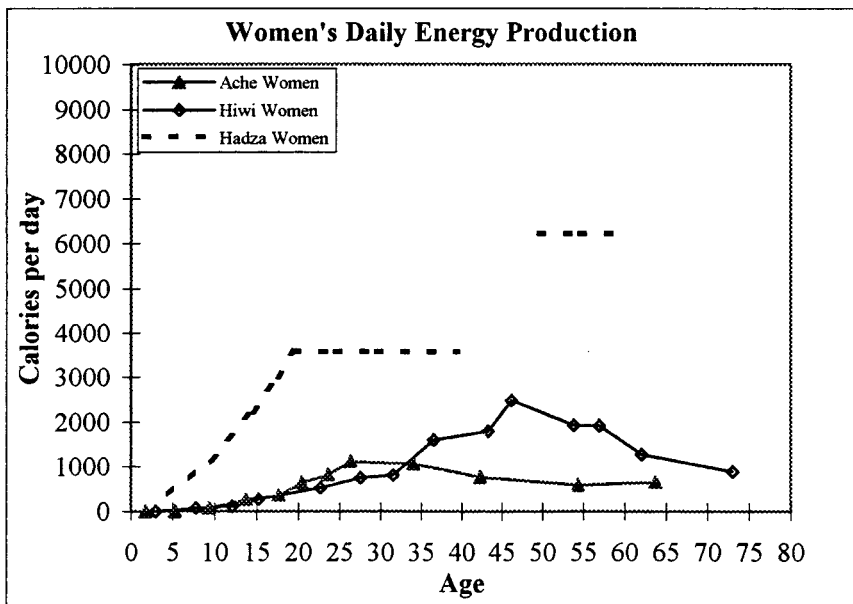
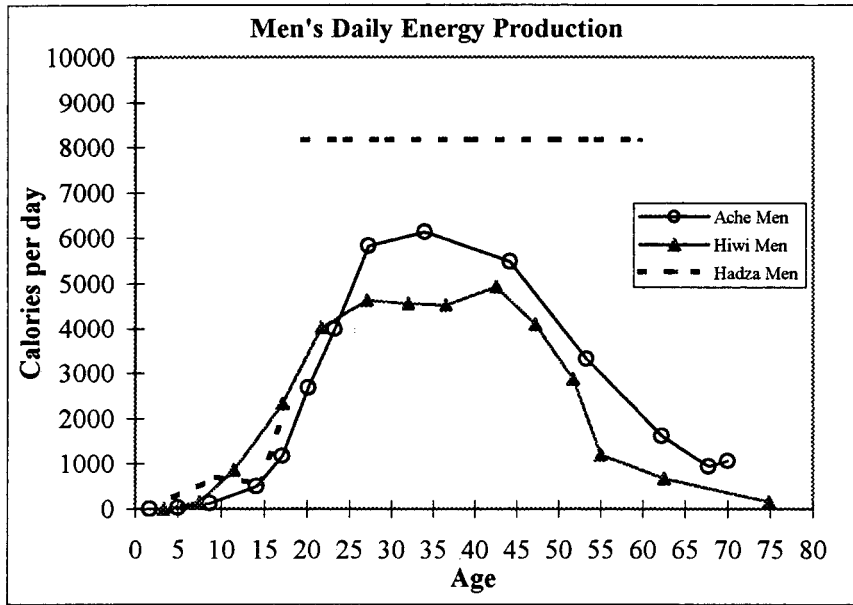


Figure 2. Daily energy acquisition data are recorded by individual among the Ache and Hiwi. Thus, the age and sex of each acquirer is known for every day sampled. Mean production for 5- or 10-year age intervals (y value) was calculated from raw data by summing all calories produced over the sample period by individuals in that age-sex class and dividing by the total sample of person days monitored for individuals in that category. This was plotted at the mean age of person days sampled (x value) in the category analyzed. Hadza production levels are given for various juvenile age categories, for all adult men combined (no age breakdown), and for all reproductive women and all women of postreproductive age combined (no age breakdown). All values are calculated as described in the notes for Tables 2 and 3.

imum adult chimpanzee life span (approximately 60 years for captive populations).

Despite the fact that the human ju-

venile and adult periods are longer than those of chimpanzees and that human infants are larger than chimpanzee infants at birth (about 3 kg

versus 2 kg), hunter-gatherer women characteristically have higher fertility than do chimpanzee females. The mean interbirth interval between offspring when the first survives to the birth of the second is more than 1.5 times longer among wild chimpanzees than among modern hunter-gatherer populations. These numbers lead to an interesting paradox. Life tables from modern human foragers always imply positive growth (see Hill and Hurtado,¹⁰ chapter 14), whereas the chimpanzee numbers presented here imply slightly negative population growth rates. Chimpanzee negative population growth may be a real

Adult men acquire much more food than do those in any other age-sex category. Although the patterns for men seem consistent for all three societies, Hadza children and postreproductive women appear to acquire substantially more food than do their Ache and Hiwi counterparts.

feature of recent habitat destruction and other human intrusion, or “natural” mortality rates may have been overestimated due to the inclusion of deaths from viral epidemics such as ebola and polio (see Hill and coworkers⁸ for a discussion).

To summarize, hunter-gatherers have a juvenile period that is 1.4 times longer than that of chimpanzees and a mean adult life span that is 2.5 times longer than that of chimpanzees. They show higher survival at all ages after weaning, but lower growth rates during middle childhood. Despite a longer juvenile period, slower growth,

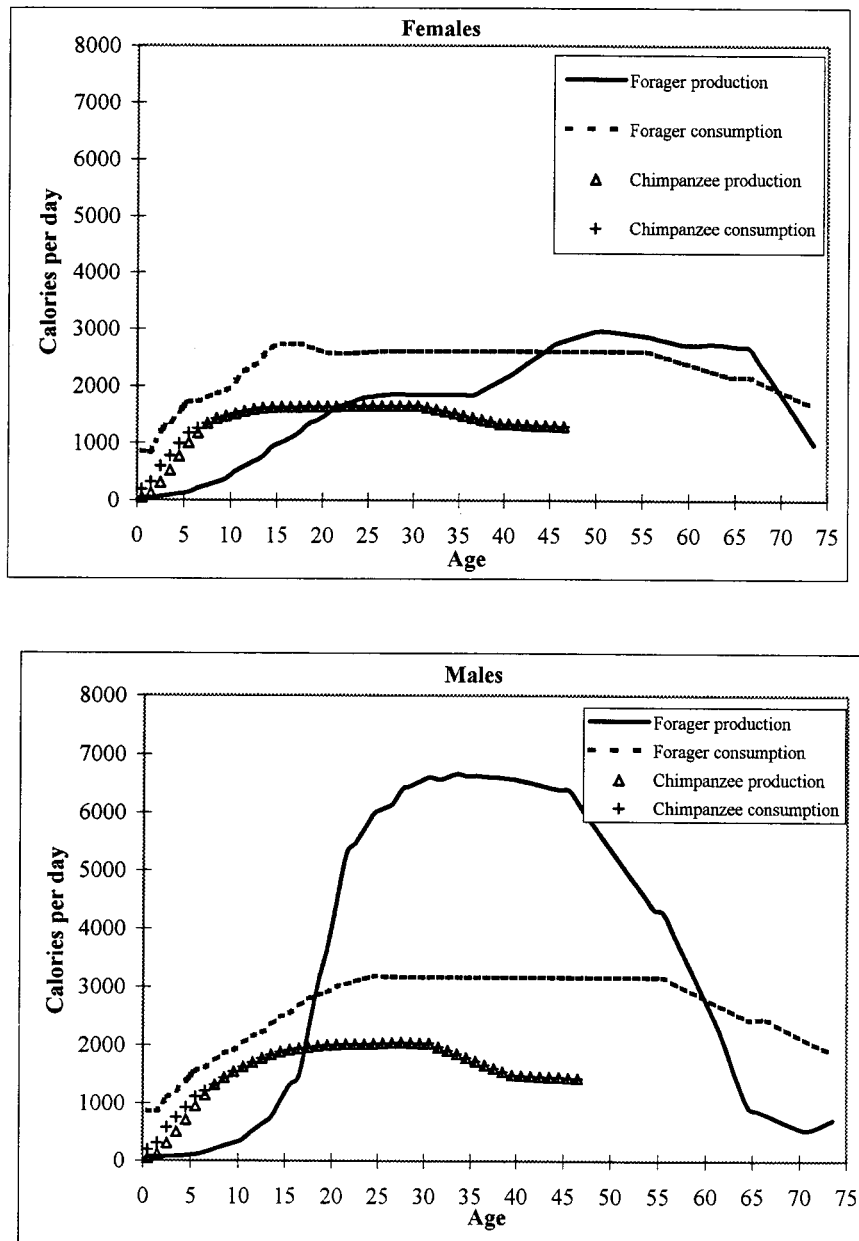


Figure 3. The mean expected daily energy consumption per individual for each age-sex category of each foraging group was estimated by first multiplying all the age-sex specific production rates for that foraging group times the proportional representation of that age-sex category as expected from the survival curves and summing expected production across all age categories. This total expected production for the group was then divided by the expected total number of individuals (as determined by the survival curve) at all ages times their proportion of a standard consumer. This procedure assumes that all populations are in steady state and that the proportional representation of each age category is determined by the probability of surviving to that age, and gives consumption per standard consumer in each group. This gives the mean consumption for a standard consumer in the group. Daily expected consumption for individuals in various age-sex categories is estimated by multiplying the proportion of a consumer represented by each age class times the mean consumption of a standard consumer. Kaplan¹⁷ provides a detailed description of these calculations and how proportional standard consumers were determined for each age-sex category. A standard consumption rate of 1 is assigned to young adult males and females; children begin at a consumption level of 0.3 that of a standard consumer. Daily energy acquisition for age-sex categories is calculated as described for Figure 2 and averaged across the Ache, Hiwi, and Hadza, weighting each group equally.

and a longer life span, hunter-gatherer women achieve higher fertility rates than do chimpanzee females.

The Age and Sex Profile of Energy Acquisition

Data on food acquisition by age and sex category exist for only three modern foraging populations. Ache and Hiwi food production was directly monitored by weighing all food produced by those in different age and sex categories throughout most months of various years. (See Hill and coworkers¹¹ and Hurtado and Hill¹² for definitions, methodology, and sampling plan). Hadza women's and children's plant-food acquisition was estimated indirectly from samples of in-patch return rates for different fruit and root resources over various age or sex classes during part of the wet season and part of the dry season of various years. (For details, see Hawkes and coworkers,⁶ and Blurton Jones, Hawkes, and O'Connell^{13,14}). These data were combined with sample estimates of time spent foraging and frequency across days to estimate daily food acquisition.^{13,14} Hadza men's food acquisition from hunting was measured directly by weighing all large game brought to camp.¹⁵

Although there is some cross-cultural variation, all three societies show similar patterns. Hunter-gatherer children produce little food compared to adults (Fig. 2). In the late juvenile period, daily food acquisition rates rise dramatically, especially for males. These rates continue to increase until mid-adulthood for males in all three groups and even longer for Hadza and Hiwi females. Adult men acquire much more food than do those in any other age-sex category. Although the patterns for men seem consistent for all three societies, Hadza children and postreproductive women appear to acquire substantially more food than do their Ache and Hiwi counterparts. But total food-consumption estimates for the Hadza may be unrealistically high, since the data suggest per capita consumption of about 3,400 calories per day (Tables 2, 3). That is 126% of the mean daily caloric consumption of the Ache, despite the fact that 10-year-old Hadza

children weigh only 78% of the weight of 10-year-old Ache children, and adult Hadza women weigh only 89% of the weight of Ache women. Those estimates are derived by assuming an age-structure consistent with the Hadza life-table.¹⁶ If the dependency ratio in the camps studied by the Hadza researchers was greater than expected by the life table, as Blurton Jones (personal communication) believes this to be the case, the per-capita consumption estimates would be reduced accordingly and would be more realistic.

Figure 3 shows the mean daily energy consumption and acquisition rates for all three hunter-gatherer societies as compared to the rates for chimpanzees of the same age and sex. The food-consumption rates of forager children and adults is estimated from body weight and total group production.¹⁷ Chimpanzee energy acquisition, while not measured directly, can be estimated from body size and caloric requirements, since very little food is transferred between age-sex categories after weaning. Daily food acquisition and consumption are virtually the same for chimpanzees from the juvenile period onward. The human consumption-acquisition profile is strikingly different from that of chimpanzees, with chimpanzee juveniles acquiring considerably more energy than forager children do until about the age of sexual maturity. No children in any forager society produced as much as they consumed until they reached their mid- to late teens. Thus, human juveniles, unlike chimpanzee juveniles, have an evolutionary history of dependency on adults to provide their daily energy needs. This can be appreciated by realizing that by age 15 the children in our forager sample had consumed over 25% of their expected life-time energy consumption but had acquired less than 5% of their life-time energy acquisition.

The area in Figure 3 where food acquisition is greater than consumption (where the solid line for each species is above the dotted line) represents surplus energy provided during the later part of the life span. These averaged data imply that hunter-gatherer men provide most

of the energy surplus that is used to subsidize juveniles and reproductive-aged women. Although based on averaging only three societies, this trend can be confirmed by comparing the food-acquisition rates of adult males and females from a sample of ten hunter-gatherer societies in which food acquisition has been measured with a systematic sample (Table 2).

Our proposal is that the shift to calorie-dense, large-package, skill-intensive food resources is responsible for the unique evolutionary trajectory of the genus *Homo*. The key element in our theory is that this shift produced co-evolutionary selection pressures, which, in turn, operated to produce the extreme intelligence, long developmental period, three-generational system of resource flows, and exceptionally long adult life characteristic of our species.

A THEORETICAL TEST: WOULD NATURAL SELECTION ACTUALLY PRODUCE THE CO-EVOLUTIONARY EFFECTS PROPOSED BY THE THEORY?

