Reproductive Ecology
and
Human Evolution

Peter T. Ellison

editor

Aldine de Gruyter
New York

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The Embodied Capital Theory of Human Evolution

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This paper presents a theoretical approach to life history evolution with the goal of shedding new light on important problems in human evolution and the evolution of primates, in general. Life history theory (LHT) in biology organizes research into the evolutionary forces shaping the timing of life events, with a particular focus on age-schedules of fertility and mortality (Cole 1954; Gadgil and Bossert 1970; Partridge and Harvey 1985). We integrate standard approaches to life history evolution with an economic analysis of capital investments and energy production to generate new theoretical models capable of addressing many of the fundamental problems in the evolution of our species. We refer to this approach as *the embodied capital theory of life history evolution*.

After presenting a brief introduction to this theoretical perspective we apply the theory to understanding major trends in primate evolution and the specific characteristics of humans. We first address the evolution of brain size, intelligence, and life histories in the primate order. We then consider the evolution of the human life course, including mortality and longevity, reproduction, learning and development, the timing of energy production, the sexual division of labor, and pair bonding. Together, these analyses illustrate both continuities and discontinuities between humans and other primates.

THE EMBODIED CAPITAL THEORY OF LIFE HISTORY EVOLUTION

According to the theory of evolution by natural selection, the evolution of life is the result of a process in which variant forms compete to harvest

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energy from the environment and convert that energy into replicates of those forms. Those forms that can capture more energy than others and can convert the energy they acquire into replicates more efficiently than others become more prevalent through time. This simple issue of harvesting energy and converting energy into offspring generates many complex problems that are time-dependent.

Two fundamental trade-offs determine the action of natural selection on reproductive schedules and mortality rates. The first trade-off is between current and future reproduction. By growing, an organism can increase its future energy capture rates and thus its future fertility. For this reason, organisms typically have a juvenile phase in which fertility is zero until they reach a size at which some allocation to reproduction increases fitness more than allocation to growth would. Similarly, among organisms that engage in repeated bouts of reproduction (humans included), some energy during the reproductive phase is diverted away from reproduction and allocated to maintenance so that it can live to reproduce again. Natural selection is expected to optimize the allocation of energy to current reproduction and to future reproduction (via investments in growth and maintenance) at each point in the life course so that genetic descendents are maximized (Gadgil and Bossert 1970). Variation in optimal energy allocations across taxa and across conditions is shaped by such ecological factors as food supply, disease, and predation rates.

A second fundamental life history trade-off is between offspring number (quantity) and offspring fitness (quality). This trade-off occurs because parents have limited resources in which to invest in offspring and each additional offspring produced necessarily reduces average investment per offspring. Most biological models (Lack 1954; Lloyd 1987; Smith and Fretwell 1974) operationalize this trade-off as number versus survival of offspring. However, parental investment may affect not only survival to adulthood but also the adult productivity and fertility of offspring. This is especially true of humans. Thus, natural selection is expected to shape investment per offspring and offspring number so as to maximize offspring number times their average lifetime fitness.

The embodied capital theory generalizes existing life history theory by treating the processes of growth, development, and maintenance as investments in stocks of somatic or embodied capital. In a physical sense, embodied capital is organized somatic tissue—muscles, digestive organs, brains, and so forth. In a functional sense, embodied capital includes strength, speed, immune function, skill, knowledge, and other abilities. Since such stocks tend to depreciate with time, allocations to maintenance can also be seen as investments in embodied capital. Thus, the present-future reproductive trade-off can be understood in terms of optimal investments in own embodied capital versus reproduction, and the quantity-quality trade-off

can be understood in terms of investments in the embodied capital of off-spring versus their number.

The embodied capital theory allows us to address problems that have not been addressed with standard life history models. An exclusive focus on physical growth per se is an impoverished way of understanding development. The large human brain, for example, is a stock of embodied capital that supports a great deal of learning and knowledge acquisition during both the juvenile and adult periods. The growth in knowledge may be as important as growth in body size with respect to providing benefits through time.

Models of investment in embodied capital have produced some fundamental results. Of central interest here, the models show that investments in embodied capital affecting adult income or energy capture coevolve with investments affecting mortality and longevity (Kaplan and Robson 2000b; Kaplan et al. 2000b). The longer the time spent growing and learning prior to reproducing, the more natural selection favors investments in staying alive to reap the benefits of those investments. Similarly, any investments that increase energy capture rates later in life select for additional investments to reach those older ages. The converse is also true. Ecological features or investments that increase the probability of survival to older ages also produce selection for greater investments in income-related embodied capital. A central thesis of this paper is that these co-evolutionary effects have been particularly important in primate and hominid evolution.

EMBODIED-CAPITAL EVOLUTION AMONG PRIMATES

Relative to other mammalian orders, the primate order can be characterized as slow-growing, slow-reproducing, long-lived, and large-brained. Although there is a great deal of variation within the order in terms of life history characteristics and brain size, the radiation of the order over time has involved a series of four directional grade shifts towards slowed life histories and increased encephalization (i.e., brain size relative to body size).[1]

The first grade shift, beginning about 60 mya with the evolution of prosimians, is towards a longer lifespan (Kaplan and Robson 2000a), probably owing to the safety of the arboreal habitat (Austad and Fischer 1991, 1992). The second major grade shift began about 35 mya with the evolution of the anthropoid lineage and involves a large increase in both brain size and lifespan, relative to prosimians. This shift is evident among extant monkeys. The major defining characteristic of the anthropoids is the reorganization of the sensory system from one in which olfaction and hearing are relatively dominant to one dominated by binocular, color vision and

by a switch in feeding behavior from insects to plant foods using a manipulating hand and hand-eye coordination (Fleagle 1999). Apes represent the third major grade shift in primates. Controlling for the allometric relations between brain size and body size, the great apes have the largest brains among nonhominid primates and also live more than twice as long as most monkeys. This shift is most likely due to increased emphasis on complex, extractive foraging techniques (Byrne 1997b; Parker and Gibson 1979). Comparison of intercepts among prosimians, monkeys, and apes in regression analyses of brain size on body size confirm the existence of these grade shifts (Allman, McLaughlin, and Hakeem 1993; Barton 1999). The fourth major grade shift occurs with the divergence of the hominid line, particularly the evolution of genus *Homo*. Controlling for body size, *Homo sapiens* has a brain about three times as large and a lifespan about twice as long as chimpanzees and gorillas, our closet living relatives.

