

# PERSPECTIVES IN ETHOLOGY

Volume 13

**Evolution, Culture, and Behavior**

Edited by

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**Kluwer Academic / Plenum Publishers**  
New York, Boston, Dordrecht, London, Moscow

2000

*Chapter 2*

**THE EVOLUTION OF LIFE HISTORY,  
INTELLIGENCE AND DIET AMONG  
CHIMPANZEES AND HUMAN FORAGERS**

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**ABSTRACT**

Compared to those of other primates and mammals, human life histories exhibit at least four distinctive characteristics: (a) an exceptionally long lifespan, (b) an extended period of juvenile dependence, (c) support of reproduction by older, post-reproductive males and females, and (d) male support of reproduction through the provisioning of females and their offspring. Another distinctive feature of our species is a large brain size and its associated psychological attributes: increased capacities for learning, cognition and insight. Humans and chimpanzees, compared to other primates, lie closely on a dietary continuum that emphasizes difficult-to-acquire foods. However, the extreme commitment of humans to such a diet has led to distinctive life history traits and age profiles of food production. What underlies these features is a qualitative difference in the role of males through their provisioning of meat to females and young. Meat is a pre-eminently provisionable resource of great value to growth and reproduction, but its acquisition comes at the cost of both skill and risk. The commitment of human males to specialize in this enterprise is the foundation of the four distinctive characteristics of human life histories. In this

*Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior*  
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

chapter, we propose a theory that unites and organizes these observations through comparisons of the behavior, biology, and life histories of chimpanzees and humans.

## 1. INTRODUCTION

Chimpanzees and humans share approximately 98.5% of their genes (Goodman, 1999). The two species' cognitive capacities and social behavior also express striking commonality in their high levels of socially-transmitted behaviors, patterns of food procurement that include extractive foraging and the hunting and social exchange of meat, fission/fusion male-bonded social systems, similar patterns of social alliances and conflict resolution, and cognitive behaviors which suggest a concept of the minds of others as well as quantitative representation. The impressive display of commonalties shared by chimpanzees and human foragers in numerous aspects of their biology and behavior pushes us to consider whether many of the differences between the two species are a matter of degree or, if we explore the major parameters of their life course and feeding niche, we will find distinctions which set the two species apart. In other words, what are the major distinctions between human foragers and apes in their adaptive niches? And, can we best understand the distinctively human life history traits as co-evolved features associated with human entrance into a unique feeding niche?

Our theory is that those four life history characteristics as well as extreme intelligence are co-evolved responses to a dietary shift towards high-quality, nutrient-dense, and difficult-to-acquire food resources. The underlying logic is the following. First, high levels of knowledge, skill, coordination and strength are required to exploit the suite of high-quality, difficult-to-acquire resources that humans consume. The attainment of those abilities thus requires time and a significant commitment to development. This extended learning phase, during which productivity is low, is compensated by higher productivity during the adult period, with an intergenerational flow of food from old to young. Since productivity increases with age, the time investment in skill acquisition and knowledge leads to selection for lowered mortality rates and greater longevity, because the returns on the investments in development occur at older ages. This in turn will favor 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 characteristics of the feeding niche, with associated food sharing, provisioning of juveniles, and increased grouping led to lower mortality during the juvenile and adult periods, because provisioning assists

recovery in times of illness or injury and reduces risk by limiting juvenile time allocation to foraging. These buffers against mortality also favor a longer juvenile period and higher investment in other mechanisms to increase life span.

Thus, we propose that the long human life span co-evolved with the 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 only consume 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 the Earth's terrestrial and coastal ecosystems.

## 2. CHIMPANZEE CULTURE AND HOMINID EVOLUTION

The recognition and identification of socially transmitted, locally variable, adaptive behavior patterns among chimpanzees have been the focus of numerous recent books and publications (Byrne, 1995; Heltne & Marquart, 1989; McGrew, Marchant, & Nishida, 1996; Whiten et al., 1999; Wrangham et al., 1994). It is clear that chimpanzees use socially transmitted behavioral patterns to solve many of the most critical challenges posed by natural selection, such as finding food, acquiring mates, forming social alliances, and raising young. These behavioral patterns vary from one study location to another and arguably can be identified as local social traditions. In a comprehensive review of chimpanzee cultures, Whiten and associates (1999), using 151 years of chimpanzee observations from seven long-term studies, found 39 behavior patterns that were customary or habitual in some communities but were absent in others and could not be explained by ecological differences. Furthermore, studies of captive chimpanzees indicate that chimpanzee cognition and intelligence may combine features of learning processes, self-awareness, and ability to communicate that are critical underpinnings to human culture. Finally, some essential features of chimpanzee and human social behavior are shared, indicating that certain features of chimpanzee social organization that strongly affect life history strategies are similar to those of humans.

Food-procurement patterns of chimpanzees are notable for two critical features which link them to human behavior: The inclusion of extractive foraging techniques and the hunting of meat (Gibson, 1986; Parker & Gibson, 1979; Stanford, 1998, 1999). The behavior patterns involved indicate slow acquisition of skills during development (Boesch & Boesch, 1999;

Goodall, 1986) as well as variability from one study site to the next (Whiten *et al.*, 1999). Chimpanzee use of tools as aids to extractive foraging has been well documented (Boesch-Achermann & Boesch, 1994; Byrne, 1997; Sugiyama, 1997). Tool use has been described at all the major study sites for chimpanzees and includes a long list of sponging, fishing, digging, and cracking behaviors, all of which give chimpanzees access to drinking and food resources which are much less efficiently extracted by bare hand or perhaps not at all. Furthermore, in some sites such as the Tai Forest, stone bashers and anvils are regularly used. Of the 39 behaviors that Whiten and associates felt confident enough to label cultural traditions, 19 were patterns of extractive foraging (an additional 14 extractive foraging behaviors were identified but failed to achieve these researchers' criteria of habitual status in any one community). Although the calories gained from both extractive foraging and hunting are a relatively small percentage of the total diet as measured both by time spent feeding and by caloric value, this aspect of chimpanzee behavior indicates a species' interest in hard-to-acquire, nutritionally dense foods which is expressed in ecologically diverse habitats (Goodall, 1986; Tutin *et al.*, 1992; Whiten *et al.*, 1999).

Another feature of chimpanzee behavior that has attracted the attention of evolutionary socioecologists is a pattern of group formation which is unusual by nonhuman primate standards. Chimpanzee social organization is characterized by male philopatry, female migration at puberty, bonding between male relatives, and the collaboration of bonded males in the defense of resident females against other male-bonded groups and sometimes in hunting as well (Nishida & Hosaka, 1996; Stanford, 1998; Wrangham & Peterson, 1996). This complex of organization patterns is clearly shared with humans, another species characterized by male bonding and collaboration for aggression and defense.

The alliances formed by chimpanzees for the purposes of gaining and defending mates, social status, and feeding territories, are supported by a repertoire of behaviors also shared by humans. De Waal (1996) and Hemelrijk (1996) describe social alliances and conflict resolution through reciprocity, reconciliation and a form of negotiation through conflictive interactions. Even more interestingly, Goodall (1986), Tutin (1979), and Stanford (1998, 1999) all describe the use of hunted meat as a medium of social exchange for access to both sex and power by chimpanzee adult males. Similar use of meat as a social token by human foragers has been proposed by Hawkes (1991) and investigated by Kaplan and Hill (1985a, 1985b). Food sharing in general is such a critical feature of the human adaptive pattern (in which adults feed young, and males and females share collected and hunted foods) that any food sharing in chimpanzees arouses great interest in the scientific community (Rose, 1997; Winterhalder, 1996).

