Chapter 13 Human Survival and Life History in Evolutionary Perspective

Michael Gurven

A PRIMARY GOAL of evolutionary anthropology is to determine and quantify differences between humans and other species, especially our primate relatives, and to reconstruct the evolutionary history of our species. As a species of seven billion individuals, humans occupy almost every habitat on the planet. Our exceptionally long lives, encephalized brains, extreme sociality, and penchant for cumulative cultural learning have all likely contributed to the biological success of *Homo sapiens*. Evolutionary anthropology has the goal of describing human universals while also explaining variation among and within human populations in genes, behavior, psychology, and culture.

This chapter focuses on human survival and life history: theoretical approaches and key features of human adaptability across time and space. I focus on small-scale societies of hunter-gatherers, because more than 90% of human history has been spent living in them. Even though domestication is a more recent feature of human societies, I also include forager-horticulturalists because they share many features with hunter-gatherers, such as natural fertility, egalitarianism, kin-based society, high work effort, and similar life spans. The first section summarizes several evolutionary approaches to studying humans. The second section characterizes human subsistence and sociality as important aspects of evolved life history. The third section integrates cultural learning and psychological adaptations related to social cognition and predator avoidance. I conclude by suggesting directions for future research.

Human Evolutionary Behavioral Sciences

Several complementary approaches comprise the evolutionary study of humans: human behavioral ecology, dual gene-culture inheritance theory, and evolutionary psychology. Each has been influential in helping to understand aspects of human nature and the human condition. This three-pronged approach to studying humans is no doubt linked to the fact that the humans studying and being studied are self-reflective, culturally rich, loquacious, and disputatious primates.

Human Behavioral Ecology

Human behavioral ecology (HBE) applies principles of natural selection to explain behavioral and cultural diversity in human populations (Borgerhoff Mulder 1991; Cronk 1991; Smith & Winterhalder 1992). It explores how features of the physical and social environment shape the suite of behaviors or "strategies" of individuals, and applies cost-benefit logic of constrained optimization to design models and to make formal predictions about the conditions that favor particular behaviors. Its roots are in biology (evolutionary biology, animal behavior, population and community ecology, life-history theory), anthropology (cultural ecology, hunter-gatherer studies), and economics (microeconomics of consumer choice). Because of its focus on the adaptive nature of behavior, the HBE tradition studies behavioral and cultural traits likely to have direct or indirect fitness consequences. These include the study of subsistence, mating, parenting, and costly social behaviors (Cronk et al. 2000). In all human societies, people extract resources from their environment; find mates; defend access to resources; protect, feed, and care for offspring; and form and maintain social partners and alliances. People trade off time and energy among these tasks. The reliance on trade-offs, borrowed from life-history theory in biology (chapter 10, this volume), is a fundamental tool in HBE. Fitness payoffs—whether measured directly, in terms of survival and reproductive success, or indirectly, as in foraging return rate, access to more sexual partners, or higher social status—result from optimal allocations made to multiple competing activities. Optima vary according to individual condition, state, and ecological setting; they also may depend on strategies employed by others in a frequency-dependent manner, often requiring game-theoretic modeling (Maynard Smith 1982).

Dual Inheritance Theory

Dual inheritance theory (DIT) or gene-culture coevolution analyzes the interaction of genetic and cultural evolutionary processes (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Henrich & McElreath 2003). While selection pressures continue to promote changes in gene frequency in human populations (Hawks et al. 2007), particularly with respect to diet, metabolism, and immune function, complex adaptive genetic design appears to remain fairly stable over recent history; the pace of cultural change is extremely rapid in comparison. Exponential population growth, rapid industrialization, and technological change in the last millennium highlight the need to include culture formally in our understanding of human adaptation to a wide range of environments. Given cultural diversity before the post-agricultural population explosion, it further behooves us to take culture seriously. Emphasis has been on the evolution of social learning strategies for obtaining behaviors in moderately noisy environments, such as prestige bias (i.e., imitate the powerful, Henrich & Gil-White 2001) and conformist bias (i.e., imitate the majority, Henrich and Boyd 1998). Reliance on these strategies can lead to both adaptive and maladaptive outcomes. The opportunity to retain skills, transmit them to others, and build on them is a main reason why humans are the only species to show the "ratcheting" of cumulative culture (Boyd & Richerson 1996; Tomasello 1999; chapter 32, this volume). To date, much work in DIT has relied on mathematical models that show the conditions favoring different learning strategies in varied environments and populations. Recent empirical studies have focused, however, on the evolution and maintenance of social norms, ethnic markers, morality, and novel technology (e.g., McElreath 2004; Mesoudi & O'Brien 2008).

Evolutionary Psychology

Evolutionary psychology (EP) studies human nature by mapping the problem-solving design features of psychological adaptations (Tooby & Cosmides 1989; Buss 1995; Crawford & Krebs 1998; Daly & Wilson 1999). The metaphor of the mind is a Swiss Army knife, or a nested network of computer algorithms, with domain-specific adaptations in the brain functionally designed to solve specific recurring problems in our ancestral past. This ancestral past has been referred to as the environment of evolutionary adaptedness (EEA). Examples of these recurring problems include finding mates, evading predators, choosing trustworthy allies, and avoiding toxins and pathogens. Attention has focused on phenotypic cues of mate choice (e.g., facial attractiveness, fluctuating asymmetry, waist-to-hip ratios, indicators of ambition, wealth and social status), sex differences (e.g., spatial abilities, mate preferences, aggression, parental investment), cooperation (e.g., cheater detection, altruistic intent, punitive sentiment), emotions (e.g., jealousy, anger, limerence, guilt) and other topics (e.g., predator-prey cognition, supernatural beliefs, aesthetics; see Buss 1999; Gaulin & McBurney 2004). Because our brains evolved in specialized ways to solve problems, individuals are best viewed as modularized "adaptation executors" rather than general-domain "fitness maximizers" (Tooby & Cosmides 1992). Psychological adaptations are believed to be instantiated as concrete neural circuits common to all members of a species. Cultural variation is "evoked" from the interaction of a context-dependent psychology and environmental cues.

Similarities and Points of Contention: Toward a Synthesis

All three of these approaches place prime importance on the role of natural selection as the sieve that shapes patterns of human variation. While evolution also occurs from founder effects in small populations, random mutation, and gene flow, only natural selection produces complex adaptations. However, alternative goals, methods, disciplinary culture, and mutual misconceptions have fomented disagreements among researchers adopting different approaches. Several recent reviews explore similarities and differences among these three subdisciplines and raise important criticisms (Winterhalder & Smith 2000; Panksepp & Panksepp 2000; Smith et al. 2001; Laland & Brown 2002; Kaplan & Gangestad 2005; Sear et al. 2007). I highlight what I view as key distinctions in five areas.

The primary goal

HBE attempts to explain behavioral variation by testing whether observed behavior matches optimal behavior predicted by an optimality model. It thereby "black boxes" the proximate psychological mechanisms (the fundamental focus of EP) that individuals employ to achieve adaptive outcomes. The reliance on the "phenotypic gambit" (Grafen 1984) in HBE and EP obviates the need to identify the genetic bases of behavior. EP focuses on the cues that minds use as critical inputs when solving specific fitness-relevant problems in the EEA. DIT stresses the role of learning rules that individuals use to choose behaviors and skills, but it neither assumes nor requires domain specificity.

Universals versus variation

Much work in EP has helped to identify human universals rather than explain intra- or interpopulation variation, whereas HBE and DIT explicitly focus on variation. Unfortunately, most EP studies are conducted among members of WEIRD (Western, educated, industrialized, rich, democratic) societies, which represent only a small portion of the tapestry of past and present human experience (Henrich et al. 2010). Debates over the relevant roles of potential genetic difference, innate predisposition, and the timing of cultural conditioning are contentious (Atran et al. 2005; Norenzayan & Heine 2005).

The role of culture

Only DIT models culture explicitly; HBE often assumes rather than explains cultural traits as constraints or parameters of the local environment, or asserts that cultural variation may be the manifestation of local equilibria in different environments. EP mostly ignores culture, as it is largely believed to be "evoked" as a developmental fine-tuning of evolved psychology.