The brain is a special form of embodied capital. On the one hand, neural tissue is involved in monitoring the organism's internal and external environment, and organizing physiological and behavioral adjustments to those stimuli. On the other, portions of the brain are involved in transforming present experiences into future performance. This is particularly true of the cerebral cortex, which is specialized towards the storage, retrieval, and processing of experiences. The expansion of the cerebral cortex among higher primates, along with their enhanced learning abilities (Armstrong and Falk 1982; Fleagle 1999), is indicative of increased investment in transforming present experience into future performance.

The action of natural selection on neural tissue involved in learning, memory, and the processing of stored information depends on costs and benefits realized over the organism's lifetime. First are the initial energetic costs of growing the brain. Among mammals, those costs are largely borne by the mother. Second are the energetic costs of maintaining neural tissue. In fact, as much as 65% of all resting energetic expenditure is used to support the maintenance and growth of the brain during the first year of a human's life (Holliday 1978). A third potential cost of the brain is decreased performance early in life. The ability to learn and increased behavioral flexibility may entail reductions in "pre-programmed" behavioral routines, which would enhance early performance. The incompetence of human infants, and even children, in many motor tasks is an example.

The benefits of the brain tissue involved in learning are realized as the organism ages. Those benefits are likely to depend, at least in part, on the impact of learning on food acquisition. Some features of the feeding niche are likely to affect the payoffs to information storage and processing and, hence, brain size. Spatial patchiness of resources tends to be associated with larger home ranges and potentially greater demands on spatial memory. The number of different species consumed potentially adds to demands for

spatial memory, learned motor patterns, processing of resource character-istics, and temporal associations. Large, nutrient-dense packages (such as big, ripe fruits) tend to be patchily distributed in space and often have very short windows of availability. There is also significant year-to-year vari-ability in abundance and location of these high-quality packages, increas-ing the demands for monitoring the environment and predicting the best time to harvest them. Diets with an emphasis on large, high-quality pack-ages are probably associated with increased brain size through several routes: by increasing the total number of species exploited, the size of the home range, and the importance of predicting the timing and location of availability. In addition, such high-quality foods as nuts, insects, and honey need to be extracted from protective casings, and their exploitation requires learned strategies and often tools.

Feeding niches with high demands for learning and information pro-cessing should select not only for increased brain size but also for increased effort at reducing mortality. This is because the brain has high costs early in life and provides benefits later in life. Thus, living longer is more beneficial. At the same time, there is ecological variability in mortal-ity risks. Life in or near trees probably increases injury risk but decreases predation risk to lower mortality risks overall. Other factors such as body size, daily activity patterns, predator density, and disease risk are also likely to affect mortality rates. The results from modeling embodied capi-tal investments discussed above suggest that those risks also affect selec-tion on brain size, since higher risks of dying reduce the expected time over which the brain will confer benefits.

Following others (e.g., Dunbar 1998; Jerison 1976; Milton 1993) we hypothesize that much of the increase in primate brain size, relative to other mammals, is due to increases in the ability to store and process learned information. We hypothesize further that the protection conferred by the arboreal environment in terms of the ability to escape predation and the types of foods available in trees favored entry into a learning-intensive feeding niche and the evolution of large brains.

These hypotheses, together with the analytical results discussed above, generate three predictions about variation among extant nonhuman pri-mates. The first is that features of the ecology that increase the productiv-ity of a large brain, such as a large home range and a diet emphasizing ripe fruits (Clutton-Brock and Harvey 1980), would be associated with both increased brain size and a longer lifespan. Second, a longer lifespan would be associated with an increased brain size, even after controlling for the feeding niche. Third, larger-brained species would allocate more effort to survival, which would be reflected in slower grow rates and later first reproduction. Results of a path analysis of 101 primate species are fully consistent with those predictions (Kaplan et al. 2000a). Home range size

and percent of fruit in the diet are strongly associated with both maximum lifespan and brain size. Controlling for feeding niche and body size, maximum lifespan is also positively associated with brain size. Finally, controlling for body size, longer-lived and larger-brained species reach their adult body weight at a later age than shorter-lived, smaller-brained species, indicating slower growth and greater effort towards survival.

THE EVOLUTION OF *HOMO:* CHIMPANZEES AND MODERN HUMANS COMPARED

Can the same principles explain the very long lives and the very large brains characteristic of the genus *Homo* and particularly of modern *Homo sapiens?* Our theory is that these extreme values with respect to brain size and longevity are coevolved responses to an equally extreme commitment to learning-intensive foraging strategies and a dietary shift towards high-quality, nutrient-dense, and difficult-to-acquire food resources. The following logic underlies our proposal. First, high levels of knowledge, skill, coordination, and strength are required to exploit the suite of high-quality, difficult-to-acquire resources humans consume. The attainment of those abilities requires time and a significant commitment to development. Higher productivity during the adult period compensates for this extended learning phase during which productivity is low, 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.