So far, food sharing is reported to be by chimpanzee mothers to offspring, for hard-to-process foods (Boesch & Boesch, 1999; Hiraiwa-Hasegawa, 1990b; Silk, 1978, 1979), by males to female sexual partners, for meat (Stanford, 1998; Tutin, 1979), and by possessors of meat to social allies and close kin (Boesch & Boesch, 1999; Stanford, 1998; Tutin, 1979), all of which are identified as typically human sharing behaviors.

The question of chimpanzee intelligence, their cognitive abilities, the mode of transmission from one generation to the next of locally variable, adaptive behavior patterns, and the extent to which chimpanzees are able to interpret the behaviors and understand the thinking processes of other chimpanzees can only be fully investigated in captivity (Boysen, 1994; deWaal, 1992; Matsuzawa, 1996; Povinelli, 1994; Tomasello, 1994). Byrne (1995) has argued cogently that great apes and humans are set apart from other primates in their ability to acquire novel behavior patterns through imitation—a quick way of acquiring a complex skill while avoiding time-consuming and potentially dangerous errors. The ability to imitate would be especially significant to a species which depends on skills-based performances for extractive foraging and hunting. Although the notion of a cognitive split between humans and apes and other primates may be defended, the intelligence of chimpanzee behavior in the laboratory suggests a theory of the mind (de Waal, 1992; Povinelli, 1994; Tomasello, 1994), some ability to manipulate numbers (Boysen, 1997), and the use and manipulation of symbols (Rumbaugh, Savage-Rumbaugh, & Sevcik, 1994).

In summary, research on chimpanzee behavior in both the wild and captivity in the past ten years provides ample evidence of communalities between humans and chimpanzees in extractive foraging and hunting, social learning and intergenerational transmission of complex behaviors, social organization, behavioral patterns of social affiliation and conflict, and intelligence and cognition. The question remains as to whether these considerable communalities in behavior between humans and chimpanzees have had the same impact on the life histories of both species and on the configuration of the feeding niches they occupy.

### **3. LIFE HISTORIES OF HUMAN FORAGERS AND WILD CHIMPANZEES**

Although both chimpanzees and humans are large-bodied, long-lived mammals, their life histories differ in various critical parameters: survivorship to age of first reproduction, life expectancy at the beginning of the

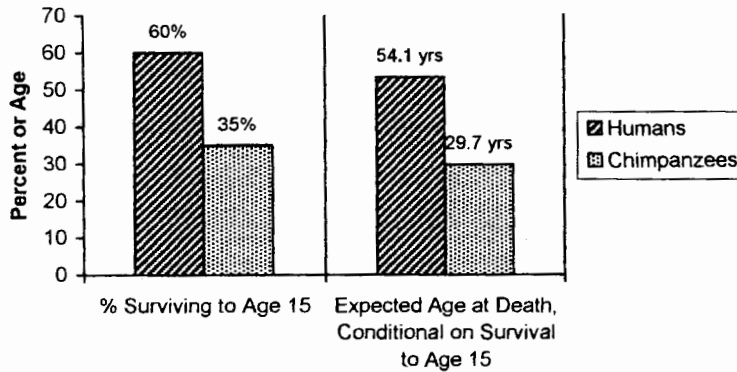


Figure 1. Survival to age 15 and adult lifespan: Human foragers and chimpanzees.

reproductive period, absolute and relative length of the post-reproductive period, spacing between births of surviving offspring, and growth during the juvenile period (Hill & Kaplan, 1999; Kaplan, 1997). The differences between traditional human forager and chimpanzee life spans are shown in Figure 1, and life history traits for the two species are compared below in Table 1.

Table 1 summarizes human life history parameters based on data from four extant groups of human foragers: Ache (Paraguay), Hadza (Tanzania), Hiwi (Venezuela), and !Kung (Botswana/Namibia); see Kaplan, Hill, Lancaster, and Hurtado (1999, table footnotes) for detailed accounts of the sources of the data and how each value was calculated. The forager data come from studies on populations during periods when they were almost completely dependent on wild foods, with little modern technology (and no firearms), no significant outside interference in interpersonal violence or fertility rates, and no significant access to modern medicine. Table 1 also presents chimpanzee life history parameters based on data from five extant groups of chimpanzees: Bossou (Guinea), Gombe (Tanzania), Kibale (Uganda), Mahale (Tanzania) and Tai (Ivory Coast). The chimpanzee data have been compiled from all published and unpublished sources that we are aware of, and, because of small sample size at individual sites, mortality data were combined to create a synthetic life table encompassing all data for wild chimpanzees (Hill *et al.*, 1999).

The data suggest that forager children experience higher survival to age 15 (60% vs. 35%) and higher growth rates during the first five years of life (2.6kg/yr. vs. 1.6kg/yr.) than do chimpanzee juveniles. Chimpanzees, however, grow faster between ages 5–10 both in absolute [2.5kg/yr. (chimpanzees) vs. 2.1kg/yr. (humans)] and proportional weight gain (16% per

Table 1. Life history parameters of human foragers and chimpanzees (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

Group	Probability of survival to age 15	Expected age of death at 15 (years)	Mean age first reproduction (years)	Mean age last reproduction (years)	Inter-birth interval* (months)	Mean weight age 5 (kgs.)	Mean weight age 10 (kgs.)
<b>Humans</b>							
Ache female	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	0.58	54.7				15.5	20
Hadza male	0.55	52.4				14.2	21.2
Hiwi female	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	0.6	56.5	19.2	37	41.3	14	19.5
!Kung male	0.56	56.5				16	22.5
<b>Forager mean</b>	<b>0.60</b>	<b>54.1</b>	<b>19.7</b>	<b>39.0</b>	<b>41.3</b>	<b>15.7</b>	<b>24.9</b>
<b>Chimpanzees</b>							
Bossou female					51		
Bossou male							
Gombe female	0.545	32.7	14.1		64.6	10	21
Gombe male	0.439	28.6				10	24
Kibale female	0.805	35.6			68		
Kibale male	0.408	40.6					
Mahale female			14.6		72		
Mahale male	0.193	23.8					
Tai female	0.094	24	14.3		69.1		
Tai male							
<b>Chimpanzee mean</b>	<b>0.35</b>	<b>29.7</b>	<b>14.3</b>	<b>27.7**</b>	<b>66.7</b>	<b>10</b>	<b>22.5</b>

\* Mean inter-birth interval following a surviving infant.

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



year vs. 10% per year (see Table 1). The earlier high weight gain in humans may be due to an earlier weaning age (about 2.5 years vs. about 5 years for human foragers and chimpanzees respectively) and by parental provisioning of highly processed foods. The later slow growth of human children between 5–10 years is intriguing. According to the allometric growth law, mammalian growth is described by the equation  $dw/dt = Aw^{0.75}$ . Most mammals show a yearly growth constant,  $A$ , of about 1 whereas the mean primate value for  $A$  is about 0.4 (Charnov, 1993). Forager children between ages 5–10 are characterized by a growth constant around 0.2.

