LIFE HISTORY TRAITS IN HUMANS: Theory and Empirical Studies

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■ **Abstract** Life history theory offers evolutionary explanations for the timing of life events, with a particular focus on age-schedules of fertility and mortality and growth. Traditional models examine trade-offs between current and future reproduction and quality versus quantity of offspring. These models can be used to understand questions concerning time of gestation, age of weaning, juvenile mortality profiles, age at maturation, adult body size, fertility rates, senescence, menopause, and the length of the life span. The trajectory of energy acquisition and its allocations is also an important part of life history theory. Modifications of these models have been developed to examine the period of learning, postweaning parental investment, and patterns of development. In this article, we combine energetic and demographic approaches in order to examine the human life course from an optimality perspective. The evolved life history solves related problems across two generations. The first set of decisions concerns how to maximize own lifetime net energy production that can be used for reproduction. The second set of decisions concerns how to maximize total offspring energy production (summed over all offspring).

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INTRODUCTION

Life history theory 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, Partridge & Harvey 1988). The focus on fertility and mortality is due to the fact that fitness, measured as the intrinsic rate of increase, is derived directly from summing reproductive output of each year lived.[1] Therefore, natural selection is expected to shape the timing of those life events. Corresponding to the age structure of death and reproduction, there is an age structure to the acquisition and consumption of energy and other resources necessary for life. As individuals grow and then reproduce, they utilize increasing amounts of energy to maintain their bodies and to produce offspring. Fundamental to life history theory is the recognition that natural selection on the timing of life events, such as growth, maturation, reproduction, and death, depends on the ecology of energy production and mortality hazards (see, for example, reviews in Lessells 1991, Roff 1992, Stearns 1992, Charnov 1993).

Compared with other primates and mammals, there are at least four distinctive characteristics of human life histories: (*a*) an exceptionally long life span, (*b*) an extended period of juvenile dependence, (*c*) support of reproduction by older postreproductive individuals, and (*d*) male support of reproduction through the provisioning of females and their offspring (Kaplan 1997; H Kaplan, K Hill, J Lancaster & AM Hurtado 1999). In this article, we develop an evolutionary economic approach to understanding the interaction of resource production and mortality risks in shaping human life histories.

The first section presents a basic, nontechnical introduction to life history theory. The second section examines theoretical and empirical treatments of fundamental issues in human life history evolution, such as maturation and age of first reproduction, life span, interbirth intervals and family size, and men's investment in offspring. The third section discusses major trends in the life histories of people living in modern developed and developing nations, with a particular focus on family size and population growth, education, and life span. Our goal here is to show how life history theory and anthropology can be combined to organize social science research on the major demographic trends that will affect standards

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[1]The intrinsic rate of increase is measured by solving the following equation for r,

$$1 = \sum_{x=0}^{\infty} l_x m_x e^{-r(x+1)},$$ where x is age, l_x is the probability of surviving from birth to age x, m_x is reproduction at age x, and r is the yearly rate of increase. Because l_x is derived from knowing the probability of dying at each age younger than x, fitness is measured directly from the age structure of fertility and mortality.

of living, crowding, urbanization, conflict and warfare, and the environment in the next century.

TIME, ENERGY, REPRODUCTION, AND LIFE HISTORY THEORY

The Trade-Off Between Current and Future Reproduction

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 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 more efficiently into replicates than others become more prevalent through time. This simple problem of harvesting energy and converting energy into offspring generates complex problems that are time dependent.

Time is the most precious resource organisms have at their disposal. Time can be converted into energy through work. The acquisition of energy takes time, and the more time available for energy acquisition, the more energy can be acquired. In addition, time, invested in growth and development in combination with energy, can be used to affect the rate at which energy is acquired from the environment. Yet, time is a limited resource, whose availability depends partially on the allocation of time and energy to increasing the expected lifespan.

Imagine an organism that is newly independent of support from its parents. It can use its time to harvest energy from the environment. It can use the energy in several different ways. However, the energy that is used for one purpose cannot be used for other purposes. It can use some or all of its energy to reproduce. Another potential use of the energy is to buy more time. By using some of the energy for physical maintenance and to defend against diseases, it can live longer to harvest more energy in the future. Another use of energy is to grow and build tissue. The allocation of energy to growth brings three benefits. Larger organisms often suffer lower rates of predation. Therefore growth can increase the length of the life span. Growth also can increase the total net energy capture per unit of time allocated to food production or acquisition. Therefore allocation of resources to growth can increase the total energy available for reproduction over the life course. Finally, larger body size can increase success in intrasexual competition for mates, ultimately affecting reproductive rate. These three benefits to growth also accrue to investments in maintenance, since physical condition will depreciate through time if no effort is allocated to maintenance. For each unit of energy acquired, the organism is assumed to face a choice between investing it in somatic effort, which increases future rates of surplus production, and investing in current reproduction.

These allocation decisions affect the number of descendants an organism leaves. The total energy allocated to reproduction will be the sum of the amounts allocated at each unit of time the organism lives. The longer it lives, the more units of time will contribute to that sum. The higher the rate of energy capture, the

greater will be the amount available for reproduction at each moment in time. The future, however, is always uncertain. Since many organisms, parasites and predators, have evolved to harvest the energy captured by other organisms, and since accidents can occur in the physical environment, there is always some probability of dying before realizing the gains from investments in future energy capture and reproduction. For this reason, Gadgil & Bossert (1970) identified the tripartite energetic trade-off among reproduction, maintenance, and growth as the fundamental problem shaping an organism's life history. Since maintenance and growth have their effects on fitness through impacts on future reproduction, this tripartite trade-off can also be thought of as a trade-off between current and future reproduction (Bell & Kofopanou 1986, Hill 1993, Lessells 1991, Stearns 1992, Roff 1992). The loss of future survival, energy capture, and reproduction because of energy allocation to reproduction now is often referred to as the cost of reproduction (Williams 1966).

The trade-off between current and future reproduction is generally measured in terms of reproductive value. Reproductive value at a specified age is the total future reproduction that an individual at that age can be expected to achieve on average before it dies[2] (discounting the future by the effects of population growth). To analyze the present-future trade-off, it is convenient to decompose reproductive value into two components: reproduction during the current time interval, and total reproduction at all future time intervals after the current one until death[3] (for reviews, see Lessells 1991, Hill 1993). The potential trade-off is due to the fact that reproductive effort expended during the current time interval may reduce reproduction at future time intervals, either by reducing future fertility or by reducing the probability of living to older ages. When allocation decisions are faced sequentially, natural selection is expected to act on reproductive effort expended at each age so as to maximize reproductive value at that age. Optimality models show that fitness is maximized at the level of reproductive effort when a small increase in reproduction during the current time interval would be exactly offset by a decrease in future reproductive value.[4]

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[2]In discrete time form, reproductive value at some age x, V_x is

$$V_x = \sum_{y=x}^{\infty} \left(l_y \big/ l_x \right) m_y e^{-r(y-x+1)},$$ where age is x, l_x is the probability of surviving to age x, and

m_y is fecundity or number of daughters produced at age y. The term l_y/l_x is the probability of living to age y, having survived to age x, and the term discounts future reproduction by the population growth rate, r, because current reproduction contributes proportionally more to the gene pool than does future reproduction in growing populations, and less to fitness in shrinking populations (see Lessells 1991).

[3]From above, this decomposition can be written as $m_x e^{-r} + \sum_{y=x+1}^{\infty} \left(l_y \big/ l_x \right) m_y e^{-r(y-x=1)}$.