Our proposal is that the shift to calorie-dense, large-package, skill-intensive food resources (Fig. 4) is responsible for the unique evolutionary trajectory of the genus *Homo*. The key

element in our theory is that this shift produced co-evolutionary selection pressures, which, in turn, operated to produce the extreme intelligence, long developmental period, three-generational system of resource flows, and exceptionally long adult life characteristic of our species. We envision two important effects of the change in feeding niche.

First, a long developmental period, parental provisioning, and a large brain are necessary foundations of the skill-intensive feeding niche, and therefore are products of selection as a result of entry into that niche. Our view is that human childhood is elongated by including a period of very slow physical growth, during which the brain is growing, learning is rapid, and little work is done. This is followed by adolescence, during which growth is accelerated so that the brain and body can function together in the food quest. Early adulthood is a time for vigorous work during which resource acquisition rates increase through on-the-job training. Thus, investment in this life history involves three important costs: low productivity early in life, delayed reproduction, and a very expensive brain to grow and maintain. The return from those investments is delayed, with extremely high productivity occurring in the middle and latter portions of the adult period. That return increases with lengthening of the adult life span because the return is realized over a greater period of time. Second, we propose that the shift in the human feeding niche operated directly to lower mortality rates because it increased food package size, which, in turn, favored food sharing, provisioning, and larger group size. Another indirect effect was that the added intelligence and use of tools associated with the feeding niche also lowered predation rates.

Underlying our theory is the hypothesis that these two effects produce co-evolutionary processes of large magnitude. Holding all else constant, ecological changes that increase the benefits of a long developmental period and a concomitant increase in later adult productivity not only produce selection pressures to delay the onset of reproduction, but also pro-

TABLE 2. PRODUCTION OF ENERGY BY MEN AND WOMEN IN FORAGING SOCIETIES

		Daily Adult Production in Calories ^a				Mean Daily Total	% Total Adult Calories	% Total Adult Protein
		Meat	Roots	Fruits	Other			
Onge ^b	men	3919	0	0	81	4000	79.7	94.8
	women	0	968	1	52	1021	20.3	5.2
Anbarra ^c	men	2662	0	0	79	2742	70.0	71.8
	women	301	337	157	379	1174	30.0	28.1
Arnhem ^d	men	4570	0	0	8	4578	69.5	93.0
	women	0	1724	37	251	2012	30.5	7.0
Ache ^e	men	4947	0	6	636	5590	84.1	97.1
	women	32	0	47	976	1055	15.9	2.9
Nukak ^f	men	3056	0	0	1500	4556	60.4	98.6
	women	0	0	2988	0	2988	39.6	1.4
Hiwi ^g	men	3211	2	121	156	3489	79.2	93.4
	women	38	713	83	82	916	20.8	6.6
IKung ^{1,h}	men	2247			974	3221	45.5	44.7
	women	0	348	348	3169	3864	54.5	55.3
IKung ^{2,i}	men	6409				6409	≥50	
	women							
Gwi ^f	men	1612	800	0	0	2412	43.0	78.7
	women	0	0	0	3200	3200	57.0	21.3
Hadza ^k	men	7248	0	0	841	8089	64.8	94.1
	women	0	3093	1304	0	4397	35.2	5.9

^a Edible portion and caloric values were taken from individual studies when available. Otherwise we assumed vertebrate meat at 85% edible, the Ache measured average for animals, and used the following conventions for calories/100 g edible: mammals 150; roots 150; fruits 70; fish 120. When not specified, protein was assumed at 20% by weight for meat and 2% for roots and fruits.

^b Onge: Data come from Bose.¹⁴⁴ We assumed that all food is produced by adults and that men and women make up equal percentages of the reported population. Caloric values (p. 156) and edible portions are taken from Meehan.¹⁴⁵ We assumed that males got all pigs, turtles, fish, and honey, whereas females acquired all crabs, bivalves, and plant products. Total caloric intake seems very low, but the Onge are the smallest foragers in this sample and had very low fertility.

^c Anbarra: Data come from Meehan¹⁴⁵; diet is found in Tables 29–32. It is assumed that women collected 85% of shellfish (p. 125) and that men obtained only birds, fish, mammals, and some shellfish (p. 149). Total person days of consumption are in each table. Women's production days come from Table 27. We assumed an equal number of production days for men.

^d Arnhem: Arnhem land data are from McArthur¹⁵⁰ (pp. 127–128 and p. 138). It is assumed that adults acquired all food, that men obtained only vertebrate meat and honey, and that women acquired all other resources.

^e Ache: Data come from all observed foraging trips between 1980 and 1996 on which KH, HK, and/or MH were present. Data prior to 1984 were published in Hill and coworkers.¹¹ Subsequent data come from forest trips between 3 and 15 days long when nearly all foods consumed were acquired from the forest. All foods were weighed on site and the edible portion was calculated from refuse samples collected after consumption. Caloric values were determined as previously published. Total production of fruits was estimated by multiplying measured collection rates for different age categories times the time spent collecting by each individual. We have made two important modifications of 1984 data because of new field measures: 1) We now estimate the edible portion of wild honeycomb to be only 35% by weight; 2) The edible portion of palm starch is estimated at only 6% by weight, with the caloric value of the edible portion being 3,920 cal/kg. These corrections and new production data have lowered previously published estimates of daily caloric intake.

^f Gwi: Meat production per hunter day is averaged from Silberbauer's¹⁴⁶ one-year observations of a band including 20 men and Tanaka's¹⁴⁷ 180-day observations (p. 111) of 10 men. We estimate Silberbauer's band to contain 20 men and 24 women because there were 80 individuals, 46.5% of whom were male and 55% were adult (p. 286, 287). For live weight meat, we assume 85% edible weight containing 1,500 cal/kg. Plant production for adult women is estimated at the observed per-capita consumption, 800 g/consumer day times 80/24 (the ratio of the total population to adult women) times 1,500 cal/kg raw plant, times 80% collected by women¹⁴⁷ (p. 70). Men are assumed to have produced 20% of the plant calories. Meat consumption per capita is the average from Tanaka¹⁴⁷ (p. 70) and Silberbauer¹⁴⁶ (p. 446). We assumed that Tanaka's raw weights are 85% edible; we also assume 1,500 cal/kg edible meat for both studies. Plant consumption is reported to be 800 g/person in both studies¹⁴⁷ (p. 70),¹⁴⁶ (p. 199). We assume that this is equally split between roots and melons, with a mean caloric value of 1,500 cal/kg raw weight. Man days hunting are reported for both studies, but calculations of the sample size of women's production and per-capita consumption are not specified in either study.

^g Hiwi: Data come from a sample of days between 1985 and 1988 when KH and MH resided with the Hiwi and weighed all food produced by a sample of camp members. Details of calculations of edible portion and food value are published in Hurtado and Hill.^{12,148}

^h IKung¹: All data on adult production and per-capita consumption are from Lee⁴² (pp. 260–271). Women's plant production (non-mongongo) was assumed to be evenly split between roots and fruits.

ⁱ IKung²: Data are from Yellen⁴³ as calculated in Hill¹⁴⁹ (pp. 182–183). Edible portion and caloric value are the same as in Lee.⁴² Only hunting data are recorded. In order to estimate per-capita consumption, adult men and women are assumed to comprise equal percentages of the band members. The percentage of the diet from meat is calculating assuming total consumption of 2,355 calories per person day, as per Lee.⁴²

TABLE 2. (CONTINUED)

- ^j Nukak: Data come from Politis¹⁵¹ (chapter 4). We assume that all food was produced by adults and that men and women make up equal percentages of the population. Edible portions and caloric values for foods come from similar Ache resources. Fruits show edible portions varying from 21% for fruits brought in and weighed with the stalk to 40% for fruits without the stalk collected in baskets. Caloric values of fruits ranged from 600 cal/kg for sweet pulpy fruits to 1,430 cal/kg for oily palm fruits. Other resources were equivalent to common Ache and Hiwi resources.
- ^k Hadza: Data on the daily caloric production of children are from Blurton Jones, Hawkes, and O'Connell.¹⁴ We assumed that 61% of the calories produced come from fruit and the remainder from roots, as for youngest girls.⁶ Daily production of women taken from Hawkes, O'Connell, and Blurton Jones.⁶ We multiplied in-patch rates by time foraging for each season (both in Table 1), and the proportion of time in patch (60% root, 66% berry) (Hawkes personal communication and Hawkes, O'Connell, and Blurton Jones,⁶ p. 350), equally weighting production in dry and wet seasons. Ekwa roots are calculated as 88% edible (Hawkes, personal communication) and 850 cal/kg edible (Hawkes, O'Connell, and Blurton Jones,⁶ p. 691). Fruits are assumed to be 50% edible and have a caloric value of 2,500 cal/kg edible⁴² (pp. 481, 484 for *grewia* sp. berries). Meat acquisition is 4.89 kg/day for adult men (over age 18) and assumed to have a caloric value of 1,500 cal/kg with the discounting for the edible portion.⁷ Honey production was assumed to be 0.78 kg/man-day for males over age 18¹⁵ (p. 86), with 35% edible and 3,060 cal/kg (as for the Ache). All food production by age and sex category was weighted by the probability of survival to that age for the Hadza,¹⁶ then divided by the total of all survival probabilities to obtain the expected per-capita consumption. The estimate of total per-capita consumption is very high, probably in part because actually sampled camps contained more juvenile consumers than the life table implies (Hawkes, personal communication). However, we cannot correct the estimate of daily consumption without a complete age-sex breakdown of the sampled camps, which currently is not available.
- ^l Chimpanzee diet: We use the Gombe diet from Goodall⁷⁶ (Fig. 10.1). The absolute amount of meat in the diet is from Wrangham and Riss.²² Kibale plant percentages are from Wrangham, Conklin-Brittain, and Hunt.⁹⁷ The Kibale meat percentage is from Wrangham and coworkers.¹⁵² The Mahale diet is taken from Hiraiwa-Hasegawa.²⁵ The absolute amount of meat in the diet was calculated from Uehara,¹⁵³ assuming adult prey at 13 kg and juvenile prey at 6 kg, on average, the percentage of adult prey was taken from Stanford.¹⁵⁴ For Tai forest chimpanzees, the absolute amount of meat in the diet was calculated from Boesch and Boesch²⁰ (Table 7.4).

duce selection pressures to invest more in survival during both the juvenile and adult periods. At the same time, ecological changes that lower mortality rates during the juvenile and adult periods also produce selection pressures that favor a longer juvenile period if it results in higher adult productivity. If both types of change occur (increased payoffs for time spent in development and lower mortality rates), great changes in both mortality rates and time spent in development may result. Furthermore, if those changes are accompanied by large increases in productivity after adulthood is reached, we expect additional increases in time spent in development and in survival rates. Our proposal is that the skill-intensive feeding niche, coupled with a large brain, is associated with a significant amount of learning during the adult period.

To test this hypothesis, we developed a model to determine whether or not natural selection would actually result in co-evolution of the developmental period and the life span. This model builds on two bodies of theory, life-history theory in biology and human-capital theory in economics. Life-history theory is based on the premise that organisms face trade-offs in the allocation of their time and effort. Gadgil and Bossert² offered the

first explicit treatment of allocations trade-offs with respect to reproduction and longevity. They postulated that during the life course selection acts on the allocation of energy to

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each of three competing functions: reproduction, maintenance, and growth. Energy allocated to reproduction will necessarily reduce the quantity available for maintenance and growth.

Maintenance and growth may be seen as investments in future reproduction, for they affect both the probability that an organism will survive to reproduce in the future and the amount of energy it will be able to harvest and transform into reproduction. Thus, one fundamental trade-off is between current and future reproduction.

Human-capital theory in economics^{18,19} is designed to analyze investments in education and training through the course of life. Central to this theory is the notion of foregone earnings: Time spent in education and training reduces current earnings in return for increased earnings in the future. The economic trade-off between current and future earnings is directly analogous to the trade-off between current and future reproduction in biology.

Charnov,^{1,9} building on earlier work on optimal age at first reproduction, developed a mathematical model of the trade-off between growth and reproduction for mammals. His model is designed to capture determinate growth, in which an organism has two life-history phases after attaining independence from its parents. These are a prereproductive growth phase in which all excess energy, remaining after maintenance requirements have been met, is allocated to growth and a

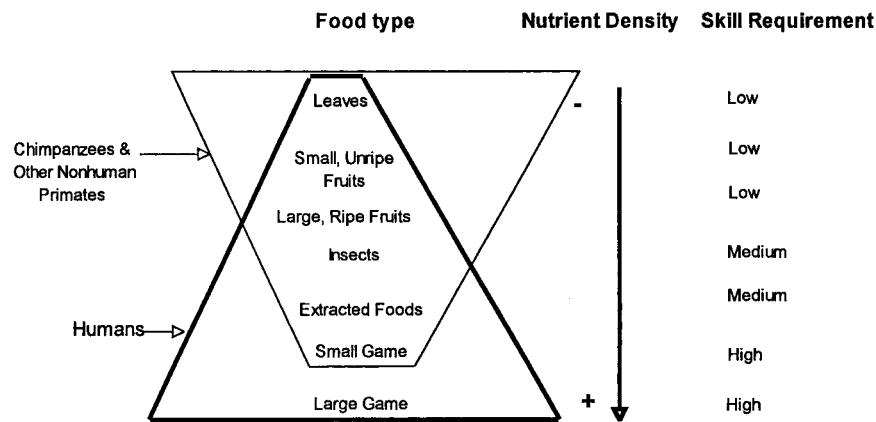


Figure 4. The feeding ecology of humans and other primates.

reproductive phase in which all excess energy is allocated to reproduction. By growing, an organism increases its energy capture rate, and thus increases reproductive rate. During adulthood the fundamental trade-off is between the expected length of the reproductive span (which is shorter with each additional year spent growing, because of the increased probability of dying before reproducing) and the adult reproductive rate (which is higher with every year spent growing because of increased energy stored in the form of adult body mass). The model predicts the amount of time mammals will grow before switching to the reproductive phase by selecting the time that maximizes expected energy for reproduction over the life course.