Methods

HBE often tests optimality models using behavioral data collected during long-term fieldwork, often among traditional populations, while EP has principally relied on controlled experiments among student populations. DIT constructs mathematical models underlying the epidemiology, or cause and spread, of ideas and the adaptive or maladaptive consequences.

The role of fitness

EP takes a functional design approach to adaptive problems to characterize the structure of psychological mechanisms. It is less attuned to behavioral outputs and their fitness-maximizing potential, even though it is assumed that psychological adaptations on average result in fitness-maximizing behavior in the trait-specific EEA. HBE focuses explicitly on behavior, and often measures direct fitness or indirect proxies of fitness. According to EP, individuals living in novel environments are not expected to display evidence of fitness-maximizing behavior if their adaptations evolved in a different ecology; this results in "mismatches" between observed behavior and theoretical predictions. However, adaptive behavior is not difficult to find in modern societies (e.g., Nettle & Pollet 2008) despite the common perception that the past few hundred years have severed the link between adaptive design and fitness outcomes. Given the trade-offs associated with allocations of scarce resources to potentially competing modules, selection should act on functional output, which may require compromised design in any single module.

A common goal of evolutionary anthropology is to understand how and why our evolved psychology produces phenotypically plastic responses in different socioecological contexts, and the extent to which psychology and behavior are currently adaptive and maximize fitness. At the population level, an aim is to understand how the cultural landscape of humans jointly alters behavior and gene frequencies (Boyd & Richerson 1985; Laland et al. 2001). Several of the differences noted above are beginning to fade as lines between the three fields become blurry: HBE practitioners often run experiments and study people in developed countries, a growing number of DIT and EP researchers conduct fieldwork and experiments, and life-history theory and the logic of optimization have recently influenced EP while HBE and DIT have increasingly paid more explicit attention to psychology. Practitioners in HBE, and in EP to some extent, have also started to study culture, norms, and historical trends. The number of collaborations among practitioners who use these disparate perspectives is growing (e.g., the Cross Cultural Experimental Games Project, the Culture and the Mind Project, and the Inheritance of Inequality in Pre-Modern Societies Project). Substantial advances in our understanding of human culture, psychology, and behavior will require the methods and theoretical insights of all three approaches.

Human Life History

Table 13.1 summarizes some key life-history differences between humans and our nearest primate relatives, chimpanzees (*Pan troglodytes*). Compared to other mammals, and even other primates of similar body size, humans have long lives, large brains, and bodies that grow and develop

Table 13.1. Comparison of life-history traits among traditional human hunter-gatherers, living in natural fertility conditions, and wild chimpanzees

Trait	Definition	Unit	Humans	Chimpanzees	Difference
Brain volume	Total volume of brain	cm^3	1201	400	200%
Juvenile period	Weaning to menarche	Years	12.9	5	158%
Adult life span	Life expectancy at age 15	Years	37.7	14	148%
Maximum life span	Oldest observed individual	Years	121	66[a]	83%
Fertility rate	Inverse of interbirth interval	#/yr	0.29	0.18	71%
Juvenile survival	Probability of living to age 15	Percentage	57	42	36%
Interbirth interval	Time between successive births	Months	41.3	66.7	–71%
Extrinsic mortality rate	Young adult mortality rate	Percentage per year	1.1	3.7	–70%
Neonate mass	Mass at birth	kg	3.4	1.4	143%
Age at menarche	Birth to menstruation	Years	15	10	50%
Age at first reproduction	Birth to reproduction	Years	19.1	13	47%
Age at last reproduction	Birth to last reproduction	Years	39	27.7	41%
Adolescence	Menarche to first reproduction	Years	4.1	3	37%
Fetal growth rate[b]	Conception to birth	g/day	12.6[a]	6.1[a]	107%
Total fertility rate	Total number of live births	Live births	6.1	5	22%
Gestation length	Conception to birth	days	269[a]	228[a]	18%
Body size	Average adult female mass	kg	47	35	34%

[a] Not specific to natural fertility or wild populations

[b] Fetal growth rate = neonate mass (g) /gestation length (days)

References
Brain volume: Aiello & Dean 1990
Juvenile period: Walker et al. 2006
Extrinsic mortality rate, adult lifespan, juvenile survival: Gurven & Kaplan 2007; Hill et al. 2001
Maximum life span: Finch 2007
Neonate mass: Lee et al. 1991
Age at first and last reproduction: Kaplan et al. 2000; Walker et al. 2006
Interbirth interval, total fertility rate: Gurven & Kaplan 2007; Kaplan et al. 2000
Age at menarche, gestation length: Walker et al. 2006; Wood 1994
Adolescence, body size: Walker et al. 2006

slowly (chapter 10, this volume). This evolved human life history has a number of derived or exaggerated features that likely contributed to the success of *Homo sapiens* (Hill & Kaplan 1999; Kaplan et al. 2000; Gurven & Walker 2006): (1) a diet comprising high-quality, nutrient-dense foods that come in large packages; (2) learning-intensive, technology-intensive, and often cooperative, food acquisition techniques; (3) an encephalized brain that facilitates the learning and storage of rich context-dependent information, effective imitation of conspecifics, and development of creative solutions to fitness-relevant problems; (4) a long period of juvenile dependence to support brain development, growth, and learning; (5) low juvenile and adult mortality rates, generating a long productive life span; (6) a three-generational system of downward resource flows from grandparents to parents and children; (7) pair bonds and biparental investment, with men specializing in energetic support and defense, and women combining energetic support with direct care of children; (8) cooperative arrangements among kin and unrelated individuals (including upward resource flows) that reduce variance in food availability through sharing, divisions of labor, and mutual aid.

One feature of human life history that has received considerable attention is survival beyond the age of last reproduction. Postreproductive longevity is a robust feature of hunter-gatherers and of the human life cycle, but it is rare in mammals, including primates. A hunter-gatherer who survives to age 15 can expect to live an additional 30 to 44 years, and a survivor at age 40 can expect to live an additional 20 to 28 years (fig. 13.1). Much of the variation in age-specific life expectancies among preindustrial populations occurs in the first few years of life, where the force of selection, measured as the fitness elasticity of survival, has the greatest relative impact on the life course (Jones 2009). Age trajectories of adult mortality, however, show a roughly similar profile across the life course. The remarkably detailed demographic studies of !Kung, Hadza, Ache, and Agta hunter-gatherer populations living traditional lifestyles confirm this pattern (Howell 1979; Blurton Jones et al. 1992; Hill & Hurtado 1996; Early & Headland 1998), and their mortality profiles resemble those from ag-

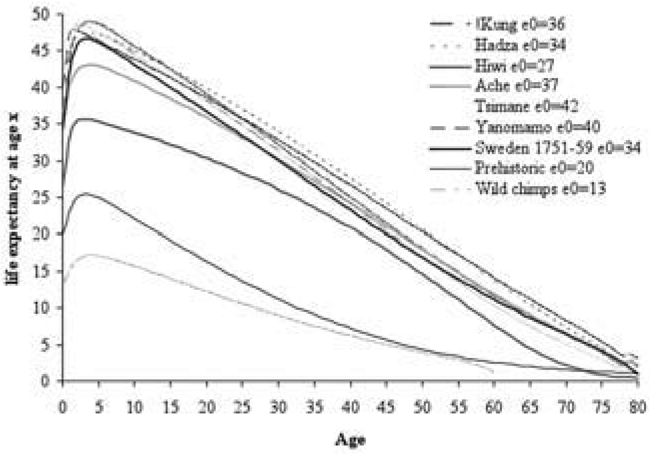

Fig. 13.1. Age-specific life expectancy, e_x. Average number of years of life remaining conditional on reaching age on *x*-axis. All curves are based on life-table estimates using the Siler method. Populations include hunter-gatherers (!Kung, Hadza, Hiwi, Ache), forager-horticulturalists (Tsimane, Yanomamo), earliest historical European data (Sweden, 1751–59), and a composite of 12 prehistoric populations of mortuary samples. These contrast with a composite of four wild chimpanzee populations. Life expectancies at birth (e_0) are given in the legend. See Gurven and Kaplan (2007) for additional methodological details.

ricultural populations, even in Europe until the nineteenth century (fig. 13.1). The rate of mortality increase in most subsistence populations follows a Gompertz-like pattern, with the mortality rate doubling every seven to nine years. Reports of short life span in early paleodemographic studies are likely due to high rates of contact-related infectious disease and violence, and to methodological problems such as poor age estimates of older individuals, biased preservation of the skeletons of infants and older individuals, and improper use of model life tables (Pennington 1996; O'Connell et al. 2002).