Second, we believe that the feeding niche specializing on large, valuable food packages, and particularly hunting, promotes cooperation between men and women and high levels of male parental investment because it favors sex-specific specialization in embodied capital investments and generates a complementarity between male and female inputs. The economic and reproductive cooperation between men and women facilitates provisioning of juveniles, which both bankrolls their embodied capital investments and acts to lower mortality during the juvenile and early adult periods. Cooperation between males and females also allows women to allocate more time to child care and increases nutritional status, increasing both survival and reproductive rates. Finally, large packages also appear to promote interfamilial food sharing. Food sharing assists recovery in times of illness and reduces risk of food shortfalls owing both to the vagaries of foraging luck and to variance in family size resulting from stochastic mortality and fertility. These buffers against mortality also favor a longer juvenile period and higher investment in other mechanisms to increase lifespan.

Thus, we propose that the long human lifespan coevolved 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.

This theory generates a series of test implications. We must show that (1) humans do, in fact, exhibit lower mortality rates, especially in adulthood, than apes; (2) the human diet differs from the ape diet in the proportional contribution of difficult-to-acquire, high-quality foods; (3) difficulty of acquisition is positively associated with age-effects on return rate for both apes and humans; (4) the greater proportion of high-quality foods in human diets causes a shift in energy production towards older ages, favoring a longer adult lifespan; (5) hunting and the acquisition of large packages of food favor sex-specific investments in embodied capital and male-female cooperation; and (6) large packages also promote interfamilial food sharing and cooperation, and those adaptations lower mortality. In this paper, we consider the first five test implications. We only briefly consider interfamilial sharing and cooperation in the discussion since the sixth prediction has been confirmed elsewhere (Gurven, Hill et al. 2000; Kaplan and Hill 1985; Winterhalder 1996).

Mortality and Survival

About 60% of hunter-gatherer children survive to age 15, compared with 35% of chimpanzees (Table 13.1, Figure 13.1).[2] Chimpanzees spend less time as juveniles than humans, with age at first birth for chimpanzee females about 5 years earlier than among hunter-gatherer women. In natural habitats chimpanzees have a much shorter adult lifespan than humans. At age 15 chimpanzee life expectancy is an additional 15 years, compared with 39 more years among human foragers. Importantly, women spend more than a third of their adult life in a postreproductive phase, whereas very few chimpanzee females survive to reach the postreproductive phase. Less than 10% of chimpanzees ever born survive to age 40, but more than 15% of hunter-gatherers survive to age 70!

Composition of the Diet

There are ten foraging societies and five chimpanzee communities for which caloric production or time spent feeding were monitored systematically (Kaplan et al. 2000a: Table 4). Modern foragers' diets all differ

Table 13.1. Life History Characteristics and Diet of Human Foragers and Chimpanzees

	Human Foragers		Chimpanzees
LIFE HISTORY CHARACTERISTICS			
Maximum lifespan	~120		~60
Probability of survival to age 15	0.6		0.35
Expected age of death at 15 (years)	54.3		29.7
Mean age first reproduction (years)	19.7		14.3
Mean age last reproduction (years)	39		27.7**
Interbirth interval* (months)	41.3		66.7
Mean weight at age 5 (kg)	15.7		10
Mean weight at age 10 (kg)	24.9		22.5
COMPOSITION OF DIET (%)			
Collected	9		94
Extracted	31		4
Hunted	60		2
CONTRIBUTIONS BY SEX (%)	Men	Women	
Adult calories	68	32	Sexes
Adult protein	88	12	Independent
Caloric support for offspring	97	3	
Protein support for offspring	100	0	

*Mean interbirth interval following a surviving infant.

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

considerably from that of chimpanzees. Measured in calories, the major component of forager diets is vertebrate meat. This ranges from about 30% to around 80% of the diet in the sampled societies with most diets consisting of more than 50% vertebrate meat (equally weighted mean = 60%, Table 13.1), whereas chimpanzees obtain about 2% of their food energy from hunted foods.

The next most important food category in the forager sample is extracted resources, such as roots, nuts, seeds, most invertebrate products, and difficult-to-extract plant parts such as palm fiber or growing shoots. They may be defined as non-mobile resources that are embedded in a protective context such as underground, in hard shells, or bearing toxins that must be removed before they can be consumed. In the sample of ten forager groups, extracted foods account for about 32% of the diet as opposed to 3% among chimpanzees.

In contrast to hunted and extracted resources, which are difficult to acquire, collected resources form the bulk of the chimpanzee diet. Collected resources such as fruits, leaves, flowers, and other easily accessible
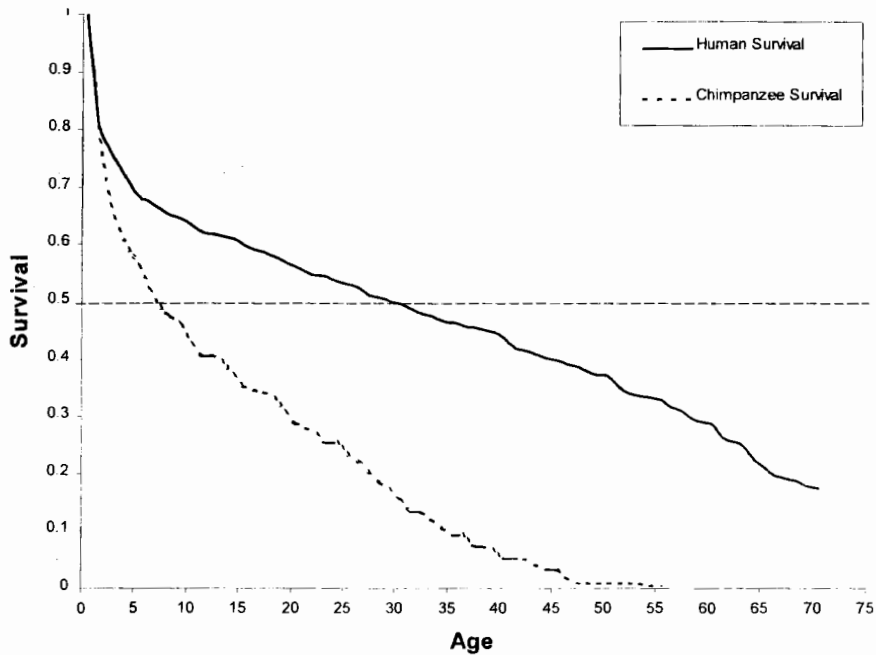
Figure 13.1. Survival curves: Human foragers and chimpanzees

plant parts are simply gathered and consumed. They account for 95% of the chimpanzee diet, on average, and only 8% of the forager diet.