[4]This would occur when $\dfrac{\partial \sum_{y=x+1}^{\infty} \left(l_y \big/ l_x \right) m_y e^{-r(y-x)}}{\partial m_x} = -1.$
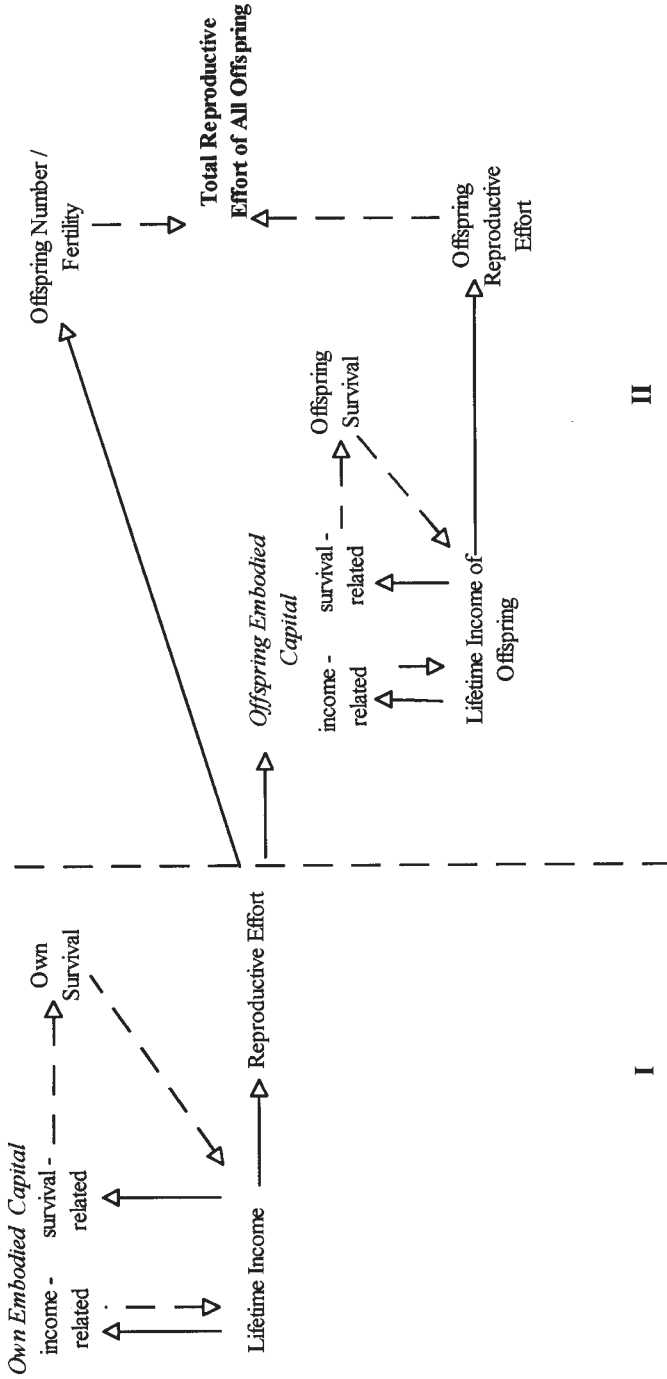
Figure 1   Multigeneration model of life history investments and effects of those investments. (Dotted arrows) The impacts of investments; (solid arrows) investment options. (Adapted from Kaplan 1996.)

The concept of embodied capital (Kaplan et al 1995), borrowed from the concept of human capital developed in economics, is a more general way of thinking about investments in future reproduction. Development can be seen as a process in which individuals and their parents invest in a stock of embodied capital. In a physical sense, embodied capital is organized somatic tissue. In a functional sense, embodied capital includes strength, immune function, coordination, skill, and knowledge, all of which affect the profitability of allocating time and other resources to alternative activities such as resource acquisition, defense from predators and parasites, mating competition, parenting, and social dominance. Since such stocks tend to depreciate with time because of physical entropic forces and direct assaults by parasites, predators, and conspecifics, allocations to maintenance such as feeding, cell repair, and vigilance can also be seen as investments in embodied capital. The embodied-capital view of life history evolution is depicted in Figure 1.

The first part of Figure 1 shows own embodied capital that is due to parental investment in the prior generation. Income-related embodied capital, for example, produces income (defined here in the general sense of the total value of time allocated to alternative activities, such as resource acquisition, child care, rest, etc), which can then be further invested in reproductive effort, or in more embodied capital. Embodied capital, in turn, can be divided into stocks affecting the ability to acquire the resources for reproduction and stocks affecting the probability of survival.

Investments in income-related capital, such as in growth, physical coordination, social alliances, skills, and knowledge, affect lifetime income through the value or productivity of time in the future. Among humans, this seems especially critical since even in ancestral hunter-gatherer environments a great deal of skill and learning are required in order to eventually acquire energy at a rate much higher than any other primate (Figure 2). The delayed payoffs from learning and skills have probably increased even more with subsequent technological advances and economic specialization.

Investments in survival-related capital, such as immune function, predator defense, and tissue repair, affect lifetime income through increasing the expected life span of earnings. However, an organism that does not reproduce leaves no descendants. Thus, the optimization problem acted on by natural selection is to allocate lifetime income among investments in future income, survival, and reproduction at each age so as to maximize the time-discounted surplus energy for reproduction over the life course (Charnov 1993; Hill & Hurtado 1996; Kozlowski 1992; Kozlowski & Wiegert 1986, 1987; Roff 1986; Stearns & Koella 1986). Since the costs and benefits associated with alternative allocations are likely to vary with phylogenetic history, local ecology, and individual condition, optimal distributions of effort to current versus future reproduction are likely to vary as well.

The life histories of most complex, multicellular plants and animals include a growth or developmental phase in which reproductive effort is zero. Thus, the determination of age of first reproduction is a fundamental question in life history
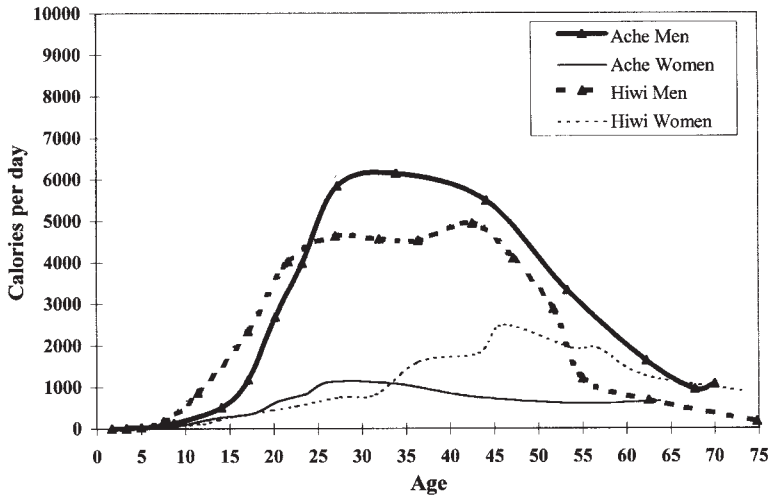
Figure 2 Age-sex–specific daily energy acquisition for Ache (3645 person days) and Hiwi (4756 person days) foragers. All food acquired by focal individuals was weighed each day, refuse was estimated, and caloric values of edible portion was determined (K Hill & AM Hurtado, unpublished data). Mean daily per capita intake is 2712 calories for Ache and 1793 calories for Hiwi. Note that a long period of learning is required in order to obtain high daily production later in life. This energy is used to subsidize children under age 15 and reproductive-aged women.

theory. Some organisms, especially many plant species, engage in one burst of reproduction and then die, whereas others engage in repeated bouts of reproduction. The former are referred to as semelparous and the latter as iteroparous (Cole 1954). Those that are iteroparous can be subdivided further into indeterminate and determinate growers. Determinate growers have fairly discrete and nonoverlapping growth and reproductive phases. During the growth phase, all excess energy is allocated to growth, and during the reproductive phase, growth ceases altogether (Charnov 1993). Indeterminate growers only allocate a portion of their excess energy to reproduction during the reproductive phase, so they continue growing after beginning to reproduce and often throughout adulthood.

Senescence, or the decrease in body function with increasing age, seems to be an inevitable effect of natural selection, at least among sexually reproducing organisms. This is due to the fact that the force of selection on characteristics expressed later in life is weaker than selection on traits expressed earlier in life (Fisher 1958, Medawar 1952, Williams 1957). Medawar (1952) proposed that deleterious mutations would accumulate at later ages, because few individuals reach those ages and therefore selection would be increasingly weak with age. He speculated that senescence was the result of mutation accumulation at loci affecting older ages, due to increasingly weak selection. Williams (1957) then intro-

duced the concept of antagonistic pleiotropy to account for the evolution of senescence. On the assumption that the strength of selection decreases with age, Williams proposed that selection may often increase the prevalence of genes, which have beneficial effects early in life and deleterious effects late in life. Hamilton (1966) produced the first formal model of the sensitivity of fitness to age-specific changes in fertility and mortality. He found that any gene that causes a proportional decrease in survival at any age after age of first reproduction and a concomitant proportional increase at an earlier age will increase fitness and increase in prevalence. This will lead to senescence.

Hamilton realized that this formulation was correct for organisms with no parental care. In his model, the only effect of living longer is the increase in total fertility due to the additional fertility realized at later ages. However, if individuals engage in parental care or, more generally, any form of kin assistance, the value of living longer depends also on contributions made to kin at those ages. This is most evident in humans, where we must account for the evolution of a post-reproductive period.

The incorporation of kin assistance into models of senescence required further developments. Building on Hamilton's initial formulation of kin selection and inclusive fitness, Charlesworth & Charnov (1981) extended the theory to include the relative reproductive values of the altruist and the recipient. This is necessary because the likely benefits and costs of assistance depend on the impacts of the assistance on the total expected future fitness of the two individuals. To see this, imagine an altruistic act that saves the life of a newborn and another act with the same cost that saves the life of a young adult. Both individuals have the same expected reproductive output at the beginning of adulthood. The infant, however, has some probability of dying before reaching reproductive age, and thus the effect of saving its life on its total expected reproduction must be devalued by the probability of its reaching reproductive age. Similarly, a self-sacrificing act that occurs later in life is less costly than one that occurs earlier in life. Charlesworth & Charnov (1981) showed mathematically that effects on mortality require weighting of the benefits by the recipient's reproductive value (as well as by degree of relatedness) and costs by the actor's reproductive value, whereas effects on fertility only require weighting by degree of relatedness.