Human adult mortality rates tend to be about 1% to 1.5% per year, while chimpanzee rates are about three times greater (Hill et al. 2001). Chimpanzees, under the most favorable conditions in captivity, show much higher rates of adult mortality and a significantly shorter life span than do foraging humans under the worst conditions (Gurven & Kaplan 2007). This is true in spite of the available evidence, which suggests that members of both species seem to die from relatively similar macro-causes, with the exception of predation (table 13.2). The majority of deaths are due to infections and illness. Despite the cultural importance of dangerous predators, as represented by mythologies, stories, songs, and games, death by predation is rare among extant foragers. Grouping patterns, weapons, warning displays (e.g., fires), and other cultural means of avoiding predators contribute to the reduced impact of predation on human survivorship (Wrangham et al. 2006). In contrast, predation by leopards is a substantial cause of death among Taï chimpanzees (Boesch & Boesch-Achermann 2000); lions may also be predators of Mahale chimpanzees (Tsukahara 1993), while snakes are a common source of fear and predation among primates more generally (Isbell 2009). Violent death caused by other humans, however, appears to be a common feature of human societies, accounting for 12.5% of 3,328 documented hunter-gatherer and horticultural deaths. Although violent death rates are comparable among human and chimpanzee populations (table 13.2), nonlethal aggression is more common among chimpanzees than among humans (Wrangham et al. 2006) and violent death rates are greater in farming societies than among hunter-gatherers (Keeley 1996). Infanticide is commonly practiced in many small-scale societies. Infants at greatest risk of being abandoned or killed are those who are sickly, unwanted, fathered out of wedlock, and/or female, as well as those viewed as bad omens, such as twins (Milner 2000).

While humans senesce more slowly than chimpanzees, it is still an open question whether the pace of aging has slowed down in recent history. Adult mortality has declined, but this does not mean that the rate of functional, physiological decay has fallen in tandem with it. Aging is

Table 13.2. Causes of death among humans and chimpanzees. Human data (*n* = 3,221) come from seven groups of hunter-gatherers and forager-horticulturalists (see Gurven & Kaplan 2007 for details). Chimpanzee sample (*n* = 289) is based on known reported deaths from Kasekela (Williams et al. 2008), Mahale (Nishida et al. 2003) and Taï (Boesch & Boesch-Achermann 2000) communities. The similar prevalence of violent deaths among humans and chimpanzees mirrors the conclusions of Wrangham et al. (2006), using different samples.

	Humans		Chimpanzees	
Cause	*n*	% known	*n*	% known
All illnesses	2333	72.4	128	50.4
Respiratory[a]	292	22.2	35	13.8[c]
Gastrointestinal[a]	239	18.1		
Fever[a]	107	8.1		
Other[a]	317	24.1		
Senescence	306	9.5	28	11.0
Accidents	166	5.2	6	2.4
Violence	354	11.0	35	13.8
Homicide[b]	164	6.0		
Warfare[b]	137	5.0		
Predation			28	11.0
Human-caused			11	4.3
Other	62	1.9	18	7.1
Total	3221	100.0	289	100.0

[a] Illness breakdown does not exist for all human groups. These percentages are based on a risk set of 1,644 individuals, and adjusted to sum to 72.4%.

[b] Information on violence-related deaths does not exist for all human groups. These percentages are based on a risk set of 2,272 individuals, and adjusted to sum to 11.0%.

[c] Respiratory illness accounts for 48% of all illnesses in Gombe, 20% in Mahale, and 0% in Taï.

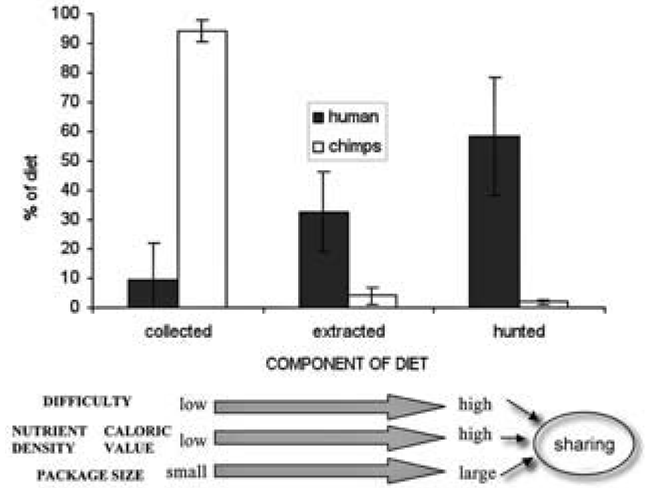

Fig. 13.2. Diets of human foragers and chimpanzees. Adapted from Kaplan et al. 2000, table 3 and figure 4.

Fig. 13.3. A Hadza man tracks an animal he has shot in the bush near Lake Eyasi, northern Tanzania. Successful hunting requires the acquisition of knowledge and skills, a process that starts in childhood but extends well into adulthood. Photo courtesy of Frank Marlowe.

often tricky to define and measure. The crudest but best available method for making inferences about past aging patterns uses historical mortality data to measure age-related changes in mortality. For example, longitudinal analysis of European mortality data suggested that senescence has slowed over the past couple of centuries, where senescence was defined in several different ways (Gurven & Fenelon 2009). This observation is consistent with the notion that reductions in "extrinsic" age-independent mortality (e.g., infectious disease, accidents, and other nondegenerative causes), should lead to greater investments in repair and maintenance, thereby resulting in longer life span, as originally hypothesized by Williams (1957; chapter 10, this volume). It is likely that low extrinsic mortality is a critical factor underlying the life history of long-lived species such as humans, clams on the ocean floor, giant tortoises, and trees on high, dry plains. Whereas other long-lived species with low extrinsic mortality often inhabit microbe-free and predator-free microenvironments, the lower extrinsic mortality of early humans may have come from effective group defense against predation and from the nurturing of sick and injured individuals (Gurven et al. 2000; Sugiyama 2004). Among early humans, low juvenile-adult mortality was likely a prerequisite for further reductions in adult mortality and the further slowing of the life course.

Intraspecific variation in adult mortality rates plays a vital role in shaping life-history traits by altering the valuation of present versus future benefits and costs (chapter 10, this volume). With a shorter expected time horizon, present payoffs (e.g., enjoying a cigarette) are preferred despite future costs (e.g., lung cancer), and future benefits (e.g., cardiovascular health) will be devalued if they require present costs (e.g., exercise and dietary restraint, Hill 1993). Life history traits such as physical growth and reproductive maturation are accelerated in populations that experience high mortality (Walker et al. 2006). Psychology and behavior are similarly affected by the same temporal trade-offs. Individuals with uncertain future prospects are more likely to discount the future and adjust behavioral strategies in a facultative manner; in modern societies, they exhibit earlier menarche, younger age at first sexual intercourse, higher reproductive rates, higher frequency of risk-taking and invest less in education and personal health (e.g., Hill et al. 1997; Chisholm 1999; Bereczkei & Csanaky 2001; Brumbach et al. 2009).