The chimpanzee juvenile period is shorter than that for humans, with chimpanzee females giving birth for the first time about five years earlier than hunter-gatherer women. This juvenile period is followed by a dramatically shorter adult lifespan for chimpanzees. In the wild, surviving 15-year old chimpanzees have a life expectancy of only age 30, whereas hunter-gatherers can expect to live an average of 39.2 additional years, provided they have survived to age 15. Importantly, women spend more than a third of their adult life in a post-reproductive phase, whereas few chimpanzee females spend any time at all in a post-reproductive phase. The differences in terms of overall survival and lifespan are striking when comparing survival probabilities for the two species (Figure 1). Less than 10% of chimpanzees ever born survive to age 40, but more than 15% of hunter-gatherers ever born survive to age 70!

Finally, despite the fact that the human juvenile and adult periods are longer, and that human infants are larger than chimpanzee infants at birth (about 3 kg vs. 2 kg), hunter-gatherer women are characterized by higher fertility than chimpanzee females (Figure 2). The mean inter-birth interval (IBI) between offspring (when the first survives to the birth of the second) is over 1.5 times longer among wild chimpanzees than among modern forager populations. Table 1 indicates that forager women may have somewhat longer reproductive spans on average than chimpanzee females, since over 80% of women in foraging societies survive to the age of last birth, whereas chimpanzee last birth is expected to be about 2.5 years (half an inter-birth interval) before the end of the average lifespan. These numbers lead to an interesting paradox. Life tables from modern human foragers always imply positive growth (discussed in Hill & Hurtado, 1996, Ch. 14), whereas the chimpanzee numbers presented here imply slightly negative population growth rates.

To summarize, human foragers show a juvenile period 1.4 times longer than chimpanzees and a mean adult lifespan 2.5 times longer than chimpanzees. Human foragers show higher survival at all post-weaning ages, but lower growth rates during mid-childhood. Despite a longer juvenile period, a slower growth, and a long post-reproductive lifespan, forager women achieve higher fertility rates than chimpanzee females.

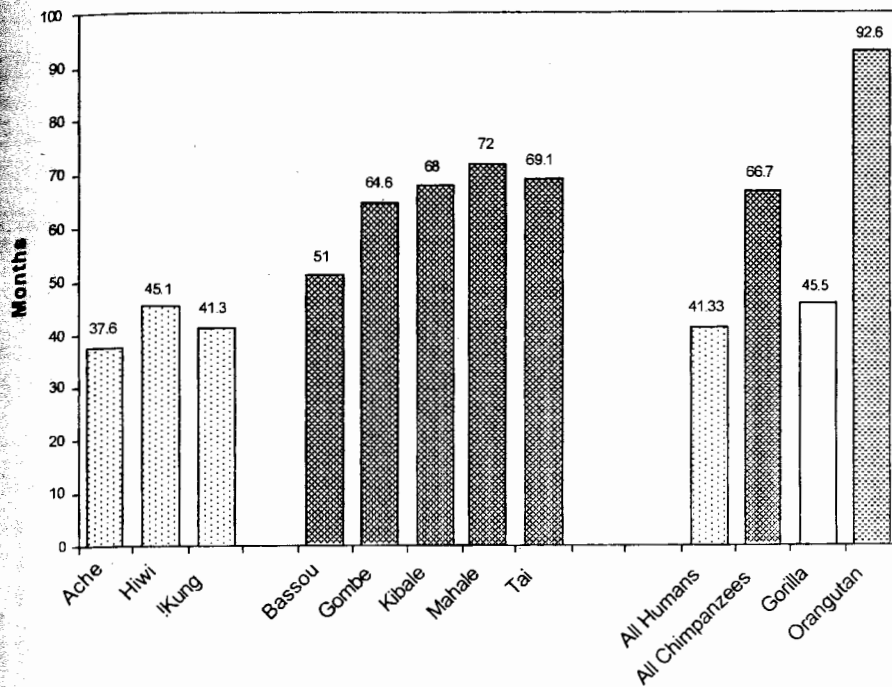


Figure 2. Birth spacing of human foragers and great apes (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

#### 4. CONSUMPTION AND PRODUCTIVITY THROUGH THE LIFE COURSE: CHIMPANZEES AND HUMAN FORAGERS

##### 4.1. Components of the Diet

A comparison of the diets from ten foraging societies and several chimpanzee communities (for which caloric production or time spent feeding were monitored systematically) is summarized in Table 2. Human and nonhuman primate diets can be subdivided into vertebrate animals; roots, nuts, seeds, and other plant parts (leaves, flowers, pith, etc.); and invertebrate animals. Modern human foragers all differ considerably in diet from chimpanzees (see Table 3). Measured in calories, the major component of human forager diets is vertebrate meat, with an approximate range of 20% to 80% of the diet in the sampled societies. Most diets consist in more than 50% of vertebrate meat (equally weighted mean = 60%); the emphasis on vertebrate meat would be even more clear if any Arctic foraging societies

Table 2. Diet of human foragers and chimpanzees (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

		Hunter-Gatherers							Chimpanzees						
		Onge	Anbarra	Arnhem	Ache	Nukak	Hiwi	!Kung <sup>1</sup>	!Kung <sup>2</sup>	Gwi	Hadza	Gombe	Kibale	Mahale	Tai
Sample* kg/person day**		1,256	3,654	276	3,645	941	4,756	866	928	?	?	Sample* kg/person day**			
meat		0.59	1.34	1.821	2,126	764	1,350	690	1,602	417	1,940				
roots		0.21	0.43	0.456	0	0	0.268	150	600?	600?	1,214				
seeds, nuts		0	0	0	0	0	0	1,365	0	0	0				
fruits		0	44	10	22	747	82	150	600?	600?	621				
other plant		0	0	3	255	0	36	0	0	0	0				
invertebrate		20	127	67	308	375	57	0	0	0	255				
<b>Total</b>		<b>1,243</b>	<b>1,085</b>	<b>2,357</b>	<b>2,712</b>	<b>1,886</b>	<b>1,793</b>	<b>2,355</b>	<b>1,617?</b>	<b>4,030</b>					
Non foraged*		0	1,116	0	trace	378	626	trace	trace	0	trace				
<b>Dietary percentage of foraged foods</b>															
meat		79	75	77	78	41	75	29	68?	26?	48	1.5	0.9	2.5	2.1
roots		19	8	19	0	0	15	6	0	37?	30	0.0	0.1	0	1.4
seeds, nuts		0	0	0	0	0	0	58	0	0	0	5.1	0	0	7
fruits		0	4	0	1	40	5	6	0	37?	15	60.2	78.5	57.7	67.6
other plant		0	0	0	9	0	2	0	0	0	0	29.3	21.3	33.4	15.5
invertebrate		2	12	3	11	20	3	0	0	0	6	3.9	0	6.4	5.6
collected		0.0	4.0	0.6	0.8	20?	4.6	4.9	?	37?	15	94.2	99.1	91.1	92.3
extracted		21.9	20.3	30.1	24.3	40?	21.6	63.4	?	37?	36	3.8	0	6.4	5.6
hunted		78.0	75.7	69.4	74.9	40	73.7	31.7	68.0	26.0	48	2	0.9	2.5	2.1

\* Person days sampled including all men women and children as equal consumers.

\*\* This is the weight of the edible portion for meat and field weight for all other resources.

† Percentages from day when measured as reported.

‡ Percentages from day when measured as reported.

