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A Theory of Fertility and Parental Investment in Traditional and Modern Human Societies

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ABSTRACT This paper has two interrelated goals. The first is to offer a general theory of fertility and parental investment across a broad spectrum of human societies. The second is to provide a perspective that unifies traditionally separate domains of anthropology. The basic foundation for the analysis is life history theory and evolutionary biological models of optimal fertility regulation. This tradition is combined with human capital theory in economics to produce a more general theory of investments in embodied capital within and between generations. This synthesis results in a series of optimality models to examine the decision processes underlying fertility and parental investment upon which natural selection is expected to act. Those models are then applied to the hunting and gathering lifeway. This analysis focuses both on problems that all hunting and gathering peoples face and on the production of variable responses in relation to variable ecologies. Next, this consideration of optimal parental investment and fertility behavior in hunter-gatherers is united with existing models of the proximate determinants of human fertility. The analysis of proximate mechanisms is based on the idea that natural selection acts on the final phenotypic outcome of a coordinated system of physiological, psychological and cultural processes. The important conditions affecting parental investment and fertility in modern socioeconomic contexts are then discussed. An explanation of modern fertility and parental investment behavior in terms of the interaction of those conditions with the physiological and psychological mechanisms that evolved during our hunting and gathering history is proposed. The proposal is that skills-based competitive labor markets increase the value of parental investment in children and motivate better-educated, higher income parents to invest more per child than their less-educated, lower-earning counterparts. It is also suggested that the deviation from fitness maximization associated with low modern fertility is due to excess expenditures on both parental and offspring consumption, indicating that our evolved psychology is responding to cues in the modern environment that are not directly related to the fitness impacts of consumption.

The principal strength of anthropology is its scope. The field encompasses both the evolution of the hominid line and the variation among and within cultures through time. A principal weakness of the discipline is the lack of an overarching theory that unifies the field. There is one especially critical point of disjunction. It is the relationship between biological processes of evolution and behavior. Instead of treating that relationship as a fundamental theoretical problem to be solved, the field has been content, for the most part, to skirt the issue by separating the discipline into the subfields. The physical processes of genetics, physiology and anatomy, and their evolution have been allocated to biological or physical anthropology. Behavior and psychological processes associated with ideology, meaning and values are the province of cultural anthropology. In fact, with the emergence of postmodernism, the subfields of anthropology are more separate today than ever before.

While this separation has the advantage of avoiding conflict among anthropologists, it has many disadvantages. First, the study of behavior is now an integral part of the biological analysis of all other organisms. The insights derived from behavioral biology do not inform most anthropological research into human behavior. Second, it is generally agreed that the evolution of physical processes is shaped by behavior; for example, natural selection on the shape, size and thickness of bone depends on the behavior that involves those skeletal processes. However, physical anthropologists, not being trained in the analysis of behavioral variation, generally must treat behavior as a given. Although they are free to speculate about the behavior of ancient hominids on the basis of their physical findings, there is no well-developed investigation into the evolution of behavior itself. Third, there is no continuity in the study of contemporary humans with the rest of the hominid line.

The generally accepted view among cultural anthropologists is that culture has liberated contemporary humans from most constraints of biological evolution, and cultures are free to vary within very broad constraints. The issue of when and how culture emerged, and how an evolutionary process could give rise to a phenomenon that is not subject to evolution has received very little treatment. This lack of continuity creates a fourth problem. Culture has become the unexplained explanator. Explanations of variation among groups as the result of cultural variation simply begs the issue of why the cultural variation takes the shape that it does.

These weaknesses are especially evident in the study of human fertility. The fertility rate of any organism is likely to be under relatively strong selection, because it contributes directly to fitness, as measured by 'r' in the Euler-Lotka equation. For this reason, under many conditions, organisms exhibit fertility rates that maximize fitness (the most complete data are available for birds: Daan et al., 1990; Dijkstra et al., 1990; Lack, 1968; Linden and Moller, 1989; for a general discussion, see Clutton-Brock, 1991; Stearns, 1992). The physiology of human fertility is increasingly well studied. We now know a great deal about ovarian and sperm function and other physiological factors affecting the probability of conception and the production of a live birth (see Wood, 1994, for a review).

The human system of fertility regulation seems very well organized to respond adaptively to variable environments. For example, one critical feature of the environment affecting the fitness costs and benefits of fertility is the presence of a nursing infant. The birth of a new offspring, shortly after the birth of an existing offspring, reduces the lifelihood of either or both children surviving (Blurton Jones, 1986, 1987; Lantz et al., 1992; Palloni et al., 1994). The impact of breastfeeding on fertility is well documented (Short, 1984; see also Jones and Palloni, 1994). The evolution of the physiology underlying the contraceptive effect of breastfeeding is almost surely due to natural selection on birth spacing. In fact, there is some data suggesting that humans, under traditional conditions, adopt birth-spacing patterns that maximize fitness (Blurton Jones, 1986, 1987—see below). A second critical feature of the environment is food supply. Although their demographic effects are not well documented, the impacts of fluctuations in food supply and net energy balance on reproductive function in women are significant (Ellison, 1990, 1995; Ellison et al., 1989; Huffman et al., 1978; Hurtado and Hill, 1990; Leslie and Fry, 1989; Lunn et al., 1984; Prentice and Whitehead, 1987; Worthman et al., 1993) and are similar across most mammals. Women seem particularly sensitive to fluctuations in food supply and in energy balance at the time of conception (ibid.), and this is probably related to the system of fat storage for lactation (see Kaplan, 1996a, for a discuson). Again, the organization of the response system to variation in net energy balance suggests that natural selection has acted upon it so that fertility is scheduled to maximize fitness.

The adaptive functioning of this physiological system depends on behavior. The length of the interbirth interval depends, in part, on the frequency and duration of breastfeeding. Similarly, the energetic balance of women depends not only of food availability in the environment, but also upon how much work women do, the production of men and children, and intrafamilial sharing patterns. Since behavioral choices and the physiological controls interact in determining fertility rates, it seems likely that natural selection would shape both and act to coordinate them in a single adaptive system.

Unfortunately, very little attention has been focused on the evolution of the psychological processes underlying the behavioral decisions impacting fertility. In general, patterns of breastfeeding, work, and sharing are treated as purely cultural phenomena with little or no evolutionary analysis. We do not know if cultural and individual variation in behavior affecting fertility is adaptive and we do not know the causes of that variation. This deficit greatly reduces our ability to understand human fertility variation across time and space.

This paper presents an approach to human fertility and parental investment that unifies evolutionary and behavioral perspectives within a common theoretical framework. It combines life history theory from biology with human capital theory from economics to develop a general theory for explaining human fertility and parental investment. It also integrates proximate approaches to the mechanisms underlying fertility variation with an evolutionary analysis regarding the action of natural selection on fertility and parental investment.

The paper begins with a general model of the action of natural selection on life history traits. This model builds on and generalizes existing life history theory in biology (see Charlesworth, 1980, Charnov, 1993, Hamilton, 1964, Kozlowski, 1992, Lessells, 1991, Roff, 1992, and Stearns, 1992, for general reviews and Hill, 1993, for a review of the application of life history theory to humans) to incorporate investments in attributes, such as skill and knowledge, that affect the ability to extract resources from the environment. While this extension of existing theory is probably useful for understanding the life history characteristics of many other organisms, it is particulary critical for humans, who invest heavily in both their own and offspring's income-generating attributes. To accomplish this extension of the theory, the concept of embodied capital, borrowed from the economic theory of human capital investment, is introduced and applied to two major life history allocation tradeoffs between 1) current and future reproduction and 2) quantity and quality of offspring. Quantitative models of fertility and parental investment, based on the second tradeoff, are then presented.

The next section applies those models to the ecology of the hunter-gatherer lifestyle, characteristic of fully modern humans. The focus on hunter-gatherers is based on the fact that most natural selection on human life histories occurred in the context of a hunting and gathering lifeway. This discussion considers the physiological and psychological mechanisms that might have evolved to respond to ecological variation affecting the costs and benefits of alternative regimes of parental investment and fertility. Attention is also focused on the coordinated action of selection on behavior and physiology and on the integration of proximate and ultimate levels of explanation.

Since most people now live in socioecological settings that are significantly different from the forager lifestyle, it is important to consider how our evolved physiology and psychology responds to modern environments. The next section considers the demographic transition in light of specific features of modern economies and their interaction with evolved mechanisms regulating fertility and parental investment. The forces of supply and demand for labor in skills-based competitive labor markets are analyzed and proposed to explain cultural changes towards low fertility and high investment in children's education. Worldwide and intrasocietal variation in fertility and parental investment behavior are then discussed in

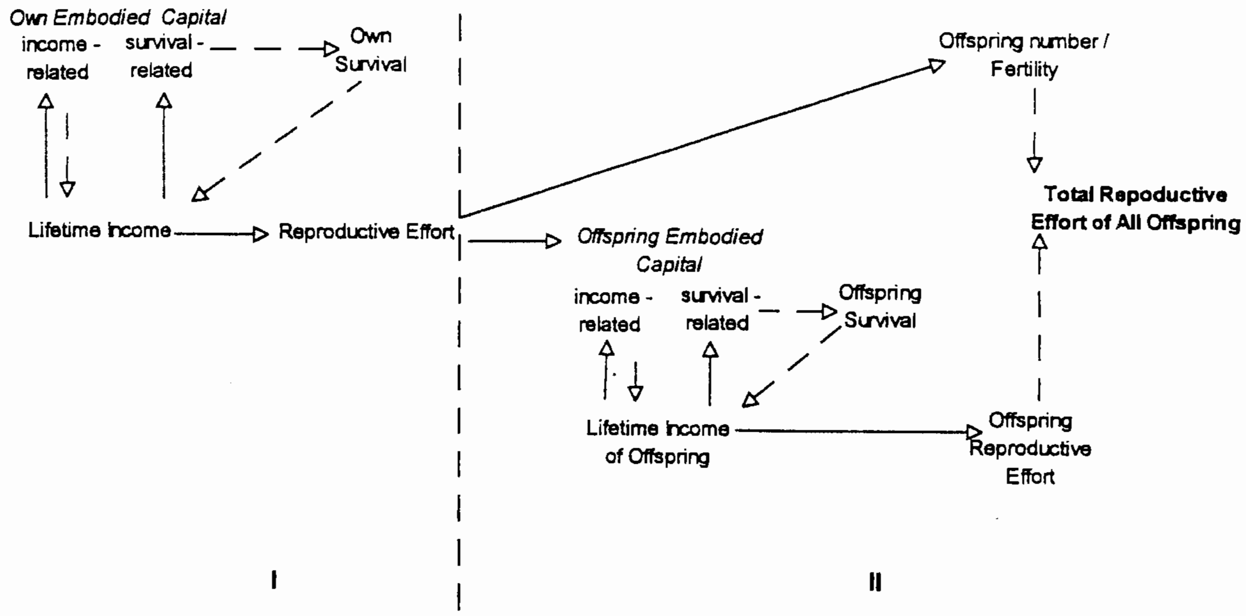

Fig. 1. Decision model for life history of investments.

terms of variable payoffs to investment in embodied educational capital.

This paper has two interrelated goals. The first is to offer a general theory of fertility and parental investment across a broad spectrum of human societies. The second is to provide a perspective that unifies traditionally separate domains of anthropology.

A GENERAL MODEL FOR THE EVOLUTION OF LIFE HISTORIES

Figure 1 illustrates the basic model underlying the analysis. The figure depicts two fundamental life history tradeoffs. The first is the tradeoff between current and future reproduction (Fig. 1, Part I); the second is the tradeoff between quantity and quality of offspring (Fig. 1, Part II). Natural selection is expected to act on those tradeoffs so as to maximize the long term representation of the genes underlying life history traits. The traits associated with highest fitness are expected to vary with ecological factors affecting the shape of those tradeoffs.

With respect to the former tradeoff, early reproduction is favored by natural selection, holding all else constant. This is due to two factors. First, the production of offspring will be a positive function of the length of the reproductive span. Since the probability of death in any time period is always nonzero, earlier reproduction tends to increase the length of the reproductive period. Second, shortening generation length by early reproduction increases the total reproductive output of the lineage.

These forces favoring early reproduction are balanced by benefits derived from investments in future reproduction. Those investments, referred to as "somatic effort," include growth and maintenance. The allocation of time and energy to growth has three major benfits. Larger organisms often suffer lower rates of mortality. Therefore growth can increase the length of the lifespan. Growth also can increase the efficiency of 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 it in reproduction.

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 somatic effort. 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, 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 due to physical entropic forces and to 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.

In the first part of Figure 1, we begin with *lifetime income.* Income is defined here in the general sense of the total value of time allocated to alternative activities, such as resource acquisition, child care, rest, etc. At each age, an individual's income will be a function of his or her embodied capital. Income can be invested directly in reproductive effort, or in 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.

The solid arrows depict investment options. The dotted arrows depict the impacts of investments. Investments in income-related capital, such as in growth, physical coordination, skills and knowledge, affect lifetime income through the value or productivity of time in the future. Investments in survival-related capital, such as immune-function, predator defense, and tissue repair, affect lifetime income through increasing the expected lifespan of earnings. However, an organism that does not reproduce leaves no descendants. Thus, the optimization problem acted upon 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 and Hurtado, 1996; Kozlowski, 1992; Kozlowski and Weigert, 1986, 1987; Roff, 1986; Stearns and 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 vs. future reproduction are likely to vary as well.

Within each broad area of allocations, there are subproblems that must be solved. For example, energy invested in the production of antibodies to infection cannot be invested in cell repair, growth or even other antibodies. Similarly, time invested in learning one skill competes with time allocated to learning other skills.

The subproblem involving the allocation of reproductive effort is the quantity-quality tradeoff. This tradeoff 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., Lack, 1954, 1968; Lloyd, 1987; McGinley and Charnov, 1988; Rogers and Blurton Jones, 1992; Smith and Fretwell, 1974) operationalize this tradeoff as number vs. survival of offspring. Natural selection is expected to shape investment per offspring and offspring number so as to maximize offspring number times their survival.

In more general form, individuals can invest not only in capital embodied in their own soma, but 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 second part of the figure 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 their own and their offsprings' embodied capital optimally, then the "dynas-

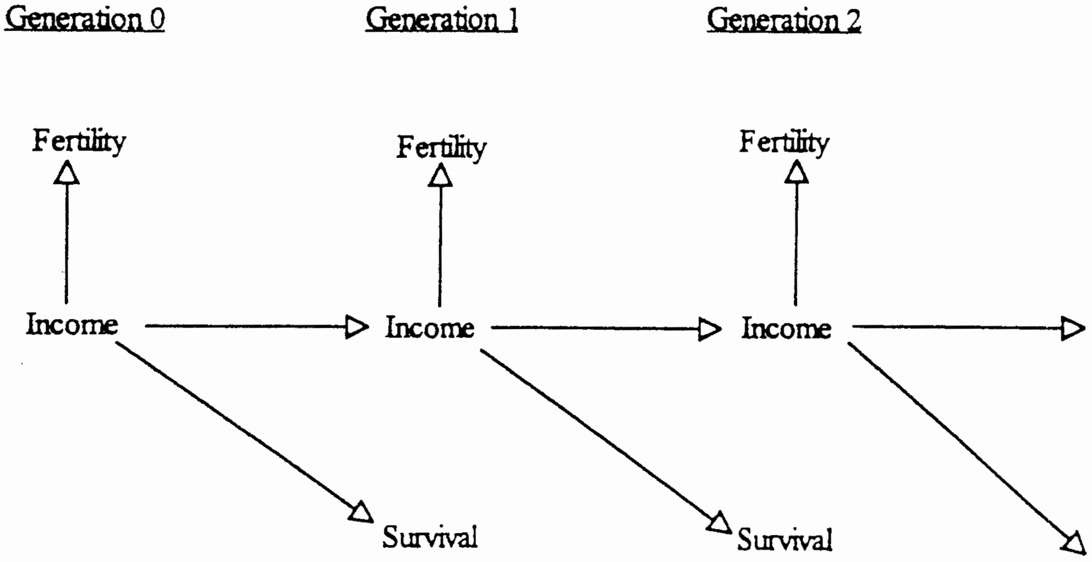

Fig. 2. Multigenerational recursion for fitness effects of parental investment.

tic" or multigenerational fitness of the lineage is maximized. The multigenerational decision path is illustrated in Figure 2.

In this model the diversity of life histories is 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 it 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 that 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 tradeoff shows that optimal investment in each component depends, in part, on investments in other components and in the effects of those investments. One result is that the value of investments in income-related capital depends on the probability of surviving to future ages.[1] If the expected future lifespan 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 is increasing through time, higher investments in survival are favored. Another result 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 probabilities

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[1] Becker (1975) and Ben-Porath (1967) obtain similar results in the analysis of investments in human capital.

of predation is probably an important determinant of why birds, bats and primates allocate more resources to maintaining physical condition and senesce at late ages for their body size.

Quantitative models of fertility and parental investment

A simple two-stage model of optimal fertility. Since the principal focus of this paper is the determinants of fertility, I will now focus on solutions to the quantity-quality tradeoff. Imagine an asexual organism whose life history consists of two periods, adult and juvenile. No offspring are produced during the juvenile period. During the adult period, the adult works and produces income, I, which is divided between resources for maintenance or own survival, I_m, and resources for reproduction, I_r. Assume that the decision concerning how much to invest in own survival vs. reproduction has already been made (i.e, it is outside the scope of the model) and as a result, all adults have the same fixed adult lifespan. The decision variables for adults in the model concern the allocation of I_r between quantity and quality of offspring. They are: number of offspring to produce (b), resources to be invested in the survival of offspring to the adult period (i_s), and resources to be invested in the embodied capital of offspring (i_l), which determines their adult income. To simplify further, assume that 1) the period of parental investment is short enough that juvenile mortality has no effect on total investment given to offspring, and 2) the length of the juvenile and adult periods is fixed or outside the scope of the model. Many of these assumptions have been relaxed in more realistic models without altering the fundamental conclusions from this simple model (see below and Kaplan, 1994b).

Let us begin with adults in generation zero. They produce b offspring. There is a fixed amount of energy, k, required to produce an offspring plus variable amounts of investment, i_s and i_l, that can be allocated to the survival and adult income of offspring, respectively. Assuming that all offspring receive equal investment and that there are no fixed costs of quality that do not depend on offspring number,[2] the budget for reproduction in generation zero can be written as

$$I_r^0 = b^0(k^0 + i_s^0 + i_l^0), \qquad (1)$$

where the superscripts all mark generation. This assumes a linear cost function with respect to offspring number, based upon the underlying assumption of replicability in offspring production.

A simple "dynastic" function to approximate long-term fitness in a nongrowing population is

$$W = \prod_{t=0}^{\omega} b^t s_\alpha^{t-1}, \qquad (2)$$

where W is fitness of an adult in generation zero and s_α is the proportion of offspring that survive to adulthood (age alpha). This estimate is based pon a counting convention that starts with an adult in generation zero and determines the number of adult descendants produced in subsequent generations. It is based upon several simplifying assumptions, following Charnov (1993). First, it assumes population size stationarity and no effects of generation time. This allows us to estimate fitness in terms of expected lifetime reproduction, R_0, instead of the expected instantaneous growth rate, r, of alleles in the ancestor's genome. Thus, equation (2) is essentially a multigenerational recursion of R_0 and the entire product is equal to the expected number of living descendants of an individual in generation zero after $\omega - 1$ generations have passed, where ω is a large enough number to capture the effects of decisions made in generation zero.[3] The assumption of asexual reproduction means that offspring are genetically identical to parents (with the exception of mutations), thus the reproduction of descendants is equally valuable to fitness as is one's own reproduction

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[2] Becker and Lewis (1973) present a more general budget constraint that includes fixed costs of quality. For the sake of simplicity those costs are ignored here, but are discussed below.

[3] It is possible to rewrite this multigenerational fitness function as a single-generation function. However, such formulation would "bury" the intergenerational tradeoffs of interest here (see Mathematical Appendix, Part I).