The data suggest that humans specialize in rare but nutrient-dense resource packages or patches (meat, roots, nuts) whereas chimpanzees specialize in ripe fruit and low-nutrient-density plant parts. These differences in nutrient density are also reflected in human and chimpanzee gut morphology and food passage time, with chimpanzees specialized for rapid processing of large quantities and low-nutrient, bulky, fibrous meals (Milton 1999).

The Age Profile of Acquisition for Collected, Extracted, and Hunted Resources

In most environments, fruits are the easiest resources that people acquire. Daily production data among Ache foragers show that both males and females reach their peak daily fruit production by their mid to late teens. Some fruits that are simply picked from the ground are collected by two- to three-year-olds at 30% of the adult maximum rate. Ache children acquire five times as many calories per day during the fruit season as dur-

ing other seasons of the year (Kaplan 1997). Similarly, among the Hadza, teen girls acquired 1,650 calories per day during the wet season when fruits were available and only 610 calories per day during the dry season when fruits were not. If we weight the wet- and dry-season data equally, Hadza teen girls acquire 53% of their calories from fruits compared with 37% and 19% for reproductive-age and postreproductive women, respectively (all calculated from Hawkes, O'Connell, and Blurton Jones 1989).

The acquisition rate of extracted resources, in contrast to that of fruits, often increases through early adulthood as foragers acquire necessary skills. Data on Hiwi women show that root acquisition rates do not reach an asymptote until about age 35–45 (Kaplan et al. 2000a: Figure 8 for details) and the rate of 10-year-old girls is only 15% of the adult maximum. Hadza women appear to attain maximum root digging rates by early adulthood (Hawkes, O'Connell, and Blurton Jones 1989). Hiwi honey extraction rates by males peak at about age 25. Again the extraction rate of 10-year-olds is less than 10% of the adult maximum. Experiments done with Ache women and girls clearly show that young adult girls are not capable of extracting palm products at the rate attained by older Ache women (see Kaplan et al. 2000a: Figure 9 for details). Ache women do not reach peak return rates until their early twenties. !Kung (Ju/'hoansi) children crack mongongo nuts at a much slower rate than adults (Blurton Jones, Hawkes, and Draper 1994), and Bock (1995) has shown that nut cracking rates among the neighboring Hambukushu do not peak until about age 35. Finally, chimpanzee juveniles also focus on more easily acquired resources than adult chimpanzees. Difficult extraction activities such as termite and ant fishing or nut cracking are practiced less by chimpanzee juveniles than by adults (Boesch and Boesch 1999; Hiraiwa-Hasegawa 1990; Silk 1978).

Human hunting differs qualitatively from hunting by other animals and is the most skill-intensive foraging activity. Unlike most animals that either sit and wait to ambush prey or use stealth and pursuit techniques, human hunters use a wealth of information to make context-specific decisions, both during the search phase of hunting and then after prey are encountered. Specifically, information on ecology, seasonality, current weather, expected animal behavior, and fresh animal signs are all integrated to form multivariate mental models of encounter probabilities that guide the search and are continually updated as conditions change. Various alternative courses of action are constantly compared and referenced to spatial and temporal mental maps of resource availability (Leibenberg 1990). 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^2 of tropical forest in their lifetimes. Almost all for-

agers surveyed use more than 200 km² in a single year, and many cover more than 1,000 km² in a year (Kelly 1995: Table 4.1). Male chimpanzees, on the other hand, cover only about 10 km² in a lifetime (Wrangham 1975, 1980).

In addition, humans employ a wide variety of techniques to capture and kill prey, using astounding creativity (Kaplan et al. 2000b). Those kill techniques are tailored to many different prey under a wide variety of conditions. For example, from 1980 to 1996 our sample of weighed prey among the Ache includes a minimum of 78 different mammal species, at least 21 species of reptiles and amphibians, probably more than 150 species of birds (more than we have been able to identify), and more than 14 species of fish. Finally, human hunters tend to select prey that is in prime condition from the perspective of human nutritional needs rather than prey made vulnerable by youth, old age, or disease as do so many carnivorous animals (Alvard 1995; Stiner 1991).

The skill-intensive nature of human hunting and the long learning process involved are demonstrated dramatically by data on hunting return rates by age. Hunting return rates among the Hiwi do not peak until age 30–35, with the acquisition rates of 10- and 20-year-old boys reaching only 16% and 50% of the adult maximum, respectively. The hourly return rate for Ache men peaks in their mid thirties. The return rate of 10-year-old boys is about 1% of the adult maximum, and the return rate of 20-year-old juvenile males is still only 25% of the adult maximum. Frank Marlowe (Harvard University, unpublished data) obtains similar results for the Hadza. Also, boys switch from easier tasks, such as fruit collection, shallow tuber extraction, and baobab processing, to honey extraction, and hunting in their mid to late teens among the Hadza, Ache, and Hiwi (Blurton Jones, Hawkes, and O'Connell 1989, 1997; Kaplan et al. 2000b). Even among chimpanzees, hunting is strictly an adult or subadult activity (Boesch and Boesch 1999; Stanford 1998; Teleki 1973).