**Table 3. Production of energy by men and women in 10 foraging societies (after Kaplan, Hill, Lancaster, & Hurtado, 1999).**

		Mean daily adult production (calories)	% total adult calories	% total adult protein
<b>Ongce</b>	men	4,000	79.7	94.8
	women	1,021	20.3	5.2
<b>Anbarra</b>	men	2,742	70.0	71.8
	women	1,174	30.0	28.1
<b>Arnheim</b>	men	4,578	69.5	93.0
	women	2,012	30.5	7.0
<b>Ache</b>	men	5,590	84.1	97.1
	women	1,055	15.9	2.9
<b>Nukak</b>	men	4,556	60.4	98.6
	women	2,988	39.6	1.4
<b>Hiwi</b>	men	3,489	79.2	93.4
	women	916	20.8	6.6
<b>!Kung<sup>1</sup></b>	men	3,221	45.5	44.7
	women	3,864	54.5	55.3
<b>!Kung<sup>2</sup></b>	men	6,409	>>50	
	women			
<b>Gwi</b>	men	2,412	43.0	78.7
	women	3,200	57.0	21.3
<b>Hadza</b>	men	8,089	64.8	100
	women	4,397	35.2	0

were included in the sample. In contrast, chimpanzees spend about 2% of their feeding time eating meat. Unfortunately, the diet of wild primates is not usually expressed in calories as is the human forager's. Field workers usually estimate the food energy acquired from the time spent feeding on various food types, and rarely express their data in terms of calories consumed. The absolute intake of meat per day also varies tremendously, the chimpanzee per capita meat intake being estimated at about 10–40 grams per day, whereas human diets range from 270 to about 1,400 grams per person per day. Even though chimpanzee males eat much more meat than do females and juveniles (Boesch & Boesch, 1999; Stanford, 1998, 1999; Wrangham, Van, & Riss, 1990), 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 (an extracted resource), which make up an average of about 15% of the energy in the forager diet, and are important in about half the societies in our sample (Table 2). In contrast, the chimpanzee diet is primarily (over 90%) comprised of collected (as opposed to extracted or hunted) foods. However, within the category of collected foods (which includes leaves,

flowers, pith, unripe and ripe fruit), chimpanzees concentrate on the resource of the highest quality and most difficult to acquire, ripe fruit, over 60% of their feeding time being spent on that resource type alone. Only two foraging societies eat large amounts of ripe fruit: the Gwi San of the Kalahari Desert, who consume melons for water and some nutrients during much of the year, and the Nukak of Colombia who extensively exploit tropical palm fruits. Likewise, other, less nutritive 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, with the exception of the Ache who regularly extract starch and growing shoots from tropical palms.

Figure 3 summarizes the comparison of the diets of human and non-human primates presented in Table 2. Extensive overlap between the human foragers' and chimpanzee diets is obvious, yet the data indicate that humans specialize in rare but nutrient-rich resource patches (meat, roots, nuts) whereas chimpanzees specialize in ripe fruit and plant parts with a low density of nutrients. The human diet especially features foods coming in packages that are not only nutritionally dense, but also require skills to obtain. Chimpanzees, on the other hand, depend mostly on collected, ripe fruits with small supplements of insects, extracted foods and small game. Big game (larger than the body size of the individual hunter) is a human prerogative. These fundamental differences in diet are reflected in the gut morphology and food passage times of chimpanzees and humans (Milton, 1999). Chimpanzees are more committed to the rapid passage of bulky, fibrous meals processed in the large intestine whereas humans process

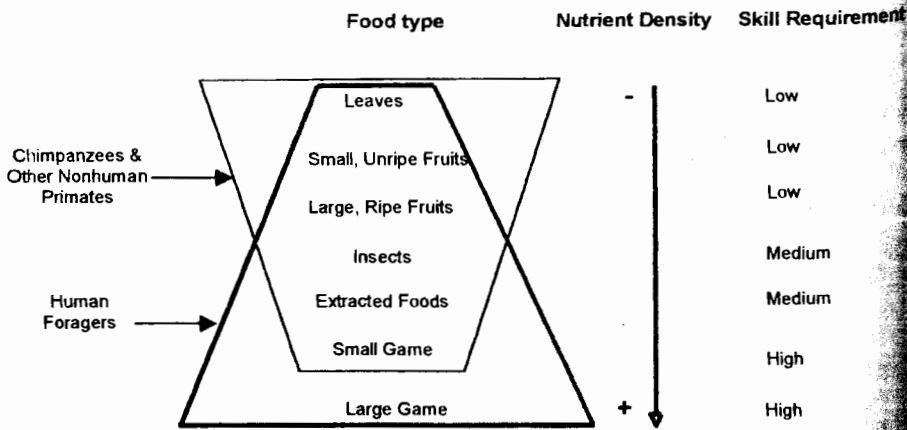


Figure 3. Feeding ecology of human foragers and other primates (after Kaplan, 1997).

nutritionally dense, lower volume meals amenable to slower digestion in the small intestine.

#### 4.2. Difficulty of Acquisition

The key feature of our theory linking feeding niche to life history concerns the relationships between difficulty of acquisition and the age patterning of production for humans and chimpanzees. In order to compare difficulty of acquisition across ecologies, it is useful to rank resources into three different classes going from most easily to most difficult to acquire. *Collected resources* are the easiest to acquire; they are sessile, plant resources which can be gathered and consumed without significant processing. Examples of collected resources are most fruits, leaves, flowers, and sprouts. *Extracted resources* are more difficult to acquire, because their consumption involves extraction of the food contents (most often the reproductive or energy storage organs of plants or animals) from a protective environment such as hard shells or the underground, or because the food is saturated with toxins which may demand extensive processing. Examples of extracted resources are roots and tubers, nuts, insects in protected nests, honey, palm fiber, and some seeds. Lastly, *hunted resources* are the most difficult to acquire, because they are mobile and engage in either evasion or active defense. Hunted resources in relatively large packages are especially dangerous to hunt even if prey body size is less than that of an individual hunter. Clearly, this categorical scheme is rough, because it does not take into account variation within categories or dependence on technology. However, the three categories do capture the major differences between human and chimpanzee strategies for food acquisition.

A breakdown of forager and chimpanzee foods by our three acquisition categories show that 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 (Kaplan et al., 1999). 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. Even though the categories may be somewhat rough, humans are clearly much more dependent than chimpanzees on food resources that require complicated techniques to obtain. It is also the case that there is a wide variability in human diet based on the availability of nutrients in the local environment. In all environments, however, humans tend to eat the best, most concentrated food using their skills in extraction and hunting.

### 4.3. The Age and Sex Patterning of Food Acquisition and Consumption among Chimpanzees and Humans

Data on food acquisition by age and sex category only exist for three modern foraging populations. Ache and Hiwi food production was monitored directly throughout most months of various years by weighing all food produced by foragers of different age and sex categories (Hill *et al.*, 1984; Hurtado & Hill, 1990). 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/sex classes, during part of the wet and part of the dry season of various years (Hawkes *et al.*, 1989, 1995; Blurton Jones *et al.*, 1989, 1997). These data were combined with sample estimates of time spent foraging and frequency of foraging across days to estimate daily food acquisition (e.g., Blurton Jones *et al.*, 1989, 1997). Men's food acquisition from hunting was measured directly by weighing all large game brought to the camp (Hawkes *et al.*, 1992).