Human Ecological Niche

In comparison with non-human primate diets, the vast majority of human hunter-gatherer diets consist of nutrient-dense, calorically rich resources (fig. 13.2). Quantitative data based on behavioral sampling (summarized in Kaplan et al. 2000) and an independent survey of 229 human groups both show that animal foods constitute over 60% of modern hunter-gatherer diets (Cordain et al. 2000; fig. 13.2), whereas the diets of nonhuman primates depend heavily on leaves and fruits (chapter 7, this volume). Ethnographies from different foraging societies suggest that meat acquisition requires a high level of skill and coordination, as hunters navigate over large ranges and integrate extensive cues, signs, and context-specific knowledge concerning animal behavior and ecology (fig. 13.3; see Blurton

Fig. 13.4. Hadza women roast tubers of ekwa, *Vigna frutescens* (Fabaceae). Humans appear biologically adapted to including cooked food in their diet, because without the extra energy provided by cooking, many raw foods are inadequately processed by the relatively small human intestinal system. For example, cooking renders foods so soft that humans have much lower daily chewing times than other primates in relation to body mass. Cooking also increases the range of edible items and the net energy gain, thus allowing high reproductive rates. Photo courtesy of Richard Wrangham.

Jones & Konner 1976; Leibenberg 1990). Other foods have also often been shown to be difficult to acquire and process. For example, roots, tubers, nuts, and palm hearts must first be located and then extracted from a solid substrate.

The reliance on difficult-to-acquire foods that slow-growing children and even adolescents may be ill-equipped to obtain on their own is a critical starting point for several theories attempting to distinguish human life history evolution from the general primate pattern (chapter 10, this volume). The two most prominent of these are the grandmother hypothesis (GH) and the embodied capital model (ECM). GH argues that postreproductive life span evolved because helping daughters reproduce and improving grand-offspring survivorship both yield greater fitness gains than giving birth past age 50. Part of the initial motivation for this idea came from observations of older "hard-working" Hadza women who collected and distributed tubers in the African savanna. ECM argues that contributions of older men and women helped to increase postreproductive life span, and that this period coevolved with the longer developmental (training) period early in life, and with increased brain size (Kaplan et al. 2000; Kaplan & Robson 2002).

The control-of-fire hypothesis complements these models by arguing that human use of fire for cooking helps increase the efficiency of provisioning by promoting food digestibility and energy, and by allowing early weaning through increased availability of weaning foods (Wrangham 2009; Wrangham & Carmody 2010). It also reduces extrinsic mortality by detoxifying certain foods, helping to eliminate food-borne pathogens, and deterring predators (fig. 13.4).

According to GH, body size is the primary determinant of age profiles of productivity. Limited production of juvenile foragers is due to the strength-intensive nature of hunting and foraging activities. Development according to ECM requires additional investments in brain-based capital, due to the learning-intensive nature of the human foraging and social niche. ECM argues that high levels of knowledge, skill, coordination, and strength are required to exploit the resources human foragers consume, and that the attainment of those abilities requires extensive learning. As mentioned in the previous section, while these and other theories may help to explain a substantial slowing of the human life course, an initial lowering of extrinsic juvenile-adult mortality, perhaps due to helping behavior, sharing, and/or cooking, was an important prerequisite to help push humans into the highly cooperative, slow-growing, and long-living life-history niche. Allowances usually made for pregnant and lactating women, who are less able to forage themselves but nonetheless receive ample food, enable a high level of human fertility with short interbirth intervals. The average forager female has about six births (table 13.1), which places a substantial burden on household feeding requirements.

Optimal Foraging Behavior

Food acquisition is a vital activity that has affected selection on primate physiology, behavior, and social organization (chapter 7, this volume). While much has been written about the feeding habits of particular primate species (e.g., Garber 1987), there have been few comprehensive optimality studies of food choice other than tests of ideal-distribution theory, the effects of dominance relationships (e.g., Janson & Chapman 1999; Koenig & Borries 2006), and consideration of feeding trade-offs in the presence of potential predators (chapter 8, this volume).

Studies of human foraging behavior were some of the first applications of evolutionary and ecological theory made by cultural anthropologists. Despite their simplicity, these studies have helped researchers to predict the suite of resources that comprise human diets in different locales, and the optimal choice of resource patches and habitats. Hunter-gatherers have knowledge of hundreds of animal and plant species, yet their diverse diets tend to focus on a much more limited set of species. Optimality models usually assume that a forager's goal is to maximize the rate of caloric intake per unit of time spent foraging (Smith 1981). The most influential optimal foraging models are the "prey choice model" and the "patch choice model" (MacArthur & Pianka 1966; Charnov 1976; Stephens & Krebs 1986).

The prey choice model predicts that a forager should pursue any resource encountered if the expected gain from pursuit outweighs the expected gain of continued search for randomly encountered food items, i.e. the long-term rate of caloric gain. This simple model has been used to predict the suite of resources people target in forest, arctic, desert, and marine environments in ethnographic and archaeological contexts (e.g., Hill & Hawkes 1983; Smith 1991; Gremillion 2002; Thomas 2007a). Adjustments to the models have been made to account for unique characteristics of human foragers (Stephens & Krebs 1986; Giraldeau & Caraco 2000), where search may not be random, encounters may be simultaneous, foragers may be sensitive to risk, and novel techniques or technology are employed. For example, improvements in technology that increase the average caloric return rate—such as shotguns instead of bows and arrows, or trucks and snowmobiles instead of walking and/or dogsleds—have each been demonstrated to decrease the number of resource types (i.e., diet breadth) pursued, as increased efficiency leads to a preference for only highly profitable resources. Domesticated hunting dogs have also been shown to increase prey encounter rates (Koster 2008) and reduce prey handling times (Ikeya 1994). The prey-choice model has also been used to explain dietary transitions. The reduced processing or handling costs of seeds and grains raise the profitability of those resources. Historical declines in the abundance of megafauna in North America have been posited as important catalysts in the subsequent adoption of plant and animal domestication (see Kennett & Winterhalder 2006).

The patch-choice model, based on Charnov's marginal value theorem (Charnov 1976), addresses the question of how long to spend in a resource patch where the rate of caloric gains declines as more time is spent in that patch. Gains might decline during foraging due to prey depletion or resources becoming more difficult to obtain over time. As in the prey choice model, the caloric benefits of remaining in the patch are compared to the foregone benefits of abandoning the patch and moving to the next one. It is often in a forager's best interest to leave patches before they are depleted. While not rigorously tested in humans, most empirical examples instead focus on the amount of time spent foraging in different habitats that vary in their mean profitabilities (see Kaplan & Hill 1992 for review). Case studies show that while foragers spend more time in more profitable patches, less profitable patches are also frequently targeted, but often in ways that make adaptive sense (Smith 1991; Sosis 2002; Thomas 2007b).

The limitations of optimal foraging models help highlight unique aspects of human social organization that require explanation. Optimal foraging models are best applied to animals with herbivorous or carnivorous diets who do not cooperate in production or distribution and who forage by random search. This is because most models maximize a single currency (calories) and do so from only one individual's perspective. Humans are omnivores; they consume a mixture of macro- and micronutrients, they coordinate and cooperate during foraging activities, and they share resources and information. These characteristics have themselves become the focus of much study (see below). Model adjustments emphasize the importance of mixed diets, cognitive limitations of the forager, risk preferences, field processing and transport costs, central-place foraging, information gathering and sharing, and divisions of labor by sex and age (Barlow & Metcalfe 1996; Winterhalder et al. 1999; Stephens et al. 2007). Unfortunately, many of these model adjustments have yet to be rigorously developed or tested in humans. For these reasons, traditional optimal foraging models sometimes make predictions that do not hold most of the time: men should actively gather roots and other plant products, and women should hunt (see below).

Group mobility, group size, and territoriality have also been considered in light of spatial and temporal resource patchiness (Dyson-Hudson & Smith 1978; Cashdan 1983), per-capita production rates over time and space (Beckerman 1983), Fretwell's ideal-free distribution theory, and member-joiner conflict (Smith 1985). Resource predictability and abundance are important factors underlying land tenure regimes and group defense; a recent formalized version of the "economic defensibility model" seems to explain cross-cultural variability in territorial behavior among hunter-gatherers (Baker 2003). The fluid composition of hunter-gatherer groups and of post-marital residence rules has been considered an adaptive response to fluctuating resource availability, demographic stochasticity, mating opportunities, and intergroup raiding (Kelly 1995; Marlowe 2005).

