

H. S. Kaplan¹ and J. Bock²

¹University of New Mexico, Albuquerque, New Mexico, USA

²California State University, Fullerton, California, USA

Abstract

The embodied-capital theory generalizes existing life history theory in evolutionary biology 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, etc. In a functional sense, embodied capital includes strength, immune function, coordination, 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. There are two trade-offs affecting natural selection on fertility. The first is the trade-off between present and future reproduction. By growing, an organism can increase its energy capture rates in the future and thus increase its future fertility. This can be understood in terms of optimal investments in own embodied capital vs. reproduction. The second trade-off is between quantity and quality of offspring, where quality is a function of parental investment in offspring and reflects its ability to survive and reproduce. This can be understood in terms of investments in the embodied-capital of offspring. Natural selection has resulted in physiological and psychological mechanisms by which individuals adjust fertility onset and fertility rates in relation to changing environmental conditions. Embodied-capital theory links several existing theories of demographic transition and, in so doing, provides a new perspective on each one. It rationalizes the shift from natural fertility to parity-specific fertility in terms of a changing quality/quantity trade-off, as a transition from high fertility/low parental investment to low fertility/high parental investment. It also shows why the shift to lower mortality rates can lead to lower fertility, but for very different reasons than traditional demographic transition theory proposes.

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B13 morality (Austin [1954], p. 112). The second sense of morality is found to be indicative of changes of state and not part of the basis of law.

Fertility Theory: the Embodied-capital Theory of Life History Evolution

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The goal of this article is to provide an introduction to the embodied-capital theory of life history evolution and the empirical research upon which it is based. The embodied-capital theory generalizes existing life-history theory in biology by treating the processes of growth, development, and maintenance as investments in stocks of somatic or embodied-capital (see Kaplan (1996, 1997) and Kaplan et al. (2000) for more complete treatments). In a physical sense, embodied capital is organized somatic tissue—muscles, digestive organs, brains, etc. In a functional sense, embodied capital includes strength, immune function, coordination, skill, knowledge, and other abilities. Since such stocks tend to depreciate in response to metabolic activity (e.g., the production of free radicals and mutations associated with mitosis) and aging, allocations to maintenance can also be seen as investments in embodied capital. The general theory is introduced and then applied to human hunting and gathering societies, which characterized most of our species' evolutionary history. This framework is then used to develop models of modern fertility behavior as the result of an interaction between historically novel conditions and the evolved psychological, cultural, and physiological mechanisms governing human parental investment and fertility.

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1. The Embodied-capital Theory of Life History Evolution

Hominids lived as hunter-gatherers for the vast majority of their evolutionary history (more than 2 million years). Agriculture originated only 10,000 years ago and has been practiced by the majority of the world's population for just two or three millennia, a relatively brief period of time for selection to act. The shift to a fully mercantile, highly urbanized economy with competitive wage-labor markets and a vast array of consumer goods since the mid-nineteenth century is completely novel. Since natural selection is an historical process, humans should be well adapted to the foraging lifestyle, but there is no reason to expect that they will respond adaptively (in the sense of maximizing reproductive fitness) to today's novel circumstances (see Kaplan et al. (1995a, 1995b) for evidence that modern fertility behavior does not maximize fitness). Therefore, an evolutionary explanation of human fertility and parental investment has three requirements: it must be consistent with our general understanding of evolution by natural selection; it must explain the behavior of humans living under traditional hunting and gathering conditions characteristic of our evolutionary history with adaptive models; and it must be able to predict the pattern of

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modern responses to novel conditions. Our approach to these requirements has been to follow a four-step procedure (Kaplan [1996], Kaplan and Lancaster [2000]). The first step is to develop a model of natural selection on fertility and parental investment for organisms in general. The second step is to apply that model to the specific selection pressures acting on human hunter-gatherers. The third step is develop a model of the proximate physiological, psychological and cultural mechanisms produced by selection and how they would interact to determine fertility and parental investment behavior. The fourth step is to generate predictive models of how those mechanisms would respond to conditions currently prevailing in the world. The theory is both ecological and psychological, integrating socioeconomic influences with a theory of mind to identify the processes by which salient features of the social and physical environment relate to people's reproductive and parenting behavior across diverse social, cultural, economic, and ecological contexts.