Net Food Production and Longevity

Figure 13.2 compares humans and chimpanzees in terms of age-profiles of production. The chimpanzee net production curve shows three distinct phases. The first phase, lasting to about age 5, is the period of complete and then partial dependence upon mother's milk. Net production during this phase is negative. The second phase during which net production is zero is independent juvenile growth, lasting until adulthood, about age 13 for females. The third phase is reproductive, during which females, but not males, produce a surplus of calories that they allocate to nursing.

Humans, in contrast, produce less than they consume for close to twenty years! Net production becomes increasingly negative until about
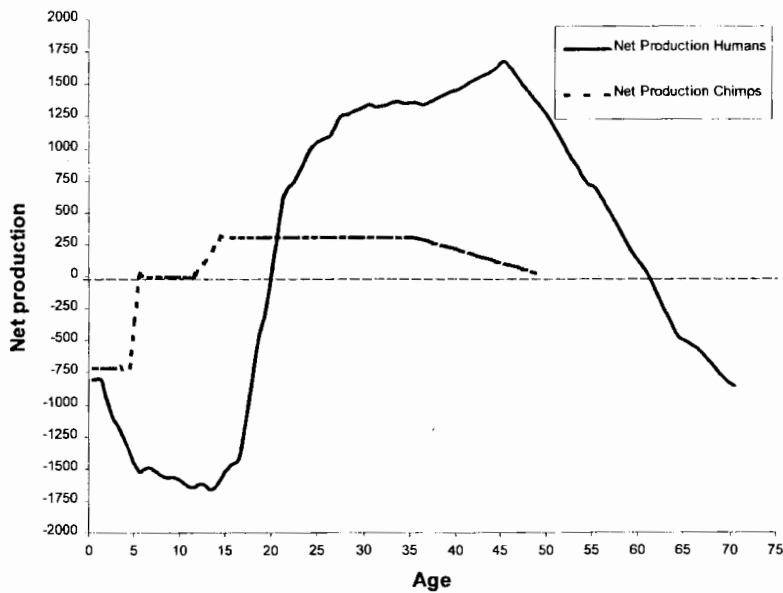
Figure 13.2.   Net food production: Human foragers and chimpanzees

age 14 (with growth in consumption owing to increased body size out-
stripping growth in production) and then begins to climb. Net production
in adulthood among humans is much higher than among chimpanzees
and peaks at a much older age. Peak net production among humans
reflects the payoffs to the long dependency period. It is about 1,750 calo-
ries per day, but it is not reached until about age 45. Among chimpanzee
females, peak net production is only about 250 calories per day (Kaplan et
al. 2000b) and since fertility decreases with age, net productivity probably
decreases during the adult period.

The survival curves in Figure 13.1 also reveal why the human age-pro-
file of productivity requires a long adult lifespan. Only about 30% of chim-
panzees ever born reach 20, the age when humans produce as much as
they consume, and less than 5% ever born reach 45, when human net pro-
duction peaks. The relationship between survival rates and age-profiles of
production is made even clearer in Figure 13.3. This panel plots net
expected *cumulative* productivity by age, multiplying the probability of
being alive at each age times the net productivity at that age and then
cumulating over all ages up to the present age. The thin and bold lines
show *cumulative* productivity by age for chimpanzees and humans,
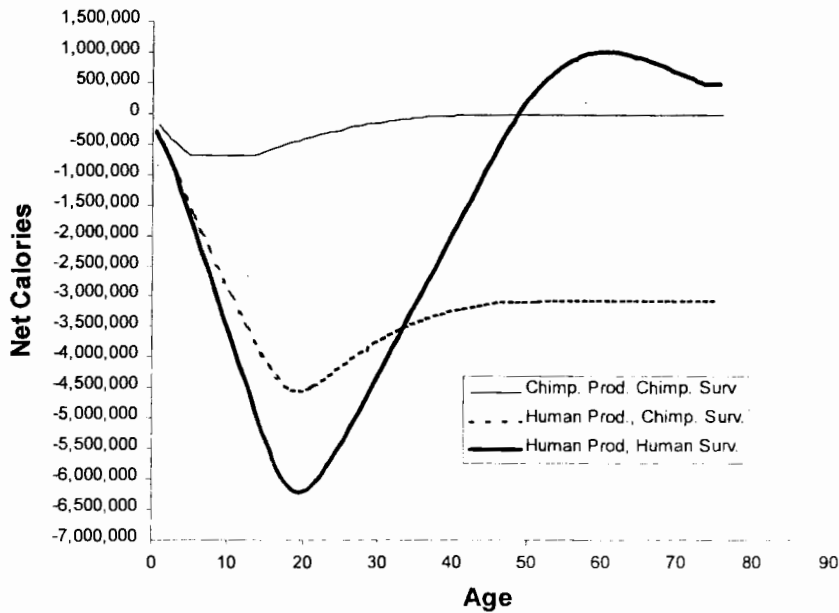respectively. The long human training period is evident when the troughs

Figure 13.3. Cumulative expected net caloric production by age: Humans and chimpanzees (adapted from Kaplan and Robson 2000a)

in the human and chimpanzee curves are compared. The dashed line is a hypothetical cross of human production profiles with chimpanzee survival rates. It shows that the human production profile would not be viable with chimpanzee survival rates because expected lifetime net production would be negative.

Sex-Specific Embodied Capital Investment and Cooperation between the Sexes

The evidence discussed above suggests that the same principles explaining the covariance among life history traits and brain size among nonhuman primates explains the extreme values exhibited by humans with respect to difficulty of the foraging niche, mortality rates, delay to peak productivity, and investments in intelligence and learning. There is, however, a major discontinuity between humans and other primates. Among humans, men and women specialize in different forms of embodied capital with correspondingly different foraging niches and activity budgets, and then share the fruits of their labor. The reproductive and economic cooperation between men and women is unparalleled in other

primates. In this section we present theory to help explain this discontinuity and some of the evidence upon which the theory is based.