All three societies show a similar pattern, presented separately for males and females in Figures 4 and 5. Forager children produce little food compared to adults. In the late juvenile period, daily food acquisition rates

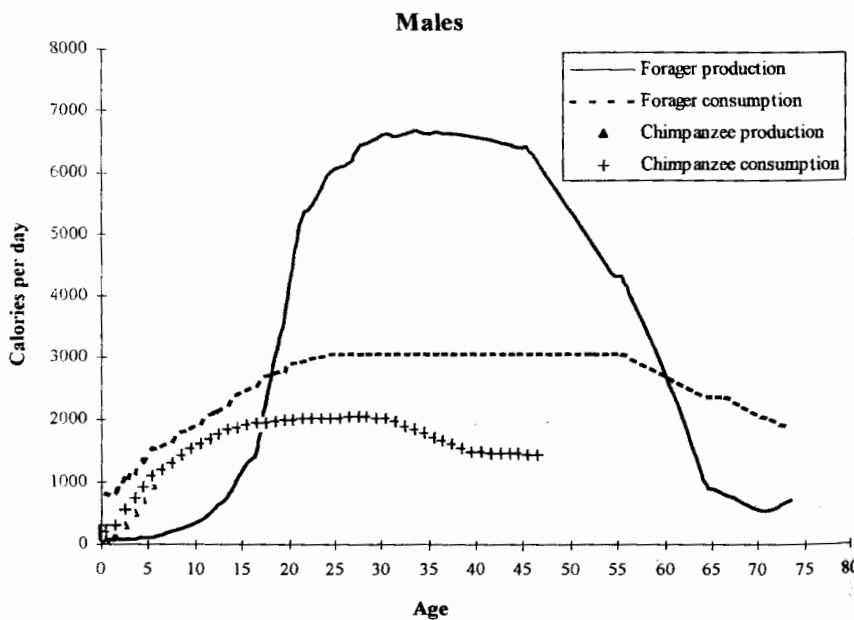


Figure 4. Production and consumption of food: Male foragers and chimpanzees (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

rise dramatically (especially for males) and keep increasing until mid-adulthood (males) or even later (some females). Adult men acquire much more food than any other age/sex category. Although the patterns for men seem consistent for all three societies, Hadza children and post-reproductive women appear to acquire substantially more food than their Ache and Hiwi counterparts (Hawkes et al., 1992, 1997, 1998).

The food consumption rates of forager children and adults can be estimated from body weight and total group production (see Kaplan, 1994). 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. This means simply that daily food acquisition and consumption rates are virtually the same for chimpanzees from the juvenile period onward. Figures 4 and 5 show the mean daily energy consumption and acquisition rates for all three hunter-gatherer societies, compared to chimpanzees of the same age and sex.

The human consumption-acquisition profile is strikingly different from that of chimpanzees, with young chimpanzees acquiring considerably more energy than forager children until about the age of sexual maturity. In particular, consumption is greater than acquisition for female

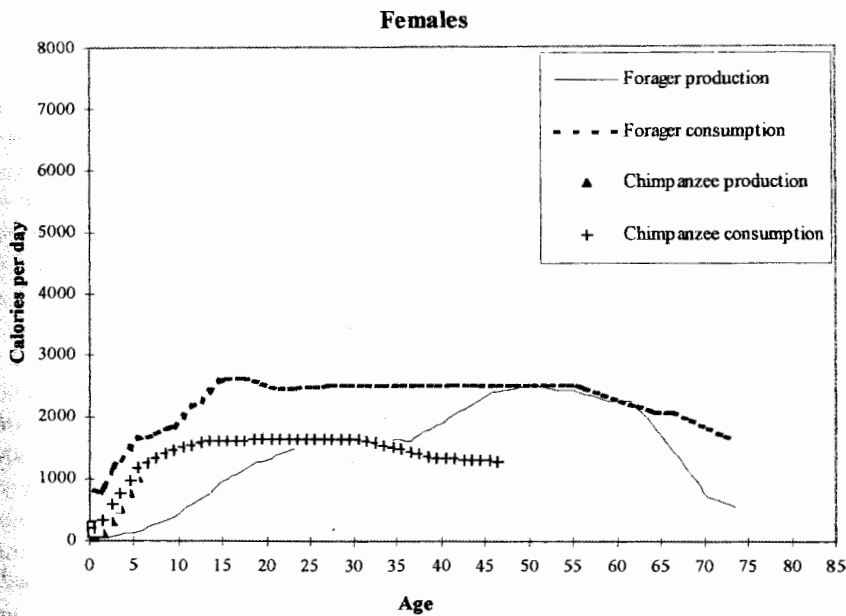


Figure 5. Production and consumption of food: Female foragers and chimpanzees (after Kaplan, Hill, Lancaster, & Hurtado, 1999).



chimpanzees under 10. This reflects several facts of life of chimpanzees. First, they have a long lactation period (nearly 5 years) during which the infant gradually learns to feed itself. Once weaned, nutritional deficits are small and are covered by maternal food sharing of hard-to-acquire foods (Hiraiwa-Hasegawa, 1990a, 1990b; Silk, 1978). By the age of 10 (early adolescence), the chimpanzee youngster is entirely self-feeding, and for the rest of her life produces what she consumes with little surplus. Female chimpanzees do not have more than one nutritionally dependent offspring at a time, and offspring births are widely spaced (5–1/2 yrs.). In contrast, before their late teens children in any forager society produce less than young chimpanzees do. Thus, human juveniles, unlike chimpanzee juveniles, have an evolutionary history of dependency on adults to provide their daily energy needs. Notice that by age 15, the children in our forager sample have reached over 25% of their lifetime energy consumption, but less than 5% of their lifetime energy acquisition.

The areas in Figures 4 and 5 where food acquisition is greater than consumption (where for each species the solid line is above the dotted line) represent surplus energy provided during the later part of the lifespan. The averaged data imply that hunter-gatherer men provide most of the energy surplus that is used to subsidize juveniles and women of reproductive age. While based on only three societies, this average trend can be confirmed by comparing food acquisition rates of adult males and females in the ten forager societies in which food acquisition has been measured within a systematic sample (Table 2).

Food acquisition levels indicate that forager women take much longer to reach peak productivity than men do. Forager males begin to acquire more energy than they consume in their late teens; however, their peak productivity builds slowly from the early twenties to the early thirties and is then sustained for 20 or more years at a level of approximately 6,500k/cals. per day. In contrast, forager women consume more than they produce until menopause, at which time their consumption matches production for perhaps 20 additional years (although, as mentioned above, there is variability among forager groups).

The causes for this disparity between the age when production and consumption are matched and the absolute levels of peak production are quite different for the two sexes. Male energy acquisition depends largely on the hunting of meat. In order to understand why hunting requires so much learning and practice, a detailed analysis of the skills involved in successful hunting must be carried out. Although a thorough treatment of the topic is beyond the scope of this chapter, a few illustrative comments will prove useful. Not all hunting niches necessarily require intensive learning and cognitive machinery. Sit-and-wait ambush predators, or those who simply move until they encounter vulnerable prey and then chase them

down, may not show great increases in success rate dependent on learning. However, the human hunters that we and others (Lee, 1979; Liebenberg, 1990) have observed use a multitude of information to make contingency-specific decisions both during the search phase of hunting and after encountering prey. 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 which guide the search and are continually updated as conditions change. Various alternative courses of action are constantly compared and referenced to spatial and temporal mental maps of resource availability. 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 (aged 35+) had hunted in an area of nearly 12,000 km<sup>2</sup> of tropical forest in their lifetimes (Hill & Hurtado, 1996). Almost all foragers surveyed used more than 200 km<sup>2</sup> in a single year, and many covered more than 1,000 km<sup>2</sup> in a year (Kelly, 1995, Table 4.1). Male chimpanzees, on the other hand, cover only about 10.3 km<sup>2</sup> in a lifetime (Wrangham, 1975; Wrangham & Smuts, 1980).