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2. *The Action of Natural Selection on Fertility and Parental Investment*

Natural selection acts on variability in the traits of individual organisms within populations. Traits (and the genes which code for those traits) whose *average* effects on the individuals possessing those traits act to maximize their long-term production of descendents through time increase in frequency relative to other traits. (Technically, selection acts on the 'inclusive fitness' of genes coding for traits. Inclusive fitness includes effects both on the reproductive success of the individual bearing the gene and on other individuals, related by common descent, who also bear the gene. For example, selection on genes affecting alarm calls in response to predators depends both on their effects on the reproductive fitness of the caller (who may risk a greater threat of predation) and on relatives bearing those genes (whose lives may be saved by the call).) Fertility is the most direct contributor to an organism's fitness (i.e., the number of descendents it produces). In fact, all other fitness components, such as mortality, only affect fitness through their effects on fertility (for example, mortality rates affect fitness by affecting the probability of living to the next reproductive event). All else constant, any increase in fertility increases an organism's fitness. However, there are two trade-offs affecting natural selection on fertility.

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The first is the trade-off between present and future reproduction. By growing, an organism can increase its energy capture rates in the future and thus increase 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 growth. Similarly, among organisms that engage in repeated bouts

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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 on age of first reproduction and on the adult reproductive rate is expected to maximize total allocations of energy to reproduction over the life course, and it depends on ecological factors, such as mortality rates (Charnov [1993]) and the effects of body size on both energy capture (Charnov [1993]) and vulnerability to predation (Werner [1986]).

The second trade-off is between quantity and quality of offspring, where quality is a function of parental investment in offspring and reflects its ability to survive and reproduce. In general, natural selection on offspring number and investment per offspring is expected to maximize the number of offspring that survive to reproduce themselves during an organism's lifetime (Smith and Fretwell [1974]). Ecological factors, such as food supply, disease and predation rates, also affect the optimal fertility rates and optimal expenditures on offspring.

Virtually all complex organisms exhibit flexibility in both age at first reproduction and fertility rates. Natural selection has resulted in physiological and psychological mechanisms by which individuals adjust fertility onset and fertility rates in relation to changing environmental conditions. For example, plants often exhibit many thousand-fold variation in fertility rates in relation to yearly and season variation in rainfall and other environmental factors. Extensive research on many bird species has shown that this phenotypic plasticity tracks fitness fairly well (see Godfray et al. ([1991]) for a review). Birds under variable conditions adjust clutch sizes in ways that tend to maximize the number of surviving young produced during the life course. The pervasiveness of adaptive phenotypic plasticity in fertility among nonhumans suggests that humans are also likely to possess adaptations to adjust fertility onset and fertility rates in relation to changing environmental conditions.

3. The Embodied-capital Theory and its Application to Fertility and Parental Investment Among Traditional Humans

The embodied-capital theory treats the present–future reproduction trade-off in terms of optimal investments in own embodied capital vs. reproduction, and the quantity–quality trade-off in terms of investments in the embodied-capital of offspring. Models based on the theory allow us to address problems that have not been addressed with standard life history models. First, an exclusive focus on physical growth *per se* is an impoverished way of understanding human development. The large human brain, a stock of embodied capital, supports a great deal of learning and knowledge acquisition during both the juvenile and adult

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periods. Second, parental investment among humans affects not only survival to adulthood, but also the adult socioeconomic status of offspring. This is true not only in modern societies, but also among traditional hunter-gatherers. These 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 co-evolve with investments affecting mortality and longevity. 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 produce increased 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. These co-evolutionary effects have been particularly important in human life-history evolution.