Here we extend Charnov's model in three ways. First, we broaden the concept of growth from body size alone to include all investments in development. Development can be seen as a process in which individuals and their parents invest in a stock of embodied capital, a term that generalizes the concept of human capital to all organisms. In a physical sense, embodied capital is organized somatic tissue. In a functional sense, embodied capital includes strength, immune function, coordination, skill, knowledge, and social networks, all of which affect the profitability of allocating time and other resources to alternative activities such as resource acquisition, defense from predators and parasites, mating competition, parenting, and social dominance. Because such stocks tend to depreciate with time due to

physical entropic forces and direct assaults by parasites, predators, and conspecifics, allocations to maintenance efforts, such as feeding, cell repair, and vigilance, can also be seen as investments in embodied capital. In our model, the energy capture rate increases with embodied capital (that is, time spent in development).

Second, in Charnov's model, organisms have no control over mortality rates, which are exogenously determined; the only variable of choice for the organism is age at first reproduction, or time spent in development. In our model, the organism can exercise control over mortality rates by allocating energy to mortality reduction. We include this second choice variable to determine if time invested in development and energy allocated to mortality reduction co-evolve. Our theory predicts that increased investment of time in development due to the exploitation of difficult-to-acquire, high-quality resources selects for increased longevity or lower mortality rates. Third, our model allows learning to continue after physical growth has ceased to analyse the effects on the increase in return rates from foraging during the adult period (see Figs. 2 and 3) as a consequence of "on-the-job" training.

Thus, the model has two choice variables upon which selection can act: age at first reproduction, a proxy for time spent in development and physical growth, and allocation of energy to lowering mortality. It also has three ecological parameters: factors affecting the pay-offs to investments in development, factors affecting mor-

talidity rate, and the growth in productivity after adulthood due to learning. The formal model is presented in Box 1.

The six main results of the mathematical model confirm the co-evolutionary selection pressures predicted by the theory. Ecological factors increasing the productivity of investments in developmental embodied capital (in the context of the present theory, a skill-intensive foraging niche) increase both time spent as a juvenile and investments in mortality reduction. Ecological factors that lower mortality rates increase both time spent in development and investment in mortality reduction. Finally, the greater the growth rate in production during the adult period, due to large brains and "on-the-job" training, the more it pays to invest in development and mortality reduction. These results all show that investments in development and investments in mortality reduction and longevity co-evolve.

EMPIRICAL TESTS OF THE THEORY

Composition of the Diet

Figure 4 illustrates our proposal about the differences between the diets of nonhuman primates and humans. While the diets of nonhuman primates vary considerably by species and by local ecology, the inverted triangle in Figure 4 represents the greater importance of lower quality, easier-to-acquire foods in the diets of most nonhuman primates (excluding insectivores). The upward-pointing triangle in Figure 4 represents the greater importance of large-package-size, nutrient-dense, difficult-to-acquire foods in human diets.

Table 3 presents data on the diets of ten foraging societies and four chimpanzee communities for which caloric production or time spent feeding were monitored systematically. As far as we are aware, this is a complete sample of the available data. The diet is subdivided into vertebrates, roots, nuts and seeds, other plant parts (such as leaves, flowers, and pith) and invertebrate resources. The diets of all modern foragers differ considerably from that of chimpanzees. Measured in calories, the major component of forager

Box 1. A Formal Model of Natural Selection on Age at First Reproduction and Investments in Mortality Reduction

The model treats two phases of the life course, the juvenile and adult periods. The juvenile period begins after the high mortality phase associated with infancy and weaning, is dedicated to growth and development, and lasts a variable amount of time, t , upon which selection acts. During this time, all energy is invested in either embodied capital (growth and learning) affecting future energy production, P , or in reducing mortality rate, μ . The two choice variables during the juvenile period are its length, t , and the proportion of energy invested in mortality reduction, λ (implying that $\{1 - \lambda\}$ is the proportion allocated to growth and learning). The adult production of energy at the end of the juvenile period, P_a , is determined by t , λ , and the combined ecological effects of the environment, ε , which is assumed to increase energy production (i.e., $\partial P_a / \partial \varepsilon > 0$). We can think of this as composed of two functions, $\Pi(t, \varepsilon)$, which captures the growth in production due to learning, growth, and development, and $\Psi(\lambda)$, which represents the proportional loss in production due to investments in mortality reduction during the juvenile period. Thus, we have $P_a = \rho(t, \lambda; \varepsilon) = \Pi(t, \varepsilon)\Psi(\lambda)$.

The second period is reproductive. During this period, growth in body size ceases and all excess energy is allocated to reproduction. Production grows at some constant rate, g , due to the effects of learning. Thus, production at some age, x , after adulthood, P_x , is $P_a e^{g(x-t)}$.

During both phases, the instantaneous mortality rate, μ , remains constant, at a level determined by the amount of energy production diverted to mortality reduction, λ , and by ecology factors affecting mortality (such as density of predators and diseases), θ , which is assumed to increase mortality rates (i.e., $\partial \mu / \partial \theta > 0$). Thus, $\mu = \mu(\lambda, \theta)$. The net energy available for reproduction at age x during the adult period, $P_{r,x}$, will be equal to total energy production times the proportion allocated to reproduction, $P_{r,x} = (1 - \lambda)P_a e^{g(x-t)}$.

The basic logic of the model is that an organism will maximize fitness by maximizing its lifetime energy allocated to reproduction. By increasing the length of the growth and development phase, t , the adult rate of energy capture increases, but the expected length of the reproductive period, R , decreases. This decrease results from the fact no energy is allocated to reproduction during the growth and development phase, though the organism is still exposed to mortality. Allocations to mortality reduction also have opposing effects. Allocations to growth during the juvenile period and to reproduction during the adult period are reduced by allocations to mortality reduction. Yet lowered mortality increases the length of the reproductive period by increasing the probability of reaching reproductive age and by increasing the expected time from reproductive age to death. Thus, R is determined by both t and λ . If we consider only individuals who survive infancy, R is equal to expectation of adult reproductive years lived, given the probability of dying at each age, x . Thus, the expected number of adult years during which energy is allocated to reproduction is $R = r(t, \mu(\lambda, \theta)) = \int_{x=t}^{\infty} (x - t)\mu e^{-\mu x} dx = 1/\mu e^{-\mu t}$, where $1/\mu$ is the expected adult life span conditional on reaching age t and $e^{-\mu t}$ is the probability of reaching age t , conditional on having survived infancy. The expected energy production during the adult period is $e^{-\mu t}(1 - \lambda)P_a \int_{x=t}^{\infty} e^{(g-\mu)(x-t)} dx$, which is equal to $e^{-\mu t}(1 - \lambda)P_a(\mu - g)^{-1}$ for $\mu > g$ (which we assume to hold true, because expected lifetime income otherwise would be infinite).

Selection is expected to optimize t and λ so as to maximize lifetime energy allocated to reproduction. Thus, we have the following maximization problem:

$$\text{Max}_{t, \lambda, \mu} W = e^{-\mu(\lambda, \theta)t} [1 - \lambda] P_a(t, \lambda, \varepsilon) (\mu(\lambda, \theta) - g)^{-1}. \quad (1)$$

Partially differentiating the fitness function, W , with respect to t and λ , respectively, the following first-order conditions for an optimum are obtained:

$$\frac{\partial P_a}{\partial t} P_a^{-1} = \mu \quad (2)$$

and

$$-\frac{\partial \mu}{\partial \lambda} (t + (\mu - g)^{-1}) = -\frac{\partial P_a}{\partial \lambda} P_a^{-1} + (1 - \lambda)^{-1} \quad (3)$$

Equation 2 for optimal t , taking μ as given, replicates Charnov's¹ result. Optimal t occurs at the age when the proportional increase in adult production due to a small increase in time spent in development (the left hand side of equation 2) is equal to the proportional loss in the probability of reaching adulthood (the right-hand side). The benefits and costs are measured in terms of proportions because fitness is a product of the probability of reaching adulthood and the production rate as an adult.

Equation 3 concerns optimal allocations to mortality reduction, given time spent in development. The left-hand side of the equation is the benefit of a small increase in investment in mortality reduction. It is the proportional increase in reaching adulthood, plus the proportional increase in the adult lifespan, adjusted for the growth in income due to learning, g . The right-hand side is the cost, the proportional loss in production due to increased investment in mortality reduction. This proportional cost is two-fold because allocations during the juvenile period reduce the growth rate and therefore reduce P_a (the first term), while allocations to mortality reduction during the adult period reduce the proportion of adult production allocated to reproduction (the second term).

Differentiating equations 2 and 3 with respect to the ecological parameters, ε , θ , and g , we derive our six main analytical results, confirming the co-evolutionary effects predicted by our theory. $\partial t / \partial \varepsilon$ and $\partial \lambda / \partial \varepsilon$ are both positive. This means that ecological factors increasing the productivity of investments in developmental embodied capital, as indexed by ε , not only increase time spent in development but also increase investments in mortality reduction. $\partial t / \partial \theta$ and $\partial \lambda / \partial \theta$ are both negative, meaning that exogenous or extrinsic increases in mortality, as indexed by θ , reduce both time spent in development and investments in mortality reduction. Conversely, ecological factors that lower mortality rates increase both time spent in development and investment in mortality reduction). Finally, $\partial t / \partial g$ and $\partial \lambda / \partial g$ are both positive, showing that the greater the growth rate in production during the adult period due to "on-the-job" training, as indexed by g , the more it pays to invest in development and mortality reduction. (A formal proof of the six results was developed by Arthur Robson and is available from the authors). These results all show that investments in development and investments in mortality reduction/longevity co-evolve.

diets is vertebrate meat. This ranges from about 30% to 80% of the diet in the sampled societies, with most diets consisting of more than 50% vertebrate meat (equally weighted mean = 60%). The emphasis on vertebrate meat would be even more clear if any high-latitude foraging societies were included in the sample. In contrast, chimpanzees spend only about 2% of their feeding time eating meat. Unfortunately, the diet of wild primates is not usually expressed in calories, as is that of human foragers. Field workers studying nonhuman primates use time spent feeding on specific foods as the closest approximation of energy acquired and rarely either measure ingestion rate or calculate calorie intake. The absolute intake of meat per day also varies tremendously: Chimpanzee per capita meat intake is estimated at about 10 to 40 g per day, while human meat intake ranges from about 270 to 1,400 g per person per day. Although it is true that chimpanzee males eat much more meat than do females and juveniles,^{20–22} we conclude that, in general, members of foraging societies eat more than ten times as much meat as do chimpanzees.

The next most important food category in our forager sample is roots, which make up an average of about 15% of the energy in the diet and were important in about half the societies in our sample. In contrast, the chimpanzee diet is primarily composed of ripe fruit, which accounts for over 60% of feeding time. Only two foraging societies ate large amounts of ripe fruit, the Gwi San of the Kalahari desert, who consume melons for water and nutrients during much of the year, and the Nukak of Colombia, who extensively exploit tropical palm fruits, which, however, are difficult to acquire. Other plant products are an important secondary food for chimpanzees, making up about 25% of observed feeding time. This category is unimportant for the foragers in our sample.

The data suggest that humans specialize in rare but nutrient-dense resource packages or patches (meat, roots, and nuts), whereas chimpanzees specialize in ripe fruit and plant parts with low nutrient density. These

differences in the nutrient density of foods ingested are also reflected in human and chimpanzee gut morphology and food passage time. The chimpanzees gut is specialized for rapid processing of large quantities and low-nutrient, bulky, fibrous meals.²³ However, a stronger contrast is apparent when we consider how the resources are obtained. We have categorized all foods into three types. Collected foods are those that can be

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obtained and eaten simply by gathering them from the environment. Extracted foods are non mobile but are embedded in a protective context from which they must be removed. Such foods may be underground, in hard shells or associated with toxins. Hunted foods include mobile resources that must also be extracted and processed before consumption. Collected resources include fruits, leaves, flowers, and other easily acces-

sible plant parts. Extracted resources include roots, nuts and seeds, most invertebrate products, and plant parts that are difficult to extract, such as palm fiber or growing shoots. Hunted resources include all vertebrates and some mobile invertebrates.

Table 3 shows a breakdown of forager and chimpanzee foods according to our three acquisition categories. Chimpanzees obtain an average of about 95% of their diet from collected foods, whereas the foragers in our sample obtain an average of 8% of their food energy from collected resources. On the other hand, foragers obtain about 60% of their food energy from hunted resources and about 32% from extracted resources, whereas chimpanzees obtain about 2% of their food energy from hunted foods and about 3% from extracted resources. While these categories may be somewhat rough, it is clear that humans are much more dependent on resources that can be obtained only by complicated techniques. Thus, the dietary data are consistent with our theoretical model. Humans appear to be more dependent on resources that require skill and learning to acquire.

The Age Profile of Acquisition for Collected and Extracted Resources

The proposition that difficulty of acquisition predicts the age profile of food production can be tested in two ways, by looking at the *daily* amount of different resource types produced by individuals of different age and by observational and experimental measures of *hourly* rates of acquisition of different resource types by individuals of different ages. The daily data are determined by both time allocation and rates of return per unit of time spent on a resource, whereas the hourly data are based exclusively on rates of return. Both sources of data support the proposition that juveniles cannot easily obtain extracted and hunted foods.