After potential prey are encountered, humans also employ a wide variety of techniques to obtain them, with an astounding creativity. Here are just some examples that Hill, Hurtado and Kaplan have seen among the Ache and Hiwi: Arboreal animals are shot with arrows from the ground or in a tree, driven by climbing, shaken down from branches, frightened into jumping to the ground, brought down by felling the tree with an axe, lured by imitating calls, lured by making captured infants emit distress calls, captured by spreading sticky resin on branches to trap them, and captured by constructing scaffolding 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 around the neck, or suffocated by stepping on them while trapping them in a tight spot. Burrowing prey are dug out, chopped out of tree trunks, stabbed through the ground with spears, frightened to the point where they bolt from the burrow, smoked out, and captured by introducing a lasso through a small hole. Aquatic prey are shot on the surface, driven into traps, poisoned, shot below the surface, discovered on muddy bottoms by systematically poking the bottom of a pond, and speared underwater by random thrusts in drying lakes. The wide variety of killing techniques motivates humans to search for an equally wide variety of prey. Although all groups probably specialize on the most abundant and vulnerable prey in their area, the total array of species taken is impressive, and probably much larger than that covered by most, if not all, other vertebrate predators. For example, from 1980 to 1996 their sample of weighed prey among the Ache included a minimum of 78 different mammal species, at least 21 species of

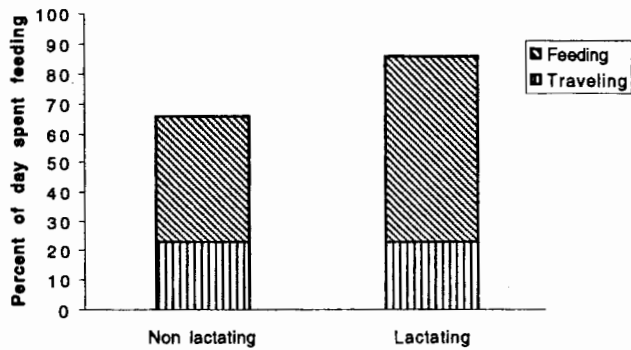
reptiles and amphibians, probably over 150 species of birds (more than they have been able to identify) and over 14 species of fish.

Chimpanzees, too, show a somewhat delayed pattern in the development of their extractive and hunting skills (Silk, 1979). Boesch and Boesch (1999) report that, although the easier forms of extractive foraging begin at age 5, skill at nut-cracking does not mature until age 10; the hunting of meat only begins at age 20 and its effectiveness continues to increase for nearly a decade. In contrast to chimpanzees and human men, women foragers show a pronounced delay in the match between food acquisition and consumption, not because they take so long to acquire the needed skills, but because of the classic trade-off faced by women between child-care and provisioning (Hurtado *et al.*, 1992). Many human female foragers consume more than they produce through infancy, childhood, adolescence, and during their reproductive careers. During this time they are nearly continuously lactating and may have older juvenile dependents as well. In other words, unlike chimpanzee females, human females can afford to consume more than they produce and have multiple dependent young as well during reproduction. It may not be until reproduction is completed that they begin to match consumption and caloric acquisition. In some circumstances reproductive females can be highly productive, collecting protein in reef environments (Bird, 1999) or extracting high-energy roots from the ground (Hawkes, O'Connell, & Blurton Jones, 1997). The important point is that women can expect help during their reproductive careers, and that this help often comes in the form of animal protein which requires skill and risk to obtain.

#### **4.4. The Effect of Men's Surplus Energy Production on the Reproductive Lives of Women**

Figure 6 compares the acquisition of calories and reproductive status of baboons (Altmann, 1980) with Ache foragers (Hill & Hurtado, 1996). Time spent foraging during the day is presented in relation to reproductive status for female baboons, foraging including both travel time and feeding time. What we see is that mother baboons are hard pressed to meet the demands of lactation. When they must produce energy beyond their own maintenance needs, their daily time budget is stretched to the limit. They cannot afford to increase their travel time, which would be energetically costly especially since they must carry their infants. Instead they increase their feeding time, by reducing resting and socializing to about 15% of the day. Mother baboons thus work harder. In fact female baboons have higher mortality rates when lactating than when cycling or being pregnant (Altmann, 1980).

### Baboon Female-Model of Time Spent Feeding and Reproductive Status



### Ache Women-Calorie Acquisition and Reproductive Status

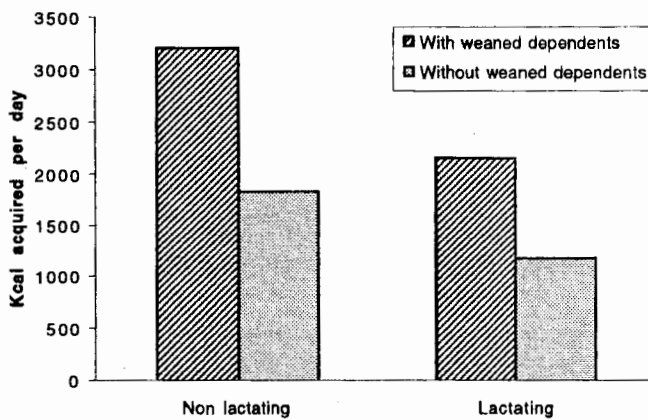


Figure 6. Food acquisition and reproductive status: Ache women and baboon females (Hurtado, Hawkes, Hill, & Kaplan, 1985; Altmann, 1980, p. 56).

Unfortunately, the appropriate data are not available for female chimpanzee productivity, mortality and reproductive status. However, their life history parameters, which include an even longer lactation period with only a single, nutritionally-dependent offspring at a time and no provisioning by other group members, suggest that they too are pressed by the same nutritional stresses as are female baboons.

In contrast, when lactating and even when they have dependent juveniles to be fed, Ache women reduce their work effort (acquisition of food

resources), although not as much as when they have only one nursing infant. Female baboons (and mother chimpanzees as well), on the other hand, never have weaned offspring that are nutritionally dependent. Once they are weaned, young nonhuman primates feed themselves for the rest of their lives whereas just the opposite is true for human juveniles. Human females, then, are able to cut back on energy production when they are nursing even though their caloric consumption and dependency ratio may have gone up, whereas nonhuman primate females increase their work effort during lactation to meet the extra caloric demands of lactation and do not assume juvenile nutritional dependency.

The provisioning of reproductive women and weaned juveniles has a powerful effect on the production of children by humans, and in more than one way: First, it reduces the energy cost and health risk of lactation to the individual mother. Remember Table 1, which shows that most forager women can expect to live out their entire reproductive careers, and that pregnancy and lactation do not raise mortality rates. Second, food provisioning lifts the burden of self-feeding from the shoulders of juveniles, and allows them to remain dependent on adults for energy until they are fully grown. Third, provisioning allows the reduction in birth spacing shown in Figure 2 (Furuichi *et al.*, 1998; Galdikas & Wood, 1990; Kaplan *et al.*, 1999). Since human weanlings do not have to be self-feeders but are provisioned by adults, they can be weaned at an earlier age. The average Inter-birth interval between successive live births of human foragers is around 41 months, which means (allowing 12 months for conception and pregnancy) that most weaning among human foragers occurs about two years and a half after birth.

In contrast, the average inter-birth interval for chimpanzees is 66.7 months, and for orangutans 92.6 months. The only great ape to approach humans in this respect is the gorilla, but the gorilla is an ape that feeds at a very low level of the food chain. The major part of its diet is made of herbaceous plants which are ubiquitous and take little acquired skills to harvest. The main requirement for weaning is that the young gorilla has developed enough gut size to process low-energy foods. On the other hand, women cut back on their work effort and do not produce surpluses during their reproductive careers because their reproduction is being underwritten by other group members, especially men, and not because their productive skills take so long to acquire.