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

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The human adaptation is narrow and specialized in that it 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 take years to learn (Kaplan et al. 2000). This adaptation has profound effects on fertility, mortality, and wealth flows. Compared with other primates and mammals, there are at least four distinctive characteristics of human life histories: (a) an exceptionally long lifespan, (b) an extended period of juvenile dependence, resulting in families with multiple dependent children of different ages, (c) support of reproduction by older postreproductive individuals, and (d) male support of reproduction through the provisioning of females and their offspring.

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The co-evolution of brains, learning and life histories is evident in Fig. 1. This figure plots net expected cumulative productivity by age (cumulating the probability of being alive at each age times the net productivity at that age) for human hunter-gatherers and wild-living chimpanzees, averaging over all available data from different groups (see Kaplan et al. 2000) for details). The long human training period is evident when the troughs in the human and chim-

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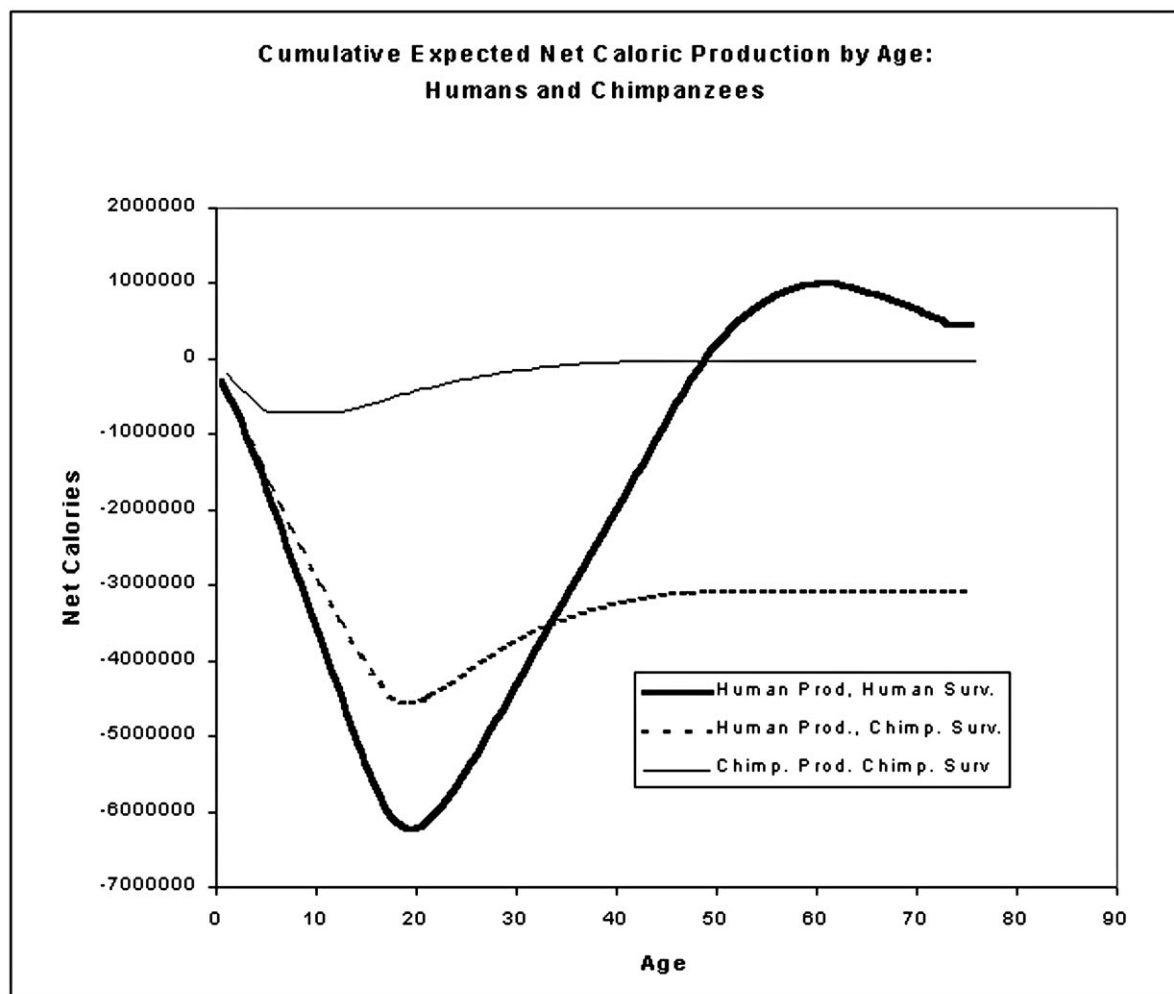