All these treatments of senescence are not specific with regard to the causes of intertemporal trade-offs. Although it is possible that at different points in the life course, a gene could, by chance, affect traits in opposite directions, it is more likely that such pleiotrop is the necessary consequence of allocation trade-offs. The principle of allocation refers to the fact that energy and/or time allocated for one function cannot be simultaneously allocated to a competing function. Kirkwood (1990) applied this allocations framework to the problem of senescence. His analysis revealed that selection would not favor allocations to maintenance sufficient to reduce senescence (depreciation) to zero. This is because at the point at which senescence does not occur, the derivative of survival with respect to energy allocated to maintenance is zero. As long as there is some payoff to energy allocated to reproduction, some energy could be diverted from maintenance to

reproduction for a net increase in fitness. At the optimum, energy allocated to different functions must have equal fitness, and therefore the optimum must occur at a point less than complete maintenance. Living organisms are designed by natural selection to die. Senescence and age-dependent increases in mortality are inevitable consequences of fitness maximization through optimization of energy allocations.

An extension of this "disposable soma theory" of aging also follows the Medawar logic. Kirkwood & Rose (1991) note that in order to survive forever, organisms must allocate considerable energy and resources to maintaining their soma. Since unavoidable causes of mortality (e.g. predation, accidents) will kill all adults before they have achieved an infinite life span, it is not worth investing the necessary energy to achieve an infinite life span. This is especially true because that energy could instead be invested into reproduction early in the life span. Thus, the somatic investment theory of senescence leads to the same conclusion as the genetic theories concerning extrinsic mortality. The rate of senescence that will evolve is directly related to the expected probability of death due to other difficult-to-avoid causes, such as predation, accidents, etc. Empirical data on aging rates, predation, and accident rates support this proposition (Austed 1993). The disposable soma theory complements the genetic approaches, however, because it specifies what types of genes might be expected lead to senescence (those affecting energy allocation to different functions).

The Trade-Off Between Quantity and Quality of Offspring

Given that lifetime allocations of energy to reproduction are maximized, there is a second fundamental life history trade-off: the allocation of reproductive effort to increasing offspring number (quantity) or to increasing offspring fitness (quality). This trade-off is presumed to result from the facts that parents have limited resources to invest in offspring and that each additional offspring necessarily reduces average investment per offspring. Most biological models (e.g. Harpending et al 1990; Lack 1954; Lloyd 1987; McGinley & Charnov 1988; Pennington & Harpending 1988; Rogers & Blurton Jones 1992; Smith & Fretwell 1974) operationalize this trade-off as number versus survival of offspring. Natural selection is expected to shape investment per offspring and offspring number so as to maximize offspring number times their survival.

Assume that parental investment increases survival to some asymptote. Under these conditions, optimal investment per offspring is reached at the investment level where the proportional decrease in number of offspring produced is equaled by the proportional increase in survival of offspring to adulthood. Since the number of offspring produced is simply (total resources)/(resources invested per offspring), it follows that the shape of the function relating survival to investment will determine the optimal level of investment per offspring (Harpending et al 1990). It also follows that optimal maternal investment per offspring will always be greater than that required to simply produce the fetus (because fetal survival without additional investment is zero, and at survival = 0, the proportional increase in survival is infinite). Likewise, optimal investment will always be less

than that required for maximal survival (since just prior to maximal survival the proportional increase from investment approaches zero). Thus, parents are selected to produce intermediate-quality offspring. Finally, the optimal amount of investment per offspring is independent of parental income (Smith & Fretwell 1974), but total parental resources divided by optimal resource investment per offspring determines lifetime fertility. All parents should produce offspring of the same quality, but parents with more resources should produce more offspring.

Although this simple model—often called the Smith-Fretwell model—provides important insights about human fertility, more complicated models that relax simplifying assumptions are useful. Kaplan (1996) has developed multigenerational model of fertility and fitness that includes both fixed costs of offspring production and investment that can affect survival and adult income of offspring. In this model, individuals can invest not only in capital embodied in their own soma, but also in the capital embodied in offspring. However, such allocations decrease resources available for the production of other offspring and, hence, decrease the total quantity of offspring produced with a given amount of income. The model also allows for a relationship between parental income and the effectiveness of investment. This eliminates the expectation that parents of varying income levels will produce offspring of equal quality.

The second part of Figure 1 shows the relationships between investments and outcomes for two generations. Here, both the parent and the offspring can invest in the offspring's survival- and income-related capital. The optimization problem for the parent is then to allocate investments in fertility and in embodied capital of offspring so as to maximize the total lifetime allocations by offspring to their own reproduction (summed over all offspring). If individuals in each generation allocate investments in own- and offspring-embodied capital optimally, then the "dynastic" or multigenerational fitness of the lineage is maximized (see Kaplan 1996).

Ecology and Life History Evolution

The diversity of life histories is presumably due to the fact that the shape of the relationships between investments and outcomes varies ecologically. For each major class of mortality (predation, disease, intraspecific violence, accidents, starvation), there will be variable relationships between the probability of dying from that cause and investments by the organism. For example, the density and characteristics of predators, in interaction with the characteristics of the organism, determine the relationship between allocations and the probability of being eaten. Some organisms, such as bivalve mollusks, tortoises, and porcupines, apparently benefit significantly from allocations to predator defense and live long lives. Feeding niche appears to interact with the benefits to investments in mortality reduction. Birds, bats, and primates appear to lower predation rates by spending less time in terrestrial habitats and by being able to escape to aerial strata (primates also reduce predation through grouping and social behavior).

There is also ecological variability in the benefits to investment in income-related capital. The relationships between body size and productivity depend on

feeding niche. The value of knowledge, skill, and information-processing ability depends on the type of foods exploited. Grazing animals probably benefit much less from investments in learning than do species who eat more variable or difficult-to-capture foods.

In addition to factors affecting the shape of each relationship between investments and outcomes, the quantitative analysis of the first trade-off shows that optimal investment in each component depends, in part, on investments in other components and in the effects of those investments. For example, the value of investments in income-related capital depends on the probability of surviving to future ages [Becker (1975) and Ben-Porath (1967) obtain similar results in the analysis of investments in human capital]. If the expected future life span is short, it pays little to invest in future earnings, favoring allocation of resources to current reproduction instead. The corollary is also true. The value of investments in survival depends on expected future income. If income increases through time, higher investments in survival are favored. A similar finding is that the value of allocations to each form of mortality reduction depends on the probability of dying from other causes. For example, if one is likely to die from predation, it pays less to invest in cell repair and immune function, which would affect future condition and the likelihood of dying from disease. Low probability of predation is probably an important determinant of why birds, bats, and primates, for their body size, allocate more resources to maintaining physical condition and senesce at later ages than other vertebrates.

A similar set of ecological factors is likely to affect the quantity-quality trade-off. Feeding niche and exposure to predators and pathogens should affect the impacts of investments in offspring-embodied capital. Organisms feeding on difficult-to-acquire resources, especially predators, tend to provision offspring to much older ages. Since infancy and early childhood is also the period during which offspring require the most direct care, maternal time given to offspring should be affected by ecological factors affecting the relationship between direct care and survival. For example, the availability of safe spaces for offspring, which should be negatively associated with mobility, and the dangers in the environment should both affect the age-specific benefits of direct maternal care. Among Ache foragers, children between the ages of 2 and 4 years spend significantly more time in tactile contact with mothers when they are on mobile foraging trips than when they are residing in a permanent reservation settlement, even when time spent being carried is omitted from the analysis (H Kaplan & H Dove, unpublished data). These theoretical considerations allow researchers to build models to examine specific life history problems and test them with empirical data.

As can be seen from the above discussion, evolutionary analysis does not entail the assumption that there is a one-to-one correspondence between genotype and phenotype. The concepts of phenotypic plasticity and evolved norms of reaction have become increasingly important in biologists' understanding of adaptation. Under many conditions, genotypes are thought to code for mechanisms that translate environmental inputs into phenotypic outputs rather than for an invariant

response. For example, the reproductive rate of most plants and animals varies positively with energy availability [because of environmental conditions associated with temperature, rainfall, prey density, population density, etc (for mammalian examples, see Wade & Schneider 1992)].

Norms of reaction to environmental and individual conditions evolve because the optimal phenotype varies with conditions, and genetic variants coding for the ability to modify phenotype adaptively sometimes can outcompete variants that produce the same phenotype in all environments. This is especially true in highly variable environments, such as that thought to characterize the evolution of *Homo* (Potts 1998). However, such phenotypic plasticity is costly. Humans, whose behavioral phenotypes are at the extreme of plasticity, have a long developmental period of low productivity, precisely because it takes so long to "program" the brain with environmental information (Figure 2). Thus, each organism represents a compromise between the benefits and costs of phenotypic plasticity.