## 5. CONCLUSIONS

The impressive array of biological and behavioral commonalities shared by chimpanzees and humans might be taken to imply that the

differences between the two species are simply ones of degree. Although some of the features discussed here involve merely quantitative differences, however, others point to distinctions of a qualitative nature. The life history and feeding niche of humans have co-evolved into a unique adaptation which formatted a completely different life course—one characterized by a long period of juvenile dependency, a late onset of reproduction, a major reduction in spacing between births, and long productive and post-reproductive periods. The feeding niche exploited by humans evolved in tandem with these life history changes. It stressed nutritionally dense, hard-to-acquire foods whose acquisition relies on a wide variety of skills-based performances.

The human adaptation is in one sense both broad and flexible, and in another sense very narrow and specialized. 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 different age- and sex- classes of individuals. The relative contributions of men and women to food production appear to vary from group to group, and even the contribution of children and teens to food production varies 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 nutrient-dense, difficult-to-acquire foods and a life history with a long, slow development, a large commitment to learning and intelligence, and an age profile of production shifted towards older ages. We do not expect to find any human population that subsists on leaves or other low quality foods, or even fruits for that matter. We rather expect humans to remain at the very top of the food hierarchy in every environment they live in (humans often exterminate all other top predators in their habitat). This dietary commitment is reflected in the extremely reduced size of the human hindgut. Humans ingest foods that are already high quality and do not require much digestive work of detoxification. They also use their great intelligence to extract and hunt those foods. In order to achieve this diet, humans are very unproductive as children, extremely productive as adults, have very costly brains, and engage in extensive food sharing both within and among age- and sex- classes of individuals.

Meat plays a special role in the evolution of human diet and behavior. It is complementary to plant foods in that it provides essential macronutrients. It is energy-dense and comes in easily divisible, large packages, which lays a foundation for food-sharing and the division of labor (Lancaster & Kaplan, 1992; Lancaster & Lancaster, 1987). It cannot be readily obtained by juveniles, because it requires learned skilled performances, nor by reproducing women, because its attainment usually involves

risk and costs to infant care. Of all types of nutritional sources, meat is the only one that can lead to surplus production through the employment of skill and cannot be readily obtained by juveniles and women under most ecological circumstances. The original division of labor in humans between male hunting and risk taking and female gathering and care of offspring rests on its unique characteristics.

The theory and the data we presented suggest that the human life-course is based on a complex set of interconnected time-dependent processes and a 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 lifecourse 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 towards the acquisition of learned skills and knowledge to obtain very high rates of productivity later in life.

## ACKNOWLEDGMENTS

The authors wish to express their appreciation to K. G. Anderson, John Bock, Michelle Cristiani, Sharon Pochron, and Troy Tucker, who helped with the preparation of tables and figures and with bibliographic research.

## REFERENCES

- Altmann, J. (1980). *Baboon mothers and infants*. Chicago, IL: University of Chicago Press.
- Bird, R. (1999). Cooperation and conflict: The behavioral ecology of the sexual division of labor. *Evolutionary Anthropology*, 8, 65-75.
- Blurton Jones, N. G., Hawkes, K., & O'Connell, J. (1989). Modeling and measuring the costs of children in two foraging societies. In V. Standen & R. Foley (Eds.), *Comparative socioecology of humans and other mammals* (pp. 367-390). London: Basil Blackwell.
- Blurton Jones, N. G., Hawkes, K., & O'Connell, J. (1997). Why do Hadza children forage? In N. L. Segal, G. E. Weisfeld, & C. C. Weisfeld (Eds.), *Uniting psychology and biology: Integrative perspectives on human development* (pp. 297-331). New York: American Psychological Association.

- Boesch, C., & Boesch, H. (1999). *The chimpanzees of the Tai Forest: Behavioural ecology and evolution*. Oxford: Oxford University Press.
- Boesch-Achermann, H., & Boesch, C. (1994). Hominization in the rainforest: The chimpanzee's piece of the puzzle. *Evolutionary Anthropology*, 3, 9-16.
- Boysen, S. T. (1994). Individual differences in the cognitive abilities of chimpanzees. In R. W. Wrangham, W. C. McGrew, F. de Waal, & P. Helte (Eds.), *Chimpanzee cultures* (pp. 335-350). Cambridge, MA: Harvard University Press.
- Boysen, S. T. (1997). Representation of quantities by apes. *Advances in the Study of Behavior*, 26, 435-462.
- Byrne, R. (1995). *The thinking ape: Evolutionary origins of intelligence*. Oxford: Oxford University Press.
- Byrne, R. (1997). The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence? In A. Whiten & R. Byrne (Eds.), *Machiavellian intelligence II* (pp. 289-311). Cambridge: Cambridge University Press.
- Charnov, E. L. (1993). *Life history invariants: Some explanations of symmetry in evolutionary ecology*. Oxford: Oxford University Press.
- de Waal, F. (1992). Intentional deception in primates. *Evolutionary Anthropology*, 1, 86-92.
- de Waal, F. (1996). Conflict as negotiation. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 159-172). Cambridge: Cambridge University Press.
- Furuichi, T., Idani, G., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enomoto, T., Okayasu, N., Hashimoto, C., & Kano, T. (1998). Populations dynamics of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*, 19, 1029-1045.
- Galdikas, B. M. F., & Wood, J. W. (1990). Birth spacing patterns in humans and apes. *American Journal of Physical Anthropology*, 83, 185-192.
- Gibson, K. R. (1986). Cognition, brain size and the extraction of embedded food resources. In J. G. Else & P. C. Lee (Eds.), *Primate ontogeny, cognition, and social behavior* (pp. 93-105). Cambridge: Cambridge University Press.
- Goodall, J. (1986). *The chimpanzees of the Gombe: Patterns of behavior*. Cambridge: Cambridge University Press.
- Goodman, M. (1999). The genomic record of humankind's evolutionary roots. *American Journal of Human Genetics*, 64, 31-39.
- Hawkes, K. (1991). Showing off: Tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology*, 12, 29-54.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. (1989). Hardworking Hadza grandmothers. In V. Standen & R. A. Foley (Eds.), *Comparative socioecology of humans and other mammals* (pp. 341-366). London: Basil Blackwell.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. (1992). Hunting income patterns among the Hadza: Big game, common goods, foraging goals and the evolution of the human diet. In A. Whiten & E. M. Widdowson (Eds.), *Foraging strategies and natural diet of monkeys, apes and humans* (pp. 83-92). Oxford: Clarendon Press.
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1995). Hadza children's foraging: Juvenile dependency, social arrangements, and mobility among hunter-gatherers. *Current Anthropology*, 36, 688-700.
- Hawkes, K., O'Connell, F., & Blurton Jones, N. (1997). Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Current Anthropology*, 38, 551-577.
- Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Science of the United States of America*, 95, 1336-1339.
- Heltne, P. G., & Marquardt, L. A. (1989). *Understanding chimpanzees*. Cambridge, MA: Harvard University Press.