Figure 1

Cumulative expected net caloric production by age: humans and chimpanzees

panzee curves are compared. Humans are not net producers until about age 18–20 years, but are very productive as adults, whereas chimpanzees begin to produce as much as they consume by about age 5 years and are much less productive as adults. In fact, peak production rates for both human males and females do not occur until the mid-thirties for the most difficult-to-acquire resources. Humans also have an expected adult lifespan of about 40 years when they become net producers, whereas chimpanzees have an expected adult lifespan (beginning at about age 13) of 14 years. 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. The human adaptation depends on about 20 years of parental support and a long life span to recoup the investments in learning.

The first major demographic transition separating our species from apes is a shift to low mortality, an increased lifespan, a long dependent development period, a large commitment to learning and intelligence, and an age profile of production shifted towards older ages with downward wealth flows across generations.

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4. Ecology and the Proximate Mechanisms Governing Fertility and Parental Investment

The mortality and production profiles discussed above have direct implications for fertility regulation. Since human parents and grandparents provision children, it is likely that natural selection would have produced mechanisms by which fertility could respond to the number of children parents could afford to raise at any given time. Figure 2 presents a conceptual model of the evolved mechanisms of fertility regulation in humans and its responsiveness to physical, biological and social conditions (*socioecology*). The figure depicts two classes of socioecological factors, one affecting survival and the other embodied capital, and three domains of evolved responses, psychology and culture, behavior, and reproductive physiology. The plain text and bold arrows refer to the traditional hunting and gathering lifeway, which we consider first. The italicized text and lighter arrows include additional factors and causal pathways existing under modern conditions.

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4.1 Traditional Foraging Societies

There are two main causal pathways regulating fertility that are both related to the energy constraints in provisioning offspring, one involving breastfeeding and the other involving the age profiles of work and food distribution. Natural selection on the timing and rate of weaning should reflect a balance between quantity effects (favoring earlier weaning) and quality effects on survival and growth of offspring (favoring later weaning). Socioecological conditions, such as the availability of easy-to-digest weaning foods and disease threats, are likely to impact the relationship between age at weaning and survival. Similarly, infant condition is likely to be individually variable and differentially affected by weaning. We expect that natural selection has acted on both infant and maternal psychology to make them responsive to those variable conditions. For example, sickly infants may be more demanding of the breast, and larger and healthier babies more interested in weaning foods. In the human case, maternal perceptions regarding breastfeeding are not only guided by her individual