ANTHROPOLOGICAL STUDIES OF MAJOR ISSUES

Despite a large literature concerning patterns of human growth, development, and demography, these topics have only recently been treated by researchers who explicitly investigate why observed patterns have evolved. Instead, most traditional studies have sought to mathematically describe these patterns and their allometries, describe the means and range of individual and cross-population variation in some of these patterns, and occasionally test hypotheses concerning atypical patterns of growth, development, fertility, or mortality. Nevertheless, some recent research is grounded in life history theory and concerns why observed patterns (and not others) have evolved or are induced by environmental cues. These studies can be logically divided into (*a*) questions of optimal trajectory of energy production and reproduction through the life course and (*b*) issues concerning the optimal allocation of available resources per offspring (and close kin). The first trade-off ties together topics such as the study of the age of sexual maturity, body size, life span, and menopause. The second trade-off encompasses interbirth interval, weaning time, family size, paternal investment patterns, and non-offspring–kin investment.

Time Trade-Offs in Production and Reproduction

Age at Sexual Maturity, Adult Body Size   Life history theory defines the age of sexual maturity as the age of first birth. Although physiological and morphological sexual maturity are indeed tightly linked to reproduction in most organisms, human females generally show a lag between these events. Adult pelvic widening, menarche, and even copulation generally precede birth by several years (Wood 1994). This "false maturation" may be an example of signaling deception by females who attempt to extract higher rates of provisioning from males by mimicking a state of reproductive readiness. But, for modeling purposes, we define sexual maturity and adulthood as the age at first reproduction.

Although chimpanzee females in the wild begin reproducing at approximately 13–15 years of age, human hunter-gatherers generally do not experience first birth until approximately 18–20 years of age (H Kaplan, K Hill, J Lancaster & AM Hurtado 1999). Both species grow at approximately the same rate during the juvenile period (Rice 1997), but humans grow for several years after chimpanzees have reached adulthood, thus often attaining larger body size. Chimpanzees show early adult mortality rates of approximately 4% per year (K Hill, C Boesch, J Goodall, A Pusey, J Williams & R Wrangham, submitted for publication), whereas human early adult mortality is around 1.5% per year (Hill & Hurtado 1996, Ch. 5). In both species, better-fed populations begin reproducing earlier and are larger as adults than are poorly fed populations. The reaction norm that produces early sexual maturity and larger body size in well-fed populations, and the general association between high mortality and early maturation and small body size among mammals (Roff 1992) invites us to develop a coherent theory of growth, mortality, age at maturity, and adult body size.

Because humans show determinate growth, energy production is allocated to growth only during the juvenile period and is then rather abruptly diverted to reproductive function. Since all energy captured from the environment, above that needed for activity and cell maintenance, is converted to body mass during the juvenile period, we can estimate size-specific energy production from the observed mammalian growth equation $dw/dt = AW^{0.7}$. The change in weight over the course of a year is predicted by the growth constant A and the current weight of an individual and decreases proportionally with larger body size (because the allometric power is less than 1).

The species-specific growth constant A is near 1 for most mammals but only about 0.4 for primates (Charnov & Berrigan 1993) and less than 0.3 for human foragers in the postinfancy growth period (Hill & Hurtado 1996). This implies that larger body size will result in a higher net energy capture rate through time, which can be converted into a higher reproductive rate during adulthood (if offspring costs stay constant over small increases in adult body size). On the other hand, each year of growth is one more year during which death can occur prior to any reproduction. Thus, the cost of a longer growth period is a lowered probability of survival to reproductive age. Since lifetime reproductive output is the summed product of energy converted to offspring at each age times the probability of survival to that age, the age of maturity that leads to maximum lifetime reproductive output can be determined. When adult mortality is independent of size, maximal reproductive output should be achieved at the point where proportional increase in production capacity (body size) per unit time is balanced by the proportional decrease in survival to first reproduction (the early adult mortality rate) (Charnov 1989). At this point, growth ceases and reproduction begins. This trade-off model further implies that the age at sexual maturity and adult body size will vary between populations with different growth rates and/or different rates of mortality for mature juveniles/young adults.

Although this conceptual model has been successfully tested in a variety of nonhuman organisms (Roff 1992, Stearns 1992), to our knowledge the model has

only been applied twice to human data. In a theoretical exercise, Stearns & Koella (1986) derive the shape of the reaction norm relating food intake and age at sexual maturity in humans and develop a model that correctly predicts the secular trends in Europe over the past two centuries in age at menarche and body size. And in a direct empirical test, Hill & Hurtado (1996, Ch. 11) show that among the Ache hunter-gatherers, both female and male fertility are increasing functions of adult body size. They then use the juvenile growth constant, young adult mortality rate, and the length of the reproductive span to estimate the age at first reproduction and body size that will maximize the fitness (measured as yearly growth rate of a population with the observed phenotype) of Ache women and men. Their model predicted very accurately the modal body weight of Ache men and women and the weight and age at first reproduction for Ache and !Kung women (Ache girls have a growth constant of 0.29 whereas !Kung girls show a growth constant of only 0.18). The model predicts that chimpanzees should stop growing sooner than humans because of higher adult mortality. Thus, chimpanzees have an earlier age at first reproduction and a smaller body size than do humans. The model also predicted correctly less variance in body size among Ache males than among females, because of the more peaked fitness curve by body size for males, and the model suggested that the sexual dimorphism in body size among the Ache is due to the steeper slope of the fertility by size curve for males. This is consistent with life history models for evolution of sexual dimorphism in body size (Charnov 1993:109–112).

Virtually all demographic studies on paternity rates in natural fertility populations show that male fertility lags behind female fertility by several years (e.g. Coale & Watkins 1986, Low 1991, Hill & Hurtado 1996, Howell 1979, Melancon 1982, Voland 1990). This might be due to male-male competition and the advantage of larger body size (see above), although some of the male delay in reproduction is probably due to female mating preference for older males (Buss 1989) irrespective of body size. In societies as diverse as Australian hunter-gatherers, African pastoralists, and European peasant farmers, average age of first reproduction for males comes long after males cease growing. We suspect that these represent cases where the male resource acquisition curve is delayed because of the need to obtain special capital in order to produce resources. This special capital may be in the form of land, cattle, or social connections and obligations. Thus, younger males who have not yet accumulated capital, who cannot produce resources (through material capital), or who cannot extract resources from others (through social capital) must wait to obtain a mate. When capital can be transferred to wives and managed effectively by women and children (e.g. herds of cattle), there should be especially strong preferences for older males who have built up a lifetime of transferable capital. Even if husbands die, resources continue to flow. Since money-based economies with easy investment opportunities meet this condition, it is somewhat surprising that women in modern societies do not show the strongest preference for older males as partners. Perhaps this is because men in modern societies contribute importantly to the quality of offspring in ways that cannot simply be purchased with income.

Despite the fact that the Ache study provides strong support for a simple model of the timing of sexual maturity and adult body size, we should exercise some caution in accepting the model unaltered. First, human growth during the juvenile phase is not constant but varies through childhood. The yearly growth constant, A, for Ache children is nearly 2 at birth, then drops to less than 0.2 during mid-childhood years, and increases again to over 0.4 during the adolescent growth spurt (K Hill & AM Hurtado, unpublished data). Also, children are fed by adults, thus a child's growth is not limited by his/her own work effort (Kaplan 1994, 1997) and should not necessarily be related to his/her body size. The fact that growth rates are slow during middle childhood and seem to be appetite mediated leads us and other researchers to suspect that body weight growth is not always limited by resource availability during childhood years. Instead, childhood growth appears to be slowed in order to allow for other developmental events that take time, such as learning (for a similar view, see Worthman 1998). Nevertheless, there may be a positive relationship between body size and production rates that can be converted into offspring near the juvenile-adult transition. Larger body size is associated with higher work output (Spurr 1998), and if net energy capture is a function of energy expenditure in general, then the trade-off outlined in the simple model above still applies.

A second problem with the simple model of age at maturity is that human productivity appears to increase long after growth has ceased and reproduction has started. Among hunter-gatherers, the hourly energy capture rate for many resources does not reach an asymptote until mid-adulthood (Figure 2) (H Kaplan, K Hill, J Lancaster & AM Hurtado 1999). This suggests that learning and skill acquisition as well as large body size are required in order to effectively obtain energy from the environment. However, if energy production is characterized by a function that includes both body size and learning in its product, and if reproduction cannot take place until growth has ceased, then proportional increases in body size will still be traded off against mortality losses, as envisioned in the classical model. However, if learning results in high energy production later in life, selection will favor any investment that can lower mortality rate prior to that time (H Kaplan, K Hill, J Lancaster & AM Hurtado 1999). Thus, the shift to a learning-and-skills–based energy production niche is likely to lower juvenile mortality and subsequently lengthen the juvenile period (with resultant larger body size).