(i.e., the coefficient of altruism is equal to one).[4]

This model assumes that survival to adulthood in generation one is a monotonically increasing function of i_s^0 and offspring income is a monotonically increasing function of i_i^0. Thus the optimization problem is to maximize long-term fitness by choosing optimum birth rates, investments in offspring survival and investment in income-generating capital of offspring, subject to the budget constraint. One special feature of the model is that the adult income of offspring does not appear directly in the fitness function. It will constitute the budget for reproduction in the next generation and therefore will be invested in grandchildren and distributed among fixed costs of fertility, investments in survival and investments in adult income (see Mathematical Appendix). This implies that births in generation t will be functions of investments in offspring income by parents of generation t − 1, as might be survival and income for individuals in generation t + 1. Thus, we have a chain of effects (see Fig. 2).

This multigenerational problem can be reduced to a set of efficiency/optimality conditions that members of each generation must satisfy in order to maximize long-term fitness. As long as offspring will optimally allocate the income they earn to reproduction and parental investment, we can reduce the multigenerational chain of effects to a two-generational problem (the set of efficiency/optimality conditions are derived in the Mathematical Appendix, Part I, as is the simplification to a two-generational problem). Using the Lagrangian method of constrained optimization (see Chaing, 1981, Dixit, 1990, Intrilligator, 1970, and Lancaster, 1968, for detailed discussions of this method), the following first-order necessary conditions for a maximum are obtained (see Mathematical Appendix, Part I):

$$\frac{1}{I^1}\frac{\partial I^1}{\partial i_i^0} = \frac{1}{(k^0 + i_{s_1}^0 + i_i^0)} = \frac{1}{s_\alpha^1}\frac{\partial s_\alpha^1}{\partial i_s^0}\,. \tag{3}$$

This result says that at the optimum marginal proportional returns to investment in offspring survival and adult income must both equal the reciprocal of total parental investment per child. From the budget constraint it is evident that the reciprocal of total parental investment per child is equal to the proportion of an offspring that a unit of investment in fertility will produce. Therefore these efficiency conditions simply state that at the margin units of investment in fertility, offspring survival and offspring income must each have the same proportional effect. *Long-term fitness can be calculated simply from the product of number of offspring born, their probability of surviving to adulthood and the income of adult offspring. This product is equal to the total adult income/consumption of next-generation descendants. This observation effectively links the biological and economic analysis of fertility and completes the multigenerational recursion that is absent from previous biological models.*

The results expressed in equation (3) have several direct empirical implications. First, if the effects of parental investment on offspring survival and embodied capital do not depend on the level of fertility,[5] optimal levels of investment in offspring survival and adult income do not depend on the income of the parent. This result accords with earlier findings (e.g., Smith and Fretwell, 1974). The fact that b cancels from each term is due to the above-mentioned proportionality of the relationship between fertility and fitness. Once investments in survival and adult income produce less than proportional increments in fitness, it no longer pays to invest in offspring quality regardless of income level. In a sense, fertility levels are the "passive" result of the functions determining the

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[4] While the assumption of asexual reproduction is clearly not empirically true for humans, this model captures the nature of the intergenerational tradeoffs between offspring number, offspring survival and adult income of offspring (as it impacts their net reproductive rate) in a simpler fashion than a more complex sexual model. The development of sexual models will be extremely useful for understanding the differences between male and female investment strategies and between investment in sons and daughters.

[5] This would be true when there are no fixed costs for offspring quality that can be shared among all offspring and the offspring production process exhibits constant returns to scale.

relationship between investment and the fitness effects of quality.[6] Once optimal levels of investment are determined (i.e., when proportional marginal impacts on fitness are unity—see equation (A3) in the Mathematical Appendix), fertility is simply the result of dividing cost per offspring into income.[7]

An additional implication of the two-stage model is derived from the fact that the middle term in equation (3) includes *all* investments in offspring in the denominator. This is due to the interaction between quantity and investments in quality in the budget constraint [equation (2)]. This interaction between quantity and quality has been discussed extensively by Becker and Lewis (1973) and Tomes (1978), and generalized to n investments by Rogers and Blurton Jones (1992). The result is illustrated graphically in Figure 3A. It shows that marginal returns to investment in a fitness component must equal the total returns divided by all investments in offspring (i.e., overall average returns). This is because the parent is trading off investment in offspring income against further fertility and each additional offspring costs the sum of fixed costs, investments in survival, and investments in income.

This interaction has several important implications. Changes in marginal returns to investment in either survival or adult income not only will affect investment in that fitness component, but will also have the same directional effects on investments in the other fitness component. For example, as discussed in greater detail below, ecological differences across hunting and gathering societies might affect the value of investment in offspring income. Skill acquisition may affect adult foraging return rate in some ecologies more than others. If provisioning of children allows them to acquire skill, it may be that optimal years of provisioning offspring may vary across contexts. According to the conditions expressed in equation (3), the optimal amount to invest in offspring survival will also change, even when the function that relates investments to offspring survival remains constant. Figure 3B illustrates this effect. In this figure, there are two relationships between investments and offspring income. The solid curve represents the low-skill case and the dashed curve represents the high-skill case. Give the shape of the two curves, higher levels of investment in offspring income are favored in the high skill case (i_h) than in the low-skill case (i_l). An additional change occurs in the investment in offspring survival (from s_l to s_h) even though there is only one function relating investments to survival. This is because the origin of the tangent line has moved from i_l to i_h. These interaction effects mean that small differences among individuals or across ecological contexts in one fitness component can have large effects on fertility through their impacts on optimal levels of investment in other fitness components. Proportional changes in investment in components which account for larger shares of total investments will have correspondingly larger effects on optimal levels of investment in other fitness components.

An age-specific model of fertility and parental investment. The above model assumes that levels of investment in a given offspring do not change as a function of how

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[6] Since fertility is, in fact, subject to integer constraints, this is not strictly true.

[7] So far, I have assumed that parents cannot invest in quality in a way that is independent of offspring number. However, investments in protection and housing of young and investments in territory or neighborhood quality could be considered fixed costs which impact the quality of all offspring but do not rise with the quantity of offspring produced (see Becker, 1991). Such investments can be incorporated into the model by defining fixed investments in survival and adult income of offspring as $\bar{i}_s$ and $\bar{i}_l$, respectively. The new budget constraint would be

$$I_t^0 = \bar{i}_s + \bar{i}_l + b^0(k^0 + i_s^0 + i_l^0)$$

This specification does not alter the first order equilibrium conditions for fertility, and variable investments in offspring survival and income. However it does show that at the optimum, marginal rates of substitution between variable and fixed investments must be equal to the fertility rate:

$$b = \frac{\partial I^1/\partial i_l^0}{\partial I^1/\partial \bar{i}_l^0} = \frac{\partial s_s^1/\partial i_s^0}{\partial s_s^1/\partial \bar{i}_s^0}$$

This is because each unit of variable investment costs b times as much as each unit of fixed investment. This means that other things being equal, exogenous factors that increase and decrease optimal levels of variable investments will have *opposite* directional effects on the level of fixed investments. Increases in variable investments lower b, and a lower b requires that equilibrium impacts of fixed investments be greater. This would occur at lower levels of fixed investments if, as required by the second order conditions, returns to fixed investments diminish with scale at the optimum.

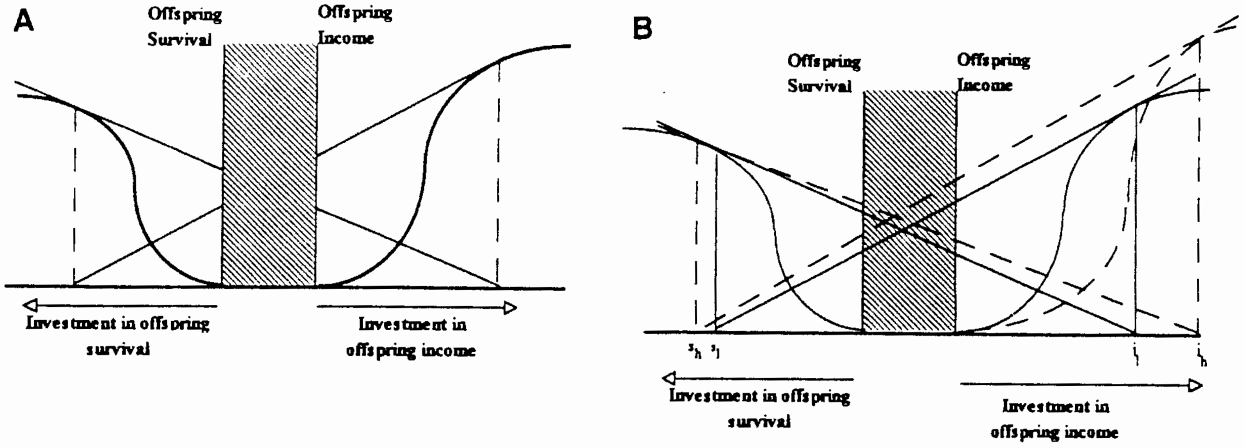

Fig. 3. **A:** Optimal investments in survival and fertility of offspring. This figure models optimal investment in offspring when there are three separable costs of producing offspring: the fixed costs of producing an offspring (the stippled area), investments in offspring survival, and investments in the adult income of offspring. The model assumes that adults have limited income and that expenditures on offspring cannot exceed total income allocated to reproduction. Fertility is then determined by dividing income allocated to reproduction by the sum of these three cost components per offspring. The S-shaped curves depict the relationship between investments and outcomes for offspring survival and fertility, respectively. The straight lines, which proceed from the x-axis through the point at which they are tangent to the S-shaped curves, represent the average benefits of producing offspring survival and income, respectively, at the optimum (the rise is equal to the outcome level and the run is equal to the sum of fixed costs, investments in offspring survival and investments in offspring income). Long-term fitness is maximized when investments in offspring survival (read from right to left) and investments in offspring income (read from left to right) occur where the dashed lines intersect the x-axis; at those levels of investment the slope of the average benefit line equals marginal benefits (the instantaneous slopes of the S-shaped curves). This figure is adapted from a more general model by Rogers and Blurton Jones (1992). **B:** Changes in optimal investments due to a change in the value of investment in offspring income.

long it lives. In essence, it assumes that all investment is given at the beginning of life and mortality occurs after the investment period. While this assumption is valid for many organisms, it is not for humans. The timing of human parental investment differs markedly from the dominant pattern among mammals. In most mammals, offspring are largely or completely energetically independent after weaning. There is some provisioning of young after weaning among chimpanzees, tamarins, marmosets (McGrew and Feistner, 1992; Feistner and McGrew, 1989) and some species of carnivores, but the length of human energetic dependence exceeds that of any other organism. Even in traditional small-scale human societies, children are not energetically independent of parents until they are adolescents or even older (Kaplan, 1994a). In fact, in some societies parents continue to provide assistance long after their children have begun to reproduce (ibid.; Blurton Jones et al., 1989).

To account for the long period humans invest in offspring it is necessary to modify the choice variables and the budget constraint. For each age of the offspring, parents must choose how much to invest in its survival and in its embodied capital affecting its future adult income. First, define p_x as the conditional probability of surviving from age x to age x + 1, given that the offspring has survived to age x. Therefore, the total probability of surviving to age y, s_y, is the product of the age-specific survival probabilities from x = 0 to x = y − 1. Assume further that 1) each p_x is a monotonically increasing function of resources received from parents that were allocated to health and avoidance of predation at age x, $i_{p.x}$, 2) investment in offspring survival at any age (x) prior to adulthood only affects survival at that age, and C) investments in survival diminish with scale:

$$s_y = \prod_{x=0}^{x-1} p_x;$$

$$p_x = p(i_{p.x}),\ \frac{\partial p_x}{\partial i_{p.x}} > 0,\ \frac{\partial^2 p_x}{\partial i_{p.x}^2} < 0.$$

Next, consider investments in embodied capital. Embodied capital can be thought of as a stock, E, that can change with age, with the amount added or subtracted at each age defined as the flow, e_x. Assume that 1) embodied capital acquired at each age is a monotonically increasing function of resources received from parents that were allocated to growth and to the acquisition of skills, $i_{e,x}$, 2) investments in embodied capital diminish with scale, 3) investment in both survival and embodied capital ends when the offspring begins reproduction (age α) and is strictly positive at all ages prior adulthood, and 4) adult income is constant through time and is a function of embodied capital at age of first reproduction:

$$e_x = e(e_{e,x}), \frac{\partial e_x}{\partial i_{e,x}} > 0, \frac{\partial^2 e_x}{\partial i_{e,x}^2} < 0$$

$$E_y = \sum_{0}^{x-1} e_x + E_0,$$

$$I = i(E_\alpha), \frac{\partial I}{\partial E_\alpha} > 0, \frac{\partial^2 I}{\partial E_\alpha^2} < 0,$$

where E_x is the stock of embodied capital at age x and E_0 is the initial stock at birth.

Finally, for simplicity, let us make the additional assumptions that 1) reproduction is asexual and care is therefore uniparental; 2) all offspring are alike and treated equally; 3) all investments are derived from income earned; 4) interest rates and population growth rates are zero; and 5) total income spent must equal total income earned, but individuals are free to borrow and lend through time at a zero interest rate. This last assumption is included so that the budget constraint does not require that income earned *in each period* must be at least as great as income spent, but only that total income earned over the adult period must be at least as great as total income spent.[8]

The discrete-time[9] budget constraint, which equates income for reproduction with fertility times investment per child, is:

$$I_r = b\left[k + \sum_{x=0}^{\alpha-1} s_x\,(i_{p,x} + i_{e,x})\right]. \qquad (4)$$

Notice that investment per child, the bracketed term, is the sum of age-specific investments in offspring survival and embodied capital, each devalued by the probability of reaching that age. From this it can be seen that holding age-specific levels of investment constant, any increases in the probability of surviving to a given age will necessary increase total expected parental investment per offspring and therefore lower fertility.[10]

Given the earlier result regarding the fitness effects of next-generation income, the fitness function for a reproducing adult can be written as

$$W = b^0 I^1 \prod_{x=0}^{\alpha-1} p_x^1. \qquad (5)$$

The first term is lifetime fertility of the parent and the second term is the adult income per offspring (i.e., income, a function of investments in embodied capital, times the probability of reaching reproductive age, a function of investments in survival). Thus the optimization problem is to maximize equation (5) by choosing optimal levels of fertility and optimal levels of investment in the survival and adult income of offspring at each age of the child, subject to the budget

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[8] This simplifies the analysis and is intuitively realistic for humans who practice exchange in various forms from kin assistance to involvement in financial markets. Incorporating effects of interest rates in more complex models should be straightforward. Many organisms also practice storage of fat and dissave in some periods. In cases in which such intertemporal exchanges are not possible, income spent must be not greater than income earned at each point time. Thus the time periods in which the income constraint is most binding should determine fertility rates.

[9] Throughout this paper discrete-time analyses will be conducted for ease of interpretation. Transforming the analyses to continuous time would be straightforward.

[10] To get a sense of the strength of this effect, I used data collected among Ache foragers on age-specific net energetic costs of rearing children (Kaplan, 1994a) and age-specific mortality rates (Hill and Hurtado, 1996) to calculate the expected total investment in an offspring at birth. If no mortality existed among Ache children, the expected total caloric costs of raising boys and girls from birth to age 18 would be about 14 million and 11.5 million calories, respectively. Taking mortality into account, the expected investment in each child at birth drops, respectively, to 10.5 million and 7.9 million. With the assumption that Ache fertility is limited by energetic budgets for investment, an increase in survival to modern levels in the US—holding caloric investment constant—would reduce observed total fertility rates of about 8.1 to about 6.0. Thus parents would have to reduce investment in offspring by about 25% to compensate for increased survival in order to maintain the same fertility levels.

constraint expressed in equation (4). This model generates the following first-order maximization conditions for fertility, and investments in age-specific survival and adult income of offspring (see Mathematical Appendix, Part II),

$$\frac{s_x^1}{\left(k^0 + \sum_0^{\alpha-1} (i_{p,y}^0 + i_{e,y}^0) \cdot s_x^1\right)} = \frac{1}{p_x^1}\frac{\partial p_x^1}{\partial i_{p,x}^0}$$

$$= \frac{\partial e_x^1}{\partial i_{e,x}^0}\frac{\partial i^1}{\partial E^1}\frac{1}{i^1}, \{x|x \in 0,1,2 \ldots \alpha - 1\}. \quad (6)$$

These equilibrium conditions show that at any age, the proportional change in fitness components (age specific survival and embodied capital) must equal one another and equal the reciprocal of *total* expected parental investment per child (including all investments at all ages), devalued by the probability of reaching that age. Again, as the optimal level of parental investment in a fitness component at any age increases, so does the optimal level of investment in that and other fitness components at all ages[11] (see Rogers and Blurton Jones, 1992, for the original derivation of this result for the case without age-structure).

APPLICATION OF THE THEORY TO HUNTER-GATHERER ECOLOGY

While the above model results outline some very general conditions for optimal fertility and parental investment, real world applications require well-informed specifications regarding the form of the relationships intrinsic to the model. Income is central to the model because it sets the budget for parental investment and fertility, and parents invest in next-generation income. Also, information is required regarding the functional relationships that relate investments to offspring survival and how exogenous/ecological factors change those relationships. This section first treats income and presents a brief overview of hunter-gather feeding/resource acquisition ecology in comparison to other primates. It then applies that discussion to the theoretical model to examine ecological determinants of variation in fertility and parental investment. It concludes with a discussion of the psychological, cultural and physiological mechanisms that may have evolved to regulate parental investment and fertility in humans.

Feeding ecology and the life cycle of productivity

Figure 4 shows age-specific production and consumption rates (measured in units of calories per day) for three different traditional groups: Piro, Machiguenga and Ache (Kaplan, 1994a). The Piro and Machiguenga practice a mixed economy of swidden horticultural, hunting, fishing and gathering, whereas data for the Ache are derived from periods during which all food was acquired by hunting and gathering. Again, there is a great deal of similarity in the age-profiles of the three groups. First, children produce much less than they consume, and production does not exceed consumption until 18–20 years of age. Childhood and even adolescence are characterized by very low rates of food production. Second, production exceeds consumption well past the reproductive period into old age. This is particularly evident among the Piro and Machiguenga. Unfortunately, sample sizes for older Ache men and women are extremely low, due to high rates of death associated with disease

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[11] The first-order conditions derived from the multi-age model of parental investment, as expressed in equation (6), require (by rearrangement) that at the optimum proportional effects on fitness components decrease as age increases:

$$\frac{s_x^1}{s_y^1} = \frac{\left(\frac{\partial\, ln\, p_x^1}{\partial i_{p,x}^1}\right)}{\left(\frac{\partial\, ln\, p_y^1}{\partial i_{p,y}^1}\right)} = \frac{\left(\frac{\partial\, ln\, e_x^1}{\partial i_{e,x}^1}\right)}{\left(\frac{\partial\, ln\, e_y^1}{\partial i_{e,y}^1}\right)},$$

$$\frac{\partial\, ln\, p_x^1}{\partial i_{p,x}^1} > \frac{\partial\, ln\, p_y^1}{\partial i_{p,y}^1}, \text{ and } \frac{\partial\, ln\, e_x^1}{\partial i_{e,x}^1} > \frac{\partial\, ln\, e_y^1}{\partial i_{e,y}^1}$$

$$\text{for } \{y > x|x, y \in 0,1 \ldots \alpha - 1\}.$$

The set of equalities shows that the ratio of the proportional marginal rates of return on investments in either survival or embodied capital at two different ages is equal to the ratio of the probabilities of surviving to those ages. Since, by assumption, investments are characterized by diminishing returns, lower proportional rates of return occur at higher levels of investment. This implies that, other things being equal, investment would tend to increase with age of offspring, as shown by the set of inequalities.

at first contact. However, data on Ache men show that they produce about twice as much as they consume in their fifties, but in their sixties, they produce about a third of what they consume.

Although we lack a comprehensive data base on food acquisition and food consumption in hunting and gathering groups, these data probably reflect some fundamental features of the life course of productivity in traditional human groups. Data collected with !Kung Bushmen also indicate that children acquire very little food (Draper, 1976; Lee, 1979) and people over sixty work almost as many hours as younger adults (Lee, 1979). Among the Hadza, older postreproductive individuals are reported to work hard (Hawkes et al., 1989) whereas children only acquire easily collected fruits and tubers (Blurton Jones et al., 1989; Hawkes et al., 1995).