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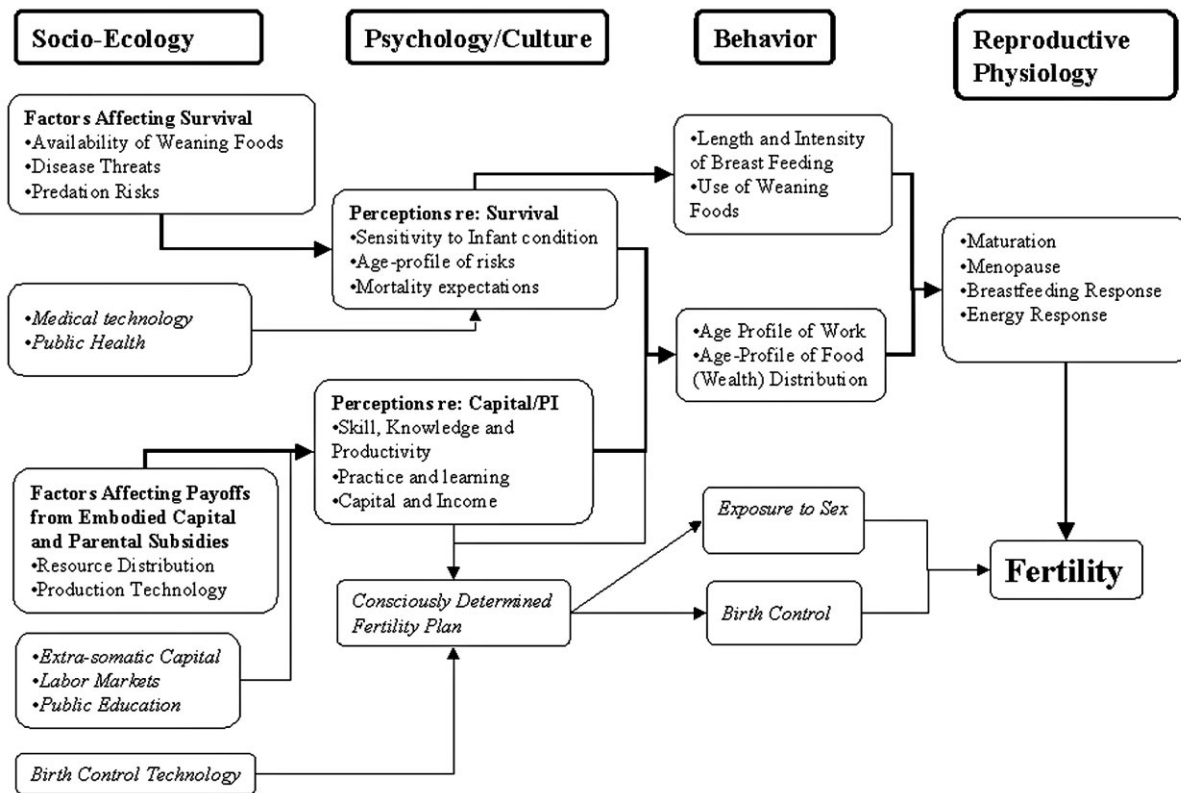


Figure 2

experience and sensitivity to her infant’s condition, but also by the cumulative experience of her group, as reflected in cultural conventions and ideas about proper breastfeeding practices. Maternal and infant psychology interact in determining the length and timing of breastfeeding. The evolved reproductive physiology translates this pattern of breastfeeding into differing degrees of fecundity.

The second causal pathway is due to the additional energy constraints involved in provisioning children. The age/sex profile of work and productivity determine the total energy available for consumption. Given some age profile of food distribution and of mortality, the fertility rate must be constrained so that energy consumed does not exceed energy produced. The longer children are provisioned and the greater proportion of their food needs subsidized by parents and grandparents, the lower the reproductive rate that can be supported with a given adult income. Natural selection should therefore act both on psychological abilities to assess the short- and long-term costs and benefits of different activity profiles and on fertility regulation so that energy flows are balanced. One fundamental trade-off with respect to activity profiles

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is between present and future production (Kaplan [1996], Bock [2000]). If children engage in easy-to-perform foraging activities, such as fruit collection, this will provide immediate caloric benefits and lower the parental subsidy required. However, time allocation to those activities detracts from time spent learning more difficult activities, such as hunting and extractive foraging. During the learning phase, those activities produce very little food, but generate high rates of production in the future. Another fundamental trade-off is between production and mortality risks, since foraging exposes people to predation, accidents, and getting lost. This suggests that parental psychology should be responsive to age-specific mortality rates and how they are affected by alternative activity profiles, and on their short- and long-term consequences for production/productivity.

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There is a growing body of evidence supporting the view that people in foraging societies are sensitive to these trade-offs and adjust behavior accordingly. In a seminal series of papers, Blurton Jones and co-workers (Blurton Jones et al. [1994a], [1994b], Hawkes et al. [1995]) show that !Kung hunter-gatherer parents consciously assess foraging risks to children and that differences between !Kung and Hadza children's productivity are due to features of the local ecology related to ease of resource extraction and dangers associated with productive tasks. Bock ([1995], [2000]), in a study of forager/agropastoralists in Botswana, shows that the age profiles of children's activity budgets reflect immediate skill and strength requirements as well as opportunities to learn. In all foraging societies for which data are available, people are aware of the many years of learning required to become a competent hunter and young men are provisioned while they learn those skills (Kaplan et al. [2000]).