The Lifespan   Human populations show high variance in infant survival rates, which affect life expectancy at birth, but this an issue primarily related to parental investment allocation per offspring. A theoretically independent issue is the average life span of those individuals who reach adulthood. This measure of life span is rarely reported by demographers, but it is much more informative concerning ecological conditions and mortality constraints experienced by a population. The early adult mortality rate is also a critical determinant of both the optimal age at maturity and the evolution of anti-aging mechanisms.

Humans have a long average as well as a maximal adult life span compared with other similar-sized mammals or large primates. The mean life expectancy of Ache hunter-gatherers who survived to adulthood during the precontact forest period was approximately 56 years (Hill & Hurtado 1996). The mean life expectancy of chimpanzees who reach adulthood in the wild is only about 28 years (K Hill, C Boesch, J Goodall, A Pusey, J Williams & R Wrangham, submitted for publication). In order to understand this difference, we need to examine initial rates of mortality in early adulthood as well as the rate at which individuals senesce. If adult mortality were constant with age, the mean expected adult life span for humans and chimpanzees would be approximately 67 and 25 years, respectively (the reciprocal of 1.5% and 4% mortality). But mortality does not remain constant through adulthood. Instead, humans, like other organisms with a distinct germ line, show increased mortality with age because they senesce.

A specific model for the evolution of the long human life span based on life history theory and modified to include economic production models has been developed (H Kaplan, K Hill, J Lancaster & AM Hurtado 1999) (see also Kaplan 1997). In that model, a large initial investment in skills and training can only be justified if a subsequent long period is available to pay back the initial investment. Likewise, a long life span will allow for a lengthy juvenile training period prior to production. This view suggests that the juvenile investment period in energy production skills and the adult productive life span should coevolve. Additionally, mathematical modeling shows that a longer juvenile training period will favor investment in mortality reduction at all ages prior to the productive period (Kaplan 1996, 1997).

The model developed suggests that at some point hominids entered a feeding niche that required long periods of training and learning but which resulted in high adult energy capture rates as a result of this training period. This would include complicated extractive foraging and especially hunting. An important component of this model is the knowledge-based and flexible problem-solving nature of human hunting rather than predation techniques based on speed and strength. Natural selection would then favor changes that increase the postinfancy life span, and the lowered mortality rate is partially due to the character of the feeding niche. This model, unlike previous mammalian life history models, clearly treats mortality rate as a decision variable instead of an exogenous constraint. A similar model has been proposed by Hawkes et al (1998), who have argued that high vegetable food production by women late in the life span, in order to subsidize the reproduction of younger women, is sufficient to favor an evolved decrease in mortality rates and longer adult life span. This model, however, does not emphasize the learning-based delayed energy production as a force for mortality reduction.

Despite the complexity of accounting for the long human life span, we do know that young adult mortality in our recent ancestors must have been lower than in other great apes, otherwise apes would not senesce faster than humans (some people live to be over 100 years of age, whereas no chimpanzee has ever lived past approximately age 60). Conclusions, based on paleodemographic stud-

ies, that some recent human populations may have never survived past age 50 (e.g. Lovejoy et al 1977, Whittington 1991) are almost certainly erroneous because of errors in sampling, assignment of age, preservation, or some other factor (for critique, see Hill & Hurtado 1996, Ch. 6).

Why humans experience lower early adult mortality is an important question that may hold the key for understanding a variety of evolved human features and aspects about the evolutionary history of our species. We can speculate that mortality in hominids began to decrease when they were effectively able to lower predation rates (through tools and sociality). Mortality might also be low relative to chimpanzees because humans care for and provision sick and injured individuals as well as all juveniles. Several studies have shown that serious illness or injury that precludes food acquisition is a common event among modern tribal populations (e.g. Bailey 1991, Sugiyama & Chacon 1999). These debilitated individuals survive only because of well-developed food sharing networks. Finally, mortality may be lower in young adults because they invest more resources in physiological mechanisms of pathogen and parasite resistance and immune function. This type of investment in mortality reduction is predicted by the economic model of life span discussed above, but it is difficult to confirm by comparison of basic metabolic rates because so many other factors affect the rates (see Aiello & Wheeler 1995 and commentary).

Whatever the evolutionary cause, humans in foraging societies have lower early adult mortality than do primates and slower senescence rates. They also show energy production techniques that require a long juvenile period for acquiring skills and do not provide maximum energy production until late in the life span (Figure 2). No current models of human life span, however, allow us to predict quantitatively how long the human life span should be, but there are several promising new models that hope to explain why humans are exceptionally long-lived for their body size.

Menopause   The complete senescence of female reproductive function occurs in humans well before other life systems have senesced (Hill & Hurtado 1996, Ch. 13) and is an evolutionary puzzle. It has long been suspected that humans are unique among mammals in this trait. This is approximately correct (Paveleka & Fedigan 1991, Caro et al 1995), although some toothed whales (Marsh & Kasuya 1986) also cease reproduction long before the end of the typical adult life span. The obvious negative impact on fitness that results from reproductive cessation makes menopause a tantalizing target for evolutionary analysis.

The most frequently proposed hypothesis for menopause is what we term the grandmother hypothesis. Originally proposed by Williams (1957) and later restated by several other human evolutionary biologists (for summary, see Hawkes et al 1989, 1998), the grandmother hypothesis suggests that as women age, they eventually reach a point where greater fitness benefits can be gained by investing in existing offspring and grandoffspring than could be expected through the continued production of offspring. The observations by Hawkes et al (1989) that postreproductive-age among Hadza foragers women produce more food than

reproductive-age women, supported by similar observations by Hurtado et al (1992) on other foraging groups and by Kaplan (1994) that in traditional societies older individuals general provision younger kin, initially provided strong evidence for this suggestion. This initial excitement over the grandmother hypothesis has led to testing for it even among mammals who do not have significantly long postreproductive periods (Packer et al 1998).

Older women do probably provision their daughters and grandchildren in many foraging societies. However, in order for this to result in menopause, a viable evolutionary scenario requires that the genetic impact of postmenopausal women on their close kin be greater than the genetic loss through cessation of reproduction. Hill & Hurtado (1991, 1996) provide the only empirical test to date of this hypothesis. Their analysis, using data from Ache foragers, suggests that the genetic contribution grandmothers make by investing in their close kin is not large enough to overcome the loss of genetic contribution through reproduction, without assuming that fertility drops to almost zero (for other reasons) in premenopausal women. Specifically, the mean genetic contribution of a 50-year-old Ache woman through increasing her offspring's fertility and her grandoffspring's survival was only one sixth of the genetic contribution she could achieve through reproduction at the rate of a 30-year-old woman. A similar theoretical conclusion was reached by Rogers (1993), who developed a model that allowed fertility at one point in life (at age of last reproduction) to be sacrificed in order to extend a female's life so that she can assist her kin later in life. This model showed that the genetic impact on close kin by grandmothers would have to be quite large in order for natural selection to favor that investment over continued reproduction.

The analyses by Hill & Hurtado (1991, 1996) estimated grandmother impact on fertility of sons and daughters by comparing the yearly fertility rate of men and women with and without a surviving mother. Likewise, a woman's impact on the survival of her grandchildren was estimated by comparing yearly survival of children with and without a living grandmother. This could be problematic, however, if other related individuals increase their own kin investment when mother or grandmother dies. Under those conditions, we might underestimate the benefits derived through grandmother investment. But this is also the social context of menopause, and the small impact of grandmothers due to compensating help by other kin must be factored in to the cost-benefit analyses. Hill & Hurtado (1996, Ch. 13) were able to show large impacts due to the absence of other kin using this same analytical technique. Even grandfathers have as large of an effect on fertility of daughters and survival of children as do grandmothers. Thus, the available evidence suggests that the grandmother effect is simply not large enough to outweigh lost fertility due to menopause.

These findings clarify some discussion about menopause. Although Williams (1957) and those following him initially thought of menopause as a single problem, it should probably be divided into two separate issues (Kaplan 1997). (*a*) Why does female fertility decline beginning in the second decade and cease in the fifth decade of life? And (*b*) why do women live far beyond the age at which they cease reproduction?

The division of menopause into fertility reduction and a postreproductive life span has led to new ideas about menopause. Most life history theorists now accept the proposition from the grandmother hypothesis that postreproductive women invest in close kin and have an impact on the reproduction and survival of those kin (but for an alternative model based only on maternal investment, see Peccei 1995). If this were not true, it would be hard to explain how there could be any selection for survival traits beyond reproductive age, since the strength of selection on survival at any given age partially depends on the expected genetic contribution over the remainder of the life span (Charlesworth 1980). However, the apparent low genetic impact of grandmother investment relative to direct reproduction suggests that another explanation is required for the age-related fertility decline terminating in menopause.