Beginning with the daily data, Figures 5 and 6 show, respectively, the daily caloric contribution of various food types acquired by Ache and Hiwi males and females as a function of age. The upper panels represent the

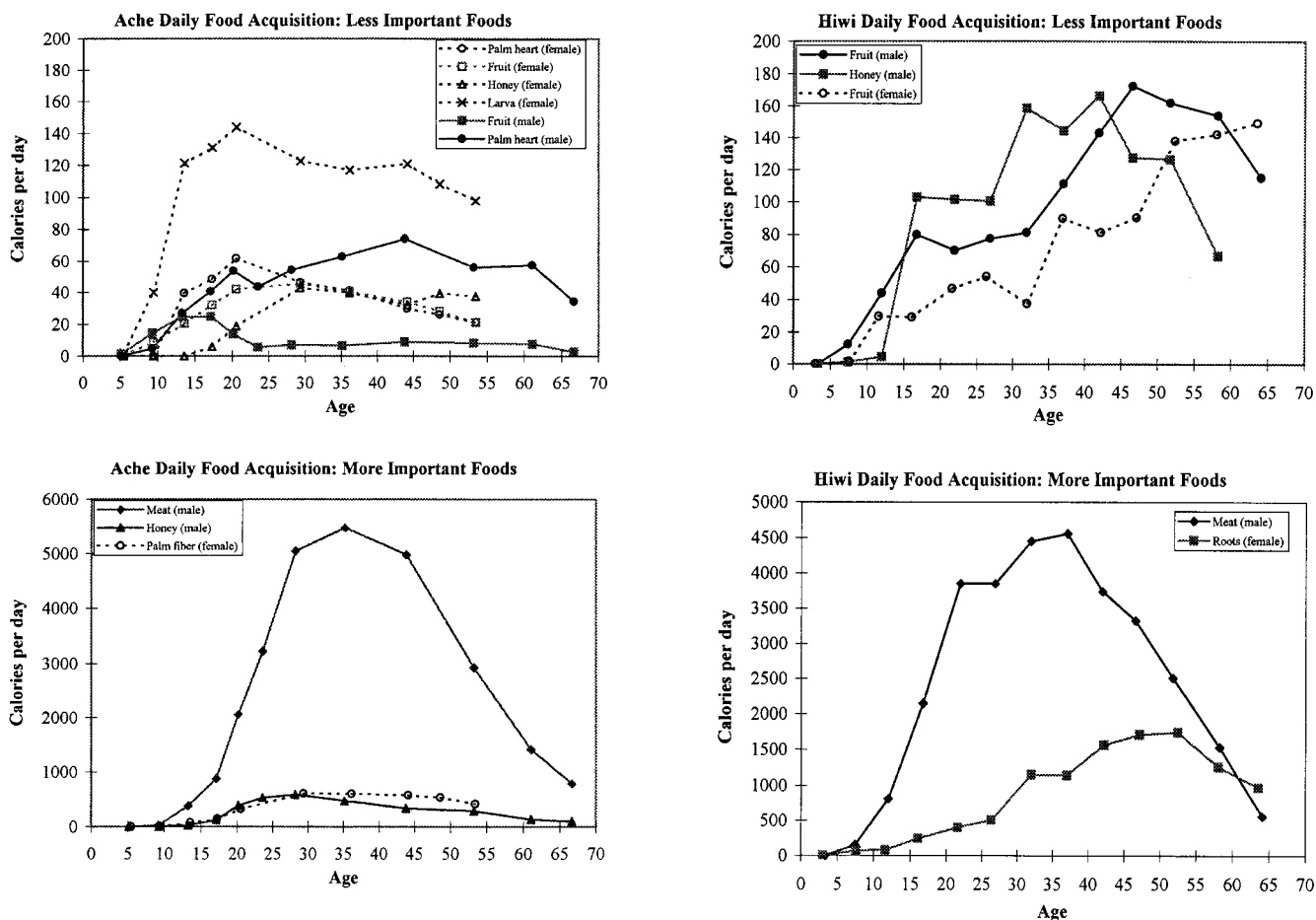


Figure 5 and 6. Age-sex specific daily energy acquisition is calculated as described for Figure 2 and Tables 2 and 3. Mean daily acquisition for each resource class was calculated by summing all the calories acquired for individuals of that age-sex category and that resource class, then dividing by all person days sampled in the relevant age category. Y values are plotted at the mean age for each class analyzed.

calorically less important foods (those for which daily production is less than 200 kcal/day); the lower panels represent the more important foods (>200 kcal/day). Among young Ache, both males and females acquire only fruits. Both sexes reach their peak rates of daily fruit acquisition in their mid- to late teens. Extracting palm hearts requires strength and some skill (about three minutes of chopping in the right spot); daily palm heart acquisition is asymptotic for both sexes by the age of 20 years. More skill and learning are required to extract honey or palm starch (knowing how to open a “window” to the resource and then extract it). The daily acquisition of these resources does not peak until individuals are in their late 20s. Daily returns from hunting do not peak until individuals are about 35 years old.

Hiwi foragers show similar production patterns with age, except that daily fruit acquisition becomes as-

ymptotic at later ages. Hiwi fruit collection is more complicated because many trips entail walking through the night to distant groves, followed by a return trip of 10 to 20 km with a heavy load of fruit. Daily honey extraction rate also reaches its peak level when these foragers are in their early 30s (these are very small nests of native bees). Female root-production rates increase four-fold from age 20 to age 40, but men’s meat production does not peak until they are about age 35.

The fact that forager children, like chimpanzees, primarily acquire ripe fruits is supported by additional data. Among the Ache, children acquire five times as many calories per day during the fruit season as they do during other seasons of the year.²⁴ Among the Hadza, adolescent girls acquire 1,650 calories per day during the wet season, when fruits were available, and only 610 calories per day during the dry season, when fruits are not

available. If we weight the data for the wet and dry season equally, teenage Hadza girls acquire 53% of their calories from fruits, compared to 37% and 19%, respectively, for reproductive-aged women and postreproductive women (all calculated from Hawkes and coworkers.⁶) Hadza boys, like Ache and Hiwi boys, switch from easier tasks, such as fruit collection, shallow tuber extraction, and baobab processing to honey extraction and hunting in their mid- to late teens.^{13,14} Chimpanzee juveniles also focus on more easily acquired resources than do adult chimpanzees. Juvenile chimpanzees practice difficult extraction activities such as collecting termites, fishing for ants, or nut cracking less than adults do.^{20,26} Hunting is strictly an adult or subadult activity.^{20,21,27}

Hourly return rates provide further evidence that important human food resources require long periods of learning and skill development. Ob-

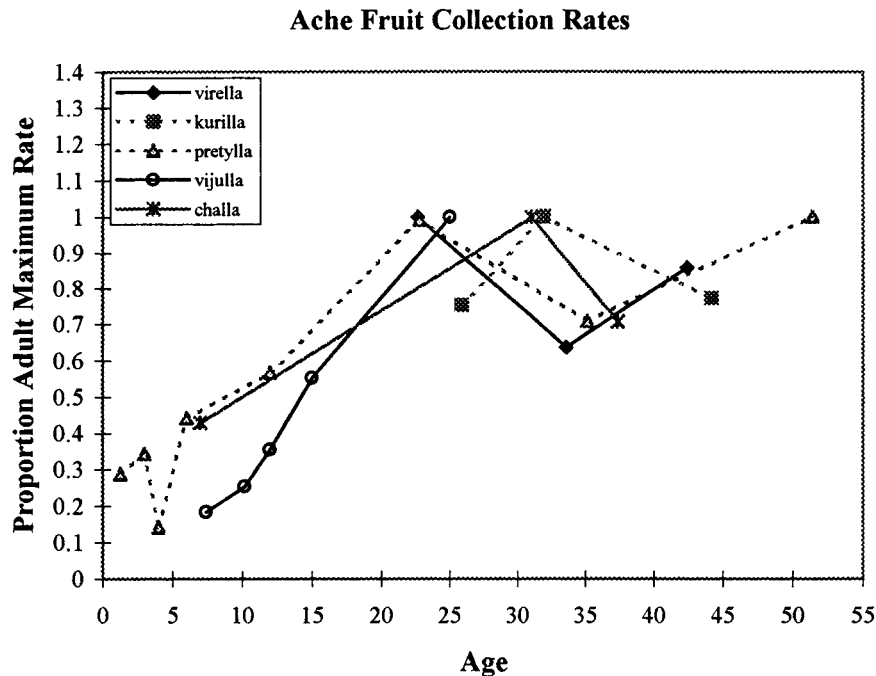


Figure 7. All Ache data, including timed counts of fruits acquired per minute, were analyzed for each age category. The mean plotted is the average from each independent monitored count for a given age class of acquirers. Fruits other than those that are simply collected from the ground or low branches were not included in the analyses. Y values are plotted at the mean age for each class analyzed.

servations of Ache fruit collection show that foragers generally acquire the maximum observed rate by about age 20 (Fig. 7). Some fruits (for example, pretylla) that are simply picked from the ground are collected by children as young as one-and-a-half to three years at 30% of the adult maximum rate. For fruits such as vijulla, which must be picked off branches, children do not reach 50% of the adult maximum rate until age 15 (Fig. 7). As mentioned earlier, fruit collection by the Hiwi (Fig. 8), unlike that done others, is labor-intensive and requires travel to distant food sites. Both males and females reach maximum return rates by about age 25.

Hadza data also show competent fruit collection by children. The Kongoro berry collection rate of young married girls is equal to the adult women's rate.⁶ Baobab collecting and processing seems to reach 50% of the adult rate by about age 12.¹⁴ Baobabs are an interesting food resource because they are both collected and extracted. While they can easily be picked off the ground, much more food energy is obtained when the pith is extracted with pound-

ing and water. Young children do not practice these activities, whereas older children do.¹⁴

In contrast to the hourly acquisition rate of fruits, that of extracted resources often increases through early adulthood as foragers acquire necessary skills. Data on Hiwi women show that their root-acquisition rates do not become asymptotic until the women are about age 35 to 45 years (Fig. 8). The root-acquisition rate of 10-year-old girls is only 15% of the adult maximum. For Hiwi males, the honey-extraction rates peak at about age 25. Again, the extraction rate of 10-year-olds is less than 10% of the adult maximum. Experiments done with Ache women and girls clearly show that the young adults are not capable of extracting palm products at the rate obtained by older Ache women (Fig. 9). Girls take longer than women to cut palms because they lack strength and because they cannot judge whether a palm will fall to the ground or get stuck in nearby tree branches. Girls take longer than women to extract the growing shoot from the palm after it is on the ground because this task requires strength and knowing where to

cut across the palm leaf stalks. Girls take longer to extract the starchy fiber from the trunk of a downed palm because they do not know how to cut open a window nor how most efficiently to pound the fiber away from the hard outer trunk wood. When these components activities of palm extraction are combined, Ache women do not reach peak return rates until their early 20s (Fig. 9).

Supporting data are also available from other groups. !Kung (Ju/'hoansi) children crack mongongo nuts at a much slower rate than adults do.²⁸ Bock²⁹ has shown that nut-cracking rates among the neighboring Ham-bukushu do not peak until about age

Hourly return rates provide further evidence that important human food resources require long periods of learning and skill development. Observations of Ache fruit collection show that foragers generally acquire the maximum observed rate by about age 20.

35. Hadza women, however, appear to obtain maximum root-digging rates by early adulthood,⁶ perhaps because they obtain a good deal of practice throughout childhood^{13,14} and thus require only adult strength in order to produce at adult rates.

Casual ethnographic observation supports the generalization that fruit collection is easily learned, extraction skills require more time to develop, and hunting is the most difficult foraging behavior. Anthropologists working with modern foragers often participate in fruit collection and can rapidly achieve aboriginal return rates. Some types of extraction can also be

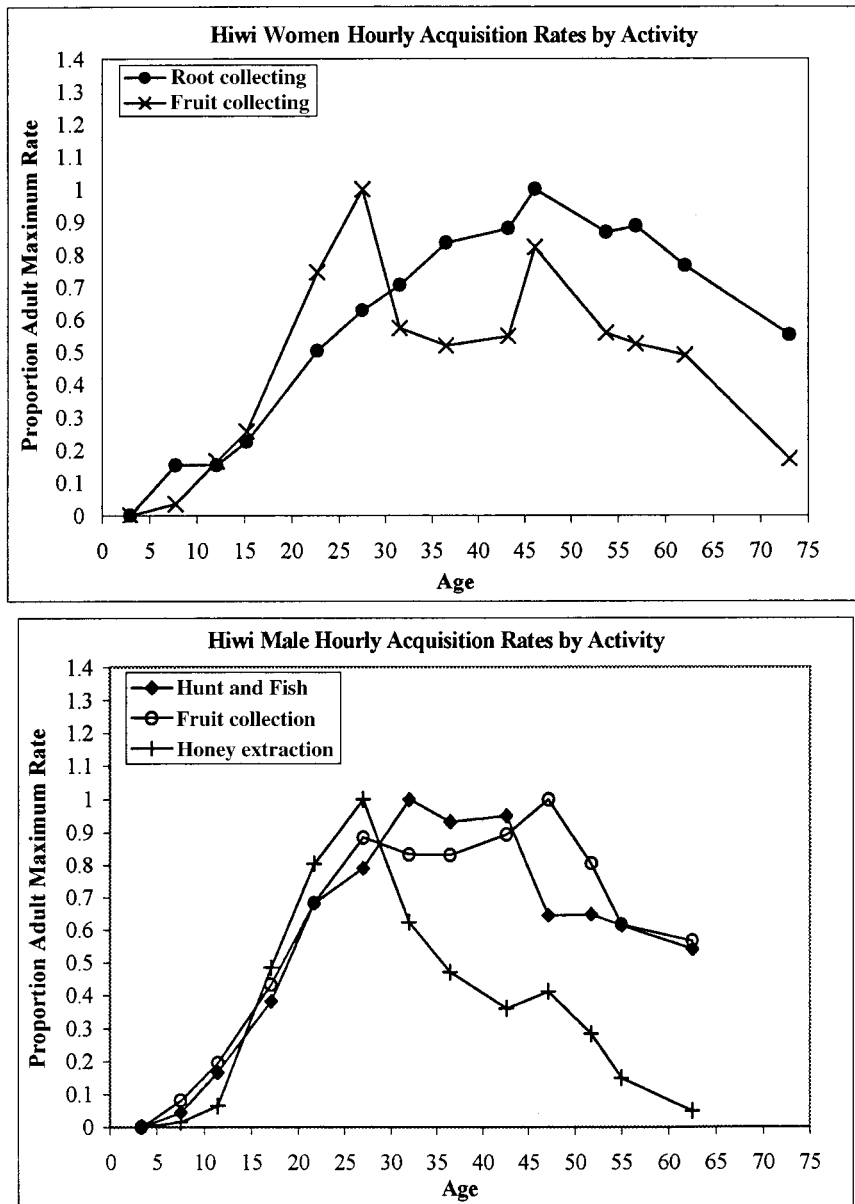


Figure 8. Because Hiwi foragers target specific resources when they leave their central camp, we recorded all time dedicated to foraging for different resource types over the sample period. Total energy production for each resource type and age-sex class was divided by the total number of hours reported to be out-of-camp foraging for that resource type to obtain the hourly return rate from foraging for that resource type. The time foraging included in-patch pursuit of resources as well as walking time to and from the patch. Y values are plotted at the mean age for each class analyzed.

mastered with practice. One of us (KH) chops down palms as fast as Ache women do and can extract the heart at a slightly slower rate. However, despite some practice, KH has not achieved the rate of palm-fiber extraction of Ache women. We know of no ethnographers who successfully dig roots or crack nuts at the rate of members of their study populations.