This pattern contrasts markedly with age profiles of production among nonhuman primates. Virtually all nonhuman primates follow the standard mammalian pattern. The period of infancy is one of nutritional dependence on the mother, with self-feeding gradually providing an increasing proportion of total food consumption. The second, juvenile period, from weaning to the onset of reproduction, is characterized by almost exclusive self-feeding. There is no significant period of nonlactational parental provisioning among nonhuman primates. The third, adult period begins with reproduction and continues to death. These differences between humans and nonhuman primates are summarized in Table 1.

My proposal is that these differences are linked to dietary differences. A close examination of the feeding ecology of human hunter-gatherers, when compared to that of nonhuman primates, yields some revealing patterns. The major difference between human and nonhuman primate diets is in the importance of nutrient-dense, skill-intensive food resources (see Fig. 5; see also Hawkes et al., 1989; Draper and Harpending, 1987, Tooby and Devore, 1987, for related ideas). While the diets of nonhuman primates vary considerably by species and by local ecology, most feed, to varying degrees, on leaves, fruits and insects, supplemented in some cases by small amounts of hunted meat and tree gums. Humans, in contrast, rarely feed on leaves. When people do consume leaves, it is as a low-calorie supplement to calorie-dense foods (David Tracer, personal communication) as a source of micronutrients. Humans also avoid most fruits consumed by primates living in the same area. When people eat fruits, they tend to be large and ripe, whereas nonhuman primates feed on a much larger array of small and unripe fruits as well. The bulk of the food acquired by human foragers is derived from difficult-to-extract, nutrient-dense plant foods and hunted game.

Calorically, the most important plant foods for humans are tubers, seeds, palm fiber and nuts. Among the Hadza, tubers are the most important plant food. The ekwa tubers that provide the bulk of the carbohydrate calories in the diet are found deep in rocky soil and require heavy labor to extract. They are rarely acquired by children or even adolescents (Hawkes et al., 1995). A similar pattern is found among Hiwi hunter-gatherers, for whom tubers are also the most important plant food. Among the !Kung, mongongo nuts are reported to be the plant food staple. While they are easy to collect, extraction of nut meat requires great skill, taking years to master (see Bock, 1995; Blurton Jones et al., 1994a). The most important plant food among the Ache is palm starch. Extraction of palm starch requires felling the tree, cutting a vertical window down the length of the trunk to expose the pulp and then pounding the pulp into mush. This is a difficult task and women do not reach peak productivity at palm fiber extraction until age 35 (A.M. Hurtado, unpublished data). Again, Ache girls younger than 15 years of age do not pound palm fiber. Seed consumption also requires a great deal of processing to extract the nutrients (Simms, 1984). Easy-to-collect fruits, in contrast, have never been reported to be the primary plant food staple in any human group.

Hill (1982) showed that whereas meat accounts for no more than 5% of total caloric consumption (and usually much less) in any nonhuman primate, hunted foods account for between 15 and 100% of total calories consumed among human foragers (see also

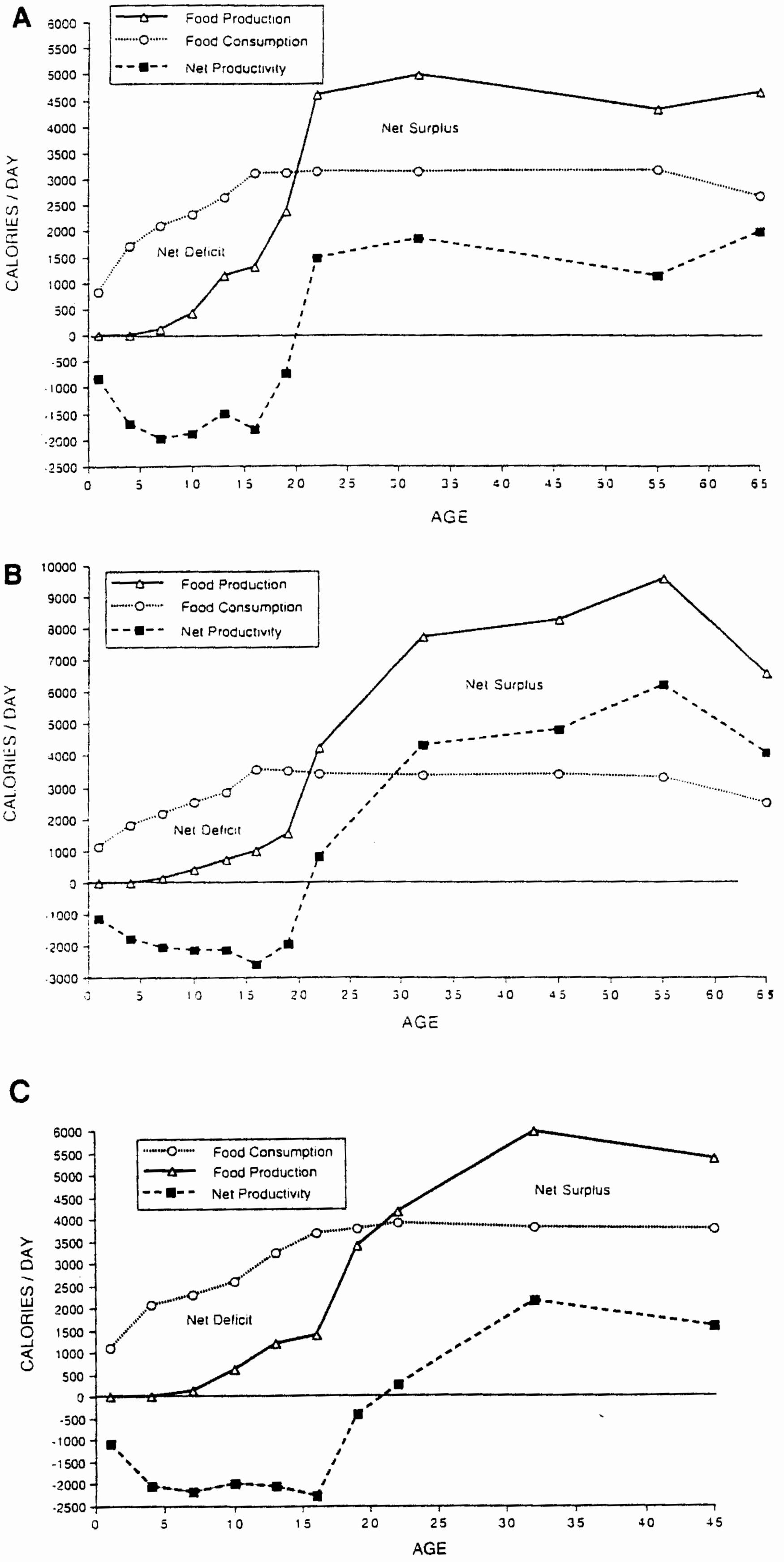

Fig. 4. **A:** Machiguenga food production and consumption by age: both sexes combined. **B:** Piro food production and consumption by age: both sexes combined. **C:** Ache food production and consumption by age: both sexes combined. All panels after Kaplan (1994a).

TABLE 1. Life history stages

Mammals/primates	Traditional humans
Infancy	Infancy
Independent prereproductive, juvenile	Dependent, prereproductive juvenile
Adult, reproductive	Adult, reproductive
	Postreproductive, productive
	Frail elderly (very short until recently)
Death	Death

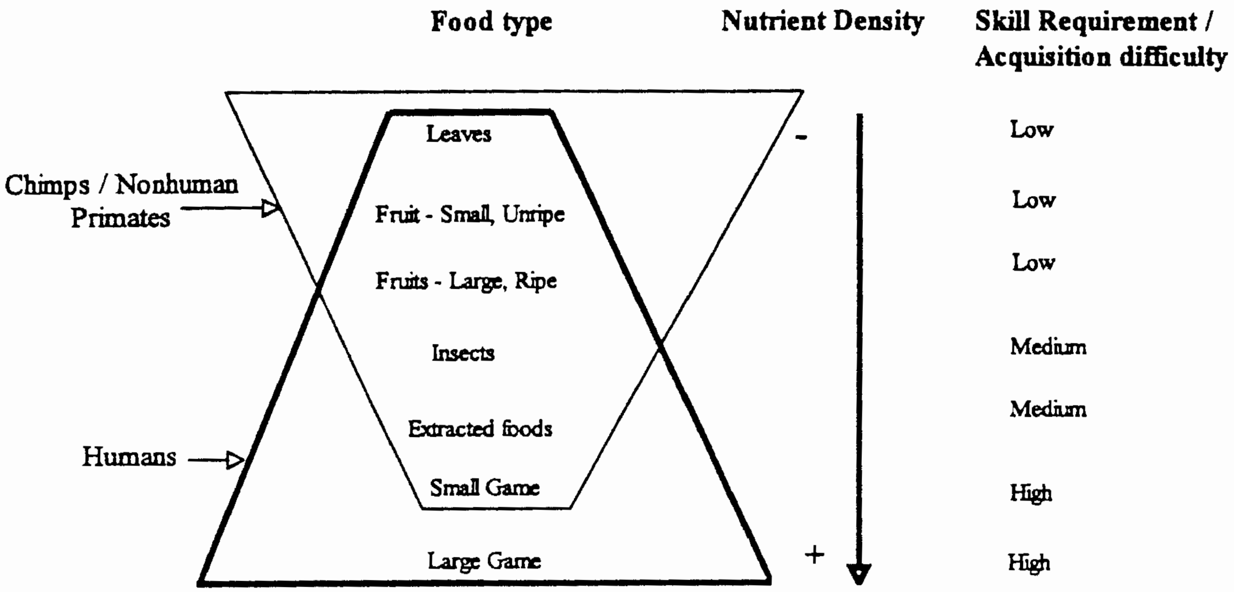

Fig. 5. The feeding ecology of humans and other primates.

Kelly, 1995). Hunting, as it is practiced by human foragers, is a very skill-intensive activity. Since people are slow runners, they rely on knowledge of prey behavior to find and kill prey. Human foragers have detailed knowledge of the reproductive, parenting, grouping, predator avoidance, and communication patterns of each prey species, and this too takes decades to learn. For example, in a test with wildlife biologists, an Ache man could identify the vocalizations of every bird species known to inhabit their region, and claims to know many more, which the biologists have yet to identify (Kim Hill, personal communication). Following most hunts, the details of the hunt and the prey's behavior are discussed, and often recounted again in camp. Even the stomach and intestinal contents of the animal are examined to determine its recent diet to be used for future reference.

The importance of skill in hunting and the long time required to obtain those skills is evident in the age patterning of hunting success. For example, among the Ache, 15–17-year-old boys acquire 440 calories of meat per day, 18–20-year-olds 1,530 calories, and 21–24-year-olds 3,450 calories, whereas 25–50-year-olds acquire about 7,000 calories of meat per day. The fourfold increase between 18 and 25 years of age exists in spite of the fact that by age 18, young men are hunting about as much as full adult mean.[12] This pattern is not unique to the Ache. From independent samples acquired in different !Kung camps, both Lee (1979) and Draper (1976) report that men under the age of 25 acquired very little meat and are known to be incompetent hunters. Among the Hadza, while boys spend a good deal of time pursuing game, their returns are quite low. Blurton Jones et al. (1989) report that during 31 days of observation, the total meat production for Hadza boys was about 2kg, mostly composed of small-to-medium-sized birds. This is less than the daily production of a single adult Hadza man.

Fruit collection, in contrast, is the least skill-intensive activity in human foraging. Fruits are also the most important food acquired by children. For example, the food production of Ache girls between 4 and 18 years of age increases from a mean of 260 calories per day when fruits are not available to a mean of 1,425 calories per day when they are in season. Boys under the age of 16 also increase production by a similar amount during fruit seasons (older adolescent boys are unaffected by fruit availability because they concentrate on hunting). Similarly, among the Hadza of Tanzania, children's food production increases markedly when baobab fruits are in season (Blurton Jones et al., 1989). In fact, Hadza children can provide as much as 50% of their total calories when fruits are in season, and may be almost entirely dependent upon their parents when they are not.

The converse applies to primates. The few, difficult-to-acquire, high-quality foods consumed by primates are also those that show developmental delays and are shared by mothers with their offspring (Feistner and McGrew, 1989; McGrew and Feistner, 1992; Silk, 1978, Teleki, 1973). Thus, those foods that are easy to procure are acquired by human and primate young alike, and those that are difficult to extract or procure are not acquired by young and are provisioned by parents. The principal difference then is that human diets are composed primarily of large, nutrient-dense, low fiber, difficult-to-acquire foods whereas nonhuman primate diets are composed primarily of foods that are easily collected. As a result, human children are provisioned.

An ecological model of fertility variation in hunter-gatherers

Since there are several phases of parental investment in humans, each requires special treatment. The first phase is infancy, the second is partial dependence on provisioning from childhood to late adolescence, and the third is assistance in reproduction by postreproductive parents. For the model, this implies that decision variables for parents concern the distribution of income to fertility and parental investment at each phase. Figure 6 presents an ecological model of parental investment and its relationship to fertility.

In the figure, there are only two direct proximate determinants of fertility, age at weaning and net energy flow to women. These determinants are chosen for two reasons. First, there is a good deal of evidence regarding those determinants (see references cited above). Second, they correspond to the constraints imposed by the different phases of the parental investment. Since humans almost never customarily nurse two infants at the same time, the intensity and length of infant investment is a critical decision variable determining fertility. The net energy flow to women represents the available energy for reproduction and investment, after accounting for the net productivity of children, postreproductive individuals, and adult men. Exposure to sex, a third proximate determinant, is probably most relevant to the onset of fertility, which for reasons of length, is not treated here.

With respect to the survival during the infancy period, there are two critical forms of parental investment, breast milk and direct care. It is useful to think of infancy in terms of a gradual transition from complete dependence on breast milk to complete dependence on other foods. The provision of breast milk increases during the first months of life as the baby grows and then supplemental foods are introduced at about 4 to 6 months of age, providing an increasing proportion of food in the child's diet as its caloric needs increasingly exceed the energy its mother can provide with breast milk (Oftedal, 1984; Vitzthum, 1994; Whitehead and Paul, 1981).

Ecological factors affect the relationship

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[12] Full adult weight is not reached until age 24 either. However, it is clear from informant reports and personal observation that the biggest effects on hunting ability in early adulthood are those of skill and knowledge.

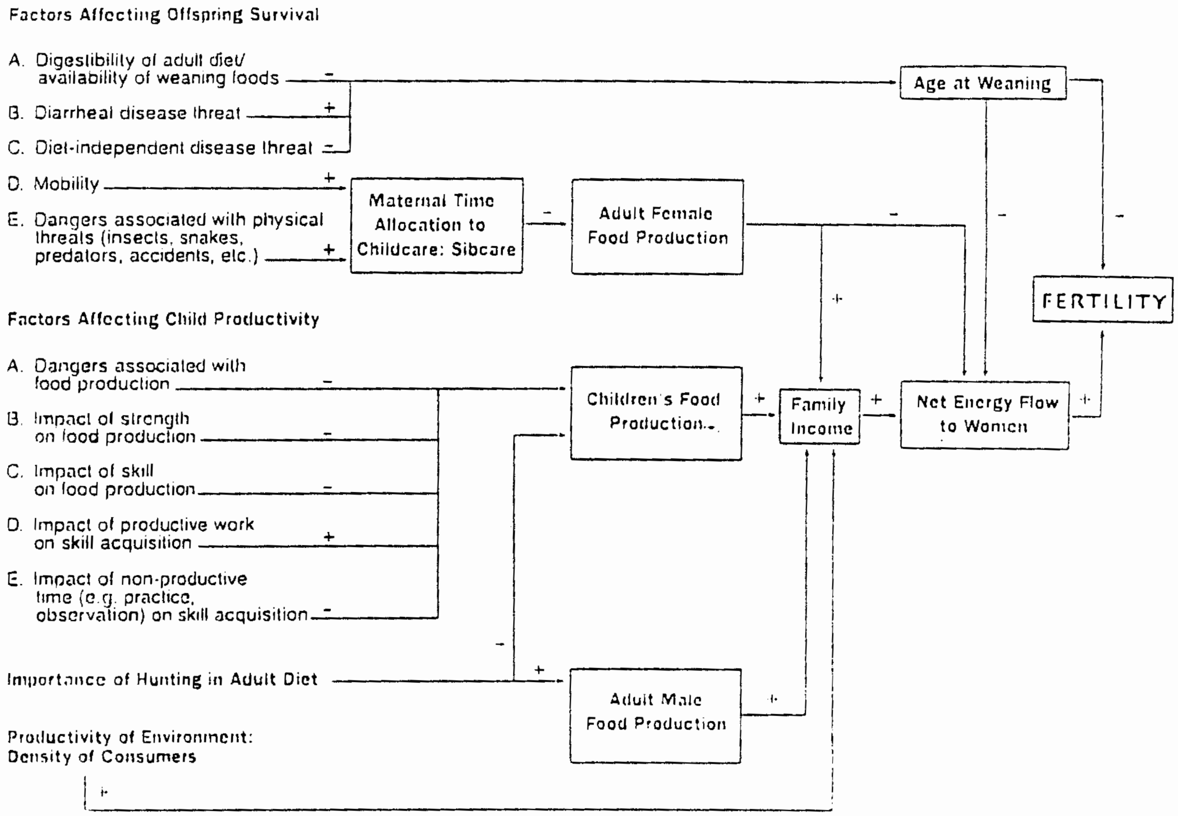

Fig. 6. Ecology and the proximate determinants of fertility.

between the rate of those transitions and offspring survival (Lee et al., 1991; Vitzthum, 1994). The digestibility of available foods is one factor. The maturation of the child's digestive system will interact with the kinds of foods available to eat in determining the optimal age to introduce new foods and the optimal proportion of milk to other foods in the child's diet at each age (Sheard and Walker, 1988). Disease organisms are another factor. The density and intensity of diseases that infect individuals through ingestion should be related to length of the breastfeeding period for two reasons. First, breast milk increases the child's immunocompetence (Hanson, 1982; Howie et al., 1990). Second, babies that are sickly require the high-quality nutrition provided by breast milk (Sheard and Walker, 1988). On the other hand, the relative importance of diseases that are unaffected by diet should be related to acceleration in the rate of weaning, since breast milk will account for less of the variance in survival (Harpending et al., 1990; Pennington and Harpending, 1988, Borgerhoff Mulder, 1992).

Since infancy and early childhood is also the period during which offspring require the most direct care, maternal food production, and hence her budget for reproduction, should be affected by ecological factors affecting the relationship between direct care and survival. The availability of safe spaces for children, which should be negatively associated with mobility, and dangers in the environment should both affect the age-specific benefits of direct maternal care. For example, among the Ache, 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 the permanent settlement, even when time spent being carried is omitted from the analysis (Kaplan and Dove, unpublished data). Women's food production both increases family income (some of which she will consume) and decreases her net energy available for reproduction due to the costs of work.

The age-specific productivity of children is also likely to depend on ecological factors. The dangers associated with acquisition of different food types should affect whether and how much children forage. This issue has received extensive treatment in a series of papers contrasting the foraging behavior of !Kung and Hadza children (Blurton Jones et al., 1989, 1994a, 1994b; Hawkes et al., 1995). In addition, as discussed above, the suite of resources available and the impacts of skill and strength on foraging return rates should determine both children's time allocation to productive labor and the total amount they produce (cf. Bock, 1995; Draper and Harpending, 1987; Hawkes et al., 1995). Children also face a potential tradeoff between early productivity and later adult production. Thus, the impacts of both productive labor and nonproductive practice on later adult productivity should also affect children's food production. For example, boys in many societies spend a good deal of time in nonproductive hunting practice. Among the Machiguenga, boys spend much time hunting small lizards and in target practice. They sacrifice the more immediately productive activities of helping the mothers in the garden and collecting wild foods, activities that their sisters perform.

The characteristics of potential food resources also affect the productivity of adults. Rates of return from hunting are likely to impact on men's food production (see Lancaster and Kaplan, 1991, for a discussion). The productivity of older people may also depend on the availability of foods that may require skill to extract, but do not require great strength or stamina. The productivity of the environment, relative to population density, is also likely to determine the net energy flow to women.