The age-related fertility decline is mainly due to decreases in coital frequency with age, increases in fetal wastage, and perhaps increases in the period of lactational anovulation following a birth (Wood 1994). Menopause takes place when the number of viable primordial follicles in the ovaries becomes too low to sustain hormonal cycling. Wood (1994) has modeled this process showing that three variables involved could hypothetically be subject to natural selection. These are the initial number of viable ova, the decay rate of viable ova, and the threshold number of viable follicles necessary to sustain reproductive function. Why has natural selection not acted on any or all of these to lengthen the reproductive span, given that women are likely to survive well past menopause? It is known that elephants retain high fertility past age 50 (Crooze et al 1981) and some whales produce offspring beyond 90 years of age (Mizrooh 1981). Kaplan (1997) considers all these factors and suggests that the premenopausal fertility decline is the outcome of a trade-off between early and late reproduction. More follicles could be produced and their decay rate could be slowed, but both adjustments require energy to be diverted from some other function. If that energy is instead spent in early reproduction, perhaps higher fitness is obtained, given the constraints faced by human females.

In any case, it has been shown that age of menopause varies between human societies (Wood 1994), and that premenopausal fertility decline is less marked in some societies than others (see Hill & Hurtado 1996, Ch. 8). Explaining why natural selection has favored female fertility decline with age continues to present a theoretical challenge despite the fact that older women react to their fertility decline by investing in already existing kin.

Quality Versus Quantity Trade-Offs in Offspring Investment

If we assume that individuals apportion resources and investment in a way that maximizes lifetime energy available for reproduction, they are still faced with a decision about how to allocate that energy. An adult may allocate all investment into one or few offspring who would likely have very high survival and subsequent fertility, or an adult can divide his or her income between many offspring who might be expected to show lower survival and fertility.

The models of parental investment discussed in the introduction assume that maximizing lifetime parental income and summed lifetime offspring (over all offspring) income will result in maximal genetic contribution over long time periods. It is important to note that the Kaplan (1996) model shows that increased payoff in either component of parental investment (income or survival-related embodied capital) will lead to increased investment in both components and that increased payoff at any age leads to increased investment at all ages. This means that small ecological changes can lead to large changes in parental investment and fertility rates.

Clutch Size and Interbirth Interval   Animals are expected to space their offspring production through time either because the required energy to support offspring is obtained over time or because raising offspring interferes in some way with the successful raising of other offspring. Humans show physiological mechanisms of fertility control that suggest our ancestors were constrained by both factors. First, the strongest determinant of whether or not an adult female will conceive when regularly exposed to copulation is whether or not she is nursing an infant (for review, see Wood 1994). Since this is true even for primaparous women who later in their life can support multiple offspring simultaneously (at different age stages), this may not mean that women cannot acquire the energy to simultaneously raise two infants. Instead, the suppression of ovulation by lactation suggests that women's bodies cannot evolve the capacity to convert food into milk at a rate high enough to support two infants simultaneously, that women cannot evolve the ability to carry two fetuses to term given optimal body size at birth, or that caring for one infant interferes with the successful care of a second. Since milk production varies greatly and can increase enormously under appropriate selection (e.g. domestic cattle), we suspect that the latter two constraints are primarily responsible for the single-offspring clutch size of humans. In particular, it has been noted that hunter-gatherer women cannot usually carry more than one infant at a time and that young children are usually carried rather than left behind by their mobile foraging mothers.

Despite the fact that adult women often show they can get access to sufficient resources to feed a nursing infant along with several other dependent children simultaneously, there is still evidence that it often difficult for women to meet the energy requirements of nursing two offspring simultaneously. Food intake during lactation is an important determinant of the effectiveness of lactational amenorrhea, and it is related to fertility rate in many natural fertility populations (Ellison 1995, Huffman el al 1978, Hurtado & Hill 1990, Leslie & Fry 1989, Lunn et al 1984, Prentice & Whitehead 1987, Worthman et al 1993, Vitzhum 1994). Thus, the observation of a strong effect of food limitation on fertility mechanisms, combined with the observation that women are usually able to obtain additional resources for additional children as their family grows, represents an unsolved paradox for life history theorists.

Given that human offspring are generally produced one at a time, we can model optimal interbirth interval (IBI) under specified conditions. Biological

models of fertility discussed in the introduction assume that parental investment in one offspring ends at the production of the next, and thus the period of parental investment is equivalent to the IBI. This is clearly not a valid assumption for humans, since offspring are generally not energetically independent of parents until their mid- to late teens (Kaplan 1994, 1997) (see Figure 2). The Kaplan (1996) models allow investment during the entire juvenile period and solve for optimal level of total investment per offspring, but it is unclear from these models how offspring should be spaced. However, one can develop a trade-off model for IBI by assuming that IBI affects survival to adulthood and that offspring number times survival to adulthood determines the fitness for any IBI. This is the typical operationalization of the Smith-Fretwell model discussed earlier. Blurton Jones (1986, 1987) was the first anthropological demographer to develop and test such an optimality model of IBI. He showed that among the !Kung, shorter IBIs were indeed associated with lower child survival, and that the maximum of his fitness estimator for !Kung women was at approximately 48 months, the most commonly observed IBI for bush-dependent !Kung women. Several researchers noted potential problems with the Blurton Jones study (Harpending 1994, Hill & Hurtado 1996:380–81; but see also Blurton Jones 1994). Hill & Hurtado (1996) also attempted to test a similar model of Ache IBI. They also showed that short IBIs were associated with higher juvenile mortality, but the effect was not large enough to cancel the benefits of higher fertility. Their analysis suggested that Ache women obtained highest fitness with the shortest observed IBI and that modal Ache fertility is lower than that which maximizes fitness.

Both the empirical studies above have serious shortcomings due to phenotypic correlations. If individuals vary either in intrinsic quality (health, physiological efficiency) or in resource acquisition abilities and kin support, those individuals who are in a better situation might show both shorter IBI and better offspring survival. Thus, Hill & Hurtado (1996) may have underestimated the true costs of short IBI for the average Ache woman, whereas Blurton Jones should not have found that modal IBI in a heterogeneous population leads to highest fitness. The problem of phenotypic correlations between life history traits that mask the real trade-offs faced by individuals has been widely discussed in biology (e.g. Lessells 1991, Van Noordwijk & de Jong 1986). It is generally agreed that the true character of life history trade-offs can only be detected by careful experimental manipulation or complex multivariate statistics. Experimental manipulation of fertility is increasingly employed in animal studies but will never be possible for humans. Although Hill & Hurtado did try to statistically control for factors that might produce phenotypic correlations, we do not know if they were successful.

The observation that average fertility is lower than the calculated optimum from a trade-off model is a common finding for modern human populations (for review, see Kaplan et al 1995) and is associated with the demographic transition of the past two centuries. However, the finding that even traditional natural fertility populations are characterized by lower fertility than appears to maximize fitness is puzzling. This finding is not unique to humans, however. The evolution of fertility rates has been intensively studied in birds and insects. Many studies show

lower than "fitness maximizing" fertility (for reviews, see Lessells 1991, Dijkstra et al 1990). This has often been shown to be due to missing costs from the optimization models. For example, most studies (like the human studies above) assume that higher fertility mainly affects offspring survival. But several studies have shown that high fertility lowers parental survival. Thus, natural selection would favor lower fertility than the models suggest. Given these problems, one can imagine a variety of possible costs of short IBI that are not included in the hunter-gatherer studies above. For example, perhaps short IBI forces other kin to provide help, thus lowering their own reproductive rates. Perhaps the true costs of fertility errors are much more serious on the side of high fertility, thus leading to a risk-sensitive strategy of lower-than-optimal fertility. Perhaps female fertility is lower than optimal because they cannot be 100% certain of the level of male investment they will receive. Many issues remain to be explored.

Paternal Investment   Models of optimal level of parental investment discussed above were primarily developed for females. Although males must also invest something to produce an offspring, the number and quality of offspring that can be produced per unit investment may vary considerably between males and through time, depending on the ease of access to, and the quality of, female mating partners. Females must invest considerably in any embryo if it is to survive and reproduce, whereas males can often gain fitness simply by fertilizing eggs. Thus, male investment in the embodied capital of offspring may be negligible if females provide the investment necessary to achieve reductions in mortality and increases in offspring income (Draper & Harpending 1987). Even when male investment is required, the investment of some individual males may still be small if other males will provide the required investment (see Hawkes et al 1995). This means that males should be opportunistically attuned to the possibility of producing an extremely cheap offspring, whereas females never experience this alternative.