Indeed, the same patterns are seen among captive animals released into the wild. Animals that have grown to adulthood in captivity can be successfully released into the wild if their feeding niche is simple (for example, if they are herbivores). However, the success rate for carnivores and apes with complex feeding strategies is much lower.

Hunting and the Role of Men in Human Reproduction

Male behavior plays a distinctive role in human life histories in two ways. First, hunting, the primary subsistence activity of adult men, is the most learning-intensive foraging strategy practiced by humans. Second, unlike most higher primates, men play a major role in the energetics of human reproduction.

We know of no ethnographers who successfully dig roots or crack nuts at the rate of members of their study populations. Indeed, the same patterns are seen among captive animals released into the wild. Animals that have grown to adulthood in captivity can be successfully released into the wild if their feeding niche is simple (for example, if they are herbivores). However, the success rate for carnivores and apes with complex feeding strategies is much lower.

Although a detailed quantitative analysis of the learning process involved in human hunting has not yet been conducted, it is clear that human hunting differs qualitatively from hunting by other animals. Unlike most animals, which either sit and wait to ambush prey or use stealth and pursuit techniques, human hunters use a wealth of information to make context-specific decisions, both during the search phase of hunting

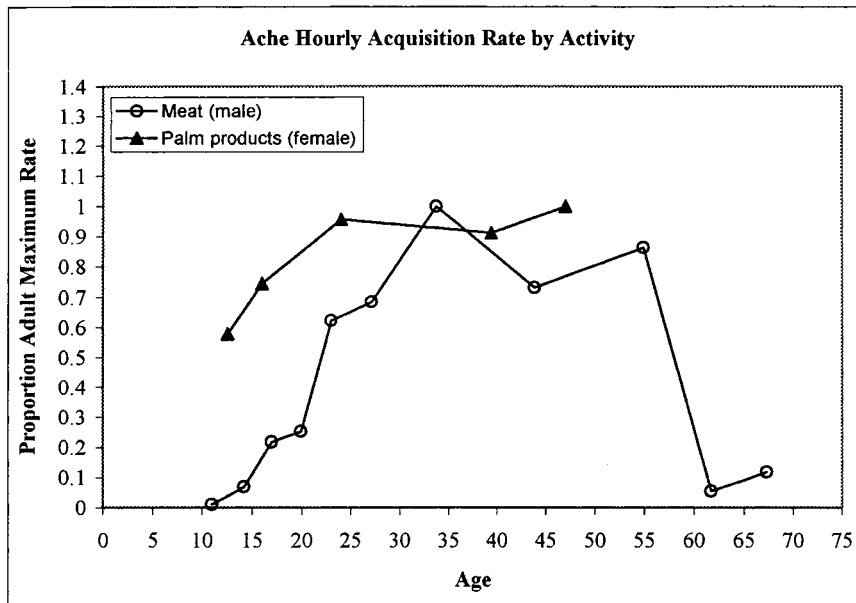


Figure 9. Data from experiments in which Ache females of different ages were asked to chop down a palm tree, extract its growing shoot (heart), and extract palm starch from the palm for at least $\frac{1}{2}$ hour. Y values are plotted at the mean age for each class analyzed. Age-specific hunting returns are based on measured kg of live weight of game acquired by Ache males between 1980 and 1984 and measured out-of-camp foraging time for males during the same time period. Y values are plotted at the mean age for each class analyzed. Differences between age categories may be due to differences in encounter rates with game or success in pursuits of game after encounter.

and then after prey is encountered. Specifically, information on ecology, seasonality, current weather, expected animal behavior, and fresh animal signs are all integrated to form multivariate mental models of encounter probabilities that guide the search and are continually updated as conditions change.³⁰ Various alternative courses of action are constantly compared and referenced to spatial and temporal mental maps of resource availability.³⁰ This information is collected, memorized, and processed over much larger spatial areas than chimpanzees ever cover. For example, interviews with Ache men show that fully adult men (those over the age of 35 years) had hunted in nearly 12,000 km² of tropical forest during their lives. Almost all foragers surveyed use more than 200 km² in a single year, and many cover more than 1,000 km² in a year (Table 4.1 in Kelly³¹). Male chimpanzees, on the other hand, cover only about 10 km² in a lifetime.^{32,33}

After potential prey are encountered, humans employ a wide variety of techniques to obtain them, using astounding creativity. Here are just

some examples that Hill, Hurtado and Kaplan have seen among the Ache, Hiwi, Machiguenga, and Yora: Arbooreal animals have been shot with arrows from the ground or a tree, driven by climbing, shaken down from branches, frightened into jumping to the ground, brought down by felling a tree with an axe, lured by imitated calls, lured by making captured infants emit distress calls, captured by the spreading of sticky resin on branches to trap them, and captured by scaffolding constructed from tree branches and vines. Ground-dwelling prey are shot with arrows, driven to other hunters or capture devices, run down upon encounter, slammed to death against the ground, strangled at the neck, or suffocated by stepping on them while they are trapped in a tight spot. Burrowing prey are dug out, chopped out of tree trunks, stabbed through the ground with spears, frightened to the point at which they bolt from the burrow, smoked out, and captured by introducing a lasso through a small hole. Aquatic prey are shot on the surface or below it, driven into traps, poisoned, discovered on

muddy bottoms by systematically poking the bottom of a pond, and speared underwater by random thrusts in drying lakes. The widely varied kill techniques are tailored to a wide variety of prey under a wide variety of conditions. Although all groups probably specialize in the most abundant and vulnerable prey in their area, the total array of species taken is impressive, and probably is much larger than that of most, if not all, other vertebrate predators. For example, from 1980 to 1996 our sample of weighed prey taken by the Ache

... it is clear that human hunting differs qualitatively from hunting by other animals. Unlike most animals, which either sit and wait to ambush prey or use stealth and pursuit techniques, human hunters use a wealth of information to make context-specific decisions, both during the search phase of hunting and then after prey is encountered.

included a minimum of 78 different mammal species, at least 21 species of reptiles and amphibians, probably more than 150 species of birds (more than we have been able to identify) and more than 14 species of fish. Moreover, human hunters tend to select prey that is in prime condition from the perspective of human nutritional needs rather than prey made vulnerable by youth, old age, or disease, as do many carnivorous animals.^{34,35}

The skill-intensive nature of human hunting and the long learning process

involved are demonstrated dramatically by data on hunting return rates by age. Hunting return rates among the Hiwi do not peak until the men reach the age of 30 to 35 (Fig. 8). The acquisition rates of 10-year-old and 20-year-old boys reach, respectively, only 16% and 50% of the adult maximum. In the 1980s, the hourly return rate for Ache men peaked when they were in their mid-30s (Fig. 9). The return rate of 10-year-old boys is now about 1% of the adult maximum, and that of 20-year-olds is still only 25% of the adult maximum.

It is not surprising that no ethnographer has ever described being able to hunt at a rate equivalent to that of study subjects. Indeed, most who hunt make kills only after being led to the game animal by a competent hunter, and then generally with a firearm (as is the case with recreational big-game hunters). These patterns also mirror the effects of acculturation in most groups. Foragers who grow up in settled communities can often collect fruits and other plant resources at rates equivalent to those obtained by older individuals who grew up in the bush (see, for example, Blurton Jones and colleagues²⁸ on the !Kung). But most young Ache men who have grown up on reservation settlements cannot hunt using traditional technology nearly as successfully as older men who grew up in the forest (unpublished data).

Chimpanzees too, appear to require many years to learn successful hunting techniques. Older males are more likely than younger adult males to ambush prey during a group hunt and perform more complicated maneuvers during the hunt.²⁰ (But see Stanford.²¹)

Although the learning process is long, investments in hunting ability by human males allow them to be highly productive as adults. The comparative analysis of diets and productivity among foragers shows that men play a major role in the energetics of human reproduction. For example, among the Ache the total expected net caloric production (food produced minus food consumed) from age 18 to death is +21,638,000 calories for males and -924,000 calories for females. The corresponding figures for the Hiwi are

+11,151,000 for males and -3,096,000 for females. Even among the Hadza, where women play a much greater role in subsistence production, males provide as least as much support for reproduction as females do, if not more. While the estimates may require revision when researchers complete their analysis of age-specific production among the Hadza, our initial approximation, based on published data, is that over the entire expected life course (including the probability of survival to each age), net production for Hadza males is +16,671,000 calories, while that of females is only +3,352,000 calories. Table 2 shows

Although the learning process is long, investments in hunting ability by human males allow them to be highly productive as adults. The comparative analysis of diets and productivity among foragers shows that men play a major role in the energetics of human reproduction.

that men provide more food energy per day than women do in all but one or two of the ten foraging societies for which there is quantitative data. Men also provide the vast majority of protein in the diet. This is critical, since higher daily protein intake increases weight gain,^{36,37} immune function response,³⁸ and survival.^{39,40}

The fact that men produce more food than women do in most low-latitude foraging societies is not conventional wisdom. This is a result of the influence of Richard Lee's^{41,42} pioneering study of the !Kung (Ju/'hoansi), which showed that women provide more food than men do. There

has been a tendency to generalize those results to all foraging societies. Table 2 shows that those results are not general; it also shows the possibility that weaknesses in Lee's study have been misleading for the !Kung as well. Lee's sample covered only 28 days of one month of 1964, and on two of those days he took women out collecting mongongo nuts in his vehicle, thus inflating the collected portion of the diet and female return rates. During much of the year, mongongo nuts are not abundant, nor are they as abundant at other !Kung study sites as at the Dobe site. Another study of !Kung food production shows much higher hunting success than Lee reported. Yellen⁴³ provided data showing that !Kung men acquired twice as much meat per day when they were in bush camps than they did in the permanent dry-season waterhole settlement where Herero raised cattle, which probably had a depressive effect on game densities. Yellen's sample of person consumption days was larger than Lee's and covered all months of the year. The daily meat consumption in Yellen's sample was about 1,600 calories per capita, which would represent 68% of all calories if total food consumption was the same as Lee reported. In addition, both Lee and Draper (p. 262 in Lee⁴²) found that !Kung men spent more hours per week on food acquisition than did !Kung women.

The fact that humans were successful in colonizing high-latitude ecologies where plant foods are not abundant and are available only for short periods also demonstrates the important role that men play in the energetics of reproduction. It is also interesting that many Neanderthal and early *Homo sapiens* are found at high latitudes where plant consumption was minimal and, in some cases, where even fuel and residential construction were provided by animal products (see Hoffer⁴⁴ for a review of east European sites). Moreover, some archeological sites beginning with *Homo ergaster* (for example, Boxgrove, England⁴⁵) contain super-abundant animal remains and evidence of spears and other hunting tools, but no evidence of plant consumption. More recent low-latitude archeological as-

semblages also often have extremely dense bone scatter, which suggests high meat consumption. At Kutikina, Tasmania, for example, bone fragments comprise nearly 20% of the weight per cubic meter of some archaeological strata.⁴⁶ On the other hand, complete assessment of plant pollen at some assemblages, among them Tamar Hat on the north coast of Africa,⁴⁷ suggests no edible plant species, despite dense faunal scatters. Such evidence suggests that adult males have often been the main, and sometimes the only food providers in foraging societies.

In another vein, the Hadza research team^{15,48,49} has argued that men do not play a major role in the energetics of human reproduction because the vagaries of hunting luck render meat an unreliable and indefensible resource. Two separate issues must be distinguished in evaluating this argument. The first concerns the sources of the caloric and nutritional subsidization of human reproduction. The second issue is whether or not the proceeds from hunting preferentially support the spouse and children of the hunter.

With respect to the first issue, the data we present clearly demonstrate that hunted foods provide a substantial proportion of the energy and essential nutrients consumed by women and children. The fact that humans in some places depend on hunting for almost 100% of their energy needs suggests that this can be a reliable means of subsistence because they have developed cultural solutions to the variability problem. The main solutions are food sharing and, to a lesser extent, food storage. The second issue is more complex and, as yet, unresolved. Hawkes and associates⁴⁹ claim that prey items are not controlled or owned because they are impossible to defend. Thus, males do not provision their families, but simply provide equally for everyone in a band by hunting. There are, however, no data to support this interpretation, other than the observation of sharing itself. In fact, there is considerable evidence that carcasses can be defended when conditions do not favor food sharing. The Ache of Paraguay, who supplied the initial data for the inde-

defensibility view of sharing share game resources widely when on long foraging treks, yet withhold even large game, sharing mainly with preferred partners when on reservation settlements.⁵⁰ Thus, the same resources are shared differently in the forest and in the reservation. The same is true in Africa, where the large game items taken by the Hadza are treated as private property by other ethnic groups who trade or sell them in the bush meat market.

In our view, human pair bonding and male parental investment is the result of complementarity between males and females. The commitment to caring for and carrying vulnerable young, common to primate females in general, together with the long period required to learn human hunting strategies, renders hunting unprofitable for women.