These two main constraints on reproduction, the length of the infancy period and the net energy flow to women, may vary in their importance in different ecological contexts. When food is abundant, the main constraint on fertility may be the health impacts of weaning. This would likely correspond to periods of maximum population growth rates (cf. Hill and Hurtado, 1996). When population density is high relative to the productivity of the environment, the net energy flow to women may be most important.

It will be a challenge to determine which constraint is binding in specific cases. One problem is that there is a bidirectional causal relationship between lactation and fertility. On the one hand, full-blown weaning is often catalyzed by pregnancy. Hormones secreted by a new fetus during the third trimester block milk production. Mothers often decide to wean their child when they realize they are pregnant (Hill and Hurtado, 1996; Short, 1984). On the other hand, earlier changes in the relative importance of supplemental foods to breast milk (and the associated change in the intensity and timing of nursing bouts) could have resulted in the production of a fertile ovulatory cycle. Since changes in nursing patterns probably interact with net energy flow to women in determining fecundity, the causal relationships are complex, and understanding them will require a great deal of further investigation.

Mechanisms underlying human responses to ecological variation

In order to adjust parental investment and fertility optimally in relation to ecological variations, humans must possess a set of mechanisms that translate environmental inputs into behavioral outputs. Many of these adjustments, especially those involving parental investment, may be accomplished through psychological processes that direct attention to functional relationships, aided by a store of cultural knowledge. Other adjustments, such as those governing fertility, may be accomplished by the physiological mechanisms discussed above.

The major adjustments in parental investment are the length and intensity of nursing, direct child care, work effort to produce food, and the age-specific provisioning of children. With respect to nursing, women should be particularly sensitive to the digestive behavior of infants and to the impacts of supplemental foods on their digestion and diarrheal disease. Since infants vary in digestive function and susceptibility to disease, women probably adjust nursing behavior in relation to individual reasons to supplemental foods. At the same time, women probably also rely on stored cultural knowledge, based on the experience of many women. Much trial and error experimentation with supplemental foods may be avoided by reliance on stored cultural knowledge (cf. Boyd and Richersen, 1985). Cultural norms are likely to proscribe the introduction of supplemental foods to newborns in most contexts, and to specify which foods are the best early supplements. However, those cultural norms also respond to changing evaluations by women. For example, Draper (1975) reports that !Kung breastfeeding and fertility patterns changed in response to decreases in maternal mobility and the availability of dairy products and corn meal, associated with increasing cultural contact. This would suggest that people can recognize the qualities of newly available foods and experiment with them to see if infants can consume them beneficially.

A similiar combination of psychological processes and cultural norms is probably involved in the adjustment of work effort and provisioning. Two major decisions for parents are how much work to require of children and how much food to give them. As discussed above, those decisions are likely to be based on the survival effects of children's work (due to environmental risks), the productivity of their labor, the impacts of activity schedules on skill development, and the health and growth effects of food. People are likely to possess psychological characteristics that make them sensitive to each of those effects, and to rely on stored cultural knowledge that incorporates generations of accumulated experience. Cultural norms are probably especially important for long-term effects, such as the impact of children's activity schedules on their later adult productivity. Trial and error learning on an individual basis would be both costly and prone to error.

The optimality conditions specified in equation (3) and depicted in Figure 3 suggest that those psychological mechanisms must be able to detect diminishing returns to investments. It is the shape of the relationship between investments and outcomes that determines the optimal amount to invest. When returns to an extra unit of investment in offspring income or survival produces a smaller fitness improvement than a comparable investment in fertility, it no longer pays to invest more in the offspring, even if the investment is beneficial. Compared to observed investments, a slightly longer nursing period, a slightly lower work requirement for children, and slightly more food given to children probably would increase their survival or adult income. However, people should be selected to possess psychological mechanisms that detect diminishing returns and to adjust investment accordingly (Harpending et al., 1990; Pennington and Harpending, 1988; Borgerhoff Mulder, 1992). In accord with this prediction, data on nutrition and health among traditional peoples do show that children are given less food than would maximize their growth rates and chances of survival (see Hill and Hurtado, 1996, for a review of the health effects of supplementing energy and protein intake in children in food-limited societies).

To summarize, the proposal here is that selection acts on the coordinated outcome of mechanisms that both regulate parental investment and fertility. Investment may be regulated by psychological mechanisms that direct attention to fundamental relationships between investments and outcomes, and that detect diminishing returns to investment. Actual decisions will be the product of those mechanisms and some reliance of cultural norms that benefit from accumulated experience. The regulation of fertility, on the other hand, may involve little or no cognition, and be wholly regulated by physiological mechanisms responsive to breastfeeding and net energy flow. This makes sense in the context of the theoretical model in so far as fertility is the "passive result" of optimal parental investment and an income budget for reproduction. If, after allocating investments to existing children, there is enough time and energy to support the next offspring, it should be produced.

PARENTAL INVESTMENT AND FERTILITY REDUCTION IN INDUSTRIAL SOCIETIES: THE COMPETITIVE LABOR MARKET THEORY

The empirical relationship between fertility and fitness, and the requirements for a theory

There is mounting evidence that people in modern state societies in the developed world

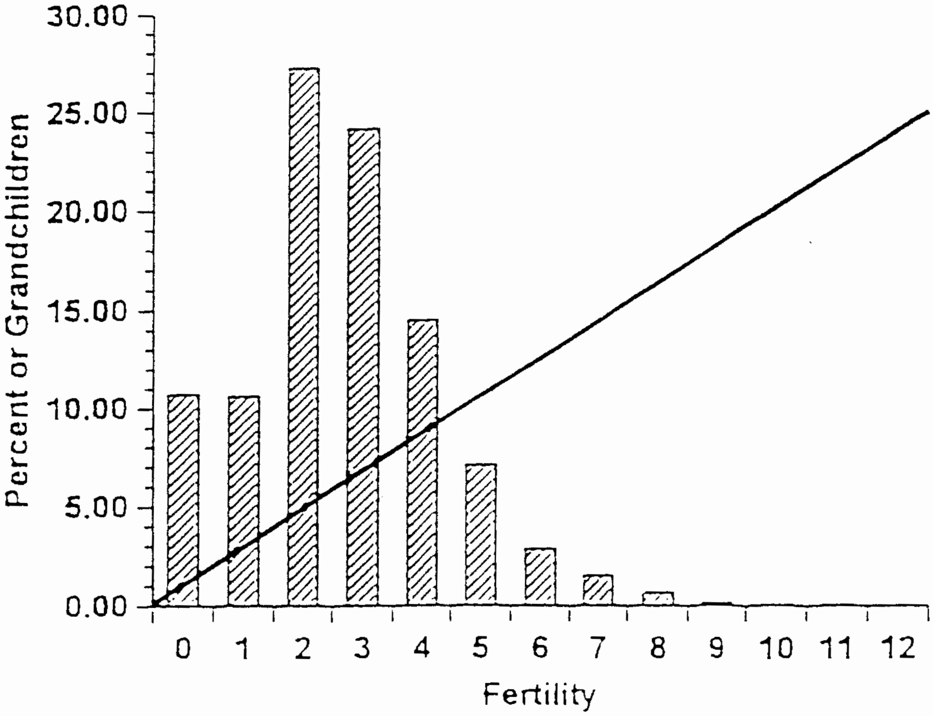

Fig. 7. Fertility and grandchildren. The bars show the percent frequency distribution of fertility in percents for Anglo men born between 1920 and 1939. The line plots the OLS estimate of the relationship between number of children and number of grandchildren among Anglo men whose children have completed reproduction. Modal Fertility is two children, but number of grandchildren is maximized with the highest number observed, 12.

do not maximize fitness through their fertility decisions (e.g., Irons, 1983, 1990, 1993, 1995; Kaplan et al., 1995; Lam, 1986; Perusse, 1993; Retherford, 1993; Vining, 1986; but see Simons, 1974, for data suggesting a positive correlation among wealth and fertility within socioeconomic groups). 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, we 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 (Kaplan et al., 1995). This contrasts sharply with the observed modal fertility of two children (Fig. 7). Higher parental fertility in modern developed societies is associated with lower achieved educational and economic status of offspring (Kaplan et al., 1995; see Blake, 1989, and Downey, 1995, for reviews), 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 to which modern behavior deviates from the predictions of simple budget constraint models of quantity-quality tradeoffs is that higher earning adults produce no more children than their lesser earning counterparts, even in well-controlled studies. Whereas available data on preindustrial societies consistently exhibit a positive relationship between resources and reproductive success (Barkow, 1989; Betzig, 1986; Boone, 1986; Borgerhoff Mulder, 1987, 1988; Cronk, 1991a,b; Flinn, 1986; Hughes, 1986; Kaplan and Hill, 1985b; Low, 1990; Irons, 1979, 1993, 1995; Mealey, 1985; Turke and Betzig, 1985; Voland, 1990; see also Chagnon, 1988), studies of postdemographic transition societies either find no relationship or a negative one (Kaplan et al., 1995;

Perusse, 1993; Retherford, 1993; Vining, 1986).[13] The models presented here predict that under most conditions, fertility should be a monotonically increasing function of resources for investment in reproduction, and when wealth does not affect the value of parental investment, fertility should increase linearly with resources.

An adequate theory of the demographic transition must accomplish two things. First, it must specify the conditions that changed, leading to a reduction of fertility and the observed relationship between wealth and fitness. Second, it must explain why those changes produced the observed responses within a larger theory of the determinants of fertility in general. In the context of the theory proposed here, it is necessary to specify the critical differences in the relationship between parental investment and child outcomes in pre- and postdemographic transition societies and to show why the suite of evolved, proximate mechanisms discussed above might produce the fertility and parental investment behavior observed in modern, post–industrial revolution labor markets.

In order for the theoretical models to explain the reduction in fertility, especially in the face of growing wealth, equations (3) and (6) require exogenous changes in the value of parental investment. The transition from high to low fertility requires that the marginal returns from parental investment decrease more slowly in modern societies than in traditional and peasant societies. In fact, the difference in the rates at which returns to parental investment diminish (as captured by the second derivatives of the functions relating parental investment to offspring survival and income) must be great enough to more than compensate for the higher real wealth in posttransition contexts. Below is an analysis [building on Becker's (1975) analysis of investment in human capital] which implies that for a large part of the range of investments, investments in offspring income in skills-based competitive market economies exhibit either constant returns to scale, i.e.,

$$\frac{\partial^2 I^{t-1}}{\partial (i_i^t)^2} = 0,$$

or with growing technology increasing returns to scale i.e.,

$$\frac{\partial^2 I^{t-1}}{\partial (i_i^t)^2} > 0;$$

see Fig. 8).

Similarly, to account for the fact that within modern societies wealth is uncorrelated with fertility, the model requires that the shape of the functions relating parental investment to offspring income and/or survival differ systematically with wealth. In particular, it requires that the cross-derivatives be greater than zero, i.e.,

$$\frac{\partial^2 I^{t-1}}{\partial i_i^t \partial I^t} > 0$$

or

$$\frac{\partial^2 S_a^{t-1}}{\partial i_s^t \partial I^t} > 0,$$

at least in the range of the optima. This means that higher earning parents must be more effective at producing embodied capital in children than lower earning parents. This part of the analysis relies on the idea that the skills affecting productivity with modern technology are cumulatively acquired and that the production of embodied capital in children depends on the capital embodied in parents (see Becker et al., 1990, for a related argument in the analysis of macro patterns in economic growth and fertility).

For these conditions to predict low modern fertility, the sum of age-specific investments in offspring must constitute a greater proportion of adult income in modern contexts than in high fertility regimes. To predict the

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[13] Studies of traditional small-scale societies suggest that fertility may be optimized to maximize the production of descendants over the long run (e.g., Blurton Jones and Sibly, 1978, and Blurton Jones, 1986, for the !Kung in Botswana, but see Hill and Hurtado, 1996, for disconfirmation among the Ache). The abrupt change in the association between wealth and fertility that occurs at the same time fertility is reduced historically (Retherford, 1993) requires explanation.

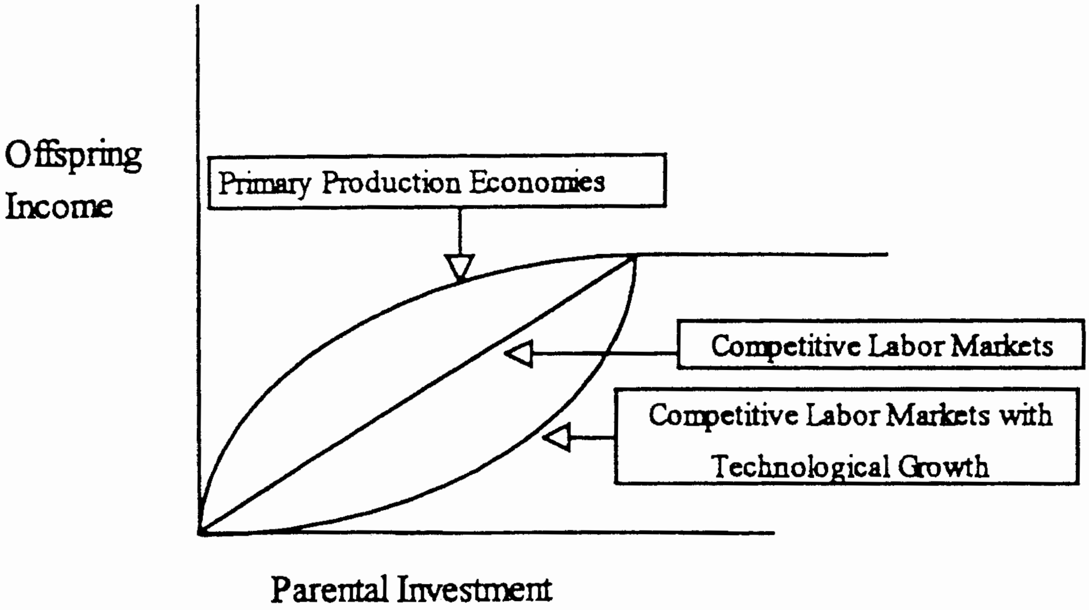

Fig. 8. Relationship between parental investment and offspring income as a function of the economy.

lack of a positive association between income and fertility, age-specific parental investments must increase proportionally with wealth. My theory is that skills-based competitive labor markets produce those conditions.

In response to those conditions, the evolved proximate mechanisms governing fertility and parental investment output a fertility much lower than the fitness-maximizing output. The psychological processes regulating desired investment per child and other expenditures produce a budget that does not permit more than two to three children. There is a conflict between the fertility schedule that our physiological response system would produce and consciously desired fertility. This has stimulated the demand for effective birth-control technology. The interaction of those processes with current socioeconomic conditions is discussed following the analysis of investment in embodied capital in competitive labor markets.

Investment in embodied capital skills-based competitive labor markets

There are qualitative differences between subsistence production and modern competitive labor markets in the relationship between investments in human capital and productivity. In subsistence-based economies the relationship between skills and productivity depends upon the activity. For example, successful agricultural production requires knowledge of weather, soil and pests in differing degrees depending upon the local ecology. Some function with eventually-diminishing returns will likely characterize the relationship between productivity and human capital. In those economies, optimal levels of investment will be determined by the diminishing impacts of further investments on productivity. However, competitive labor markets will tend to produce wage structures that equalize the present value of costs of investments with the earnings (see Becker, 1975, for a detailed presentation of this argument).

This section begins with a highly simplified analysis of supply and demand for labor in a market economy without skill differentiation in employment. This model shows how wages and the number of people employed are determined in a competitive market for labor. The second model adds skill-differentiation to the market and generates a set of predictions about equilibrium investments in offspring embodied capital by fitness-maximizing parents. This model assumes that all parents are equally effective in producing embodied capital in their offspring. The third model relaxes that assumption and allows parents with higher levels of skill to produce embodied capital in offspring at a higher rate per unit of investment. This model is designed to specify the conditions that would have to be met in order for the models of fitness-maximizing investments in offspring number and offspring quality to predict the empirical pattern of results found in modern society.

This analysis is a form of reverse optimality. We already know much about the basic empirical patterning of modern fertility and parental investment behavior. The goal here is to develop an optimality framework for analyzing optimal fertility and parental investment behavior in the context of a labor market economy, and then to determine the assumptions that would have to be met for the model to predict the observed behavior. Once those conditions are specified, empirical research can be conducted to determine if they hold in modern society.

The first model is illustrated graphically in Figure 9. The model assumes that initially most people are involved in the traditional economic sector, engaging in primary (non-wage) production. All individuals engaging in primary production are alike. However, there is trade and competitive prices for goods. Since all individuals are alike, they achieve the same base income, I_0. Fertility decisions are made according to the maximization conditions expressed in the above age-specific model, limited by the budget constraint imposed by I_0. Assume that a new technology emerges so some goods are more efficiently produced by firms that are larger than family households. Those firms will want to hire labor to combine with physical capital in an optimal mix. In Figure 9, the firms' *demand* for labor is depicted as a function of the wages paid per unit of labor (except, as is customary in supply-demand analysis, the axes are reversed with the y-axis depicting wages and the x-axis depicting the number of workers demanded). The demand curve slopes downward, because as wages decrease, profit-maximizing firms will wish to hire more workers (see, for example, Varian, 1992). The basic assumption underlying the downward sloping demand curve is that if all other inputs into the production process are held constant, each extra unit of labor will have a diminishing marginal product. Thus, if there are a thousand laborers employed in the labor market, the 1,001th worker will increase total production (and hence sales revenues) less than the one-thousandth worker. A profit maximizing firm will wish to employ units of labor as long as the revenues derived from adding the next worker are greater than the wages that must be paid (i.e., until a quantity is reached such that the marginal revenue derived from a unit of labor is equal to the cost). Thus, *the demand curve represents the marginal revenue of workers as a function the total quantity employed.*

Fitness-maximizing or, in economic jargon, utility-maximizing, individuals will attempt to get the highest possible return for their labor. With the assumption that jobs in the market sector (e.g., digging coal) require no more skill than that involved in primary production in the traditional sector, individuals in the traditional sector would be willing to switch to the market sector as long as they could sell their labor for anything greater than I_0. The *supply curve* in Figure 9 reflects this idea. The supply curve represents *the amount of labor that workers would be willing to supply as a function of wages* (again, with the traditional axes switched). At any wage below I_0, no worker would be willing to switch to the market sector; at I_0 all workers would be indifferent to switching, and wages above I_0 would induce all workers to switch. Given the assumption that all workers are alike in earning I_0 in the traditional sector, the supply curve is flat (if time spent working is held constant in both the wage labor and traditional sectors). If workers varied in traditional sector earnings, the supply curve would be upward sloping, because as wages in the market sector increase, more individuals would be willing to switch out of the traditional sector. *The market is cleared at the point of intersection between the demand and supply curves.* This means that there are no individuals left in the traditional sector who would be willing to switch the market sector at a wage some firm is willing to pay. Individuals therefore would be attracted to the labor market until the quantity of employment is reached at the aggregate level such that the

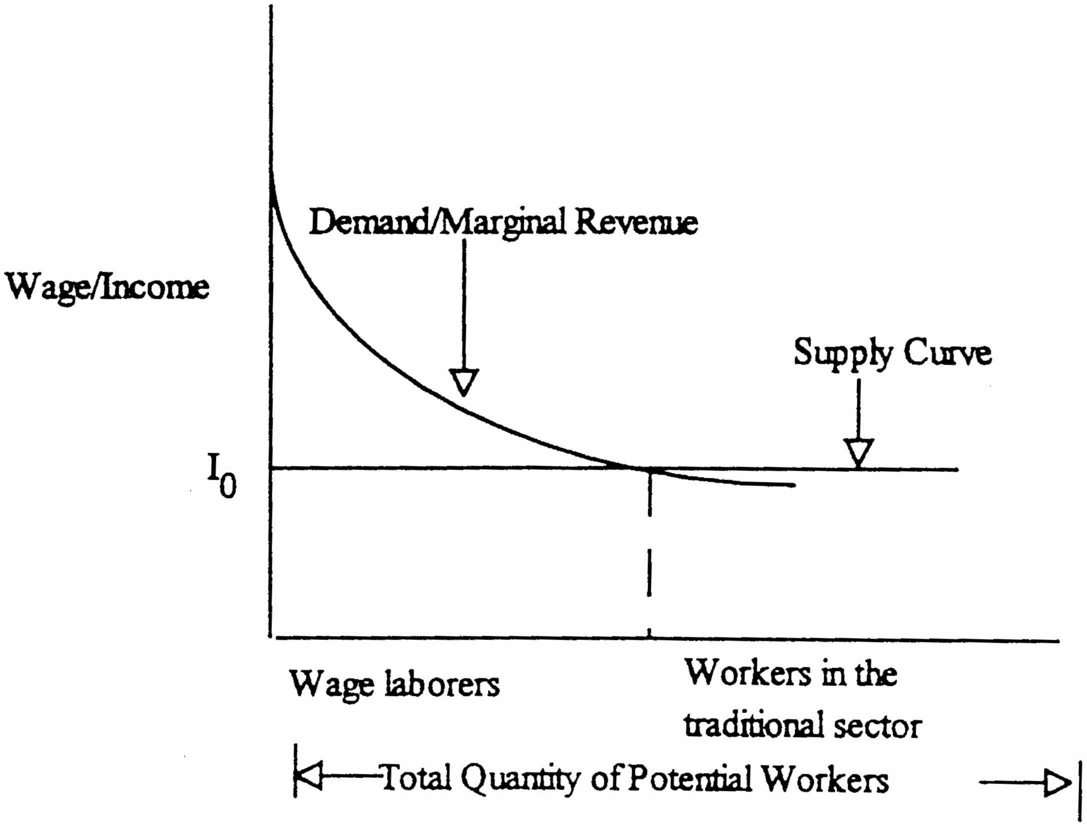

Fig. 9. Equilibrium wage rates in a two-sector economy.

marginal revenue from additional units of labor was equal to I_0. As long as the total quantity of potential laborers is greater than the intersection of the supply and demand curves for labor, the equilibrium income in both the traditional sector and the labor market would be equal.[14]

For the next model, assume that further exogenous change creates a demand for more skilled labor. Those skills can be acquired but will cost an additional amount, c, to embody. That cost could be paid by either parents or offspring, or both. In practice, it appears to be paid by both, with a large part financed by parents through the provision of additional years of support. For the purposes of this exposition, I will assume that parents pay the entire cost.[15]

According to the model results in equation (3), fitness-maximizing parents will be willing to pay those costs if the increase in the adult income of their offspring would offset the loss in fertility. Define the total parental investment in the traditional and unskilled labor sectors at equilibrium as p^* with an associated fertility rate,

$$b^* \left(= \frac{I_0}{p^*}\right).$$

The fertility of parents producing skilled offspring, b', would be

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[14] If income in the traditional sector were a decreasing function of the number of people involved in it, movement into the labor market would certainly raise the income in the traditional sector. This would have the effect of moving the equilibrium point to the left with a resultant increase in income in both sectors, although both incomes would still be equal.