Because males can sometimes achieve high fitness by successfully parasitizing the reproductive investment of other adults, there should be strong selection pressures on males for traits that improve the ability to reproduce in this way. Males usually expend a good deal of energy trying to gain copulations with fertile females (mating investment), whereas females expend little energy attempting to obtain copulations with fertile males. Thus, males have an extra allocation decision that does not apply to females. This means that male life histories are divided into energy allocated to fertilize an egg (mating investment) and energy allocated to the survival and embodied capital of various offspring. Female reproductive allocation is only concerned with improving the quality of alternative existing and potential offspring.

Since male behavior may change through time as the relative payoffs of mating and parenting investment change, some aspects of male reproductive behavior are readily recognized as life history decisions. However, the fact that male investment in mating versus parenting throughout the life course determines much of the character of the relation between the sexes means that this aspect of life history theory also encompasses marriage patterns, divorce rates, aspects of residen-

tial locality, paternal-offspring relations, and ultimately much of the social system of any society.

Although there are multitude of studies on the mating versus parenting trade-off of human males from an evolutionary perspective (for reviews, see Betzig et al 1988, Buss 1994, Geary 1998), few of these explicitly invoke life history theory. Age at first reproduction for males is the solution to trade-offs in lifetime income trajectory and was treated in an earlier section. Here we consider two additional issues: the age-related shift in balance between mating and parenting investment, and optimal fertility of males.

When males are fully adult but not yet pair bonded, they are likely to be most attractive to available females. This is because they have a high lifetime expected earning potential and have not yet committed those resources. Later, as they pair off with females that they are unlikely to abandon (due to economy of scale effects in raising offspring?), and have less of their lifetime earnings ahead of them, they are probably less attractive to females not already pair bonded with them (except in the special capital economies mentioned in an above section). Thus, males should gain higher payoffs to mating investment (more copulations with fertile females per unit effort) when they are young. Likewise, older men generally have more offspring and therefore can obtain greater fitness impact from paternal investment than can younger men (who have few or no offspring). These two forces should favor mating investment among younger men and parenting investment among older men even when men in both age categories have children (and therefore face the trade-off). Although we are unaware of any studies that test this proposition with empirical data, the Hill & Hurtado study with Ache foragers (1996, Ch. 9) shows that younger men were reported to produce a higher fraction of offspring through extramarital liaisons than were older men, who produced most of their offspring within recognized long-term marriages. We might predict that among married men, younger males will spend more time in potential mate-getting environments (i.e. environments that attract unmarried adult women) than will older men in all societies.

A second life history question addressed by recent empirical studies is that of optimal male fertility rates. Because some offspring can be produced at almost no cost to males, the average cost of an offspring should be lower than that for females. Thus, optimal fertility should be higher for males than for females. Because of phenotypic correlations, the males who achieve highest fertility will also have highest fitness in most societies. This is confirmed in studies ranging from modern American men (Kaplan et al 1995) to Ache foragers (Hill & Hurtado 1996, Ch. 12). It is particularly interesting to note in the Ache study that although the slope of fitness by fertility decreases for all cohorts of females at high fertility, no decrease in slope is observed among males of any cohort. Fitness and fertility show a linear relationship for males. If male fitness can always be increased by higher fertility well beyond the optimal fertility for any one female, males and females face a conflict of interest concerning the dedication of the males' resources to already existing offspring. This might be expected to be a point of conflict between spouses in all human societies.

HUMANS LIVING IN MODERN ENVIRONMENTS

The Demographic Transition

There is mounting evidence that people in modern state societies in the developed world do not maximize fitness through their fertility decisions (e.g. Irons 1983, 1990, 1993; Kaplan et al 1995; Lam 1986; Perusse 1993; Vining 1986; W Irons, unpublished data; RD Retherford, unpublished data). Observed fertility behavior deviates from the predictions of fitness maximization in two ways. First, and most important, observed fertility is lower than would be predicted based on models of fitness maximization. For example, Kaplan et al (1995) showed that among men in Albuquerque, New Mexico, number of third-generation descendants (i.e. grandchildren) is highest among those who produced the most (i.e. 12) children. This contrasts sharply with the observed modal fertility of two (Kaplan et al 1995). Higher parental fertility in modern developed societies is associated with lower achieved educational and economic status of offspring (Kaplan et al 1995; for reviews, see Blake 1989, Downey 1995), but the lower earning capacity of children from large families does not decrease their fertility and so there is no apparent fitness reduction associated with lowered parental investment per child.

The second way in which modern behavior deviates from the predictions of simple budget-constraint models of quantity-quality trade-offs is that higher-earning adults produce no more children than their lesser-earning counterparts, even in well-controlled studies. This violates predictions from the Smith-Fretwell model discussed earlier. Whereas available data on preindustrial societies consistently exhibit a positive relationship between resources or power and reproductive success (Barkow 1989; Betzig 1986; Boone 1986; Borgerhoff Mulder 1987; Chagnon 1988, Cronk 1991a,b; Flinn 1986; Hughes 1986; Irons 1979, 1993; Kaplan & Hill 1985; Low 1990; Mealey 1985; Turke & Betzig 1985; Voland 1990; W Irons, unpublished data), studies of low-fertility societies find either no relationship or a negative one (Kaplan et al 1995, Perusse 1993, Vining 1986; RD Retherford, unpublished data; but see Simons 1974 for data suggesting a positive correlation between wealth and fertility within socioeconomic groups).[5]

The lowering of fertility associated with modernization is generally referred to as the demographic transition by social scientists. Traditionally, the demographic transition is described as a process in which an initial decrease in mortality is followed by a decrease in fertility some years later (Davis 1945, Notestein 1945). An adequate theory of the reduction in fertility in modern states must accomplish two things. First, it must specify what changes lead to a reduction of fertility and the observed relationship between wealth and fitness. Second, it must account for

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[5]Studies of traditional small-scale societies suggest that fertility may be optimized to maximize the production of descendants over the long run (e.g. for the !Kung in Botswana, see Blurton Jones & Sibly 1978, Blurton Jones 1986; for disconfirmation among the Ache, see Hill & Hurtado 1996). The abrupt change in the association between wealth and fertility that occurs at the same time fertility is reduced historically (RD Retherford, unpublished data) requires explanation.

why those changes produced the observed responses within a larger theory of the determinants of fertility in general. From an evolutionary perspective, it is necessary to specify the critical differences between pre- and postdemographic transition societies and to show why the suite of proximate mechanisms that evolved to regulate fertility and parental investment in the past might produce the fertility and parental investment behavior observed in modern, postindustrial societies.

There have been several attempts to understand these deviations from fitness maximization in the light of human evolutionary history. Barkow & Burley (1980) suggest that low fertility is due to the historical novelty of birth control, which allows conscious control over fertility by women, in combination with human intelligence, which evolved for other reasons but leads women to consciously desire fewer children than is their biological optimum. Perusse (1993) argues that modern contraception interacts with male motivational systems to produce deviations from fitness maximization. Since modern contraception is a historical novelty, men's psychology was selected to utilize resources to attract women to engage in sexual activity. The desire to pursue sexual relationships with women, without explicit consideration of whether those relationships produced children, was sufficient, because without contraception, there is a predictable relationship between copulations with fertile females and the production of offspring.

Irons (1983) and Turke (1989)[6], who build on Alexander (1974), suggest that humans track "cultural success" as a proxy for fitness and that the costs of attaining social success rise with modernization. In a similar vein, Lancaster & Lancaster (1987) and Lancaster (1997) suggests that parents increase investment in children and reduce their total number in order to enhance offspring competitiveness on the marriage market. Boyd & Richerson (1985) provide a related explanation of low modern fertility in terms of cultural evolutionary processes. They suggest that for behaviors whose results/outcomes are difficult to predict (the effects of fertility decisions on children's outcomes will be only known many years after those decisions are made), modeling the behavior of "successful" individuals may be the most effective strategy. With modernization, the most successful individuals must sacrifice their own fertility to achieve high levels of social and economic success. Thus, those individuals (e.g. teachers, politicians, etc) are preferentially modeled, and therefore people adopt their low-fertility behavior.

Kaplan (1996) and Kaplan & Lancaster (1999) specifically model the problem from the perspective of human life history evolution. They argue (*a*) that fertility regulation among hunter-gatherers is based on a coordinated system of behavioral and physiological responses, (*b*) that because of the importance of skill in the human foraging niche (discussed above), human psychology has evolved to detect the relationship between parental investment and income of offspring when they are adults, and (*c*) that parents make decisions about how long to support and provision offspring on the basis of those assessments. Support and provisioning of offspring affects fertility through its impact on a mother's nutritional

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[6]Turke (1989) also suggests that the breakdown of extended kin networks lowers fertility because the costs of child rearing are paid directly by parents.

status. Such a system would adjust fertility in relation to the energetic demands of the family. However, when food is not the only material resource invested in children (i.e. when extrasomatic wealth, such as money or land, is also invested in children), the evolved psychology of parental investment may lead to a lower desired fertility than would be produced by the physiology of menstrual cycling with unprotected sex.