The indefensibility hypothesis also asserts that shares given up by successful hunters are never repaid in any useful currency (meat, other goods, or services) and that shares are given to everyone equally, regardless of whether they have done or will do anything to pay them back. However, recent research shows that contingent giving is typical in all societies where it has been examined. Ache and Hiwi foragers share more with those who share with them and, when they are sick or injured, receive help from those with whom they have shared

and in relation to how generously they have shared.^{50,51} Yanomamo gardeners work more hours in the gardens of non-kin who work more hours in their gardens.⁵² We believe that this type of reciprocity, often in different currencies, is the basis for all human economies, divisions of labor, and specialization, and that its critical development in the hominid line distinguishes us from our ape relatives.

Taken together, currently available evidence suggests that men generally provide a considerable portion of the energy consumed by juveniles and reproductive-aged women. This does not mean that men contribute more to society or reproduction than do women. Women process food (part of providing nutrients), care for vulnerable children, and do a variety of other important tasks in all societies. It is the partnership of men and women that allows long-term juvenile dependence and learning and high rates of survival. Indeed, analyses show that among both the Ache and the Hiwi, individual women produce less food if their husband is a high producer.⁵³ Divorce or paternal death leads to higher child mortality among the Ache,^{10,54} the Hiwi,⁵⁵ and the !Kung,⁵⁶ but not the Hadza.⁵⁷

In our view, human pair bonding and male parental investment is the result of complementarity between males and females. The commitment to caring for and carrying vulnerable young, common to primate females in general, together with the long period required to learn human hunting strategies, renders hunting unprofitable for women. The fact that human males can acquire very large packages of nutrient-dense food means that they can make a great difference to female reproductive success. That is not true of most other primates (the exception being callithricid males, who provide other necessary assistance). This difference creates a major discontinuity between humans and apes, and results in a partnership between men and women. That partnership is ecologically variable, in that the roles of men, women, and children vary with the availability of food resources in the environment and the risks posed to children.^{28,55,58-60}

When plants are abundant and

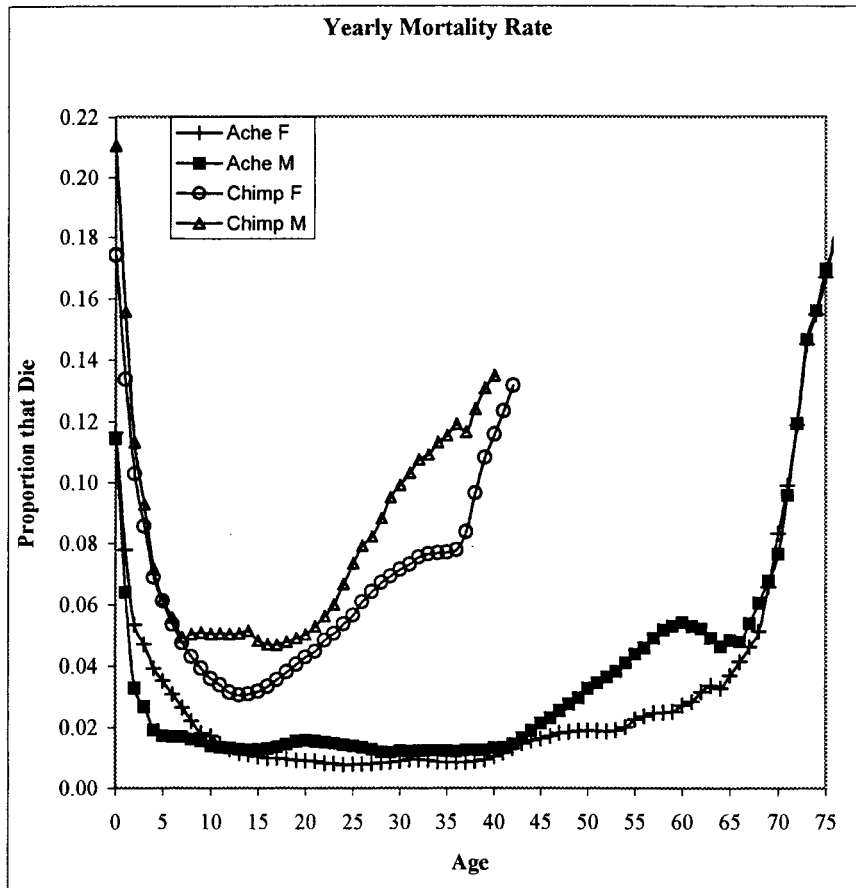


Figure 10. Yearly mortality rates for the Ache are from Hill and Hurtado¹⁰ and for chimpanzees from Hill and coworkers⁸ as described for Figure 1. Raw mortality data were smoothed using a double running average. Ages 1–5, 3 pt; ages 5–10 5 pt; ages >10, 9 pt with truncation at the end of the life table.

game is scarce (as in the Gwi environment), men specialize in providing the rarest nutrients in the environment, protein and lipid, because these nutrients are critical for growth and good health,^{61,62} while women provide more food energy. When plant foods are scarce, men's hunting provides the bulk of energy and women concentrate on the processing of food and other raw materials, and on child care. There is much to be learned about the determinants of male and female roles in foraging societies, but the primary activity of adult males is hunting to provide nutrients for others.

In sum, hunting is the human activity that requires the longest period before maximum return rates are achieved, but it also provides the highest overall return rate once maximum skill levels are reached. As a result, hunting provides the greatest energy

component of human diets in many foraging societies (Table 3) and is a fundamental feature of the human life-history adaptation. Resolution of the debate about whether hunting is primarily direct parental investment, as we contend, or mating effort, as proposed by Hawkes and coworkers,⁶³ awaits further data and sophisticated tests. Nevertheless, the nutritional support of reproduction by human males is a fundamental feature of our species.

Reduction in Juvenile and Early Adult Mortality Rates

Human foragers have longer maximum life spans than chimpanzees do, suggesting that they may have lower mortality rates over much of the life span.^{64–67} Both groups experience minimum mortality rates in the late juvenile and early adult period, a pat-

tern typical of many living organisms.⁶⁸ However, the minimum mortality rate of foragers is about 1% per year, whereas the minimum rate for chimpanzees is about 3.5% per year (Fig. 10). We propose that the character of food resources taken by humans ultimately lowers the mortality rate of juveniles and young adults in three ways. First, the hunted and extracted foods taken by humans generally come in large packages. Large, valuable packages favor food sharing, which reduces fluctuations in daily food intake, allows sick and injured

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individuals to recover at higher rates, and facilitates provisioning of children. Second, the food types taken favor larger foraging parties and residential groups, which offer protection, particularly for juveniles who associate closely with adults. Third, the food niche has led to the development of tools and an understanding of animal behavior, which can be used effectively to repel predators.

Large package size has been positively associated with the probability of food transfers or the degree of food transfer in virtually every study in

which it has been examined.^{50,63,69–75} Among the Ache and Hiwi, the percentage of foods not eaten by the acquirer's nuclear family is directly related to the mean package size of different food categories⁷² or package size within food categories.⁵⁰ Daily variability in the acquisition of different food categories also positively correlates with the percent shared in both societies. Importantly, meat comes in larger packages and is more variable than extracted resources, which, in turn, come in larger, more variable packages than do fruits. Meat is transferred most between non-kin, followed by extracted products, then fruits.⁷² Chimpanzees also share meat more than they do any other food resource.^{76,77} Thus, we propose that as humans moved into a hunting-extraction feeding niche, levels of food sharing increased dramatically over that seen among chimpanzees.

Among the Ache, individuals who are sick or injured are frequently fed by other individuals, often ones who are not kin. Those who share a greater percentage of their production are provisioned by more individuals when they are sick or injured.⁵¹ Illness and injury are common among those in foraging societies, as we might imagine, given their frequent exposure to dangers, parasites, and pathogens, and the lack of modern medical care. A systematic health survey in one reservation Ache community in 1997 showed that adults required care at the community clinic on 6% of all person days, whereas children required care on 3.5% of all person days. Sugiyama and Chacon⁷⁸ have calculated that Yora men of Peru were unable to hunt on about 10% of all person days monitored. Bailey⁷⁹ reported that Efe men came to ask for medical treatment on 21% of all man days and often had problems that precluded foraging. Most relevant to our hypothesis is how often men, women, or children are sick or injured for many days in a way that would preclude food acquisition. No data are yet available on this topic. However, we have seen a variety of serious medical problems including snakebites, injuries sustained in piranha and jaguar attacks, broken bones, large punctures, and animal bites, as well as, arrow

wounds, massive infections, and occasional illness that have kept people from foraging for more than a week at a time. Indeed, we researchers have all experienced medical problems that lasted for a week or more and prevented us from working in the field. If people were not food-subsidized during such periods, mortality rates would undoubtedly be higher.

Large, widely dispersed food patches may promote grouping among animals.^{80,81} Human women and children generally spend the day in parties that contain many individuals of the foraging band, whereas chimpanzee females and juveniles are often dispersed into parties of one or two individuals.^{76,82} This appears to have two important consequences. First,

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human males experience higher mortality from predators than do females. Eight of the nine Ache who died from jaguar attacks in the twentieth century were men, as were 14 of the 18 who died from snakebite.¹⁰ Second, human juveniles are rarely killed by predators. In recent memory and historical mythology, no Ache child has been killed by a jaguar. The only !Kung reportedly killed by a predator in Howell's⁸³ demographic study was an older man. Nevertheless, there is good evidence that chimpanzee juveniles are killed by predators^{20,76} and that adult females are probably killed more often than adult males.

Human tool use probably provides a good deal of protection from predators. Fire appears to frighten many

predators and may provide a good deal of nocturnal protection. Hunting tools can inflict serious injury or death on predators, thus providing protection for women and children, particularly when multiple males are present. The knowledge and analysis of animal behavior, fundamental to human hunting, can also be employed to fend off predators. Ache often know when the group is being stalked by a jaguar by analyzing its footprints and movement patterns. When they become aware of a predatory jaguar, they build brush walls around the camp and take turns acting as sentinels through the night.

These quantitative and qualitative data about food sharing, tools, and knowledge provide suggestive evidence that the shift to large-package, high-quality foods indirectly acted to lower mortality rates. Research on causes of death and risks of predation and illness among both humans and chimpanzees is necessary to determine the factors responsible for the more than three-fold differences in juvenile and adult mortality rates.

DISCUSSION

Primate Life-History Evolution

The life-history traits and large brains of fully modern *Homo sapiens* may be seen as the extreme manifestation of a process that defines the primate order as a whole. Our theory organizes the major evolutionary events in the primate order and the specific changes that occurred in the hominid line.

The early evolution of the primate order (60 mya to 35 mya) was characterized by small increases in encephalization. Relatively little is known about early life-history evolution except that it appears that even the more "primitive" prosimian primates were long-lived and delayed in reaching reproductive maturity as compared to mammals of similar body size. Austad and Fischer^{84,85} have related this evolutionary trend in the primates to the safety provided by the arboreal habitat. They compare primates to birds and bats, which are also slow in developing and long-lived for their body sizes. Thus, the first major grade shift that separated the primate order from

other mammalian orders was a change to a lowered mortality rate and the subsequent evolution of slower senescence rates.

The second major grade shift occurred with the evolution of the anthropoids, the lineage containing monkeys, apes, and humans, beginning about 35 mya. This was characterized by an increasing emphasis on plant foods as opposed to insects, and by more rapid increases in brain size relative to body size.⁸⁰ The major defining characteristic of the evolution of the anthropoids was reorganization of the sensory system from one in which olfaction and hearing were relatively dominant to one completely dominated by binocular color vision.⁸⁰ This grade shift is almost certainly tied to a dietary shift toward a diverse array of plant parts, particularly fruits and leaves.

The diet of the anthropoids has been characterized as both "broad and selective."^{86,87} The diet is broad precisely because it is so selective. Anthropoid primates tend to select foods on the basis of the ripeness, fiber content, nutrients, and toxicity of foods consumed early in the day.^{88–90} This selectivity requires the allocation of increased brain tissue to visual processing.^{91,92} It also requires that many different species of plants and animals be included in the diet, increasing the demands for memory and learning.^{93,94}

This grade shift is reflected in brain size. Regressions of log brain size on log body size show that the intercept is significantly lower for strepsirrhine primates (including most prosimians) than for the haplorhine primates (including all anthropoids and a few prosimians).

The third major grade shift in primates occurred with the evolution of the hominoid lineage, the branch leading to apes and humans. This shift included further encephalization. The intercept in a regression of log brain size on log body size is significantly higher for apes than monkeys, and apes clearly perform better on most tasks reflecting higher intelligence.^{93,95} Evidence on teeth and tooth wear among early hominoids suggests a diet composed mainly of soft, ripe fruits.⁹⁶ The frugivorous emphasis of

the hominoid lineage is evident in later hominoid species as well.⁹⁶ Wrangham and colleagues^{97,98} also show that the chimpanzee diet is based on a much greater percentage of ripe fruits than is the diet of other sympatric primate frugivores. (This is probably true of orangutans as well). The cognitive demands of a diet that emphasizes ripe fruits are likely to be much greater than simple frugivory. For one thing, there are greater perceptual demands in detecting the state of fruit from visual cues against a background.⁹¹ For another, the lower abundance of ripe fruits and the short

Although, as compared to humans, chimpanzees engage in relatively little extractive foraging and hunting, they do much more than monkeys. In this sense, their superior intelligence and greater encephalization than occurs in monkeys illustrates the same evolutionary forces that separate humans from apes.

time in which they are available (ripe, but not yet eaten by competitors) is likely to impose greater demands with respect to monitoring the environment, remembering the state of individual trees, and predicting when the fruits will become ripe on the basis of their current state.