Why women gather and men hunt.   The analyses in the previous section show that the principal foraging activities of humans are learning-intensive, and as a result, productivity increases with age. Therefore the lifetime payoffs associated with alternative activities depend on the time allocated to those activities. Hunting, as practiced by humans, is largely incompatible with the evolved commitment among primate females towards intensive mothering, carrying of infants, and lactation-on-demand in service of high infant survival rates. First, it often involves rapid travel and encounters with dangerous prey. Second, it is often most efficiently practiced over relatively long periods of time rather than in short stretches, owing to search and travel costs. Third, it is extremely skill-intensive, with improvements in return rate occurring over two decades of daily hunting. Fourth, it provides large (shareable) packages of food that are high in fat and protein.

The first two qualities make hunting a high-cost activity for pregnant and lactating females. The third quality, in interaction with the first and second, generates life course effects such that gathering is a better option for females, *even when they are not lactating*, and hunting is a better option for males.

Figure 13.4, which plots expected *cumulative net lifetime production* by age, disaggregated by sex, shows why this is true for Ache foragers. There is very little variation in men's time allocation to hunting, which averages about seven hours a day. For men, the effects of learning and skill acquisition are clearly visible in the steep increase in productivity until about 35. With their time allocation pattern, hunting provides higher lifetime returns than gathering. Women gather less than two hours a day (about 26% as much as males hunt), and as a result, they remain net consumers throughout their lives. The line with the open squares represents the hypothetical cumulative net production women would achieve if they hunted 26% of the time and learned at the same rate as men. Since women spend about 75% of their time either nursing or more than three months pregnant, a more illuminating way of thinking of this hypothetical line is that it plots the returns they would have if they hunted as much as men when they were unencumbered by pregnancy and lactation. For most of a woman's life, it would not pay to hunt, and she never would get enough practice to make it worthwhile, even when she is postreproductive.

Economic and reproductive cooperation among husbands and wives.
We propose that this sex-based specialization in embodied capital investments over the life course, together with the long period of parental invest-
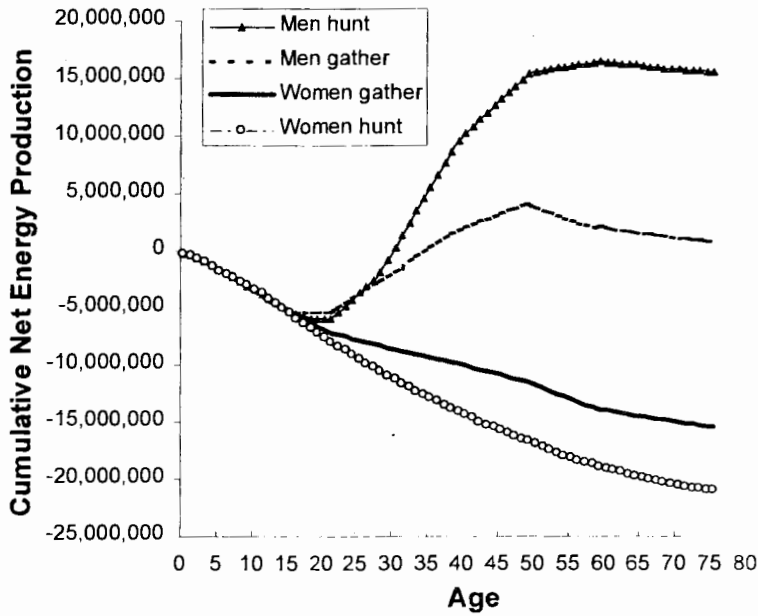
Figure 13.4.   Cumulative net energy production by Ache

ment leading to multiple child dependents, is directly responsible for high male parental investment, the universality of the marriage institution, and the extensive economic and reproductive cooperation among husbands and wives. The specialization in different skills and in the procurement of different resources generates a complementarity between human men and women that is rare among mammals. Stated simply, complementarity occurs when the value of male investment in offspring depends *positively* on the amount given by females and vice versa (with fitness held constant).[3] In contrast, male and female inputs are substitutes when the relative values of the two inputs are independent of the amount provided by the other sex (again holding fitness constant).

The specialization generates two forms of complementarity. Hunted foods complement gathered foods because protein, fat, and carbohydrates complement one another with respect to their nutritional functions (see Hill 1988 for a review) and because most gathered foods, such as roots, palm fiber, and fruits, are low in fat and protein (nuts are an exception). The fact that male specialization in hunting produces high delivery rates of large, shareable packages of food leads to another form of complementarity. The meat inputs of men shift the optimal mix of activities for women, increasing time spent in child care and decreasing time spent in

food acquisition. They also shift their time to foraging and productive activities that are compatible with child care and away from activities that are dangerous to them and their children.

On average among adults in the ten-group sample, men acquired 68% of the calories and almost 88% of the protein; women acquired the remaining 32% of calories and 12% of protein (Table 13.1). Given that on average these calories are distributed to support adult female consumption (31%), adult male consumption (39%), and offspring (31%), respectively, women supply 3% of the calories to offspring and men provide the remaining 97%! Men not only supply all of the protein to offspring but also the bulk of the protein consumed by women. This contrasts sharply with most mammalian species (>97%), where the female supports all of the energetic needs of the offspring until it begins eating solid foods (Clutton-Brock 1991) and males provide little or no investment.