Becoming "Expert": Adult Productivity

The complex feeding and social niche of humans requires substantial learning to achieve adult-level proficiency. Changes in foraging proficiency with age have now been examined among the Ache (Walker et al. 2002), Gidra (Ohtsuka 1989), Hadza (Blurton Jones & Marlowe 2002), Hiwi (Kaplan et al. 2000), Mardu (Bird & Bliege Bird 2005), Machiguenga and Piro (Gurven & Kaplan 2005), Meriam (Bird & Bliege Bird 2002; Bliege Bird & Bird 2002), Mikea (Tucker & Young 2005) and Tsimane (Gurven et al. 2006). Most of these studies show that men's hunting success peaks in the age range of 35 to 50 years, while other foraging and fishing activities peak by about age 20. Several cases of extraction activities show similar delays in productivity (albeit not as extreme), such as shellfish collecting among Gidjingali (Meehan 1982) and mongongo nut processing among Okavango Delta peoples (Bock 2002; fig. 13.5a). Conversely, among the Meriam of Mer Island, increases in children's productivity in several fishing and hunting activities closely tracked changes in physical growth (Bird & Bliege Bird 2002, 2005; Bliege Bird & Bird 2002). Tucker and Young (2005) also found few differences in productivity rates between children and adults in tuber extraction. Tests based on observational, interview, and experimental data collected among Tsimane Amerindians of the Bolivian Amazon suggest that body size alone cannot explain the long delay until peak hunting productivity (fig. 13.5b). Rates of indirect encounter (e.g., smells, sounds, tracks, and scat) and shooting of stationary targets are two components of hunting ability explained primarily by physical size alone, but more difficult components of hunting, such as direct encounter of important prey items and successful capture, require substantial skill (fig. 13.6). Those skills can take a hunter an additional 10 to 20 years to refine after achieving adult body size (Gurven et al. 2006). Similar conclusions were reached by Walker et al. (2002) based on an analysis of Ache hunting performance.

By the time hunter-gatherer men marry they are well on their way to becoming better hunters, but they still require much experience, or on-the-job training. As pointed out by Blurton Jones and Marlowe (2002) in reference to the Hadza, learning need not be completed before maturation, marriage, or reproduction (cf. Bjorklund 1997). Similarly, learning need not occur in constant increments throughout the entire prereproductive period in order for the long delay to be linked to later production as stipulated by the ECM. A combination of size-dependent learning and stepwise ratcheting up of strength and skill (or "punctuated equilibrium": Bock 2002) may characterize increases in performance during development. Furthermore, developmental milestones occur in an ordered sequence, with each one building cumulatively on prior achievements. Critical learning may occur not continuously but in dispersed stages, as has been found to be the case with physical growth (Lampl et al. 1992). This would suggest that gaps in learning during critical periods may be more detrimental to later performance and require more catch-up time than gaps that occur at other ages. Hunters raised in another culture or restricted from lengthy experience early in life rarely achieve the level of proficiency of hunters immersed in the traditional lifestyle. One experiment in which young Ache men were paid for each animal they killed over a 13-month period showed that while these men spent much more time hunting, there was no net increase in hunting return rate, encounter rates, or likelihood of a kill upon pursuit (Walker et al. 2002). These inexperienced hunters did not become highly proficient hunters, even though they likely benefited from the social transmission of relevant information on game behavior, locations, and successful hunting strategies from other men.

Many of the groups in which substantial delays in hunting performance have been reported are groups of primarily small game hunters. While the source of large game is open to interpretations of hunting and scavenging (e.g., Binford 1981; Blumenschine et al. 1994), small game was probably hunted by early *Homo*. Given that all chimpanzee hunting is directed towards small game such as red colobus monkeys (chapter 8, this volume), the first place to look for expanded hunting among early hominins is in the increased frequency and success in obtaining small game. There is evidence that small game hunting has been an important component of human diets for at least 200,000 years (Stiner 2002).

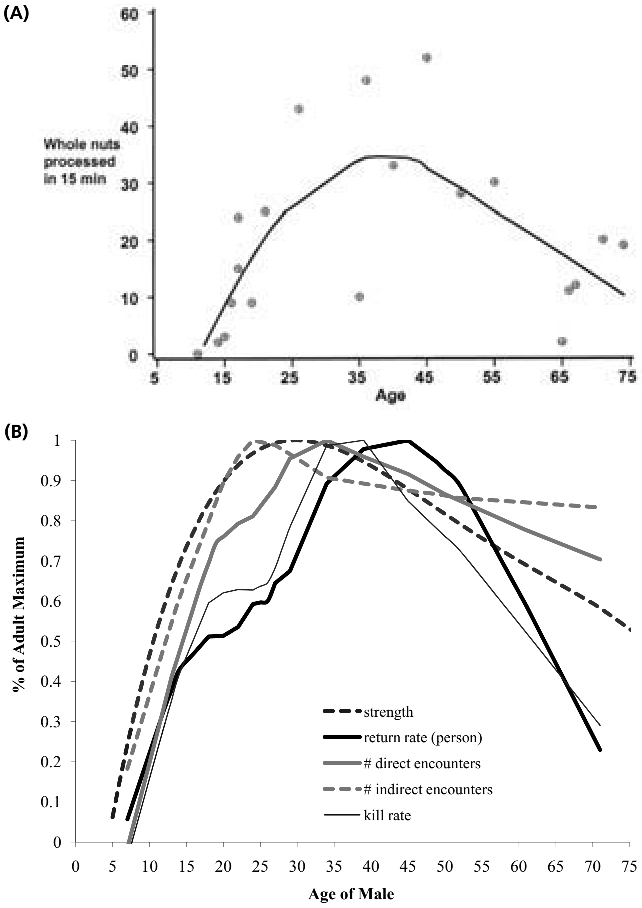

Fig. 13.5. (a) Mongongo nut processing by age. The graph depicts age-specific trends among females from four ethnic groups in the Okavango Delta in the number of nuts processed in 15 minutes. Taken from Bock 2002, figure 10. (b) Hunting performance by age. The graph depicts age-specific trends among Tsimane forager-horticulturalist men, standardized to adult maximum values. Shown in order of proficiency are muscular strength, indirect and direct encounters with animals, kill rate, and caloric return rate. Adapted from Gurven et al. 2006, figure 7. All trend lines are lowess curves.

Fig. 13.6. A Tsimane boy and his pet capuchin monkey. Caring for and playing with pets is a common occurrence in hunting societies, even though these same animals are treated as food in a different context. Pets require attention, training, and feeding. The practical value of maintaining pets likely stems from their role as educational "props" in teaching children about animal behavior. Some pets may also detect intruders and clean up scraps. Photo courtesy of Michael Gurven.

Even megafaunal "specialists" were likely hunting small and medium-sized game (Byers & Ugan 2005). The earlier practice of small game hunting by *Homo* merits investigation. It is not known whether the cognitive skills required for small versus large game hunting differ, or whether those differences depend on prey and ecology. Often, small game hunters rely on a greater variety of different prey items than do large game hunters, but such differences have yet to be studied systematically. Human hunting is nonetheless unique among primates, due to the expanded day range, the widespread sharing of spoils, and the long-distance transport of kills to a home base for processing and consumption by others (Stiner 1991).

While much attention has been given to skill-intensive aspects of male hunting, arguably many other human economic and cultural skills also take considerable time to master. Furthermore, obtaining sufficient social capital and building reliable support networks may take substantial time and skill, and may be especially helpful during periods of conflict, sickness, and injury (Simmons 1945; Wiessner 1981). Ritual knowledge and crucial roles as leaders, orators, and shamans are held mostly by older adults. Basic skills may be acquired by the time of reproductive maturation, but many more years may be required for an individual to become highly proficient. Among Tsimane forager-farmers, for example, older adults are named as experts in manufacturing activities, such as handbag weaving and bow and arrow making, and in music and storytelling. The average age of male and female experts for a large variety of skills in different domains is consistently over 40 years old. Experiments in the United States confirm that older adults are effective storytellers. Their stories are more memorable when told by them than when told by younger individuals (Mergler et al. 1984); the older adults employ more emotional modulation and show greater attention to detail (Adams et al. 2002).