In addition to eating ripe fruits, chimpanzees and gorillas also use complex techniques for extracting foods from protected substrates, such as nut-cracking, termite and ant fishing, and removal of bark to get at pith.⁹³ Gibson^{99,100} identified extractive foraging in primates as an impor-

tant selective force in primate intelligence and presented evidence in support of this idea. Furthermore, these behaviors vary between groups as social traditions. In a comprehensive review of chimpanzee cultures using 151 years of chimpanzee observations from seven long-term studies, 39 behavior patterns were found to be customary or habitual in some communities but absent from others where ecological explanations could be discounted.¹⁰¹ Of these, 19 were patterns of extractive foraging. An additional 14 extractive foraging behaviors were identified but failed to achieve habitual status in any one community. Furthermore, chimpanzee males are avid hunters. Boesch and Boesch²⁰ present data indicating that older chimpanzee males are capable of predicting escape patterns of their prey and of predicting how prey will respond to the behaviors of other chimpanzees. This appears to require even greater levels of cognitive processing than are required for extractive foraging. Although, as compared to humans, chimpanzees engage in relatively little extractive foraging and hunting, they do much more than monkeys. In this sense, their superior intelligence and greater encephalization than occurs in monkeys illustrates the same evolutionary forces that separate humans from apes. (See Lancaster and associates¹⁰² for a review of chimpanzee behavior and cognition.)

There is some debate, however, about the relative importance of diet versus group living in the evolution of primate intelligence and brain size. According to one view, the increase in brain size was largely driven by the complexities of the primate diet. Jerison^{103,104} suggested that brain tissue evolves in response to two kinds of demands: One depends on body size, based on monitoring and supporting an animal's body tissue and particularly its surface area; the other is the ability to assimilate, integrate, and remember environmental information. He therefore predicted that differences in brain size, after controlling for body mass, would be associated with an animal's ecological niche and its demands for information processing. Jerison¹⁰³ hypothesized that the

need to process information in a complex three-dimensional environment was the cause of the large brain of primates relative to the brains of other mammals.

Clutton-Brock and Harvey¹⁰⁵ tested a version of this hypothesis with intergenera comparisons within families of primates. They reasoned that frugivores need to assimilate and retain more environmental information than folivores do because fruits are more scarcely distributed than leaves, requiring more specific locational memory. They found that, after controlling for body size, both dietary emphasis (leaves versus fruits and insects) and the size of the home range predicted brain size. Milton^{23,89,106} extended their work, focusing on gut specialization and brain size as alternative routes to energetic efficiency. Leaves, while abundant, tend to contain high amounts of fiber and often toxins as well. The ability to extract nutrients from leaves depends on the size of the gut and other specializations designed to facilitate fermentation for nutrient extraction. Fruits, on the other hand, are ephemeral resources, patchily distributed but offering a higher density of easily processed energy. Milton showed in paired interspecific comparisons that gut size and brain size were inversely correlated, corresponding to the dietary emphasis on fruits versus leaves.

Another view is that brain-size evolution was driven primarily by the complexities of social life in primate groups.^{107,108} Many species of primates exhibit complex dominance hierarchies that are mediated by political alliances and relations among relatives in genetic lineages.^{109–112} It is not clear why higher primates have such complex social relations, but it appears that group living is at least partially a response to predation that significantly lowers predation. Among species that tend to eat higher-quality foods that are easy to monopolize, social relationships also mediate access to foods within groups.¹¹³

The most recently published analyses with the largest samples show that both group living and diet are associated with brain size and the size of the neocortex in primates.^{91,92} In a separate set of analyses, Allman and col-

leagues⁶⁶ have shown that group living and diet are positively associated with maximum life span in primates after controlling for body size. They also have shown a high positive correlation between brain size and life span, again controlling for body size. Smith¹¹⁴ showed that after controlling for body size, brain size in primates is positively associated with the age of first molar eruption, an indicator of the age at which individuals begin to consume adult diets, as well as with age of first reproduction and longevity. The relationship is strongest for

It seems likely that the cognitive ability associated with foraging in a complex three-dimensional environment is an important pre-adaptation for social intelligence and complex social relations. Of particular interest here are the specializations inherent in the primate visual system . . .

age of first molar eruption, probably because brain growth and postcranial morphological development compete.¹¹⁵

Kaplan and colleagues¹¹⁶ have recently conducted multivariate analyses specifically designed to test the present theory. They found that when brain size is regressed on body size, age at first reproduction, maximum life span, percent of fruit in the diet, range size, and group size in a multivariate model, all but group size were significant predictors of brain size. In addition, the frugivory and range size variables, meant to capture the cognitive demands of the diet, also predict the life-history variables (age of first

reproduction and maximum lifespan) after controlling for body weight.

Regardless of the importance of group size in determining brain size in monkeys, the grade shift in brain size between monkeys and apes is almost surely related to diet and not to group size.⁹⁵ Apes show dietary specialization, but do not live in particularly large groups. In fact, gibbons, orangutans, and to a lesser extent, gorillas, live in relatively small groups while chimpanzees and bonobos form groups of the same size as do baboons and vervets.

It seems likely that the cognitive ability associated with foraging in a complex three-dimensional environment is an important pre-adaptation for social intelligence and complex social relations. Of particular interest here are the specializations inherent in the primate visual system, including binocular vision, high visual acuity, and associated increases in the size of the lateral geniculate nucleus.^{64,65,91} Barton⁹¹ has shown that the size of the parvocellular system involved in the processing of visual stimuli increases with increasing group size among nonhuman primates. Thus, it may be that selection favoring social intelligence increases once the necessary cognitive pre-adaptations exist. This may be one reason why primates exhibit such high levels of social complexity relative to other group-living mammals, such as many herbivores. Adept social manipulation that leads to a higher position in a dominance hierarchy may be favored by natural selection, for dominance has correlated positively with measures of fitness in a multitude of primate studies.^{109–113,117} Yet this would probably be true for other social mammals as well. Many of the same abilities to store and analyze information may be employed to solve dietary and social problems.⁹⁴ Once social intelligence and social complexity evolve, the cognitive adaptations may be maintained even when dietary complexity is secondarily reduced in some species, as is the case with the derived simplicity of the diet of colobine monkeys.¹⁰⁵ Apes show remarkably sophisticated social intelligence^{94,112,118,119} and stand out in comparison to monkeys. Although this cannot be a result of

greater group size per se, it is again possible that selection on social applications of intelligence increased when the cognitive adaptations to feeding acted as a pre-adaptation.

It is useful to think of primate evolution as both a branching and a directional process. It is branching in the sense that ecological variation, intraniche competition, and segregation generate variable selection pressures that lead to the evolution of multiple species with different traits. Some are selected to rely on more easily acquired foods and travel less, to invest more in gut physiology and less in brains, and to mature more rapidly and live shorter lives. Others are selected to rely on more complex feeding strategies and exhibit their respective, correlated life histories. It is a directional process in the sense that cognitive and life-history adaptations that evolved previously act as pre-adaptations for further selection in the same direction in response to niche competition and ecological change. *Homo sapiens* is an extreme in one of those directions.

The Hominid Line

The fourth major grade shift in primate evolution occurred with divergence of the hominid line, particularly the evolution of genus *Homo*. The brain and life span of modern humans are clearly “outliers” compared to those of other mammals, and even as compared to the relatively large-brained, slow-living primates. The evolution of these extreme adaptations in the hominid line is built on a hominoid base that already showed a significant tendency toward large brains, long lives, and exploitation of high-quality foods. Available evidence on Australopithecines suggests that bipedalism preceded changes in brain size and life history.^{114,115}

Although the record is still incomplete, it appears that brain enlargement and life-history shifts co-occurred. Early *Homo ergaster* shows both significant brain expansion and an elongated developmental period,¹²⁰ but much less so than modern humans. Neanderthals display both brain sizes and dental development that are in the same range as those of modern humans. Bipedalism can be

thought of as a pre-adaptation that evolved to facilitate terrestrial locomotion, allowing for long day ranges through energetic efficiency.¹²¹ Ache men walk an average of 15 km per day, about three times the distance covered by chimpanzee males,^{32,33} even though both inhabit tropical forests. Bipedality also had the secondary effect of freeing the hands for specialization in manipulative activities. Environmental conditions in the early Pleistocene interacted with bipedality to favor an increased emphasis on extractive foraging, hunting, learning, prolonged development, and long lives for at least one line of the hominid family. It may be that this unique suite of conditions is responsible for the extreme differences between humans and other primates in intelligence, development, longevity, and resource flows across generations. The

Although the record is still incomplete, it appears that brain enlargement and life-history shifts co-occurred.

complexities of a highly variable climate also would have favored a trend toward cognitive solutions that led to new foraging opportunities. Hominids with such solutions were probably better able to withstand rapid climate and habitat change than those who were more inflexible.¹²²

The shift toward a high-quality diet based on learned foraging techniques also implies another co-evolutionary process. Just as the juvenile period and the life span co-evolved, so too did brain and gut sizes co-evolve with life-history traits and with each other.^{23,123} Many other physiological traits are probably related to this evolved complex. For example, it is likely that hidden estrus among humans is related to the male energy subsidization of adult female reproduction,⁶² and that the postreproduc-

tive life span of both sexes is related to high food production by older individuals. Almost certainly, the reason that human females have shorter inter-birth intervals than apes do¹²⁴ (and probably different physiological sensitivity to nursing stimulation) is because reproductive-aged human women are able to decrease rather than increase their food production during lactation due to subsidies by other age and sex classes.¹⁰² This commitment to food sharing is evident in human physiology and behavior. Women obtain more of the extra energy required for pregnancy and lactation by increases in energy intake¹²⁵ and reductions in energy expenditure^{12,126} rather than by an increase in fat mobilization or metabolic economy.¹²⁵ Reductions in basal metabolic rate during early pregnancy¹²⁷ are not sufficient to make up for the increased energy requirements. It is likely that this response evolved in the context of provisioning.

Figure 11 illustrates our historical hypothesis regarding the hominid diet and its impact on both pay-offs to learning and development and on mortality rates. The figure begins with two important exogenous changes. The first is a change in the distribution of foods with the emergence of African savannas in the Pleistocene, which increased the abundance of high-quality but protected plant foods (nuts and tubers, in particular) and animal foods. The second change is the pre-adaptation of bipedality, emerging in the Australopithecines as a locomotor adaptation. This adaptation frees the hands for tool use, which allows more efficient extraction and hunting and frees the hands for carrying large packages of food suitable for sharing.^{128,129} It also results in efficient terrestrial locomotion and higher daily mobility that would increase the daily encounter rate with rare but energetically rich resources. These changes led to an increased emphasis on large, high-quality, but difficult-to-acquire foods. Our hypothesis is that this feeding niche had multiple effects: It increased the premium on learning and intelligence, delaying growth and maturation; increased nutritional status and decreased mortality rates through food

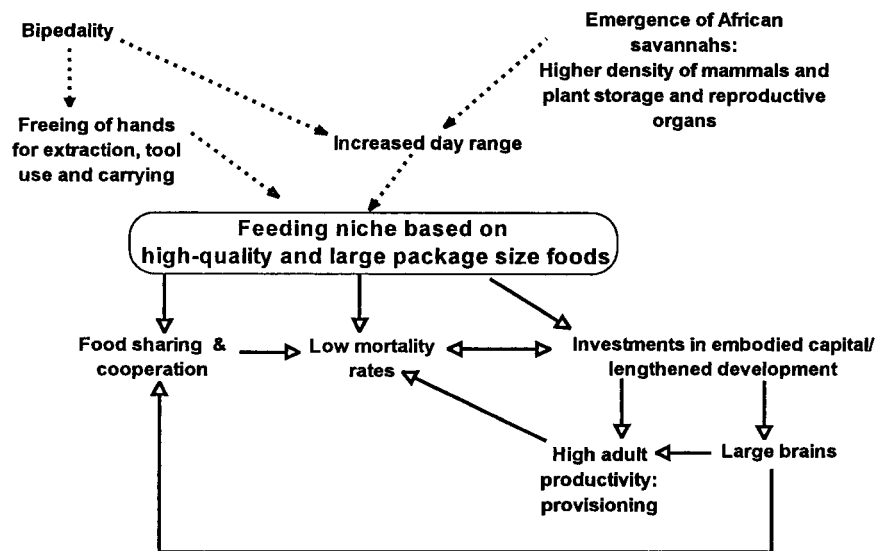


Figure 11. Ecology and co-evolutionary process in the Hominid line.

sharing (predicted by the provisioning of young sick or injured individuals); and released selection against larger group size, which lowers predation mortality.

The Grandmother Hypothesis

The present theory shares some features with a model of menopause and human life history recently proposed by Hawkes and colleagues,¹³⁰ often referred to as the grandmother hypothesis. This hypothesis proposes that humans have a long life span relative to that of the other primates because of the assistance that older postreproductive women contribute to descendant kin through the provision of difficult-to-acquire plant foods. Women, therefore, are selected to invest in maintaining their bodies longer than chimpanzee females do. Thus, both theories focus on the exceptionally long human life span. Rather than regarding the cessation of reproduction in the fifth decade of life as the critical adaptation (a feature shared with apes), both theories attempt to explain the extension of the human life span beyond menopause.^{24,130} This implies that some fertility earlier in life is given up in order to prolong the adult life span.²⁴ The theories differ in important ways, however.

First, the grandmother theory focuses on the productivity of older women, but not on investments in

learning and development. The present theory specifically links high productivity later in life to investments in a large brain and to the unique features of growth in human children. The grandmother hypothesis is silent about the expansion of the costly human brain. It also offers no explanation of why human children grow so slowly and take so long to mature, except for the fact that adult mortality rates are low. In fact, Hawkes and colleagues¹³⁰ suggest that learning is a secondary effect of a long juvenile period (determined by the long lifespan) rather than the cause of the long juvenile period. Second, the grandmother theory fails to account for why men live to about the same age as women. If the benefits of living longer derive, for women, from provisioning descendant kin and, for men from direct reproduction, there is no reason why their life spans should be so similar. Third, the grandmother model fails to capture the important role that human males play in supporting women's reproduction. It also fails to explain the age profile of production among males and why men take so long to reach their productive peaks.