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These time-allocation decisions affect fertility through maternal energetics. In addition to breastfeeding effects, fecundity responds to women's net energy flows. Seasonal changes on food intake (Bailey et al. [1992]), net energy expenditure (Hurtado and Hill [1987]) and weight (Bailey et al. [1992], Tracer [1996]) all have been shown to predict fecundity as do individual differences among women (Hill and Hurtado [1996]).

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To summarize, in this model fertility is determined by the interaction of individual psychology and cumulative cultural knowledge, beliefs and practices, behavior and reproductive physiology. Each of these domains co-evolved by natural selection to respond to ecological variability in mortality regimes and payoffs to parental subsidization of skill acquisition. The connection between psychology and fertility is indirect in that psychology adjusts parental investment (through productive behavior, wealth flows, and breastfeeding) and reproductive physiology translates parental investment decisions into fertility. The key to this system is that maximizing lifetime expected resource production through the optimal allocation of

activities and wealth flows will tend also to maximize fitness when all wealth is in the form of food and extra food translates into higher fertility.

4.2 Fertility Under Modernizing Conditions

In Fig. 2, the additional socioecological factors and causal pathways proposed to result in fertility transition are shown with italicized type and thin arrows. Our proposal is that this fertility regime results from the interaction of new socioecological conditions with the psychological processes governing parental investment and wealth flows, evolved in response to the hunting and gathering lifeway. The two critical new factors are the existence of extrasomatic capital and changes in the payoffs to embodied capital, especially in the form of education.

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Physical capital, such as land and money, is stored and invested in children in the form of inheritance and parental support for education. Unlike the traditional case where all wealth is embodied, there is no guarantee that a wealth-maximizing psychology will maximize fitness, because much wealth may never be converted into offspring and remain stored in other physical forms.

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Changes in the payoffs to embodied capital occur for two reasons. Changes in the technology of production to education-based labor markets have led to very high returns on parental investments in children's education. There are multiple inputs into the production of education-based embodied capital. Parental time inputs prepare children for school and affect their progress in school. Variation in the quality of those inputs, perhaps based on parental education, may predict both levels of parental investment and fertility. Teachers, educational materials, and the quality of student preparation all affect rates of learning (Card and Krueger [1992]).

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Changing medical technology and public health efforts greatly reduced mortality rates for all age groups. Increased survival rates during the period of parental investment increase the expected costs per child born, favoring further increases in offspring quality (Kaplan [1996]). Increased survival during the adult period increases the expected years of return of educational investments, further increasing the incentive to invest in children's education. It will be especially productive to investigate the public and private dynamics involved in this process. Increased private interest in education may have inspired more public investment in education. The quality of public education, in turn, increased the rate of return on private investments in education. Similarly, increased private interest in health (perhaps inspired, in part, by increased investment in education) also stimulated increased public investment in health. This, in turn, increased payoffs to educational investments.

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These factors, in combination with parental psy-

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chology, result in fertility being regulated by a consciously determined childbearing plan realized through birth-control technology and/or controlled exposure to sex. In response to the increased payoffs to investments in education and the expected costs of those investments, parents determine the number of children they can afford to raise, given their wealth. The low mortality rates also allow parents to plan reproduction at the outset, because the number of children born accurately predicts the number of children that will be raised to adulthood. Reproductive physiology affects fertility in the present in that it sets the broad limits within which a childbearing plan can be realized, and may actually lower fertility when plans include significant delays to first reproduction (Kaplan 2000).