Even child care abilities may improve with parity. Among several nonhuman primates, primaparous mothers have lower fertility and experience higher infant mortality than do multiparous mothers (Bercovitch et al. 1998; Robbins et al. 2006; chapter 15, this volume). While adolescent subfecundity and higher infant mortality among primaparous human mothers has also been documented, it is unclear whether any of these effects are due to inexperience and lack of proficiency among first-time mothers.

Delayed Maturation

The extension of juvenility through childhood and adolescence is seen as a prominent, recently derived feature of human life history (Bogin & Smith 1996; Bogin 1997; Dean et al. 2001; Bock & Sellen 2002). Although primate growth patterns may be highly variable, the standard primate pattern is to proceed from infancy to juvenility to adulthood (chapter 11, this volume). Four explanations for delayed maturation in primates have been proposed, rooted in concepts of social competition, risk aversion, trade-offs between growth and reproduction, and learning- and skill-based food acquisition strategies (Pagel & Harvey 1993; Leigh 2001; Pereira & Fairbanks 2002; chapters 10 and 11, this volume). Social explanations focus on intragroup competition, in which extra time is needed to develop social competency (Dunbar 1998; Barton 1999). The risk-aversion hypothesis argues that slow growth among group-living primates reduces resource competition and thereby serves to decrease the risk of dying due to fluctuations in the food supply (Janson & van Schaik 1993). A third hypothesis views optimal age at reproductive maturation as a trade-off between increased production from the benefits of growing longer (and hence larger) and the decreased probability of reaching reproductive maturity, because with each additional unit of time invested in growth there is some risk of dying (Charnov 1993). This model has been extended and applied to humans in the form of the grandmother hypothesis. As described earlier, the GH applies Charnov's (1993) model of optimal age at reproduction to explain the juvenile period as an artifact of selection on longer life span due to the indirect fitness benefits that accrue to magnanimous grandmothers (Hawkes et al. 1998).

Finally, learning- and skills-based models focus on the difficult adult foraging niche of many primates, especially humans, where much time early in life is devoted to acquiring the critical coordination, skills, and knowledge necessary for proficient adult foraging (Bogin 1997; Ross & Jones 1999). ECM extends this approach to explain delayed maturation, extended life span, and increased encephalization as a coevolutionary response to the demands of the difficult human foraging niche (Hill & Kaplan 1999; Kaplan et al. 2000; Kaplan & Robson 2002). According to this model, natural selection acts to extend life span when early learning yields high production payoffs over the duration of a longer adult life span. Similarly, longer life span creates selection pressure to grow more slowly early in life, and to spend this time learning when such investments lead to higher production payoffs later in life. The ECM also indirectly incorporates the risk-reduction hypothesis. The gains from learning act to increase the optimal level of investment in mortality reduction at all ages (Kaplan & Robson 2002). As a result, human children should have the lowest mortality of any primate. The ECM links foraging and ultimately reproductive success to brain-based "embodied" capital, which includes the suite of skills, knowledge, and abilities that affect future performance, and to the maintenance and repair mechanisms that act to reduce mortality so that later gains can be realized.

The separation of reproductive and economic maturation is an important feature of human life history. Humans are capable of reproducing before they can fully support their own needs because of the contributions made by others, such as grandmothers, husbands, in-laws, and older children. The "pooled energy budget" from others' caloric contributions not only expands women's energetic budget beyond self-production, but also enables girls to reduce their own activity, thereby permitting more resources to be allocated to growth, maintenance, and reproduction (Kramer et al. 2009).

An interesting paradox is that while poor conditions indicative of high extrinsic mortality might select for earlier maturation and a faster life history, faster physical growth and secular declines in age at menarche due to improved nutrition and health are well documented in many human populations. In a study examining juvenile growth rates in 21 hunter-gatherer and horticultural populations, societies with larger and taller adults (i.e., with better nutrition and health) developed faster and earlier, while higher juvenile mortality rates were associated with earlier menarche and age at first birth (Walker et al. 2006).

Sexual Division of Labor

One ubiquitous feature of human societies is an extensive division of labor among men and women. Apart from breastfeeding and child care responsibilities of females, such a pattern of coordination and collaboration in resource production rarely manifests in nonhuman primate societies.

Five features of hunter-gatherer socioecology are likely responsible for the sexual division of labor among foragers: (1) offspring are dependent during infancy, childhood, and even adolescence; fast fertility rates result in compound dependency of multiple offspring; (2) humans are committed to carrying children and providing high-quality childcare, traits shared throughout the Primate order which are incompatible with hunting; (3) an adequate diet requires macronutrients typically found in mutually exclusive types of foods; (4) peak efficiency in many foraging activities is delayed due to time-dependent learning; and (5) some tasks exhibit sex-differentiated comparative advantage. These conditions are common to most foraging groups, and are together responsible for a discrete sexual division of labor (Murdock & Provost 1973; Kelly 1995; Gurven & Hill 2009).

A central aspect of the division of labor is marriage and family formation. All human groups recognize marriage as a way for men and women to regulate their sexual activity and form cooperative bonds in raising children. Sometimes this bond is defined by monogamy, but mild polygyny may better characterize the spectrum of traditional human societies (Quinlan 2008). Marriage is characterized by intensive food sharing within a family, a division of labor in the organization of other household tasks, and the care of children. Among foragers, the reproductive careers of men and women are usually linked. While divorce is common in many foraging groups, many couples have the majority of their children together, and men often have their last child when their wives reach menopause. The relationship between men and women in foraging societies is arguably the most intense and multifaceted cooperative relationship in which they engage, although the reliance on husbands varies cross-culturally (Jankowiak et al. 2002).

Many individuals other than spouses contribute to the welfare of family members, leading to the claim that humans are "cooperative breeders" (Hrdy 1999, 2009). Divisions of labor among extended family members, as well as among non-kin, are not uncommon. Activities that provide benefits to others'offspring in addition to one's own occupy a relatively large percentage of post-juvenile daily energy expenditure among foragers, consistent with the notion of "pooled energy budgets" described above. While the net flow of resources is generationally downward, resource transfers and helping behavior are bidirectional and occur also among siblings and from young to old.

The Social Brain and Cultural Transmission

Humans as Cultural Animals

Does the human life history require unique cognitive abilities and elaborate culture, or did it instead promote their subsequent evolution? Attempts to answer this question have led to a flurry of studies over the past several decades detailing numerous aspects of primate culture and social cognition (e.g., Boesch & Tomasello 1998; Perry 2006; Lycett et al. 2007; Watson & Caldwell 2009). While cultural "traditions" have been well documented in primates (chapter 31, this volume), especially among chimpanzees, orangutans (*Pongo* spp.), and capuchin monkeys (*Cebus* spp.), human culture is often distinguished by the accumulation of ratchet-like modifications within and among generations, and its reliance on imitation and explicit guidance and instruction. Other aspects of cognition purported to uniquely represent "phylogenetic mind gaps" separating humans and other primates include generative computation, the combining of representations from separate cognitive domains, the ample use of mental symbols, and abstract thought (Hauser 2009). These abilities, combined with other cognitive capacities, particularly intention reading and social learning, have been linked to the development of complex symbolic language, tools, technology, institutions, and belief systems.

Social learning plays a critical role in the intergenerational transmission of knowledge and practices (fig. 13.7; chapters 11, 31, and 32, this volume). Among foragers, social learning probably increases the rate at which human children, adolescents, and adults learn how to hunt and gather efficiently. In these societies, children and adolescents spend many years listening to others tell stories about different foraging experiences before engaging in these activities themselves. Social learning may help foragers use the personal experience of others to improve their own foraging efficiency more rapidly than would be possible without such prior knowledge. Social learning of foraging skills,

Fig. 13.7. Three generations of an American matriline. Intergenerational transfers are a critical component of the human life course, including in developed countries like the United States of America. The grandmother taught her daughters to quilt, and her daughters taught their daughters. The grandmother and her husband traveled to visit their daughters and grandchildren in several US states; they also often paid for travel vacations for the extended family. Although much of the grandmother's savings were needed to cover medical expenses and a care facility because of her severe Alzheimer's disease, she still bequeathed family heirlooms and valuables to her grandchildren late in her life and upon her death. Photo courtesy of Anne Pisor.

however, is not unique to humans. In nonhuman primates, the frequency of social transmission of information strongly predicts variation in brain size, and most of this information pertains to foraging (Reader & Laland 2002).