[15] Individuals can support their own training by accepting lower income (perhaps negative) at one time for higher income earned later (see Becker, 1975, Mincer, 1974, for analyses). Parents today generally support the early part of human capital investment through high school (with the aid of government subsidization of schools) and perhaps higher education. This is often followed by an on-the-job training period that is self-financed through the receipt of lower wages (Becker, ibid.).

$$b' = \frac{I_0}{p^* + c} = b^* \frac{p^*}{p^* + c}.$$

Fitness-maximizing parents would be indifferent to raising skilled workers if

$$b^* I_0 = b' I'$$

or

$$I' = \frac{p^* + c}{p^*} I_0,$$

where I′ is the income of skilled workers.

As long as the demand curve for skilled workers is somewhere above the supply curve (which is constant at I′) and intersects it at a point less than the total number of potential workers, a new mixed equilibrium will develop (see Fig. 10). For the purposes of illustration, Figure 10 is drawn so the axis for the demand curve for unskilled workers is shifted to the right of the y-axis, to the point where the demand curve for skilled workers intersects the supply curve of skilled workers. This leads to the prediction that forces of supply and demand will automatically generate an equilibrium in which parents are indifferent to alternative levels of fertility and offspring income. Fitness gains from increased income per child will exactly equal the fitness costs of lost fertility. Becker's original 1975 analysis of investment in human capital obtains this result for individuals self-financing those investments. This model extends that result to model of fitness-maximizing parents developed with equations (1) through (3).

This model can be extended to include multiple levels of skill and investment in embodied capital. As long as the marginal revenue derived from the first worker of a given skill level is higher than the income equivalent of the fertility given up to obtain the skills, firms would offer wages high enough to attract people to make the necessary investments. This process would continue until the marginal revenue was equal to the costs of obtaining the skills. The final equilibrium, of course, will be determined by a complex set of interactions, such as the substitutability of different factors of production (including workers of differing skill levels), and the impact of income changes on the demand for consumption goods.

In addition, variance in fertility will also reflect changes in other investments due to increased investment in skill. The initial model of investment tradeoffs among fertility, survival and income of children implies that increased investment in one component of offspring reproductive value leads to increases in other components. Thus anyone investing in more skilled children will also invest more in their health and survival. This would engender even greater fertility differences among parents investing in differing skill levels for their children. In fact, one might argue the increased investment in public health at the end of the 19th century was as much a consequence of fertility reduction as a cause.

This simple graphical model is potentially capable of explaining several aspects of the empirical pattern discussed above. It explains why competitive labor markets with skill-differentials linearize the relationship between parental investment and offspring income for a large part of the observed range. It also predicts variation in fertility levels within income classes, because parents will be indifferent to alternative choices of fertility and income. In addition, the children of higher investing parents will earn more, but will not necessarily have more children than the children of less investing parents. Since optimal investment in this model does not depend upon income, skilled workers will be indifferent to producing skilled or unskilled offspring. If they produce unskilled offspring, they will have more children than unskilled workers. If they produce skilled offspring, they will have the same fertility as unskilled workers who produce unskilled offspring but more children than those unskilled workers producing skilled offspring. It also predicts investments in health will reflect investments in income-producing skills, both historically and across skill levels.

Still, several major problems remain unresolved. First, the model, as it stands, predicts that there will be a mean difference in the fertility of skilled and unskilled workers. Although both types of workers will be indifferent to raising skilled and unskilled children,

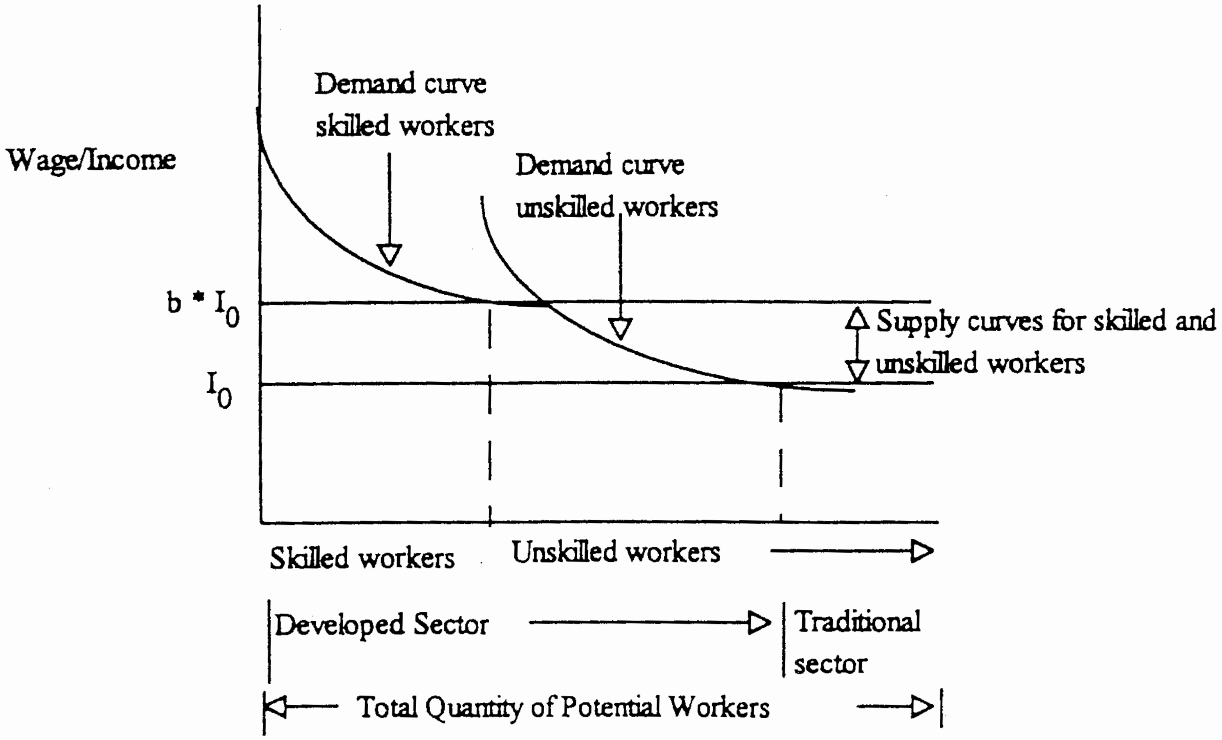

Fig. 10. Equilibrium wages in a two-sector economy with two skill levels.

skilled workers, on average, should be more fertile due to their higher income. Second, the model cannot account for sustained fertility reduction because initial decreases in fertility in one generation will be matched by increases in some future generation. Third, the model does not predict an intergenerational correlation in income (i.e., wealthier parents producing wealthier children), as is found empirically.

To explain the equality of fertility across income classes and the intergenerational correlation in fertility, the above model requires that at the optimum skilled parents invest more in children than unskilled parents. Here I follow Becker et al.'s (1990) suggestion that the production of human capital is human-capital intensive. If the qualities that increase productive output are knowledge, reading, writing, logic and mathematical skills, the production of those qualities are likely to require inputs of a similar nature. The value of many inputs, in terms of the embodied capital produced, should depend on the capital embodied in those inputs. First, consider inputs of parents' time. There is significant evidence that the nature of parent-child interaction varies with the educational level of parents (Hart and Risley, 1995; Hoff-Ginsberg and Tardif, 1995). This probably means the skills and behavior patterns that result from parental time inputs are associated with the capital embodied in parents. By the time children enter the public education system there are clear differences among them in school-related skills, and those differences are related to socioeconomic status. Second, the rate at which a child learns may depend on the knowledge and skills he or she already possesses. Much of the education offered in schools is based upon the premise that knowledge is cumulative (Cromer, 1993). Basic skills are acquired first, and those skills are used as a foundation for the acquisition of the next set of skills. This would imply that the impact of the child's time inputs would depend upon skills already in place.

In the above model, this would mean that the net increase in embodied capital at each age would be functions of both the quality of inputs, and the capital acquired at younger ages. As above, define E_x as the total amount of embodied capital at age x and e_x as the net increase in embodied capital at age x. We can think of E_x as a stock and e_x as a flow where

$$E_x = \sum_{y=0}^{x-1} e_y.$$

Next define for a given age of the child, $t_{c,x}$ as the child's time, $t_{p,x}$ as parents time, $t_{o,x}$ as other's time (such as teachers), $E_{c,x}$ as the child's existing stock of capital, $E_{p,x}$ as the embodied capital of parents, $E_{o,x}$ as the embodied capital of the others giving time to the child, and i_x as resources spent on all other inputs. Then e can be written as a function of inputs:

$$e(x) = e(t_{c,x}, t_{p,x}, t_{o,x}; E_{c,x}, E_{p,x}, E_{o,x}, i_x x, t),$$

where

$$\frac{\partial^2 e_x}{\partial t_{c,x} \partial E_{c,x}}, \frac{\partial^2 e_x}{\partial t_{p,x} \partial E_{c,x}}, \frac{\partial^2 e_x}{\partial t_{o,x} \partial E_{c,x}}, \frac{\partial^2 e_x}{\partial i_x \partial E_{c,x}},$$
$$\frac{\partial^2 e_x}{\partial t_{p,x} \partial E_{p,x}}, \text{ and } \frac{\partial^2 e_x}{\partial t_{o,x} \partial E_{o,x}}, >> 0.$$

The first four cross-derivatives or interaction terms are written to indicate that the effect of each input will be greater as the recipient's (i.e., the child's) stock of embodied capital increases. This is important because it means that at each age, optimum investment in the child will be a positive function of the skills the child already possesses and that variance in investment will increase with age. The last two terms indicate the expectation that the value of parents' and others' time inputs will also be an increasing function of their own stock of embodied capital. This means that more skilled parents should invest more and that parents should also invest more in children who are receiving inputs from higher quality schools. The rate of capital embodiment is also written as a function of time, t. This is meant to indicate that the overall level of technology and knowledge in the society will impact the rate of capital acquisition and optimal levels of investment.

If this is true, it has important implications for the above model of supply and demand for embodied capital in the labor force. After one generation, not only will there be differences in the incomes of parents but also in the value of their time inputs. Now, the optimal level of investment in children may vary with income. It is easy to imagine a positive covariance between income of parents and the child's stock of human capital in early childhood, due to the positive covariance between income and the value of parental time inputs to children's development. Even if there are diminishing returns to parental time inputs, parents with more embodied capital may actually spend more time with children if the impact of their time is greater at each level than that of the time parents with less capital spend (as depicted in Figure 11).

If the value of later inputs, such as resources and time dedicated to education, is an increasing function of the child's stock of embodied capital, then the stock of capital in children will become increasingly divergent with age. This will also mean that the total costs of embodying a given amount of capital will be a *decreasing* function of the parent's stock of capital. Although the cost of the time parents invest in children will be greater as parental income increases, the increased efficiency of later inputs will compensate for the greater expense of time by higher earning parents. Total investment in embodied capital at the optimum will therefore be positively related, both directly and indirectly, to the stock of capital embodied in parents. To show this, I will apply this line of reasoning to the supply and demand model presented above.[16]

Parents will differ in embodied capital as a function of the skill required for their jobs. If the total cost of embodying skills in their children will be lower for more skilled parents, the cost (supply) curves for each type of wage labor in the next generation would include two levels for each type of parent, as depicted in Figure 12.[17] In the figure, the

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[16] These implications are drawn on the basis Becker's (1975) more general conclusions that the amount invested in human capital will be positively related to the rate of return on investment.

[17] Of course, these supply curves are not really independent of one another because the supply of one type will depend on the wage offered in the other type, but they are drawn to reflect the costs of acquiring the skills.

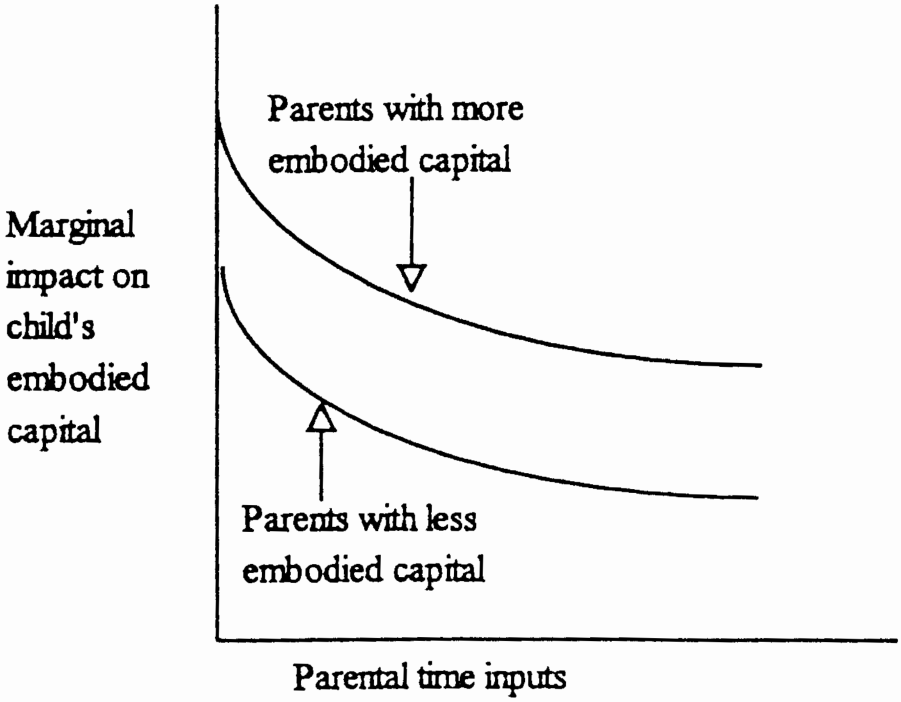

Fig. 11. Impacts of embodied capital of parents on the value of their time inputs.

x-axis is split into two sections, one for the children of more skilled parents and the other for the children of less skilled parents. There are two step functions, one representing the supply curve for more skilled laborers and the other for less skilled laborers. The step in the two curves represents the difference in the costs of embodied capital in children for the two types of parents. The way the two lines are drawn reflects the following assumptions: 1) the embodied-capital requirements of skilled jobs are greater and therefore the wage for more skilled laborers must be sufficiently higher than the wage for less skilled laborers (hence the supply curve for more skilled workers is everywhere above the supply curve for less skilled workers—otherwise no parents would be induced to support the investment in those skills); 2) it is cheaper for more skilled parents to produce skill in their children than for less skilled parents (hence the step in each curve); and 3) the difference in the costs for the two types of parents is greater for more skilled jobs than less skilled jobs (hence, C_M, the cost differential between the two jobs for children of more skilled parents, is smaller than C_L, the corresponding cost differential for the children of less skilled parents; and the step in the supply curve for the more skilled job is larger than in the curve for the less skilled job).

Superimposing the demand (marginal revenue) curves for the two types of workers produces a mixed equilibrium (see Fig. 13). The predicted equilibrium depends on the shape of both the supply and demand curves for each type of worker. Figure 13 shows one such equilibrium. In the figure, the demand curve for more skilled workers intersects the supply curve at a point that includes most, but not all, children of more skilled workers. The demand curve for less skilled workers intersects the supply curve at a point that includes most children of less skilled workers. The equilibrium wage for less skilled employment, marked by I_L, occurs at this intersection and will be *the monetary equivalent of the capital invested in the less skilled children of less skilled workers*. Even though some children of more skilled parents will elect the less skilled job, the equilibrium wage paid will be equal to the cost of acquiring those skills for the most expensive worker hired (i.e., a child of less skilled parents).

The equilibrium wage paid to skilled workers, I_M, marked by the intersection of

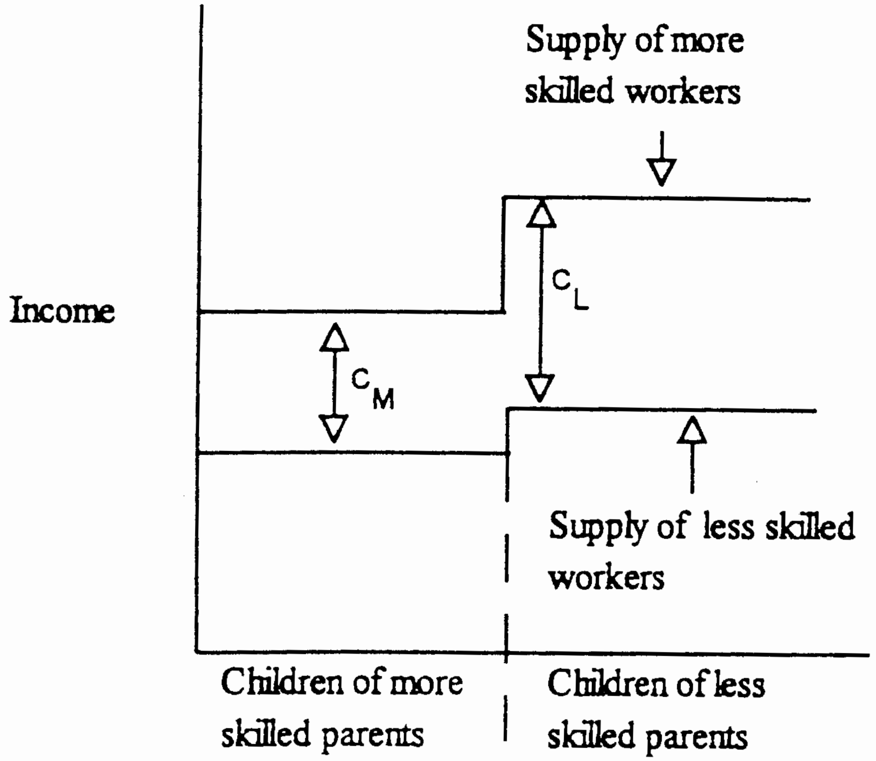

Fig. 12. Supply/cost curves for skilled and less skilled laborers in relation to skill levels of parents.