- Hemelrijk, C. (1996). Reciprocation in apes: from complex cognition to self-structuring. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 185–196). Cambridge: Cambridge University Press.
- Hill, K., Boesch, C., Pusey, A., Williams, J., & Wrangham, R. (1999). *Chimpanzee mortality in the wild*. Manuscript submitted for publication.
- Hill, K., Hawkes, K., Hurtado, A., & Kaplan, H. (1984). Seasonal variance in the diet of Ache hunter-gatherers in eastern Paraguay. *Human Ecology*, *12*, 145–180.
- Hill, K., & Hurtado, A. M. (1996). *Ache life history: The ecology and demography of a foraging people*. Hawthorne, NY: Aldine de Gruyter.
- Hill, K., & Kaplan, H. (1999). Life history traits in humans: Theory and empirical studies. *Annual Review of Anthropology*, in press.
- Hiraiwa-Hasegawa, M. (1990a). A note on the ontogeny of feeding. In T. Nishida (Ed.), *The chimpanzees of the Mahale Mountains: Sexual and life history strategies* (pp. 277–283). Tokyo: Tokyo University Press.
- Hiraiwa-Hasegawa, M. (1990b). The role of food sharing between mother and infant in the ontogeny of feeding behavior. In T. Nishida (Ed.), *The chimpanzees of the Mahale Mountains: Sexual and life history strategies* (pp. 267–276). Tokyo: Tokyo University Press.
- Hurtado, A. M., Hawkes, K., Hill, K., & Kaplan, H. (1985). Female subsistence strategies among Ache hunter-gatherers of Eastern Paraguay. *Human Ecology*, *13*, 1–28.
- Hurtado, A. M., & Hill, K. (1990). Seasonality in a foraging society: Variation in diet, work effort, fertility, and the sexual division of labor among the Hiwi of Venezuela. *Journal of Anthropological Research*, *46*, 293–345.
- Hurtado, A. M., Hill, K., Kaplan, H., & Hurtado, I. (1992). Tradeoffs between female food acquisition and childcare among Hiwi and Ache foragers. *Human Nature*, *3*, 185–216.
- Kaplan, H. K. (1994). Evolutionary and wealth flows theories of fertility: Empirical tests and new models. *Population and Development Review*, *20*, 753–791.
- Kaplan, H. K. (1997). The evolution of the human life course. In K. Wachter & C. E. Finch (Eds.), *Between Zeus and Salmon: The biodemography of aging* (pp. 175–211). Washington, DC: National Academy of Sciences.
- Kaplan, H., & Hill, K. (1985a). Food-sharing among Ache foragers: Tests of explanatory hypotheses. *Current Anthropology*, *26*, 223–245.
- Kaplan, H., & Hill, K. (1985b). Hunting ability and reproductive success among male Ache foragers. *Current Anthropology*, *26*, 131–133.
- Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (1999, in press). A theory of human life history evolution: Brains, learning and longevity. *Evolutionary Anthropology*, *8*.
- Kelly, R. (1995). *The foraging spectrum: Diversity in hunter-gatherer lifeways*. Washington, DC: Smithsonian Institution Press.
- Lancaster, J. B., & Kaplan, H. (1992). Human mating and family formation strategies: The effects of variability among males in quality and the allocation of mating effort and parental investment. In T. Nishida, W. McGrew, P. Marler, M. Pickford, & F. de Waal (Eds.), *Topics in primatology: Human origins* (pp. 21–33). Tokyo: University of Tokyo Press.
- Lancaster, J. B., & Lancaster, C. S. (1987). The watershed: Change in parental-investment and family-formation strategies in the course of human evolution. In J. Lancaster, J. Altmann, A. Rossi, & L. Sherrod (Eds.), *Parenting across the life span* (pp. 187–205). New York: Aldine de Gruyter.
- Lee, R. B. (1979). *The !Kung San: Men, women, and work in a foraging society*. Cambridge: Cambridge University Press.
- Liebenberg, L. (1990). *The art of tracking: The origin of science*. Cape Town: David Philip.

- Matsuzawa, T. (1996). Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 196–212). Cambridge: Cambridge University Press.
- McGrew, W. C., Marchant, L. F., & Nishida, T. (Eds.). (1996). *Great ape societies*. Cambridge: Cambridge University Press.
- Milton, K. (1999). A hypothesis to explain the role of meat-eating in human evolution. *Evolutionary Anthropology*, 8, 11–21.
- Nishida, T., & Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale mountains, Tanzania. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 114–134). Cambridge: Cambridge University Press.
- Parker, S., & Gibson, K. (1979). A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences*, 2, 367–408.
- Povinelli, D. J. (1994). What chimpanzees (might) know about the mind. In R. W. Wrangham, W. C. McGrew, F. D. Waal, & P. Helte (Eds.), *Chimpanzee cultures* (pp. 285–300). Cambridge, MA: Harvard University Press.
- Rose, L. M. (1997). Vertebrate predation and food-sharing *Cebus* and *Pan*. *International Journal of Primatology*, 18, 727–766.
- Rumbaugh, D. M., Savage-Rumbaugh, E. S., & Sevcik, R. A. (1994). Biobehavioral roots of language: A comparative perspective of chimpanzee, child, and culture. The question of chimpanzee culture. In R. W. Wrangham, W. C. McGrew, F. D. Waal, & P. Helte (Eds.), *Chimpanzee cultures* (pp. 319–334). Cambridge, MA: Harvard University Press.
- Silk, J. B. (1978). Patterns of food-sharing among mother and infant chimpanzees at Gombe National Park, Tanzania. *Folia Primatologica*, 29, 129–141.
- Silk, J. B. (1979). Feeding, foraging, and food-sharing behavior in immature chimpanzees. *Folia Primatologica*, 31, 12–42.
- Stanford, C. B. (1998). *Chimpanzee and red colobus: The ecology of predator and prey*. Cambridge, MA: Harvard University Press.
- Stanford, C. G. (1999). *The hunting apes: Meat eating and the origins of human behavior*. Princeton, NJ: Princeton University Press.
- Sugiyama, Y. (1997). Social tradition and the use of tool-composites by wild chimpanzees. *Evolutionary Anthropology*, 6, 23–27.
- Tomasello, M. (1994). The question of chimpanzee culture. In R. W. Wrangham, W. C. McGrew, F. D. Waal, & P. Helte (Eds.), *Chimpanzee cultures* (pp. 301–318). Cambridge, MA: Harvard University Press.
- Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 6, 29–38.
- Tutin, C. E. G., Fernandez, M., Rogers, M. E., Williamson, E. A., & McGrew, W. C. (1992). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. In A. Whiten & E. M. Widdowson (Eds.), *Foraging strategies and natural diet of monkeys, apes and humans* (pp. 19–26). Oxford: Clarendon Press.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399, 682–685.
- Winterhalder, B. (1996). Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology*, 5, 46–57.
- Wrangham, W. (1975). *The behavioral ecology of chimpanzees in Gombe National Park, Tanzania*. Unpublished Ph.D. dissertation, Cambridge University, Cambridge.
- Wrangham, R. W., McGrew, W. C., De Waal, F., & Helte, P. (Eds.). (1994). *Chimpanzee cultures*. Cambridge: Harvard University Press.

- Wrangham, R. W., & Peterson, D. (1996). *Demonic males: Apes and the origins of human violence*. Boston, MA: Houghton Mifflin.
- Wrangham, R. W., & Smuts, B. (1980). Sex differences in behavioral ecology of chimpanzees in Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, 28 (Suppl.), 13-31.
- Wrangham, R. W., Van, E., & Riss, Z. B. (1990). Rates of predation on mammals by Gombe chimpanzees, 1972-1975. *Primates*, 3, 157-170.