The evidentiary basis of the grandmother hypothesis is also very weak. There is no direct evidence that postreproductive women are the major food providers in any society. While Hadza data do suggest that older

Hadza women produce more food than younger women do, postreproductive women produce less than Hadza men (Fig. 2). Furthermore, it is unlikely that the Hadza pattern of high food production by postreproductive women is common among other foragers. Ache and Hiwi postreproductive women do not acquire even half the daily food energy acquired by adult men. !Kung data also suggest that older women produce very little, even leading the Hadza research team to ask "Why don't elderly !Kung women work harder to feed their grandchildren?" (Blurton Jones

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and coworkers,¹³ p. 388). And certainly none of the high-meat-consuming societies of Table 4 nor any of the societies in human history dwelling at high latitudes could have been mostly dependent on the food production of postreproductive women. While we agree that the age profile of production is shifted toward older ages among women as well as men, and that postreproductive women provide many important services in foraging societies, among them child care, tool making, food processing, and camp maintenance, there is no evidence to support the hypothesis that they have

been the “breadwinners” in most societies during human history.

The present theory organizes all of these facts. Both males and females exploit high-quality, difficult-to-acquire foods (females extracting plant foods and males hunting animal foods), sacrificing early productivity for later productivity, with a life-history composed of an extended juvenile period in which growth is slow, a large brain is programmed, and a high investment is made in mortality reduction and maintenance to reap the rewards of those investments.

PREDICTIONS OF THE THEORY TO BE TESTED IN FUTURE RESEARCH

Comparative Biology

The co-evolutionary selection pressures posited by our theory and supported by the quantitative theoretical model should be generally applicable. Holding pay-offs to time spent as a juvenile constant, increased survival rates during the juvenile period should select for delayed reproduction, as predicted by the models of Kozłowski and Weigert⁵ and Charnov.^{1,9} Holding constant extrinsic mortality hazards and the pay-offs to investments in mortality reduction, increased pay-offs to time spent in development as a juvenile should select for increased allocations to survival and lower mortality rates. The latter is a novel prediction of our theory. The testing of our predictions will require careful comparative research within taxonomic groups at different levels of analysis (for example, among birds, mammals, and reptiles, and among orders and genera within those higher taxonomic levels). It will be necessary to distinguish pay-off functions and mortality hazards from the actual levels achieved, given the observed allocations. For example, it will be necessary to distinguish the risk of dying from different causes, such as predation and infectious disease, from observed mortality rates due to those causes, because the observed mortality rate will be affected by allocations to predator avoidance and feeding, and by allocations to immune function.

A principal innovation of the proposed theory is the incorporation of

co-evolutionary selection among life-history traits without requiring any trait to be treated as extrinsic. This is more realistic than previous approaches, but makes for increasingly demanding empirical analysis. There are many possible pay-offs to time spent in development. The most general benefit of increased time spent in development is increased body size and its effects on energetic turnover, survival, and mating success. The co-evolutionary selection measures posited here should apply to those effects, but of primary interest in our theory are the benefits associated with learning and information storage. Varia-

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tion within birds, carnivores, pinnipeds, and primates should be particularly fertile ground for testing predictions generated by the theory with respect to learning, brain size, and life-history traits. The general prediction is that within those taxonomic groups, species that rely on more learning-intensive, complex feeding strategies will have longer developmental periods, longer life spans, and larger brains relative to body size. With respect to brain size, the correlations of brain size with life-history characteristics and feeding strategies should be reflected in those parts of the brain associated with learning and information storage, and

not with raw perceptual processing, such as sonar and visual acuity (unless, of course, those functions are more developed in organisms that learn and store information). Suggestive evidence in support of the theory is available for birds¹³¹ and primates,¹¹⁶ but rigorous testing of those predictions awaits further research and analysis.

Hominid Evolution

Following this line of reasoning, the first major increases in brain size in the hominid line should be accompanied by extensions of the juvenile period, increased longevity, and increased complexity of learned foraging strategies. Smith's analyses of tooth eruption among early *Homo ergaster* provide suggestive evidence of extension of the juvenile period beyond that of chimpanzees and Australopithecines, but to a lesser extent than that of fully modern humans. So far, the record is silent with respect to longevity and mortality rates. Our ability to test the prediction that longevity increases with brain size during hominid evolution may await new developments such as advances in the extraction of DNA from fossil remains and in understanding the genetics of aging. Nevertheless, this extension of the expected life span with increased emphasis on learning in development and brain size is a firm prediction of our theory.

Although the early evolution of the genus *Homo* could have been accompanied by increased complexity of foraging strategies with respect to either hunting or gathering, we strongly suspect that future research will demonstrate increases in both the importance of hunted foods and complex extractive technologies for gathering.^{23,121,128,129,132,133} Recently, O'Connell and associates⁴⁹ have rejected hunting as being important in early hominid evolution on two grounds. First, some archeological assemblages that include large accumulations of animal bone, thought to illustrate the hunting life-style, have now been reinterpreted as possibly resulting from natural processes. Second, recent data show that chimpanzees hunt considerably more than was previously thought. Therefore, hunting cannot be the cause of the changes

in hominid life histories and social systems.

With respect to the first point, it is premature to reject the “hunting hypothesis” simply because the causes of bone accumulation at hominid sites are not well understood and are open to various interpretations. It has never been demonstrated that early hominids did not rely heavily on hunted foods. It is also the case that too much emphasis has been placed on hunting large game (Jones presents suggestive evidence that bone accumulations at Olduvai reflect reliance on small game hunting¹³⁴). Chimpanzees hunt small game, as do many modern hunter gatherers. For example, the Ache rely heavily on small game: About 50% of the animal food in the Ache diet is small game acquired using hand-hunting techniques (no projectile weapons). In fact, it may be that the learning demands of a diet based on small game may be greatest because it can require killing many different species at regular intervals. Thus, much encounter-specific and species-specific knowledge and creativity may also be required.

With respect to the second point, Tables 1 and 2 show that humans and chimpanzees exploit very different food niches. While chimpanzees do hunt, the most successful chimpanzee hunters obtain less than 10% of the daily per capita energy intake from meat reported for any human foraging group. To claim that humans and chimpanzees both must have the same life history and social system because they both hunt is equivalent to asserting that chimpanzees must have the same social system as black and white colobus monkeys because they both eat some ripe fruit. We predict that early hominids will show a major increase in the consumption of hunted foods. Analyses of vitamins and minerals in hominid bone remains may provide new avenues for testing that hypothesis, in addition to archeological evidence.¹³⁵

It is clear that the process of hominization occurred over a long time. Our theory is silent about the dates of important events and evolutionary changes in the hominid line. Whether the process will look ratchet-like, in that small increases in longevity will precede small increases in brain size, which, in turn, lead to further in-

creases in longevity, is also an open question. Whether the process is gradual or punctuated, our theory predicts that changes in brain size, the dietary importance of meat and other difficult-to-acquire foods, gut size, and life span will be seen to co-evolve in the archeological and paleontological record. It is important to recognize that many of those changes may be quantitative as well as qualitative. For example, although chimpanzees hunt monkeys, they only pursue them in a very small proportion of their encounters with them, presumably because most of those encounters do not occur under conditions likely to result in a

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successful kill. Ache foragers only rarely ignore an encounter with monkeys, even when they hear them at a great distance, because most such encounters do result in successful kills, presumably because of the Ache’s skill and effective weaponry. The quantitative changes in brain size and life-history traits during hominid evolution should be accompanied by quantitative changes in diet and skill-intensive foraging techniques.

Modern Humans Versus Chimpanzees

There are at least two major avenues of future research with extant

hunter-gatherers and chimpanzees for testing the predictions of our theory. First, we have provided only suggestive evidence that food sharing and provisioning lower both juvenile and adult mortality rates in humans and that this is a major cause of the difference between human and chimpanzee age-specific survival probabilities. We need to know a great deal more about the frequency of illness in both species and the relationship between morbidity and mortality. What is the relationship between illness and food intake rates in both species? What is the relationship between reduced food intake and mortality? Our theory predicts that weight loss accompanying illness will be more frequent and severe, and that illness will more frequently result in mortality among chimpanzees than humans. Our theory also predicts that chimpanzee juveniles will spend more time than human juveniles in contexts that expose them to predation, and that this difference will be due to both group size and time spent in the food quest. Our theory also predicts absolutely greater frequency of predation on chimpanzees than on humans.

A second avenue of research is on the components of foraging success. A principal difference between our theory and the grandmother hypothesis is that we propose that the human life course and large brain are the results of a long learning process that is necessary for successful foraging, and that both males and females engage in this process. Recently, on the basis of some experiments among Hadza juveniles, Blurton Jones and Marlowe¹³⁶ have suggested that human foraging is not very difficult to learn. We propose that hunting, as practiced by humans, but not necessarily by other predators, is exceedingly difficult to learn and requires many years of experience. Our observations of hunters in six different groups suggests to us that it is not marksmanship, but the knowledge of prey behavior and remote signs of that behavior such as tracks and vocalizations that are the most difficult features of human hunting.³⁰

This impression is testable. We should find that marksmanship is acquired relatively early in the learning process and that naive individuals such as anthropology graduate students could be trained to be effective

marksmen with relatively little practice. In contrast, we should find that knowledge of animal behavior and signs of behavior are learned only gradually over many years. We should also find that encounter rates with prey are much more strongly age-dependent than are kill rates upon encounter. It should also be the case that kills that rely on marksmanship are less age-dependent than kills that rely on finesse and skill, such as luring animals out of holes. In addition, it should be much more difficult to train naive individuals to find prey than to shoot projectile weapons accurately. Similarly, we should find that age effects on chimpanzee hunting should be a result of differences in knowledge of prey behavior. Boesch and Boesch²⁰ provide suggestive evidence of such effects, but more research is necessary for a definitive test. An analogous set of predictions also could be tested with extractive gathering techniques and the specific knowledge required for each (Bock^{29,137} presents a series of experiments with grain processing as a model of how such research could be conducted).

CONCLUSIONS

The human adaptation is broad and flexible in one sense, but narrow and specialized in another sense. It is broad in the sense that, as hunter-gatherers, humans have existed successfully in virtually all of the world's major habitats. This has entailed eating a very wide variety of foods, both plant and animal, both within and among environments. It also has entailed a great deal of flexibility in the contributions of individuals of different ages and sex. The relative contributions of men and women to food production appear to vary from group to group. Even the contributions of children and teens to food production vary predictably with the abundance of easy-to-acquire foods.

Our adaptation is narrow and specialized in that it is based on a diet composed of large, nutrient-dense, difficult-to-acquire packages and a life history with a long, slow development, a large commitment to learning and intelligence, and an age profile of production shifted toward older individuals. We do not expect to find any human population that subsists on

leaves or other low-quality foods. Indeed, we expect humans to remain at the very top of the food hierarchy in every environment they live in (for example, humans often exterminate all other top predators in their habitat). Humans ingest foods that are already high in quality and do not require much digestive work or detoxification. And if a food contains toxins, they are generally removed prior to ingestion by processing techniques. This dietary commitment is reflected in the extremely reduced size of the human

Finally, the effect of the commitment to food sharing is evident in the reproductive physiology of human women. Provisioning permits human women, in contrast to other female primates, to reduce rather than increase their rate of energy production during their reproductive years, when they have both infant and juvenile nutritional dependents and a greatly reduced spacing between births.

hindgut.²³ Humans use their great intelligence to extract and hunt those foods. In order to achieve this diet, humans also engage in extensive food sharing both within and among age and sex classes of individuals. Finally, the effect of the commitment to food sharing is evident in the reproductive physiology of human women. Provisioning permits human women, in contrast to other female primates, to reduce rather than increase their rate of energy production during their reproductive years, when they have both infant and juvenile nutritional depen-

dents and a greatly reduced spacing between births.

The model and the data we have presented suggest that the human life course is based on a complex set of interconnected, time-dependent processes and the co-evolution of physiology, psychology, and behavior. There appears to be a tight linkage among the ordering of major psychological milestones (language learning, understanding and mastering the physical, biological, and social environment); the timing of brain growth; growth rates during childhood and adolescence; developmental changes in survivorship; behavioral, psychological, and physiological changes with the transition to adulthood; profiles of risk with age; and rates of senescence and aging. It is very likely that a species-typical life course evolved in response to the demands of a hunting and gathering lifestyle that was broad and flexible enough to allow successful exploitation of the world's environments, but specialized toward the acquisition of learned skills and knowledge to obtain very high rates of productivity later in life.

ACKNOWLEDGEMENTS

We thank K.G. Anderson, Theodore Bergstrom, John Bock, Robert Boyd, Pat Draper, Peter Ellison, Michael Gurven, Sarah Hrdy, Monique Borg-erhoff Mulder, David Lam, and Peter Richerson for helpful discussions of these issues as well as Anne Pusey and Janette Wallis for sharing data on chimpanzee development and birth-spacing. We especially thank Nicholas Blurton Jones, Eric Charnov, Kristen Hawkes, and James O'Connell whose seminal work in this area both challenged us and helped stimulate our thinking, and who took time to critique various versions of this manuscript. Arthur Robson deserves special recognition for performing the mathematical analysis to generate the results outlined in Box 1 and writing the Mathematical Appendix, which is available from the authors.

Field research on the Ache, Hiwi, and Machiguenga has been supported by grants to Kim Hill and A. M. Hurtado by the National Science Foundation (BNS-8613215, BNS-538228, BNS-8309834, BNS-8121209, BNS-9617692), the National Institutes of

Health (RO1HD16221-01A2), Fundación Gran Mariscal de Ayacucho, Caracas, Venezuela, and two grants from the L.S.B. Leakey Foundation. Further support has gone to H. Kaplan for field research on the Machiguenga and Yora by the National Science Foundation (BNS-8718886) and the L.S.B. Leakey Foundation, and for life history theory and life course evolution by the National Institute of Aging (1R01AG15906-01).

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