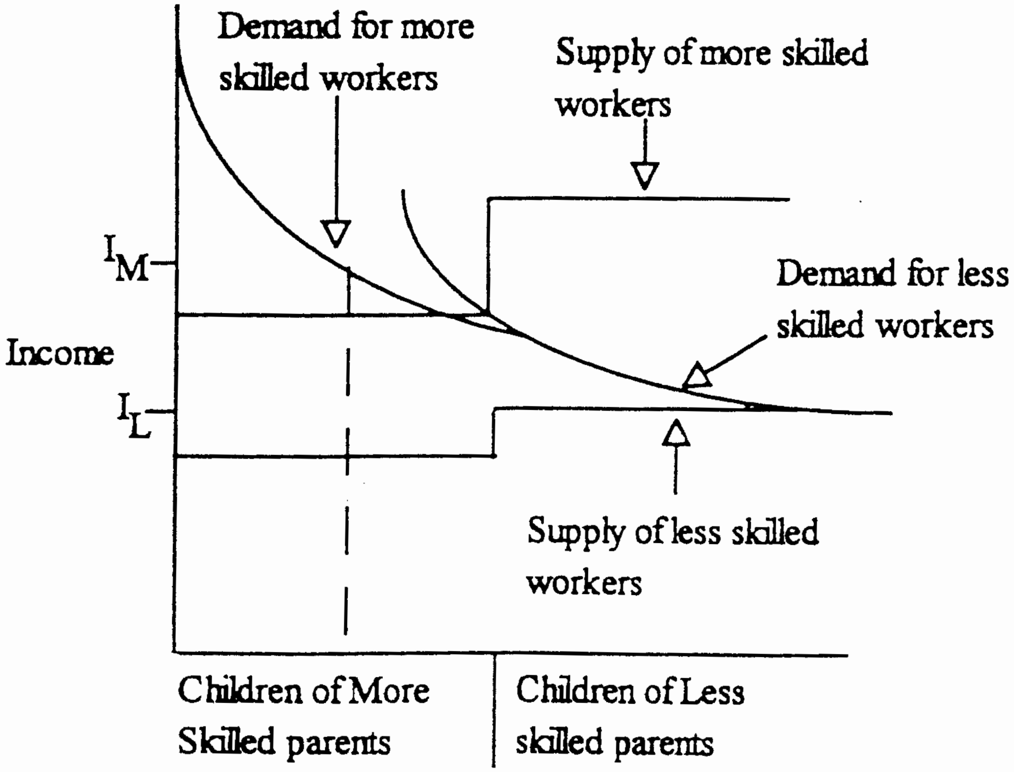

Fig. 13. Equilibrium wage rates for two skill levels with variation in skill levels of parents.

the demand curve with the dashed vertical line, will be slightly higher than the intersection of the demand curve with the cost curve. At the latter intersection, the wage difference between more and less skilled jobs is smaller than the difference in the costs of obtaining the skills for the two types of jobs, even for the children of skilled workers. This would induce some children of skilled workers to move to the less skilled jobs. This movement would, however, also drive up the wage for more skilled workers, since the demand would then exceed the supply. Movement would occur until the differences in wages equaled the differences in costs of skill embodiment. This is why the difference in the height of the two supply curves for the children of skilled parents is equal to the corresponding wage differential. Optimality requires that differences in wages of identical individuals (i.e., those with identical opportunities and return rates) who occupy jobs requiring different degrees of embodied capital should be equal to the differences in costs of acquiring that capital.

Changes in the shapes of the demand and supply curves would generate different equilibria for wages and the distribution of workers. For example, if the demand curve for more skilled workers shifter upward sufficiently, the new equilibrium would include some children of less skilled workers in the more skilled jobs.

The significant implication of Figure 13 is that the population distribution of fertility, parental investment and incomes in competitive labor markets will be determined by both demand and supply functions. The demand curves will reflect technologies of production and the attendant demands for workers with varying levels of skill. The shape of the supply curves will reflect population variance in rates of return to investment in embodied capital. The values of the cross-derivatives discussed above are critical for determining whether the model predicts a positive association between parental stocks of embodied capital and parental investments in children's stocks, and a corresponding association between children's incomes and parents' incomes. The lack of income differences in fertility requires that optimal investments increase linearly with income. If we denote optimal parental investment for the ith parent as $\bar{p}_i^0$ then equal numbers of children for all income levels requires that

$$\frac{\bar{p}_i^0}{\bar{p}_j^0} = \frac{I_i^0}{I_j^0} \approx \frac{I_i^1}{I_j^1}.$$

However, if embodied capital decreases the costs of embodying capital in offspring as well as increases income, the increased income necessary to motivate people to invest in higher levels of skills for offspring need not be as great as the fitness costs of obtaining those skills.

This within-population heterogeneity in the costs of embodying capital in children means that diminishing returns to parental investment are not determined by the environment as they would be in primary production economies, but rather by the population distribution of embodied capital production functions. First consider the highest skilled jobs in the economy. Those jobs would be filled by individuals with the lowest costs of skill acquisition in decreasing rank order until the point is reached when the next cheapest worker is more expensive than the product she produces. Her parents would therefore invest less in her than would be necessary to obtain the highest skilled jobs, and she would find employment in the next tier of skill. That tier would then be occupied by individuals in decreasing rank order until the next cheapest worker will not be paid enough to compensate for skill embodiment. This process would continue through the lowest skilled jobs in the economy.

Next, consider the related proposition that technological change in production will be positively related to the stock of embodied capital at the population level (Becker et al., 1990). If higher levels of general education of the population are associated with more rapid technical progress, the demand for more skilled workers will increase as more investment is made in education. Through time then, the demand for new levels of skill will grow. For the simple model, this would imply that skilled parents not only would have the option of producing children of equal or less skill, but will have the opportunity to reinvest the dividend from their own educational investments in even higher levels of skill for their children. As long as technology is constantly growing and generating demand for new levels of skill, sustained fertility reduction over many generations is possible.

Although the continual intergenerational reinvestment of dividends from investments in embodied capital seems hard to sustain indefinitely, it does seem consistent with the last century of technological growth and increasing investment in education (see, for example, Denison, 1985, Lesthaeghe and Wilson, 1986, and Lindert, 1986). In fact, there may be some "excess" return to education, especially at high levels, if there is a significant lag between increases in demand for skilled labor and corresponding increases in supply (see Fig. 6). Since the embodiment of skills takes time, some lags between demand and supply are likely. This would lead to higher rates of return to investments than would be expected at equilibrium. Such "excess" returns could drive fertility to a minimum level.

So far, I have considered only fertility *reduction* and not the quantitative level of fertility. I have also neglected the integer constraints on fertility and have treated fertility as if it were continuous. However, we know that minimum fertility greater than zero is one. If there were excess returns to investments in embodied capital, one might expect most people to have one child. Yet evidence suggests most people consider an only child to be undesirable and have a target fertility of two or three (see Fig. 5). There is also evidence, however, that only children do not differ in education and achievement from children raised in two-child families (Blake, 1989). Yet families with more than two children do show reductions in educational and income achievement (e.g. Blake, 1989, Kaplan et al., 1995). This suggests decreases in family size below two do not increase the total capital embodied by children.

This lack of effect may be due to several factors. Some of the costs of investment in embodied capital may be fixed (see Becker, 1991, for an analytical treatment of fixed and variable costs). The choice of a neighborhood to live in and the taxes paid for social services, including public education, are obvious examples of fixed costs. Thus the non-impact of a reduction from two to one child may reflect diminishing marginal returns to variable costs, as they represent an increasing proportion of total costs. This would be true if the two types of costs were not perfectly substitutable. Also, men in focus-group discussions in Albuquerque expressed the opinion that interactions with siblings were an important contribution to development, and that mutual assistance among siblings was helpful in attaining life goals. Regardless of the reasons for this lack of impact, there seems little positive incentive to reduce fertility below two. Moreover, since number of children is not continuous, a reduction of fertility below two requires a 50% change in fertility. This fact, coupled with the risk associated with the possible loss of an only child, creates a large disincentive. *Increasing returns to scale for increases in embodied capital, combined with a lack of increase in embodied capital with a reduction to one child, may be sufficient to account for the two-child family.*

Implications of the competitive labor market theory for empirical research and social policy

To summarize, the analysis of parental investments in competitive labor markets was combined with the evolutionary economic models presented above to suggest two characteristics of modern economies that might be sufficient to account for a period of sustained fertility reduction and to a corresponding lack of income variation in fertility. The first characteristic is the direct link between costs of investment and wage rates due to the forces of supply and demand for labor in competitive economies. The second is the increasing emphasis on cumulative knowledge, skills and technologies in the production of resources. These two characteristics may together produce the historically novel conditions that 1) investments in offspring income have nondecreasing (i.e., constant or increasing) returns to scale at the population level, and 2) embodied capital of parents is positively associated with returns to investment in embodied capital of children with diminishing returns at the individual level set by the within-population distribution of costs of skill embodiment.

These propositions generate a series of predictions. First, the principal effect of parental income on parental investment should be due to the education-based capital embodied in parents. Therefore within economic strata more educated parents should invest more in each child and should have lower fertility. Comparisons across occupational categories with similar incomes but differing levels of school-based skills (e.g. manual skills vs. clerical skills) should be useful in this regard. Conversely, holding parental skills, intelligence and knowledge constant, income should be positively associated with fertility (since optimal levels of investment should be constant, higher income allows for increased child quantity). Second, more academically able children should receive higher levels of investment (especially, school-related investment) than less able children, even within families (see Becker and Tomes, 1976, for a similar argument). Third, levels of investment at different stages of the child's development should be positively correlated with one another, contingent on the child's progress. The quantity and quality of early investments should positively affect early educational performance which should, in turn, positively affect later investments.

If these hypotheses are correct, they might explain the patterns of class mobility and ethnic differences in achievement in the US. Intergenerational correlations in income and scholastic achievement would be due to associations between parental capital and both the quality of early parental time inputs and the level of total investment during development. Stable ethnic differences, even in the face of equal access to high quality public education, should result from the above associations. Ethnic groups whose members entered this country with lower levels of academic skills (or who were prevented from obtaining those skills) may persistently experience lower levels of achievement over the generations, even without prejudice and social obstacles for educational achievement.

This view of embodied capital as the result of a production process contrasts with approaches to intelligence developed by psychometricians, such as Hernstein and Murray (1994). They argue that intelligence is a fundamental life-long attribute of a person. They admit that IQ scores are not very reliable for children younger than 6 years of age, but after that age, they are quite consistent within individuals. Presumably, the lack of early within-individual test-retest reliability is due to developmental considerations that are not associated with raw intelligence. I would argue, however, that intelligence is being "produced" during those early years of development. One input into the production process is the genetically heritable initial stock of embodied capital, E_0, but so too are interactions with parents and other features of the home environment. We cannot consider estimates of IQ, based on the scores of 6-year-olds, to be direct reflections of raw ability. While virtually all behavior geneticists would agree that there are environmental inputs to intelligence, the view expressed here suggests that intelligence is a form of produced embodied capital.

Nevertheless, the models presented here support Hernstein and Murray's (ibid.) suggestion that social mobility in skills-based labor markets produces cognitive sorting among income groups. In fact, if genetically heritable inputs into embodied capital increase the rates of return to both investment in own and offspring embodied capital, the process of cognitive sorting by income may be even more extreme than they imagined. If the view expressed here is correct, parent-offspring covariance in embodied capital will be due to both genetic covariance, and the covariance between own embodied capital and rates of return to investment in offspring embodied capital. The empirical analysis of those relationships will be a challenging and rewarding task.

These models, on the other hand, should make us more optimistic about the potential of compensatory programs to increase scholastic performance and later adult income of traditionally "underachieving" sectors of the society. There is considerable uncertainty as to the long-term effects of compensatory early education programs (Barnett, 1985; Consortium for Longitudinal Studies, 1983; Hood, 1992; Schweinhart et al., 1993; Zigler and Styfco, 1994). However, effects are measurable in such areas as dropout rates, delinquency, adult employment and marital stability, especially in the case of programs which are multidimensional, high quality, and involve parental participation. Becker and Tomes (1976) argue that compensatory programs may fail due to a decrease in parental investment in response to increases in government investment. However, our models suggest that parents will increase investment in children's educational development in response to the better academic performance stimulated by the compensatory program. Perhaps the empirical pattern of significant early improvements in scholastic ability produced by programs such as Head Start followed by later regression towards the mean is well explained by consideration of the cumulative nature of school-based knowledge acquisition (Consortium for Longitudinal Studies, 1983). Even though graduates of compensatory programs will have an advantage in the first years of school, they will again begin to fall behind if the assistance is not continued during primary and secondary school and if the quality of home and neighborhood inputs is low. Sustained compensatory programs may very well be effective, especially for children with high levels of natural ability. In addition, this model suggests the effectiveness of compensatory programs will depend on the skills and knoweldge embodied in the teachers and staff employed by those progarms (see Becker et al., 1990, for a similar line of reasoning). Traditionally, due to low levels of funding, those programs have not been able to offer competitive salaries to attract highly qualified personnel. Even the most qualified teachers in Head Start earn no more than $15,000 (Zigler and Styfco, 1994).

Similar predictions can be made regarding international differences in scholastic achievement. In less developed countries both parents and teachers have lower average levels of education-based capital. The theory would predict that for each year a child spends in school, she will learn less than her counterpart in a more developed country. This would lower the rate of return on investment in the child's education. Since wages for different levels of embodied capital are probably determined globally, the costs of obtaining skills in the developed world could set wage rates for the developing world, effectively pricing children of less educated parents out of the market. Thus would tend to cause a decrease in parental support for schooling in the developing world, further augmenting the difference. Firms with knowledge-intensive production technologies would preferentially locate where human capital is the least expensive to acquire, lowering the demand for educated workers in less developed countries and further lowering the payoffs to investment in education (see Becker et al., 1990, for an independent derivation of these results for understanding economic growth). The high fertility exhibited in developing countries, especially in rural areas, may be due to *low rates of return on investments in embodied capital.*

A minority of people in developing countries, however, do have access to high-quality education and are children of educated parents. This theory would predict that these individuals with high rates of return to education are most likely to pursue higher education. Therefore regressions of income on education, traditionally used to assess rates of return, would create the illusion of high rates of return to education in the developing world, even when they are really low for the majority. This may explain contradictory findings in the economic literature on rates of return to education in the developing world (see Lam and Schoeni, 1993, for a discussion).

The implication of this argument for development programs is that increased efficiency of human capital production may be the key to increasing educational achievement and attracting knowledge-based jobs to less developed countries. It also suggests that development programs must compensate for the low education of parents and the poor quality of school systems, if the goal is to reduce fertility and increase parental investment in the embodied capital of children. The theory would suggest that an emphasis on quality of education would automatically increase quantity of education through increased voluntary participation.

With respect to historical data, the timing of fertility transitions in specific areas should coincide with increased investment in education, increases in return rates to education, and increasing employement of skilled labor in production. There is evidence that in the last half of the 19th century (and in some places earlier), the practice of fertility limitation within marriage became widespread in the industrializing world (Coale, 1986; Knoedel, 1986; Van de Walle, 1986; Coale and Treadway, 1986). This was accomplished largely by abstinence, and later by other methods of birth control. The earliest reductions in fertility should be found in the sectors of society first engaged in school- and knowledge-based occupations (see Livi-Bacci, 1986, for some supporting evidence). At the initial stage of demographic transitions, the relationship between wages and fertility should be most negative, followed by a leveling out of the relationship as most occupations require some schooling (Retherford, 1993).

The graphic models presented here assume that increases in education of offspring are financed by decreases in parental fertility. It is also likely that increases in *own* education were financed through reductions in parental reproduction, perhaps mediated by postponement of reproduction. Both possibilities must be investigated empirically. The relative importance of the two should affect and reflect the timing of changes in educational attainment, changes in return rates to education and the financing of education.

The rise and fall of fertility associated with the North American baby boom provide an interesting test case. Data from the Albuquerque men sample show that pre- and postboom total fertility rates are almost identical (about one child less than during the boom period), and that age at first reproduction was much later for the pre- and postboom periods. If the graphic models are substantially correct, we should find that the reduction from three to two children during the lower fertility periods has a greater impact on both own and children's income than it does during the high-fertility period.

Variation within cohorts should reflect two processes which must be distinguished. First, some variation should be due to indifference between options in a mixed equilibrium. Some human capital acquisition may be financed by reductions in salaries early in adulthood in return for higher salaries later in adulthood (see Becker, 1975, for a detailed discussion). Therefore, lifetime incomes of individuals pursuing alternative patterns of income flow may actually be identical (after interest rates are taken into account), even though some will receive relatively high salaries early in adulthood while others show much more salary growth later in the life course. If the total incomes over time are equal, there may be no net fertility effect, even though the timing of reproduction may differ due to the timing of investments in capital. Second, individuals with similar incomes early in adulthood may actually have very different lifetime incomes if those with higher education also engage in on-the-job training. It is also possible that there may be alternative fertility-income combinations to which people are indifferent (determined by supply-demand equilibria in the labor market). These two effects could be responsible for the confusing pattern of results obtained in cross-sectional analyses of income and fertility. Analysis must clearly be focused on the pattern of income flow through the life course and its relationship to the timing of reproduction and total fertility.

Proximate mechanisms and deviations from fitness maximization

Both the data on modern fertility behavior and casual introspection suggest that most people do not attempt to maximize fitness consciously. The demographic transition is characterized by a fertility desire that is much lwoer than what the nutritional status-lactation system would produce. The above analysis suggests that the decrease in desired fertility associated with the demographic transition may be due to changing payoffs to investment in embodied capital and to the forces of supply and demand in labor markets. Those forces tend to compensate increased expenditures in embodied capital with income sufficient to make the marginal worker indifferent to a higher expenditure–higher income position and a lower expenditure–lower income position. However, it is possible that this response is not fitness-maximizing and current fertility is much lower than that which would maximize fitness.

People report that given their desired expenditures on self and on each child produced, their time-resource budgets do not allow more than two or three children (unpublished focus group discussions with men in Albuquerque). This suggests that the psychological and cultural processes regulating budget allocations are not well adapted to fitness maximization under current conditions. To see this, imagine the variant individual with a different allocation budget. This individual seeks housing, just large enough to accommodate her family. Four children share each bedroom. Furnishings are sparse and are of the cheapest quality. Each adult and child has two, perhaps three, changes of clothing. Food is purchased so that an optimal nutrient balance is maintained at the cheapest price. No resources are allocated to vacations and other "luxury" items. This individual invests enough so that her children survive at the same rate as do other children, go to the same schools that other children go to, and receive the same postsecondary education. Presumably, this individual with the same income as others in her neighborhood could raise many more children than do her neighbors.

People appear to believe that their children would suffer if they did not own a large wardrobe and electronic games and have their own bedroom. They also appear to believe that a significant proportion of their resources should be allocated to their own consumption in the form of clothing, vehicles, vacations, dining, stereos, and the like. It also appears as if we desire children in the same way we desire other consumer goods. We would be unhappy without children, but we are not motivated to maximize the production of descendants. In fact, as wealth has increased over the course of the last century, none of the increase has been allocated to increased fertility, and all has been allocated to increased consumption and investment in embodied capital. Such a motivational system may have maximized fitness in a hunting and gathering context when outlets for expenditures were few and directly related to offspring survival, self and offspring mating success, and the income for reproduction of self and offspring.

We understand very little about the psychological and cultural processes underlying current consumption patterns. In a hunting and gathering context, the principal forms of income are food, childcare time, and the treatment received from other members of the band. Selection on allocation mechanisms embodied in human brains must have been mediated through the effects of, and on, these three forms of income. The effects of the first two are relatively straightforward to consider. However, people in hunting and gathering groups appear to invest quite heavily in *social capital*, attributes stored in others that affect their treatment of an individual. The exchange of gifts and food, assistance in work, time allocated to socializing, and gossip all reflect the importance of social standing.