Complementarity of investments is also evident in the behavior of married couples. For example, as the amount of food that men acquire increases, their spouses forage less and allocate more time to other activities, such as child care. For every 1,000 additional calories that husbands acquire, Hiwi and Ache women decrease time spent foraging by 0.8 and 0.5 hours, respectively (Hurtado et al. 1992). Couples also have a number of behaviors that help each other increase foraging return rates. For example, among the Ache, men cut most of the palms from which their wives extract palm fiber, the main carbohydrate staple. Women often help their husbands spot game. In fact, women spend about 11% of their out-of-camp time helping others acquire food, 55% of which is spent helping their husbands. Among both the Ache and Hiwi (and most other foragers, for that matter), women cook and process most of the food that their husbands acquire and consume (Hurtado et al. 2000). Among the Hiwi, spouses adjust their activities and time use according to what the other spouse is doing and the weaning status of their youngest child. The husbands of nursing women increase time spent in activities in camp that are compatible with child care as their infants get older. This suggests that as breastfeeding duration and frequency decrease, men do more child care. Moreover, reproductive age women are more likely to be out foraging when their husbands are in camp than when their husbands are out of camp. Thus spouses take turns staying in camp with some of their shared offspring while the other goes out to forage, sometimes accompanied by one child (Hurtado et al. 2000).

In this sense, humans are more like birds than mammals. Most bird species produce altricial chicks that cannot fly or defend themselves effectively, and as a result, they are especially vulnerable to predation when they are unprotected. However, finding food for both the parents and the young requires time away from the nest. Male and female investments are com-

plements since the value of the food brought by one sex is greater if the other sex protects the chicks (either through specialization in care and feeding or turn-taking at the nest). Male parental investment and monogamy are extremely common among bird species with altricial young and rare among species with precocial young who feed themselves.

Male and female investments are much less complementary among mammals because mothers and infants tend to stay together to facilitate nursing. Most mammalian young follow their mothers during feeding (or are cached in hidden places) so that care and feeding can be done simultaneously (or do not trade off against one another as sharply). In principle, mammalian males could have evolved to lactate as well. Mother's milk and father's milk would be perfect substitutes because milk is milk, regardless of who provides it.

The extensive cooperation among human men and women would only make sense if the reproductive performance of spouses were linked. Ache juvenile mortality increases when fathers are poor hunters or are deceased (Hurtado and Hill 1992). Thus, for females in a stable pair bond, whatever they can do to increase their husbands' strength and survivorship will be mutually beneficial. Behavioral cooperation between the sexes would also make sense if the probability of defection was relatively low.

The fact that humans are unique in raising multiple dependent offspring of different ages reduces the payoffs to defection and increases the benefits for men and women to link their economic and reproductive lives over the long run. Men and women who divorce and remarry during the time they are raising offspring will face conflicts of interest with new spouses over the division of resources. If they marry someone with children from previous marriages they may disagree with their spouses over the allocation of food and care to their joint children relative to children from the previous marriage. Those conflicts increase the benefits of spouses staying together and having all or most of their children together.

Data on divorce and reproduction show that people are responsive to those costs and benefits. Among the Ache, who marry and divorce frequently when they are young, reproduction solidifies marital bonds. A good measure of pair bond stability is the extent to which there is overlap in the timing of last births between spouses. Among the Ache, most men are five to six years older than their spouses (Hill and Hurtado 1996). When women reach menopause in their late forties, men have the option to continue reproducing with younger women but they do not generally do so. Overall, 83% of all last births for women also represent a last birth for the fathers of these children. In addition, the last child of 90% of Ache men who had fathered at least two children with the same spouse was also the last child of the wife. Last, as the number of shared offspring increases, the difference in spouses' ages at the time of the birth of their last child

decreases (Hurtado et al. 2000). For the minority of couples whose year of last birth differed greatly and men established new families with younger women, spouses usually had only one shared offspring.

Finally, human females evidence physiological and behavioral adaptations that are consistent with an evolutionary history involving extensive male parental investment. Human females decrease metabolic rates during pregnancy (suggesting that they lower work effort) and store fat (suggesting that they are being provisioned) (Lawrence and Whitehead 1988; Pike 1999; Poppitt et al. 1993), whereas nonhuman primates do not (Lancaster et al. 2000). In addition, nonhuman primate females increase work effort during lactation and, as a result, have increased risk of mortality. Human female foragers, in contrast, tend to decrease work effort during lactation and focus on high-quality care (Hurtado et al. 1985; Lancaster et al. 2000). These phenotypes could not have evolved if women did not depend on men for most of their food provisioning throughout human history.

Specialization in nutrient extraction and multiple dependency of young may be the critical factors favoring the greater relative importance of selection for cooperative rather than competitive arrangements between human mates. The investments by men may also explain why humans manage to have both shorter interbirth intervals and higher rates of juvenile and adult survival than chimpanzees (see Table 13.1).

DISCUSSION AND CONCLUSIONS

The analyses in this paper have applied embodied capital theory to understanding primate radiations in brain size and longevity, the evolution of the human life course, and sex-specific specialization in embodied capital investments. In each case, the theory has led to new insights and empirical results, some of which contravene alternative theories that have heretofore been widely accepted.

Embodied capital theory organizes the relationships of ecology, brain size, and longevity among primates, which existing debates about primate brain size evolution have failed to do. One debate pits ecological and social intelligence hypotheses against each other. According to "the ecological hypothesis," increases in brain size are largely driven by the complexities of the diet. Jerison (1973, 1976) hypothesized that the need to process information in a complex three-dimensional environment was the cause of the large brain size of primates relative to other mammals. He therefore predicted that differences in brain size, after controlling for body mass, would be associated with an animal's ecological niche and its

demands for information processing. Milton (1981, 1993; Milton and Demment 1988) extended this approach by focusing on gut specialization and brain size as two alternative routes to energetic efficiency. Leaves, while abundant, tend to contain high amounts of fiber and often toxins as well. The ability to extract nutrients from leaves depends on the size of the gut and other specializations designed to facilitate fermentation for nutrient extraction. Fruits, on the other hand, are ephemeral resources that are patchily distributed but offer a higher density of easily processed energy.