Specifically, Kaplan & Lancaster (1999) propose that the emergence of competitive labor markets in the context of an increasingly technological economy greatly enhanced the economic payoffs to investment in the skills and formal education of children. The resources that parents deemed necessary to invest in children required a lower fertility than the lactation-energy balance hormonal system would produce. In response to this, people in Europe and America lowered their family sizes at the end of the last century through behavioral means (e.g. coitus interruptus, cessation of sex, rhythm method). This led to an increased demand for efficient contraceptive technologies that generated further reductions in fertility. Contraception is the outcome, not the cause, of lowered fertility trends (see Barkow & Burley 1980, Perusse 1993). They suggest further that parents who are more educated and therefore earn more are more efficient at educating their children. As a result, optimal levels of investment increase with increasing education of parents. Fertility and income become uncorrelated as increases in income are compensated for with increased investment.

The Kaplan-Lancaster model generated a series of predictions about variation in parental investment and fertility in developed nations and the pace of fertility decline in developing societies. Tests of those predictions that have been conducted to date have supported the model. For example, they found that (*a*) education has become an increasingly important determinant of age at first reproduction and fertility during this century; (*b*) holding education constant, increases in income generally increase fertility; (*c*) holding income constant, more-educated parents invest more per child than do less-educated parents, in terms of both time and monetary expenditures; (*d*) the child's scholastic abilities and earlier parental investments are associated with the likelihood of providing support for higher education; and (*e*) the level of parental investment children receive is positively associated with their educational attainments. Kaplan (1996) also predicted that fertility reduction in the developing world would be determined by the payoffs to education, and that in many situations, the payoffs would be low because of poor schools and low educational achievement of parents. Consistent with this view, initial results from research in Cape Town, South Africa (H Kaplan, D Lam, KG Anderson & J Lancaster, unpublished data) show that (*a*) youths from disadvantaged backgrounds tend to fail more grades in primary school than do advantaged youths, and increasingly so as their parents have less education; (*b*) early school performance predicts school performance in secondary school; and (*c*) poor performance in secondary school predicts the likelihood of dropping out of school.

There are also alternative and complementary explanations that require consideration. The increasing effectiveness of birth control technologies are proba-

bly relevant (Easterlin et al 1980, Barkow & Burley 1980, Potts 1997), because cost-effective birth control lowers unwanted fertility. Cultural transmission of fertility values is also receiving increased attention (Boyd & Richerson 1985, Zei & Cavalli-Sforza 1977, Cleland 1985, Cleland & Wilson 1987)). Changing kin networks and the decreased involvement of extended kin in child rearing has been postulated as a cause of the shift to fewer, higher-quality children (Turke 1989). Clearly, future research must focus on testing alternative models within the same study to determine whether some alternatives can be excluded and whether a complete explanation requires the amalgamation of several models.

In fact, the life multigenerational history model presented above suggests another, more general explanation of the demographic transition. Adults not only face a trade-off between quantity and quality of children, but also between investment in own embodied capital and reproduction (see Figure 1). A new model developed (H Kaplan, K Hill, J Lancaster & AM Hurtado 1999) shows that payoffs to investment in embodied capital depend not only on the productivity of those investments, but also on the length of time over which the returns are realized. The lowering of mortality, resulting from large investments in public health during the last century in developed nations (and more recently in developing nations), has increased the length of time over which such investments would be realized. According to the model, the effects of the increased importance of education in determining wages and of a longer productive life interact to produce even larger increases in investments in embodied capital. This may be why demographers note that the decrease in fertility associated with modernization is generally preceded by a decrease in mortality rates (Davis 1945, Notestein 1945).

Additionally, in modern society, people face a tremendous array of consumption goods, including housing, clothing, electronic equipment, vehicles, etc. The medium of exchange for obtaining those goods, of course, is money, which can be converted into any one of them. As diminishing returns to consumption of one good is reached, money can then be allocated to other goods. With all the goods available, there is always some good of which little has been consumed and returns to purchasing some amount of it are still high. The same can be said for investment in an offspring's embodied capital, which appears to include investments not only in schooling but also in goods associated with social training and social status, such as hobbies and sports, clothing, and toys, with much of these investments being commitments to favorable placements of children in the mating market. Our best guess at this time is that the low fertility exhibited in modern societies is due to the combined effects of lowered mortality, higher payoffs to investments in our survival and health and in offspring income, a perceived lack of diminishing returns to other forms of consumption, and increasingly effective birth control technologies.

The existence of extra-somatic wealth may be the critical condition to which our evolved proximate mechanisms do not respond so as to maximize fitness. This would imply that it is not only in postdemographic transition settings that deviations from fitness maximization are likely to be observed. When there is heritable wealth, such as cattle or land, the breast-feeding/energy-balance system

may generate higher fertility than parents desire. Adjustments to this situation may involve primarily differential inheritance, such as primogeniture and illegitimacy, but it may also include late age of marriage (Coale & Treadway 1986) or even celibacy (Boone 1986), and lowered rates of polygyny by wealthy men (Luttbeg et al 1999). Thus, perhaps we should not be surprised to find deviations from fitness maximization as soon as there are forms of extra-somatic wealth [see, however, Rogers (1990) for a model suggesting that reduced fertility in the context of heritable wealth may be fitness maximizing; see also Borgerhoff Mulder (1998) for a recent review of attempts to understand fertility reduction from an evolutionary perspective]. The extremely low fertility in modern societies may reflect the extreme importance of extra-somatic wealth and the multiple ways in which it can be used, as well as increased payoffs to investment in education-based embodied capital.

CONCLUSION

In this paper, we have attempted to integrate the traditional emphasis of life history theory on age schedules of fertility and mortality with an in-depth consideration of the production and consumption of energy through the life course. We introduced the concept of embodied capital to examine trade-offs between current and future reproduction and between quantity and quality of offspring. In comparison with the rest of the primate order (one that, in general, exhibits relatively high levels of investment in embodied capital for mammals), humans are an outlier with extraordinarily high investments in embodied capital. As a result, the human life course is characterized by extremely low productivity during a long developmental, learning phase, followed by a period of extremely high productivity during the adult phase (as shown in Figure 2). Unlike most primates, weaning does not mark the transition to self-sufficient energy acquisition for growth, and sexual maturity does not mark the transition to self-sufficient energy acquisition for reproduction. We proposed that this investment in embodied capital is due to our feeding niche, which emphasizes high-quality, difficult-to-acquire extracted and hunted foods.

The high level of investment in embodied capital affects virtually all the life history characters typical of our species. Growth is both slow and prolonged. Reproduction is delayed as a result. Increases in productivity continue into mid-adulthood, well after reproduction has begun, and people remain quite productive well into old age, after reproduction has ceased. Adult mortality rates are extremely low, and aging occurs very slowly. Children are provisioned for many years after weaning, and parents support multiple dependent young. The high productivity of males and of older people results commonly in a three-generational system of resource flows, in which both grandparents and men assist women in the production and support of offspring.

This commitment to intensive investment in embodied capital (both for self and offspring) also appears to be related to responses to modernization. Changing technologies of production and improved public health may have interacted to

increase the payoffs to investments in skill and education, investments in health and longevity, and investments in child quality with greatly reduced fertility. Although such increases in investments may be a predictable consequence of our evolutionary heritage, they may not be adaptive in the strict sense of being currently fitness maximizing.

The most basic features of the psychological and physiological mechanisms underlying our set of responses to environmental variation evolved in the context of a hunting and gathering ecology. Given that environmental dangers, disease threats, food supply, and the importance of skill in food acquisition are likely to have varied across hunter-gatherer ecologies and through time, we can expect that optimal life history allocations would have varied as well. The ability to alter allocations to survival, maintenance, reproductive effort, fertility, and parental investment in response to changing net energy intake rates must have been under selection.

Part of the response system is under physiological control. The probability of having a fecund menstrual cycle varies positively with seasonal variation in net food intake rates in food-limited populations (see Hill & Hurtado 1996, Ch. 10 for review). Part of the response system is under behavioral control. Since the behavioral and physiological responses interact in determining the final outcome (e.g. rates of breast-feeding and food intake interact in determining probability of an ovulatory menstrual cycle), it is likely that selection would have produced a coordinated physiological/psychological response system that yields adaptive life history adjustment in relation to changing conditions characteristic of hunter-gatherer ecologies.

Most people today live under conditions that are very different from those of the Pleistocene. What kinds of responses do we expect in relation to modern environments and to variability within modern environments? Very little is known about the answer to this question. It is perhaps the most fundamental question facing the social, behavioral, and medical sciences today. The strength of anthropology's four-field structure is that it allows us to examine our species in the light of both its long-term evolution and its flexible responses to different ecological, cultural, and social environments. The combination of anthropology's traditional strengths with the theoretical foundations provided by life history theory should provide a powerful tool for investigating the major demographic trends that will affect standards of living, crowding, urbanization, conflict and warfare, and the environment in the next century.

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