Today, income comes in different forms. Money can substitute for food, time and social status. However, resources and social status are measured in other currencies as well. Education and occupation appear to affect social status independent of income. Money spent on consumption also appears to affect social status. Thus it would appear that there is a translation problem. Our brains evolved to detect the impacts of alternative allocations of time and food to self and offspring. Now, they must track the effects of modern resources. We appear to be sensitive to the diminishing returns associated with each expenditure, but we overemphasize material expenditures that have no direct effects on fitness. Why this is so and to what extent is social status competition is involved remain questions for future investigation.

My suspicion is that in addition to the demographic transition, people, during last several thousand years of human history, may have experienced other conditions in many parts of the world that would have generated nonoptimal fertility behavior (cf., Hill, 1984). The problem arises when people notice that the fertility output of the nutritional-state system is too high for their desired parental investment behavior. With growing population density and agriculture, ownership of physical assets (particularly land) emerged, and parents realized that passing down assets to children could dramatically affect their adult outcomes. Given that there were probably economies of scale (the opposite of diminishing returns) associated with physical assets and social status, people often responded in two ways. One was to devise differential inheritance patterns, such as sex-biased inheritance and primogeniture, which effectively divides offspring into cheap and expensive categories (see Boone, 1986; Hrdy and Judge, 1993). The second was to control the age of marriage through asset transfers, and this was probably the first major form of cognitive control over fertility (i.e., parents deciding when their children could reproduce). While such decisions may have had desired effects on children's adult outcomes as well as on parents' own reproductive careers, they may not have been fitness-maximizing.

CONCLUSIONS

This paper has attempted to unite several independent research traditions and bodies of theory to develop a general approach to understanding human fertility and parental investment. The basic foundation for the analysis is life history theory and existing evolutionary biological models of optimal fertility regulation (Alexander, 1974; Blurton Jones, 1986; Blurton Jones et al., 1989; Borgerhoff Mulder, 1992; Charnov, 1993; Charnov and Krebs, 1974; Harpending et al., 1990; Hill, 1993; Hill and Hurtado, 1996; Hurtado et al., 1992; Lloyd, 1987; McGinley and Charnov, 1988; Pennington and Harpending, 1988; Rogers, 1990; Rogers and Blurton Jones, 1992; Smith and Fretwell, 1974). This tradition was combined with human capital theory in economics (Becker, 1975, 1991; Becker and Barro, 1988; Becker and Lewis, 1973; Becker et al., 1990; Becker and Tomes, 1986; Ben-Porath, 1967; de Tray, 1973; Mincer, 1974; Willis, 1973, 1987) to produce a more general theory of investments in embodied capital within and between generations. This synthesis allowed consideration of the impacts of parental investment on next-generation income for reproduction as well as on offspring survival, resulting in a series of optimality models to examine the decision processes underlying fertility and parental investment upon which natural selection is expected to act.

Optimality models are very useful tools for analyzing the evolution of physiological and behavioral traits. First, they allow the research to explicitly model the action of natural selection on traits when those traits are associated with both fitness benefits and costs. Second, they provide a yardstick against which actual behavior can be compared. If people's behavior deviates from predictions of the models, those deviations provide a basis for learning. One set of possibilities to consider is that the behavior is optimal, but model assumptions are incorrect. Another set is that evolved proximate mechanisms generate nonoptimal behavior in current conditions. The specific deviations from predictions should provide useful clues for further theory building and empirical work. The analysis of those optimality models showed that when the cost of achieving a given level of child quality is independent of number of children produced, maximizing total income for reproduction among offspring (i.e., summed over all offspring) is equivalent to maximizing fitness. Additional results are 1) optimal parental investment in offspring survival depends positively on optimal investment in offspring income, and vice versa, and 2) optimal fertility increases linearly with income and parental investment is independent of income, unless the payoffs to parental investment depend on parental income (as proposed in the case of modern competitive labor markets).

Although natural selection is an optimizing process (see Grafen, 1991, for a discussion), it is also an historical process with changing directions of selection and cumulative add-ons. Thus there is no reason to believe a priori that current designs are optimal. This caveat is especially critical for the analysis of modern human behavior, since people now live under conditions that are different from those characterizing the long stretches of hominid evolutionary history. For this reason, the analysis here proceeded in four steps (cf. Tooby and Cosmides, 1992).

The first step was to develop the optimality models for analyzing the action of natural selection on fertility and parental investment. The second step was to apply those models to the hunting and gathering lifeway. It is most likely that the proximate mechanisms underlying human physiology and behavior would produce optimal responses in hunting and gathering contexts, given that natural selection has acted on those mechanisms predominately among populations of foragers.[18] This analysis focused both on problems that all hunting and gathering peoples face and on the production of variable responses in relation to variable ecologies. It was proposed that hunter-gatherers adjust the length and intensity of the breastfeeding period to the quality of weaning foods and disease risk. The work effort of men, women and children is adjusted in relation to payoffs to maternal childcare, the relative efficiencies of men and women in the food quests, and the costs and benefits of child food production in terms of dangers, immediate productivity and future productivity.

The third step was to unite this consideration of optimal parental investment and fertility behavior in hunter-gatherers with existing models of the proximate determinants of human fertility (e.g., Bongaarts and Potter, 1983; Ellison, 1990, 1995; Ellison et al., 1989; Henry, 1961; Huffman et al., 1978; Leslie and Fry, 1981; Lewis et al., 1991; Lunn et al., 1984; Prentice and Whitehead, 1987; Worthman et al., 1993; see Wood, 1994, for a review). The analysis of proximate mechanisms was based on the idea that natural selection acts on the final phenotypic outcome of a coordinated system of physiological, psychological and cultural processes. It was proposed that physiological mechanisms are the direct proximate determinants of fertility in hunting and gathering societies, and these respond to lactational and nutritional status in women. The fertility outputs of physiological mechanisms that translate lactational and nutritional status depend on behavioral inputs that are the result of psychological decision processes and cultural traditions. Natural selection will act to co-adapt physiology and behavior because they jointly produce the fertility and offspring quality outcomes that directly determine fitness. Culture was analyzed as a store of beliefs and practices that acts to accumulate the experiences of many individuals through time, especially regarding the relationships between behavior and fitness-related outcomes. In that sense, it provides a set of behavioral rules for people to adopt as a first-guess approximation of the best behavioral strategy, but also responds to changing psychological evaluations of those relationships when conditions change.

The fourth step was to identify the important conditions affecting parental investment and fertility in modern socioeconomic contexts, and to propose an explanation of observed fertility and parental investment behavior in terms of the interaction of those conditions with the physiological and psychological mechanisms that evolved during our hunting and gathering history. This fourth step built on an existing tradition of identifying special features of modern life that produce deviations from fitness maximization (Barkow and Burley, 1980; Blurton Jones, 1989; Boyd and Richersen, 1985; Irons, 1983, 1990, 1993, 1995; Lancaster, in press; Lancaster and Lancaster, 1987; Perusse, 1993; Turke, 1989).

Barkow and Burley (1980), after considering and rejecting quality-quantity arguments, suggest that the historic novelty associated with low fertility is the emergence of conscious control over fertility by women. Their proposal combines three conditions. First, modern contraception allows conscious control over fertility.[19] Second, the high level of intelligence in humans, which was selected for other reasons, leads women to consciously desire fewer children than is their biological optimum. Third, conditions favoring women having the power to control their fertility must combine with the first two conditions to produce low fertility. I agree that high intelligence has a cost, be-

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[18] This is not to say that natural selection has not had sufficient time to act on agricultural populations to have a significant impact on human traits. The importance of the farming and herding lifeway in the evolution of some human traits has yet to be evaluated.

[19] In this and another paper (Burley, 1979), the author's argue that concealed ovulation is an adaptation to prevent women from exercising conscious control over fertility.

cause it can be used to recognize tradeoffs that are biologically irrelevant. However, my theory turns the causal arrow in the other direction. I would argue that efficient techniques for modern contraception were developed in response to the conscious desire to lower fertility, and that it is the changes in the economic system that produce this desire. Women in traditional societies desire much higher fertility than modern women and men.

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. Perusse presents evidence to show that in modern society, unmarried wealthier men have more sexual relations with potentially fertile women than do poorer men. However, because of contraception, they do not have higher fertility. I have argued elsewhere (Kaplan, 1993) that this argument begs the question of why wealthier men marry at higher rates. They willingly marry and produce few children. They also have relations with fewer other women than do wealthy unmarried men. The fertility desires of both men and women have dropped, and this fact must be explained.

Turke (1989) and Irons (1983), 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 and Lancaster, 1987; Lancaster, in press) suggests that parents increase investment in children and reduce their total number in order to enhance offspring competitiveness on the marriage market. These views are most similar to the one expressed here. Those earlier papers, however, are less explicit about the specific features of modernization that drive low fertility. The competitive labor market model provides one possible system-level causal process that drives parental investment to high levels.

Turke (1989) also suggests that the breakdown of extended kin networks lowers fertility because the costs of child rearing are paid directly by parents. Again, I would reverse the causal direction here. Skill-differentiated labor markets tend to favor geographic mobility because both the opportunities for acquiring skills (e.g. universities) and the location of industries are not uniformly distributed across space. Moreover, as embodied capital becomes the primary asset that people possess and as financial markets for borrowing and saving become well developed, there is less need to depend on kin for the buffering of risk and for storing social assets. Thus, it is the emergence of those markets that drives both lower fertility and the breakdown of kin networks.

Boyd and Richersen (1985, P. Richersen, personal communication) provide an 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 ("indirect bias" in their terminology) 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. My theory, in contrast, proposes that most individuals explicitly recognize the tradeoff between fertility and their children's adult outcomes (and this was evident in focus group discussions with men in Albuquerque), and therefore they strategize individually to determine their behavior. This is not to say that people do not observe the outcomes of others and associated those outcomes with their behavior, but that they do not blindly model the behavior of the more successful individuals.

To summarize, I proposed that skills-based competitive labor markets increased the value of parental investment in children and motivate better educated, higher income parents to invest more per child than their less educated, lower earning counterparts. The analysis underlying this proposal also led to a series of predictions about cultural variation in parental investment and fertility within developed societies and about the pattern of fertility change in the developing world. It was also suggested that the deviation from fitness maximization associated with low modern fertility is due to excess expenditures on both own and offspring consumption, indicating that our evolved psychology is responding to cues in the modern environment that are not directly related to the fitness impacts of consumption.

While many of these proposals eventually may be refuted by empirical evidence, I hope that this analysis has showed the promise of a more unified approach to the field of anthropology.

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LITERATURE CITED

Alexander RD (1974) The evolution of social behavior. Ann. Rev. Ecol. System. *5*:325–383.

Barkow JH, and Burley N (1980) Human fertility, evolutionary biology, and the demographic transition. Ethol. Sociobiol. *1*:163–180.

Barkow J (1989) Darwin, Sex, and Status. Toronto: Toronto University Press.

Barnett WS (1985) The Perry Preschool Program and its long-term effects: A benefit-cost analysis. High/Scope Early Childhood Policy Papers No. 2. Ypsilanti, MI: High/Scope Educational Research Foundation.

Becker GS (1975) Human Capital. 2nd ed. New York: Columbia University Press.

Becker GS (1991) A Treatise on the Family. 2nd ed. Cambridge, MA: Harvard University Press.

Becker GS, and Barro RJ (1988) A reformulation of the economic theory of fertility. Q. J. Econ. *103*:1–25.

Becker GS, and Lewis HG (1973) Interaction between quantity and quality of children. In TW Schultz (ed.): Economics of the Family: Marriage, Children, and Human Capital. Chicago: University of Chicago Press, pp. 81–90.

Becker GS, and Tomes N (1976) Child endowments and the quantity and quality of children. J. Political Econ. *84*:s143–s163.

Becker GS, and Tomes N (1986) Human capital and the rise and fall of families. J. Labor Econ. *4*:s1–s39.

Becker GS, Murphy KM, and Tamura R (1990) Human capital, fertility and economic growth. J. Political Econ. *98*:s12–s37.

Ben-Porath Y (1967) The production of human capital and the life cycle of earnings. J. Political Econ. *75*:352–365.

Betzig LL (1986) Despotism and Differential Reproduction: A Darwinian View of History. Hawthorne, NY: Aldine.

Blake, J (1989) Family Size and Achievement. Los Angeles: University of California Press.

Blurton Jones NG (1986) Bushman birth spacing: A test for optimal interbirth intervals. Ethol. Sociobiol. *7*:91–105.

Blurton Jones NG (1987) Bushman birth spacing: A direct test of simple predictions. Ethol. Sociobiol. *8*:183–203.

Blurton Jones NG, and Sibly RM (1978) Testing adaptiveness of culturally determined behavior: Do Bushman women maximize their reproductive success by spacing births widely and foraging seldom? In NG Blurton Jones and V Reynolds (eds.): Human Behavior and Adaptation. London: Taylor and Francis, pp 135–157.

Blurton Jones NG, Hawkes K, and O'Connell JF (1989) Modeling and measuring the costs of children in two foraging societies. In V Standen and R. Foley (eds.): Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals. Oxford: Blackwell.

Blurton Jones NG, Hawkes K, and Draper P (1994a) Foraging returns of !Kung adults and children: Why didn't !Kung children forage? J. Anthropol. Res. *50(3):*217–248.

Blurton Jones NG, Hawkes K, and Draper P (1994b) Differences between Hadza and !Kung children's work: Affluence or practical reason? In ES Burch Jr and LJ Ellanna (eds.): Key Issues in Hunter-Gatherer Research. Oxford: Berg, pp. 189–215.

Bock J (1995) The Determinants of Variation in Children's Activities in a Southern African Community. PhD dissertation, Department of Anthropology, University of New Mexico.

Bongaarts J, and Potter RG (1983) Fertility, Biology and Behavior: An Analysis of Proximate Determinants. New York: Academic.

Boone J (1986) Parental investment and elite family structure in preindustrial states: A case study of late medieval-early modern Portuguese genealogies. Am. Anthropol. *88:*859–878.

Borgerhoff Mulder M (1987) On cultural and reproductive success: Kipsigis evidence. Am. Anthropol. *89:* 617–634.

Borgerhoff Mulder M (1988) Reproductive consequences of sex-biased inheritance for the Kipsigis. In V Standen and R Foley (eds.): Comparative Socioecology of Mammals and Man. London: Blackwell, pp. 405–427.

Borgerhoff Mulder M (1992) Reproductive decisions. In EA Smith and B Winterhalder, (eds.): Evolutionary Ecology and Human Behavior. Hawthorne, NY: Aldine de Gruyter, pp 339–374.

Boyd R, and Richersen PJ (1985) Culture and the Evolutionary Process. Chicago: University of Chicago Press.

Burley N (1979) The evolution of concealed ovulation. Am. Nat. *114:*835–858.

Chagnon N (1988) Life histories, blood revenge, and warfare in a tribal population. Science *239:*985–992.

Chaing AC (1981) Fundamental Methods of Mathematical Economics. New York: McGraw-Hill.

Charlesworth B (1980) Evolution in Age Structured Populations. Cambridge: Cambridge University Press.

Charnov EL (1993) Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology. New York: Oxford University Press.

Charnov EL, and Krebs JR (1974) On clutch size and fitness. Ibis *116:*217–219.

Clutton-Brock TH (1991) The Evolution of Parental Care. Princeton, NJ: Princeton University Press.

Coale AJ (1986) The decline of fertility in Europe since the eighteenth century as a chapter in human demographic history. In AJ Coale and SC Watkins (eds): The Decline of Fertility in Europe. Princeton, NJ: Princeton University Press, pp 1–30.

Coale AJ, and Treadway R (1986) A summary of the changing distribution of overall fertility, marital fertility, and the proportion married in the provinces of Europe. In AJ Coale and SC Watkins (eds): The Decline of Fertility in Europe. Princeton, NJ: Princeton University Press, pp 31–181.

Consortium for Longitudinal Studies (1983) As the Twig is Bent: Lasting Effects of Preschool Programs. Hillsdale, NJ: Erlbaum.

Cromer A (1993) Uncommon Sense: The Heretical Nature of Science. New York: Oxford.

Cronk L (1991a) Human behavioral ecology. Ann. Rev. Anthropol. *20:*25–53.

Cronk L (1991b) Wealth, status and reproductive success among the Mukogodo. Am. Anthropol. *93:* 345–360.

Daan S, Dijkstra C, and Tinbergen J (1990) Family planning in the kestrel (*Falco tinnunculus*): The ultimate control of covariation of laying date and clutch size. Behavior *114:*83–116.

Denison EF (1985) Trends in American Growth, 1929–1982. Washington, DC: Brookings Institute.

De Tray DN (1973) Child quality and the demand for children. J. Political Econ. 82:S70–S95.

Dijkstra C, Bult A, Bijlsma S, Daan S, Mejier T, and Zijlstra M (1990) Brood size manipulations in the kestrel (*Falco tinnunculus*): Effects on offspring and parent survival. J. Anim. Ecol. *59:*269–286.

Dixit AK (1990) Optimization in Economic Theory. 2nd ed. Oxford: Oxford University Press.

Downey DB (1995) When bigger is not better: Family size, parental resources, and children's educational performance. Am. Sociol. Rev. *60:*746–761.

Draper P (1975) !Kung women: Contrasts in sexual egalitarianism in foraging and sedentary contexts. In R Reiter (ed.): Toward an Anthropology of Women. New York: Monthly Review Press, pp. 77–109.

Draper P (1976) Social and economic constraints on child life among the !Kung. In RB Lee and I DeVore (eds.): Kalahari Hunters and Gatherers. Cambridge, MA: Harvard University Press, pp. 199–217.

Draper P, and Harpending H (1987) Parental investment and the child's environment. In J Lancaster, J Altmann, A Rossi, and L Sherrod (eds.): Parenting across the lifespan: Biosocial Dimensions. New York: Aldine, pp, 207–235.

Ellison P (1990) Human ovarian function and reproductive ecology: New hypotheses. Am. Anthropol. *92:*933–954.

Ellison P (1995) Understanding natural variation in human ovarian function. In RIM Dunbar (ed.): Human Reproductive Decisions: Biological and Social Perspectives. London: MacMillan.

Ellison PT, Peacock NR, and Lager C (1989) Ecology and ovarian function among Lese women of the Ituri forest. Am. J. Phys. Anthropol. *78:*519–526.

Feistner ACT, and McGrew WC (1989) Food-sharing in primates: A critical review. In PK Seth and S Seth (eds.): Perspectives in Primate Biology. New Delhi: Today and Tomorrows Printers and Publishers, pp. 21–36.

Flinn M (1986) Correlates of reproductive success in a Caribbean village. Ethol. Sociobiol. *9:*1–29.

Grafen A (1991) Modeling in behavioural ecology. In JR Krebs and NB Davies (eds.): Behavioral Ecology: An Evolutionary Approach. 3rd ed. Oxford: Blackwell Scientific, pp. 5–31.

Hamilton WD (1964) The genetical evolution of social behavior. J. Theor. Biol. *7:*1–52.

Hanson LA (1982) The mammary gland as an immunological organ. Immunol. Today *3:*168–172.

Harpending JC, Draper P, and Pennington R (1990) Cultural evolution, parental care, and mortality. In A Swedlund and G Armelegos (eds.): Health and Disease in Traditional Societies. South Hadley, MA: Bergin and Garvey, pp 241–255.

Hart B, and Risley T (1995) Meaningful Differences in the Everyday Experience of Young American Children. Baltimore: Brookes.

Hawkes K, O'Connell J, and Blurton Jones N (1989) Hardworking Hadza grandmothers. In V Standen and RA Foley (eds.): Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals. London: Basil Blackwell, pp 341–366.

Hawkes K, O'Connell JF, and Blurton Jones N (1995) Hadza children's foraging: Juvenile dependency, social arrangements and mobility among hunter-gatherers. Curr. Anthropol. *6(4)*:688–700.

Henry L (1961) Some data on natural fertility. Eugenics Q. *8*:81–91.

Hernstein RJ, and Murray C (1994) The Bell Curve: Intelligence and Class Structure in American Life. New York: Free Press.

Hill J (1984) Prestige and reproductive success in man. Ethol. Sociobiol. *5*:77–95.