According to "the social brain" or "Machiavellian intelligence" hypothesis (Barton and Dunbar 1997; Byrne 1995, 1996; Dunbar 1992, 1998; Milton 1981, 1993; Milton and Demment 1988), the expansion of the brain is driven primarily by the complexities of social life in primate groups. Many species of primates exhibit complex dominance hierarchies that are mediated by political alliances and relations among relatives in genetic lineages (Harcourt 1988a, 1988b; Walters and Seyfarth 1987). Discussions of life history associations with brain size have focused primarily on the metabolic costs of growing large brains (Foley and Lee 1991; Martin 1996), or on whether the relationship between brain size and longevity is real or a statistical artifact (Allman et al. 1993; Barton 1999; Economos 1980; Foley and Lee 1991; Martin 1996). There has been virtually no discussion on how selection might work on both longevity and brain size.

The embodied capital theory and our empirical results show how features of ecology, including both mortality risks and information processing demands, interact in determining optimal allocations to the brain and survival. They also suggest an alternative interpretation of primate social intelligence. Coevolutionary selection on brains and longevity owing to the complexity and the navigational demands of the primate diet may have produced preadaptations for the evolution of social intelligence. Given that primates have long lives with enduring social relationships, and given that many species of primates eat foods whose distribution generates within-group competition, there would be selection for the application of existing enhancements in memory and information processing abilities to the management of social interaction. Many animals live in social groups, but primates are notable in terms of the complexity of their social arrangements. Perhaps social pressures alone are not sufficient to select for markedly increased brain size, but they might select for the extension of existing abilities to social problems. This may be why apes display remarkable social intelligence even though group size is not particularly large (Byrne 1995, 1997a). Orangutans, for example, are mostly solitary, but it takes about seven years for a young orangutan to become independent of its mother (presumably because of the learning-intensive nature of the diet). If this view is correct, it also suggests that the assumption of extreme domain-specificity in intelligence may be unwarranted.

There is growing interest in the evolution of human life histories, especially longevity. One model, recently proposed by Hawkes and colleagues (1998) and often referred to as the "Grandmother Hypothesis," proposes that humans have a long lifespan because of the assistance that older postreproductive women contribute to descendant kin through the provisioning of difficult-to-acquire plant foods. Women, therefore, are selected to invest in maintaining their bodies longer than chimpanzee females do. This model offers no explanation for why men live so long. In contrast to this female-centered view, Marlowe (2000) proposes that reproduction by males late in life selects for the lengthening of the human life course, with effects on females being incidental. The data we presented regarding the interdependence of men's and women's economic and reproductive lives cast doubt on both those theories and on the view that the sexual division of labor is primarily caused by conflicts of interest between mates (Bird 1999). Cooperative arrangements between men and women help bolster their individual chances for survival and the number of surviving children they produce.

The embodied capital theory explains why both men and women have long lives. Both men and women exploit high-quality, difficult-to-acquire foods (females extracting plant foods and males hunting animal foods), sacrificing early productivity for later productivity; both have a life history characterized by an extended juvenile period where growth is slow and much is learned; and both make a high investment in mortality reduction to reap the rewards of those investments. It also explains many other facts, such as the expansion of the costly human brain, the sex-specific investments in embodied capital, and the economic and reproductive cooperation among men and women.

The complementarity in embodied capital investments between men and women is a distinctive feature of the human adaptation that is qualitatively different from other primates. It is not just men and women that cooperate in nuclear families, however. Food sharing among families is pervasive in human groups. This is true of both hunted and extracted resources and of the foods acquired by women and men (Gurven, Allen et al. 2000; Gurven, Hill et al. 2000; Kaplan and Hill 1985). Food sharing not only buffers the risk of day-to-day variation in food supply owing to foraging luck, it also allows people to recover from illness and injury (Gurven, Hill, and Hurtado 2000). Food sharing may be one reason why humans have such low mortality rates and can afford to invest in learning-intensive foraging strategies (see Kaplan et al. 2000a for a fuller treatment). Moreover, food sharing buffers variance in family size resulting from unpredictable mortality. Larger families are reported to receive larger shares of food in most societies for which data are available (Gurven, Hill et al. 2000). Interfamilial food sharing may also be a necessary support for long-term child dependence since families with multiple, surviving young

could not support themselves without the assistance of families with low dependency ratios.

The human adaptation is broad and flexible in one sense, and very narrow and specialized in another sense. It is broad in the sense that as hunter-gatherers, humans have existed successfully in virtually all of the world's major habitats. This has entailed eating a very wide variety of foods, both plant and animal, and a great deal of flexibility in the contributions of different age and sex classes of individuals. The human adaptation is narrow and specialized in that it is based on extremely high investments in brain tissue and learning. In every environment, human foragers consume the largest, highest-quality, and most difficult-to-acquire foods using techniques that often take years to learn. In terms of embodied capital, males specialize in acquiring hunting skills at the expense of very low productivity during the adolescent and early adult years, and females specialize in extractive activities that are compatible with child care and in the care and training of offspring. The human feeding niche and parental investment system is also specialized in that it depends upon cooperation between men and women and food sharing among families. It is this legacy that modern humans bring to the complex economies existing today, where education-based embodied capital determines income and the economy is a complex web of specialization and cooperation between spouses, families, and larger social units. We are only beginning to explore the implications of this legacy for understanding modern behavior.

NOTES

1.   See Kaplan et al. 2000b for details on this section.
2.   The hunter-gatherer 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. The chimpanzee data are compiled from all published and unpublished sources of which we are aware and to which we had access (Hill et al. 2001; Kaplan et al. 2000b).
3.   Technically, complementarity occurs when marginal rates of substitution along fitness isoclines or indifference curves change as the ratio of the two inputs change, making those curves convex to the origin.

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