Among humans, language helps improve the reliability and efficiency of social learning. It involves a specific set of cognitive adaptations (Pinker 1994) and is posited as an important component of the "hominid entry into the cognitive niche" (Barrett et al. 2007). Language lowers the cost of transmitting information by allowing more precise ways of sharing information about the world. It helps to improve coordination among group members and reap the gains of mutualistic cooperation (Alvard & Nolin 2002). Novel solutions to local problems, obtained either directly from personal experience or from others, can be communicated effectively and to a broad audience. In many domains, language allows the communication of much more information than can ever be gained by personal experience in a single lifetime. The rapid accumulation of sequenced skills allows for complex tool manufacture and other cultural adaptations, and accounts for the ratchet-like cumulative nature of human culture (chapter 32, this volume). Culture, leading to the development of tools, clothing, and fire, has influenced selection on genes affecting diet, nutrition and digestion, disease resistance, dentition, and cognition (Durham 1991; Laland et al. 2001).

The ability to imitate and learn from others has cognitive prerequisites that may be uniquely human (Caro & Hauser 1992; Premack & Premack 1996). A variety of learning mechanisms appear to bolster the specialized learning of language, food preferences and aversions, and danger (Gallistel 1990). The decoding of other actors' mental states to infer their intentions (as distinct from outcomes), "theory of mind," and other mental representations are important for effective social learning (Tomasello 1999) and for maintaining long-term cooperative interactions. Even humans' closest relatives, chimpanzees, have limited social cognition and do not achieve full-fledged humanlike belief-desire psychology (Call & Tomasello 2008; chapter 30, this volume). Imitation and emulation therefore go beyond the mimicking of physical movements; behavioral adjustments help an actor achieve an intended goal (chapter 31, this volume).

Much learning in small-scale societies may be observational, or may involve a combination of approval, disapproval, and correction by others. Effective pedagogy may require additional psychological adaptations for purposefully transmitting information to others willing to learn (Csibra & Gergely 2006). Anecdotal reports that overt teaching is absent in these societies may be surprising, but even slight corrections can effectively guide naïve individuals towards target behaviors or skills (Castro & Toro 2004). Much learning in infancy and childhood is likely transmitted vertically from parents to offspring (Hewlett & Cavalli-Sforza 1986). Among adolescents and adults, horizontal transmission among peers and kin is also common. Preferred models for cultural learning include successful, skillful, and influential group members (Henrich & Gil-White 2001).

Cognitive and Social Niches

Human diets are inherently risky: foraging luck is often highly variable, and food sharing is a fundamental solution. Hunters, in particular, often return to camp empty-handed after a full day's search, especially when pursuing large game (Hawkes et al. 1991). Food sharing among families buffers against the risk of daily food shortfalls associated with hunting large, mobile packages. Cultural norms governing resource distribution likely coevolve with systems of production in ways that help motivate and reward productive effort among group members (Gurven 2006). Among the Lamalera, for example, shares of whale meat are given to participating hunters and to nonhunters who contribute productive capital (e.g., specialist sail and boat makers; Alvard & Nolin 2002). In any group-oriented production system, however, actual decisions and transactions may deviate from the normative patterns (e.g., see Altman 1987, Bailey 1990); there is room for social navigation towards selfish ends by skillful actors. Widespread sharing is vulnerable to exploitation by cheaters who consume resources without providing or sharing them in turn. Indeed, much gossip and conversation around the campfire concerns accusations of repeated stinginess, greed, or laziness, as well as identification and condemnation of possible second-party defections on kin obligations (Wiessner 2005). These conversations often focus on actor intentions, beliefs, and circumstances, in addition to the outcome, in order for the participants to form their opinions.

A growing body of evidence shows that food is not shared equally among all band members in most hunting and gathering societies, except under special circumstances (Gurven 2004; Kaplan & Gurven 2005). People have preferred partners, with whom reciprocal exchange is greatest. Efficient sharing requires the monitoring of contributions made by other group members, and the monitoring requires not just observing others but also inferring the intentions of others. Identifying acts of cheating may be difficult in real-life situations. Thus, the ability to negotiate profitable partnerships requires social intelligence and the ability to understand how one's actions will affect future access to vital resources. Moreover, some food sharing may act as investment in social capital that affects future cooperative interactions. The encephalized primate brain required for navigating a difficult feeding niche must therefore also be a social brain that can strategically share game and other resources (Stanford 1999).

Cognitive substrates for solving economic and social problems may be shared. Selection should act on the total effects of increased abilities, summed over all routes through which those abilities affect fitness. For example, inferences about an animal's behavior, such as its likely escape strategies if it detects the hunter's presence, are critical for hunting success. Other humans and prey are both intentional agents, and so animal "mind reading" and human mind-reading may involve similar cognitive abilities. Hunters often use visual cues, folklore, and observations of tracks and spoor to test their hypotheses about animal behavior. Leibenberg (1990) has argued that such inferences, with empirical verification, form the basis for protoscientific thinking. In a review of the comparative anatomy of primate brains, Rilling (2006) notes that selection uniquely modified the human brain to deviate from the rules of brain design that prevail among other primates. The human brain displays unique modifications in the prefrontal cortex associated with symbolic thinking, knowledge of appropriate social behavior, decision making, planning, cognitive control, and working memory. Bering and Povenilli (2003) propose that the critical divide between the minds of apes and humans is not just a difference of 1,000 cm^3 that enables humans to do the same things much better, but rather a novel ability to think about things that cannot be directly observed by the senses. Humans are often fanatical about thinking about and discussing the hidden world of causation, such as what others are thinking, what their ulterior motives are, how a tool works, or why people get sick (chapter 32, this volume).

In addition to its role in negotiating sharing decisions in foraging societies, the social brain of humans is an ecological brain that helps facilitate coordination and cooperation among group members. Divisions of labor among kin and unrelated group members require coordination and task specialization. Effort is often allocated to different tasks in coordinated ways so as to maximize group production, which must then be distributed among coordinating group members. The chief benefit of such social organization is the formation of synergistic economies of scale in which the sum of the joint production of *n* actors is greater than the sum of each of the *n* actors producing alone. Age and sex-based specialization and task complementarity enable human foragers to reap gains from such economies of scale. The evolution of complex human social organization over the past five millennia has often involved increasing returns to scale in production, as in intensive agriculture, irrigation networks, patron-client relations, and armies.

Other Psychological Adaptations

I briefly highlight two additional categories of psychological adaptation to complement the above discussion on life history, subsistence, and cognition. Encounters with predator and prey are common, and salient fitness-relevant experiences among primates (chapter 8, this volume) and human hunter-gatherers are no exceptions. Even though death by animal predators is very low among hunter-gatherers (table 13.2), fear of attack from lions, snakes, and jaguars is common, and much cultural lore emphasizes these animals. Species-typical investments may have led to mortality reduction from predation, thereby contributing to the lower level of extrinsic mortality in human populations as compared with that in primate populations. Evading predators and hunting prey (i.e., avoiding being killed and killing when hungry) is likely to have selected for certain cognitive mechanisms. Fear helps organize one's bodily resources towards seeking escape routes or avoiding predators and dangerous situations altogether (Öhman & Mineka 2001). As described earlier, predator and prey are intentional agents, and so detecting and making decisions about such agents may represent evolved features of the "agency system" (Byrne & Whiten 1988; Barrett 2005). These include monitoring of directional eye gaze, autonomous movement, cause and effect contingency, reasoning about belief and desire, and the types of mind-reading skills outlined earlier (see Barrett 2005 for a summary). These kinds of adaptations, as part of a "predator-prey inference system" (Barrett 1999), are likely present in many mammalian species. However, two distinctions can be made in the human case. First, no evidence exists for evolved perceptual templates for true predators among humans, thus suggesting a diverse set of predators over human history and/or the substantial influence of social learning of fear in response to certain animals, as has been observed among rhesus monkeys (Mineka et al. 1984). Although fear and phobia of snakes and spiders have long been described (Agras et al. 1969; LoBue & DeLoache 2008), snakes, other than constrictors, and spiders do not prey on humans, but rather attack in self-defense. Second, current data suggest that predator-prey inference systems require attention to actor goals and intentions, but not necessarily to beliefs. The latter type of attention may instead require a developed "theory of mind" (Baron-Cohen 1995).