A great deal of further research is necessary, however, before we can understand why these changes in socioecology have resulted in such low levels of fertility and high levels of parental investment and wealth consumption. It does not appear that people are simply maximizing family wealth because net wealth of families would be maximized by higher fertility than is currently observed. It is also clear that people are not maximizing personal consumption; in that case, they would have no children. One possible hypothesis is that the social dynamics of small groups in hunting and gathering economies resulted in greater fitness for those of higher social standing and selected for a psychology in which relative social position of self and offspring is valued highly. Such a psychology would also emerge if people judged the well-being of themselves and their children based upon the wealth and consumption of others. This psychology may have been fitness maximizing under traditional conditions. If relative, as opposed to absolute, wealth and social standing guide human decisions regarding wealth flows, parental investment, and fertility, it is possible that 'run-away' consumption and investment in children's education result from the interaction of this psychology and modern education-based labor markets and consumption possibilities.

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5. Implications of Embodied-capital Theory for Understanding Current Fertility Transitions

Embodied-capital theory links several existing theories of demographic transition and, in so doing, provides a new perspective on each one. It rationalizes the shift from natural fertility to parity-specific fertility in terms of a changing quality/quantity trade-off, as a transition from high fertility/low parental investment to low fertility/high parental investment. It also shows why the shift to lower mortality rates can lead to lower fertility, but for reasons that are very different from what traditional demographic-transition theory proposes. According to the latter, lower mortality precedes and drives lower fertility, because fewer children

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are required to maintain the population equilibrium and cultural ideologies evolve to maintain population equilibrium. According to the present view, mortality rates are but one important factor in the overall rate of return on investments in embodied capital.

This model can further serve to organize research on fertility transitions, with the fundamental expectation g that exogenous factors affecting the rate of return on parental investment in the embodied capital of offspring will predict the timing of fertility decline and its distribution within populations. Understanding these dynamics may provide insights into the course of fertility reduction and its variation across countries and among individuals within countries. For example, most studies of predemographic transition societies show that there is a positive association between wealth and fertility (Borgerhoff Mulder [1992]). There is some evidence for a negative relationship during the demographic transition. (Kaplan et al. [1995a, Vining [1986]) and no relationship after the transition is complete (Kaplan et al. [1995a]). It may be that only the wealthy can take advantage of high levels of investment in children’s embodied capital when there are few schools and limited public expenditures on health and education. The process of demographic transition may progress through different sectors of the society as more and more people can take advantage of increased rates of return due to changes in the economy and changes in public investments. These same dynamics, in combination with international transfers of educational and health technology, may also explain the national differences in the timing of fertility reduction.

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Understanding these dynamics also requires an understanding of how people process the mix of information derived from direct assessment, observation of others, and cultural guidelines. Theoretical work modeling the action of natural selection on information processing suggests that the relative reliance on direct experience and on cultural sources should vary according to environmental conditions (Bock [1999]). Cultural learning should be a better guide for behavior when environments are relatively stable than when they are changing (Bock [2001]). The rapid change in economics of production, public education and public health may lead people to reject existing cultural models, look for new models, and assess costs and benefits of alternative course of action more consciously on the basis of direct experience.

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International family planning programs present one set of new models, promoting lower fertility and greater investment in children’s education. When those models are consistent with individual assessments of costs and benefits, the direction of change is clear. It is less clear, however, how people will respond to family-planning messages in the short and long run if the payoffs to investment in embodied capital are low, either because schools are poor or because

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employment opportunities for educated people are limited (as appears to be the case in many sub-Saharan African countries).

6. Conclusion

According to embodied-capital theory, fertility and parental investment behavior result from the interaction of exogenous conditions with an evolved response system shaped by natural selection. In addition, a distinctive feature of the learning-intensive nature of human psychology is that information about the environment and guidelines for behavior are obtained through cultural sources as well as through direct personal assessment (Bock [1999, 2001]). Given the very limited capacities for cultural transmission displayed by nonhuman primates (Lefebvre [1995]), it is evident that the capacity for culture itself evolved by natural selection. We still know very little about the mix of physiological, psychological, and cultural processes underlying decisions regarding wealth flows, educational investments and consumption patterns, or how those processes relate to fertility decisions. Understanding the complex interplay of exogenous conditions, cultural forces, and evolved response systems in the determination of family structure and fertility presents a formidable challenge, but one that promises great rewards.

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