A second area where evidence of functional design is expected comes from the relatively high level of paternal investment among humans. This high level should be reflected in evolved motivational adaptations that help facilitate long-term mateships and high-investment paternal care. Physiological data on male-female and male-offspring bonding mechanisms and hormones that promote such bonds suggest that human males were selected to increase cooperative sentiment with female partners and to help raise highly dependent offspring (Gray et al. 2004). In other primates that show significant paternal care, such as cotton-top tamarins and common marmosets, a male's prolactin levels increase in synchrony with his mate's; an expectant father seems physiologically responsive to his mate's pregnancy and his offspring's imminent birth (Ziegler et al. 2006). A similar response is found among humans, but not among other nonpaternal species (Storey et al. 2000). Male couvade pregnancy symptoms are not uncommon in cultures with high levels of partner intimacy and paternal care (Elwood & Mason 1994). Vasopressin and oxytocin have also been found to help modulate attachment, support, and pair-bonding behavior in male rodents (Heinrichs & Domes 2008). Studies among humans are underway; for example, humans with a certain vasopressin receptor subtype (V1aR) associated with monogamous behavior in rodents were happier in their marriages and felt greater affiliation with their partners (Walum et al. 2008).

Future Directions

I have documented key life-history features of humans and their associated foraging niche, as well as the cooperativeness, social maneuvering, mind reading, and cumulative culture that go along with our encephalized brains. These features evolved in the context of humans living as hunter-gatherers in a world of other hunter-gatherers. There is still an open question regarding the extent to which evolution has continued to shape the genetics underlying human behavior, personality, and cognition, in addition to the well-documented recent adaptations to climate, pathogens, and regional diet. As the size of populations around the world has exploded since the advent of agriculture, the selective sweeps of many favorable alleles have been detected; the future may shed light on their relevance (Hawks et al. 2007). As genome-wide scans become more affordable, the exploration of gene-by-environment interactions will help shed light on both ancient (e.g., Varki & Nelson 2007) and recent (e.g., Bersaglieri et al. 2004) adaptations.

Much of evolutionary behavioral science that is related to "surviving and growing in a difficult and dangerous world" in anthropological populations has emphasized the efficiency of subsistence behavior, cooperative production and sharing, the value of social learning, and life-history variability. Many components of these themes remain to be explored in detail. For example, no systematic study of age-related changes in navigational skills, tracking skills, knowledge of animal behavior, techniques employed, or motivation has been conducted in traditional populations to elucidate the extent of on-the-job learning that is required to attain proficiency in hunting. Systematic research can also help reveal the relative importance of intergenerational social learning while at the same time exploring the functional significance of childhood and adolescence. Why do many human activities require years of learning before peak proficiency is gained? Such activities would include the food-production tasks and their subcomponents listed above, but also unstudied activities like child care and tool manufacture. To clarify the significance of the human social brain, more research is needed on age-specific changes in the accrual of social capital. How and why does it take so long for humans to become adept social adults?

Almost all studies of kin cooperation and human life history among small-scale societies emphasize their indirect effects on fitness (e.g., the presence of a maternal grandmother on her offspring's fertility or her grand-offspring's mortality), or on caloric contributions to the diet, but little attention has been paid to the specific resource transfers that could potentially affect the fitness of kin, especially nonfood contributions. For example, how do older adults acting as leaders, mediators of conflict, coordinators of group activity, and repositories of cultural knowledge affect the fitness of others? Are these benefits directed preferentially towards kin? What about the contributions made by young adults? Here both the EP and HBE approaches can make important contributions. DIT can also contribute by assessing whether cultural transmission across three generations, rather than just two, increases the fitness value of postreproductive individuals in ways not captured by the direct transfer of resources.

The popularity of the GH has led to a focus on grandmothers as caretakers and helpers whose support helps bolster high fertility, slow growth, and long life span, but many other individuals, including even juveniles and adolescents, are also likely to be important contributors (fig. 13.8; Kramer 2005). The "pooled energy budget" concept is essential to all models of human life history in which members of a group contribute to help subsidize slow juvenile growth and female fertility (Hrdy 1999, 2005; Reiches et al. 2009). Future work is needed to clarify who helps, under what conditions, and in what way, and how potential conflicts of interest are resolved. Indeed, the stability of helping behavior among cooperative breeders is not easily reconciled with standard evolutionary models of altruism (Bergmüller et al. 2007). Similarly, the extensive flow of resources and information among non-kin also requires further explanation, as simple models such as reciprocity and

Fig. 13.8. A key adaptation in the evolution of human reproduction and life history is the significant enhancement of alloparental caregiving. In many societies, postreproductive grandmothers are important in reducing the burden on the baby's mother. Thus the mother can work less while recovering from pregnancy and nursing her infant. This, along with subsidies from others, helps the mother return to a fertile, ovulatory state, thereby contributing to the short interbirth intervals characteristic of humans. Photo © Pete Leonard/Corbis.

kin selection cannot explain many of the sharing norms of hunter-gatherers. Complex divisions of labor, group augumentation, and the strategic use of sharing as social insurance are themes that have not been adequately addressed. We also need better studies of multicurrency trades, as well as models of how sharing norms, ownership rights, production schemes, and intergenerational nutrient flows might work in human populations.

To better elucidate the evolution of an extended life span in humans, more attention to the differences in physiology and disease etiology between humans and other primates, such as chimpanzees, will be informative (e.g., Nissi et al.

2009). Also needed is a better understanding of the costs and benefits of investments in innate and adaptive immune response in pathogen-rich and energy-limited environments (McDade 2003). The fields of evolutionary medicine and ecological immunology aim to understand health and disease in ecological and evolutionary contexts, invoking life-history trade-offs, host-parasite dynamics, and other evolutionary principles. Understanding human growth, development, aging, and health in light of the evolutionary history of our species is a major aim of biodemography (Finch & Kirkwood 2000), of evolutionary physiology (Garland and Carter 1994), and of the developmental origins of health and disease (DOHaD) paradigm (Gluckman & Hanson 2006). Each of these areas has benefited, and will continue to benefit, from collaborations with anthropologists working in preindustrial and transitional populations as well as with primatologists who work with wild and captive ape and monkey populations.

Conclusion

Future study of human behavior from an evolutionary perspective will require a synthesis of the three approaches (HBE, DIT, EP) in a diverse range of study populations (Henrich et al. 2010). The functional design of the mind should not be ignored in behavioral ecological studies, just as behavioral outcomes, constrained optimality, and fitness should not be ignored in psychological studies. A better understanding of trait change over time will require a greater appreciation of gene-culture coevolution. Comparative phylogenetic approaches will also be useful for making sense of existing cultural variation (Borgerhoff Mulder 2001; Nunn et al. 2006). The role of initial conditions and both social and physical ecology in shaping the patterned unraveling of history may be best illuminated through further integration of HBE with DIT. Yesterday's decisions and outcomes are today's parameters and constraints. To explain the behavioral diversity that exists within and among human populations is a daunting yet exciting goal. To what extent is such diversity due to reaction norms in variable environments (HBE), to different cultural trajectories in similar or different environments (DIT), to genetic variation, or to a combination and interaction of all three? The future offers hope for further integrating knowledge about humans across the social and biological sciences. Further communication across traditional disciplinary divides can push the biological study of humans to be further consilient with mammalian behavioral biology and to elucidate the origins and maintenance of derived human features.

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