Hill K (1982) Hunting and hominid evolution. J. Human Evol. *11*:521–544.

Hill K (1993) Life history theory and evolutionary anthropology. Evol. Anthropol. *2*:78–88.

Hill K, and Hurtado AM (1996) Ache Life History: The Ecology and Demography of a Foraging People. Hawthorne, NY: Aldine de Gruyter Press.

Hoff-Ginsberg E, and Tardiff T (1995) Socioeconomic Status and Parenting. In M Bornstein (ed.): The Handbook of Parenting. Vol. 2. Hillsdale, NJ: Erlbaum.

Hood J (1992) Caveat Emptor: The Head Start Scam. Policy Analysis No. 187. Washington, DC: Cato Institute.

Howie PW, Forsyth JS, Ogston SA, Clark A, and Florey CduV (1990) Protective effect of breast feeding against infection. Br. Med. J. *300*:11–16.

Huffman SL, Chowdhury AMK, Chakborty J, and Mosley WH (1978) Nutrition and postpartum amenorrhea in rural Bangladesh. Popul. Studies *32*:251–260.

Hughes A (1986) Reproductive success and occupational class in eighteenth-century Lancashire, England. Soc. Biol. *33*:109–15.

Hrdy SB, and DS Judge (1993) Darwin and the puzzle of primogeniture. Hum. Nature *4*:1–45.

Hurtado A, and Hill K (1990) Seasonality in a foraging society: Variation in diet, work effort, fertility and the sexual division of labor among the Hiwi of Venezuela. J. Anthropol. Res. *46*:293–345.

Hurtado A, Hill K, Kaplan H, and Hurtado I (1992) Tradeoffs between female food acquisition and child care among Hiwi and Ache foragers. Hum. Nature *3*:185–216.

Intrilligator M (1970) Mathematical Optimization and Economic Theory. Englewood Cliffs, NJ: Prentice-Hall.

Irons W (1979) Cultural and biological success. In N Chagnon and W Irons (eds.): Evolutionary Biology and Human Social Behavior. North Scituate, MA: Duxbury, pp. 257–272.

Irons W (1983) Human female reproductive strategies. In SK Wasser (ed.): Social Behavior of Female Vertebrates. New York: Academic, pp 169–213.

Irons W (1990) Let's make our perspectives broader rather than narrower: A comment on Turke's "Which Humans Behave Adaptively, and Why Does it Matter?" and on the so-called DA-DP debate. Ethol. Sociobiol. *11*:361–375.

Irons W (1993) Monogamy, contraception, and the cultural and reproductive success hypothesis. Behav. Brain Sci. *16*:295–296.

Irons W (1995) Cultural and Reproductive Success in Traditional Societies. Unpublished manuscript. Department of Anthropology, Northwestern University.

Jones RE, and Palloni A (1994) Investigating the determinants of postpartum amenorrhea using a multistate hazards model approach. Ann. N.Y. Acad. Sci. *709*:227.

Kaplan H (1993) The problem of resource accrual and reproduction in modern human populations remains an unsolved evolutionary puzzle. Behav. Brain Sci. *16*:297–298.

Kaplan H (1994a) Evolutionary and wealth flows theories of fertility: Empirical tests and new models. Popul. Dev. Rev. *20*:753–791.

Kaplan H (1994b) A Theory of Human Parental Investment and Fertility. Department of Anthropology, University of New Mexico, Albuquerque.

Kaplan H (1996a) The Evolution of the Human Life Course. Unpublished manuscript. Department of Anthropology, University of New Mexico, Albuquerque.

Kaplan H (1996b) The Competitive Labor Market Theory of the Demographic Transition and the Evolutionary Economics of Human Fertility and Parental Investment. Unpublished manuscript. Department of Anthropology, University of New Mexico, Albuquerque.

Kaplan H, and Hill K (1985a) Food sharing among Ache foragers. Curr. Anthropol. *26*:223–245.

Kaplan H, and Hill K (1985b) Hunting ability and reproductive success among male Ache foragers. Curr. Anthropol. *26*:131–133.

Kaplan H, Lancaster JB, Bock J, and Johnson S (1995) Does observed fertility maximize fitness among New Mexican Men? A test of an optimality model and a new theory of parental investment in the embodied capital of offspring. Hum. Nature *6*:325–360.

Kelly R (1995) The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways. Washington, DC: Smithsonian Institution Press.

Knoedel J (1986) Demographic transitions in German villages. In AJ Coale and SC Watkins, (eds.): The Decline of Fertility in Europe. Princeton, NJ: Princeton University Press, pp. 337–389.

Kozlowski J, (1992) Optimal allocation to growth and reproduction: Implications for age and size at maturity. Trends Ecol. Evol. *7*:15–19.

Kozlowski J, and Wiegert RG (1986) Optimal allocation of energy to growth and reproduction. Theor. Popul. *29*:16–37.

Kozlowski J, and Wiegert RG (1987) Optimal age and size at maturity in annuals and perennials with determinate growth. Evol. Ecol. *1*:231–244.

Lack D (1954) The Natural Regulation of Animal Numbers. Oxford: Oxford University Press.

Lack D (1968) Ecological Adaptations for Breeding in Birds. London: Methuen.

Lam D (1986) The dynamics of population growth, differential fertility, and inequality. Am Econ. Rev. *76:*1103–1116.

Lam D, and Schoeni RF (1993) Effects of family background on earnings and returns to schooling: Evidence from Brazil. J. Political Econ. *101:*710–740.

Lancaster JB (in press) An evolutionary history of human reproductive strategies and the status of women in relation to population growth and social stratification. In PA Gowaty (ed.): Evolution and Feminism. New York: Chapman and Hall.

Lancaster JB, and Kaplan H (1991) Human mating and family formation strategies: The effects of variability among males in quality and the allocation of male effort and parental investment. In A Ehara, T Kimura, O Takenaka, and M Iwamoto (eds.): Primatology Today. Amsterdam: Elsevier.

Lancaster JB, and Lancaster CS (1987) The watershed: Change in parental-investment and family-formation strategies in the course of human evolution. In JB Lancaster, J Altmann, AS Rossi, and LR Sherrod (eds.): Parenting Across the Life Span: Biosocial Dimensions. Hawthorne, NY: Aldine de Gruyter, pp 187–205.

Lancaster JB (1968) Mathematical Economics. New York: Macmillian.

Lantz P, Partin M, and Palloni A (1992) Using retrospective surveys for estimating the effects of breastfeeding and childspacing on infant and child mortality. Popul. Studies *46:*121–139.

Lee PC, Majluf P, and Gordon IJ (1991) Growth, weaning and maternal investment from a comparative perspective. J. Zool. (Lond.) *225:*99–114.

Lee RB (1979) The !Kung San: Men, Women and Work in a Foraging Society. Cambridge: Cambridge University Press, p. 236.

Leslie PW, and Fry PH (1989) Extreme seasonality of births among nomadic Turkana pastoralists. Am. J. Phys. Anthropol. *79:*103–115.

Lessells CM (1991) The evolution of life histories. In JR Krebs and NB Davies (eds.): Behavioral Ecology: An Evolutionary Approach. 3rd ed. Oxford: Blackwell Scientific, pp. 32–68.

Lesthaeghe R, and Wilson C (1986) Modes of production, secularization, and the pace of fertility decline in western Europe, 1870–1930. In AJ Coale and SC Watkins (eds.): The decline of Fertility in Europe. Princeton: Princeton University Press, pp. 261–292.

Lewis PR, Brown JB, Renfree MB, and Short RV (1991) The resumption of ovulation and menstruation in a well-nourished population of women breastfeeding for an extended period of time. Fertil. Steril. *55:*529–536.

Linden M, and Moller A (1989) Cost of reproduction and covariation of life history traits in birds. TREE *4:*367–371.

Lindert PH (1986) Unequal English wealth since 1670. J. Political Econ. *94:*1127–1162.

Livi-Bacci M (1986) Social-group forerunners of fertility control in Europe. In AJ Coale and SC Watkins (eds.): The Decline of Fertility in Europe. Princeton, NJ: Princeton University Press, pp. 182–200.

Lloyd DC (1987) Selection of offspring size at independence and other size-versus-number strategies. Am. Nat. *129:*800–817.

Low B (1990) Occupational status, landownership, and reproductive behavior in 19th-century Sweden: Tuna Parish. Am. Anthropol. *92:*457–468.

Lunn P, Austin S, Prentice AM, and Whitehead R (1984) The effect of improved nutrition on plasma prolactin concentrations and postpartum infertility in lactating Gambian women. Am. J. Clin. Nutr. *39:*227–235.

McGinley MA, and Charnov EL (1988) Multiple resources and the optimal balance between size and number of offspring. Evol. Ecol. 2:77–84.

McGrew WC, and Feistner ATC (1992) Two nonhuman primate models for the evolution of human food sharing: Champanzees and callitrichids. In JH Barkow, L Cosmides, and J. Tooby (eds): The Adapted Mind: Evolutionary Psychology and the Generation of Culture. New York: Oxford University Press, pp. 229–248.

Mealey L (1985) The relationship between social status and biological success: A case study of the Mormon religious hierarchy. Ethol. Sociobiol. *11:*83–95.

Mincer J (1974) Schooling, Experience and Earnings. Chicago: National Bureau of Economic Research.

Oftedal OT (1984) Milk composition, milk yield and energy output at peak lactation: A comparative review. Symp. Zool. Soc. Lond. *51:*33–85.

Palloni A, Aguirre G, and Lastiri S (1994) The effects of breast-feeding and the pace of childbearing on early childhood mortality in Mexico. Bulletin of Paho *28:*93–110.

Pennington R, and Harpending H (1988) Fitness and fertility among the Kalahari !Kung. Am. J. Phys. Anthropol. *77:*303–319.

Perusse D (1993) Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels (with comments). Brain Behav. Sci. *16:*267–323.

Prentice A, and Whitehead R (1987) The energetics of human reproduction. Symp. Zool. Soc. Lond. *57:* 275–304.

Retherford RD (1993) Demographic Transition and the Evolution of Intelligence: Theory and Evidence. Unpublished manuscript. Program on Population, East-West Center, Honolulu, Hawaii.

Roff DA (1986) Predicting body size with life history models. Bioscience *36:*316–323.

Roff DA (1992) The Evolution of Life Histories: Theory and Analysis. New York: Chapman Hall.

Rogers AR (1990) Evolutionary Economics of Human Reproduction. Ethol. Sociobiol. *11:*479–495.

Rogers AR (1994) Evolution of time preference by natural selection. Am. Econ. Rev. *84:*460–481.

Rogers AR, and Blurton Jones NG (1992) Allocation of Parental Care. Department of Anthropology, University of Utah, Salt Lake City, unpublished manuscript.

Schweinhart LJ, Barnes HV, and Weikart DP (1993) Significant Benefits: The High/Scope Perry Preschool Study through Age 27. Monographs of the High/Scope Education Research Foundation, No. 10. Ypsilanti, MI: High/Scope Press.

Sheard NF, and Walker WA (1988) The role of breast milk in the development of the gastrointestinal tract. Nutr. Rev. *46*:1–8.

Short RV (1984) Breast feeding. Sci. Am. *250*:35–41.

Silk JB (1978) Patterns of food-sharing among mother and infant chimpanzees at Gombe National Park, Tanzania. Folia Primatol. *29*:129–141.

Simms S (1984) Aboriginal Great Basin Foraging Strategies: An Evolutionary Approach. Ph.D. Dissertation, University of Utah.

Simons JL (1974) The Effects of Income on Fertility. Chapel Hill, NC: Carolina Populations Center.

Smith CC, and Fretwell SD (1974) The Optimal Balance Between Size and Number of Offspring. Am. Nat. *108*:499–506.

Stearns SC (1992) The Evolution of Life Histories. New York: Oxford University Press.

Stearns SC, and Koella J (1986) The evolution of phenotypic plasticity in life history traits: Predictions for norms of reaction for age- and size-at-maturity. Evolution *40*:893–913.

Teleki G (1973) The Predatory Behavior of Wild Chimpanzees. Lewisburg, PA: Bucknell University Press.

Tomes N (1978) A Model of Child Endowments and the Quality and Quantity of Children. PhD dissertation, Department of Economics, University of Chicago.

Tooby J, and Cosmides L (1992) The psychological foundations of culture. In JH Barkow, L Cosmides, and J Tooby (eds.): The Adapted Mind: Evolutionary Psychology and the Generation of Culture. New York: Oxford University Press. pp. 19–136.

Tooby J, and Devore I (1987) The reconstruction of hominid behavioral evolution through strategic modeling. In W Kinzey (ed.): The Evolution of Human Behavior: Primate Models. Albany: SUNY Press, pp. 183–237.

Turke PW (1989) Evolution and the demand for children. Popul. Dev. Rev. *15*:61–90.

Turke P, and Betzig L (1985) Those who can do: Wealth, status and reproductive success on Ifaluk. Ethol. Sociobiol. *6*:79–87.

Van de Walle F (1986) Infant mortality and the European demographic transition. In AJ Coale and SC Watkins (eds.): The Decline of Fertility in Europe. Princeton, NJ: Princeton University Press, pp. 201–33.

van Schaik CP (1989) The ecology of social relationships amongst female primates. In V Standen and RA Foley (eds.): Comparative Socioecology. Oxford: Blackwell, pp. 195–218.

Varian HR (1992) Microeconomic Analysis. 3rd ed. New York: W.W. Norton.

Vining DR Jr (1986) Social versus reproductive success: The central theoretical problem of human sociobiology. Behav. Brain Sci. *9*:167–216.

Vitzthum V (1994) Comparative study of breastfeeding structure and its relation to human reproductive ecology. Ybk Phys. Anthropol. *37*:307–349.

Voland E (1990) Differential reproductive success with the Krummerhorn population (Germany, 18th and 19th centuries). Behav. Ecol. Sociobiol. *26*:65–72.

Whitehead RG, and Paul A (1981) Infant growth and human milk requirements: A first approach. Lancet *2*:161–163.

Willis RJ (1973) A new approach to the economic theory of fertility behavior. J. Political Econ. *81*:S14–S64.

Willis R (1987) Wage determinants: A survey and reinterpretation of human capital earnings functions. In O Ashenfelter and R Layard (eds.): Handbook of Labor Economics. Amsterdam: North Holland, pp. 525–602.

Wood JW (1994) Dynamics of Human Reproduction: Biology, Biometry and Demography. New York: Aldine de Gruyter.

Worthman C, Jenkins C, Stallings J, and Lai D (1993) Attenuation of nursing-related ovarian suppression and high fertility in well-nourished, intensively breastfeeding Amele women of lowland Papua New Guinea. J. Biosoc. Sci. *25*:425–443.

Zigler E, and Styfco SJ (1994) Head Start: Criticisms in a constructive context. Am. Psychol. *49*:127–132.

MATHEMATICAL APPENDIX

Part I

The Lagrangian method of constrained optimization combines the partial direct and indirect effects of the choice variables on the objective function to be maximized with their effects on the budget constraint (see Chaing, 1981, Lancaster, 1968, Dixit, 1990, Intrilligator, 1970, for introductions to the technique). In this case, λ can be interpreted as the marginal fitness return of a unit of income at the optimum.

Since the solution of the choice variables for maximizing a monotonic transform of fitness will be the same as that for maximizing fitness, we can write the Lagrangian function (L) for maximizing log fitness as

$$\underset{b^0, i^0_s, i^0_t}{\text{Max}}\, \text{L} = \log \text{W} + \lambda(I^0_r - \text{b}^0(k^0 + i^0_s + i^0_t))$$

$$= \sum_{t=0}^{\omega}(\ln b^t + \ln s^{t-1}) + \lambda(I^0_r - b^0(k^0 + i^0_s + i^0_t)). \quad \text{(A1)}$$

Setting the partial derivatives of the Lagrangian function with respect to b^0, i^0_s and i^0_t, respectively, equal to zero leads to the following first-order necessary conditions for an interior solution[A1]:

[A1] Second order conditions require that second derivatives of investments in offspring survival and income are characterized by diminishing returns to scale in the neighborhood of the optimum, i.e.,

$$\frac{\partial^2 s^1_s}{\partial(i^0_s)^2}, \frac{\partial^2 I^1}{\partial(i^0_t)^2} << 0.$$

$$0 = \frac{\partial \log \mathrm{L}}{\partial b^0} = \frac{1}{b^0} - \lambda(k^0 + i_s^0 + i_i^0) \text{ or}$$

$$\lambda = \frac{1}{b^0\,(k^0 + i_s^0 + i_i^0)}$$

$$0 = \frac{\partial \log \mathrm{L}}{\partial i_{s,1}^0} = \frac{1}{s_\alpha^1} \cdot \frac{\partial s_\alpha^1}{\partial i_s^0} - \lambda\, b^0 \text{ or}$$

$$\lambda = \frac{1}{b^0 \cdot s_\alpha^1} \frac{\partial s_\alpha^1}{\partial i_s^0}$$

$$0 = \frac{\partial \log \mathrm{L}}{\partial i_i} = \frac{\partial \log \mathrm{W}}{\partial I^1} \frac{\partial I^1}{\partial i_i^0} - \lambda\, b^0$$

$$= \frac{1}{I^1} \frac{\partial I^1}{\partial i_i^0} - \lambda\, b^0 \text{ or } \lambda = \frac{1}{b^0} \frac{1}{I^1} \frac{\partial I^1}{\partial i_i^0}.$$

The calculus leading to these conditions is straightforward except in the case of the impacts of investments in the adult income of offspring. The adult income of offspring does not figure directly in the fitness function. It will be invested in next generation offspring and distributed among fixed costs of fertility, investments in survival and investments in adult income. Thus, we have a chain of effects (see Fig. 2):

$$\frac{\partial \log \mathrm{W}}{\partial I^1} = \frac{\frac{\partial b^1}{\partial I^1}}{b^1} + \frac{\frac{\partial s_\alpha^2}{\partial I^1}}{s_\alpha^2} + \frac{\partial I^2}{\partial I^1}\left(\frac{\frac{\partial b^2}{\partial I^2}}{b^2} + \frac{\frac{\partial s_\alpha^3}{\partial I^1}}{s_\alpha^3}\right)$$

$$+ \ldots \prod_{t=1}^{w-2} \frac{\partial I^{t+1}}{\partial I^t}\left(\frac{\frac{\partial b^{w-1}}{\partial I^{w-1}}}{\partial^{w-1}} + \frac{\frac{\partial s_\alpha^w}{\partial I^{w-1}}}{s_\alpha^w}\right)$$

$$\frac{\frac{\partial b^1}{\partial I^1}}{b^1} + \frac{\frac{\partial s_\alpha^2}{\partial I^1}}{s_\alpha^2} + \sum_{i=1}^{w-1}$$

$$\left[\left(\frac{\frac{\partial b^i}{\partial I^i}}{b^i} + \frac{\frac{\partial s_\alpha^{i+1}}{\partial I^i}}{s_\alpha^{i+1}}\right)\prod_{t=1}^{i-1} \frac{\partial I^{t+1}}{\partial I^t}\right]. \qquad \text{(A2)}$$

Fortunately, since at the optimum a unit of income must have the same effect on fitness regardless of which component it is spent on, we can estimate its effect on next generation income only. An increase in income in any generation will always have a linear effect on fitness, if all income is optimally allocated to increasing fitness. To better illustrate this idea, I will examine the equilibrium conditions more carefully.

The first equilibrium equation governing fertility shows that a proportional increase in fertility results in a proportional increase in fitness. The cost of a change in fertility, however, depends on the level of parental investment. Each offspring costs the sum of fixed costs, the investment in survival and the investment in adult income. If we treat that sum as a constant for a moment and label it p, it is clear that each unit of investment in fertility produces 1/p offspring. Since each increase in fertility causes a 1/b increase in log fitness, a unit of investment in fertility increases log fitness by 1/pb. This also means that if all other expenditures are held constant and any increase in income was dedicated to an increase in fertility, proportional changes in income would produce a proportional increase in fitness (unitary income elasticity):

$$\frac{\partial W}{\partial I} \frac{I}{W} = 1, \qquad \text{(A3)}$$

with the factor of proportionality being 1/p. This means that the fitness function is quasilinear.

Of course p is not constant but composed of choice variables. One of the choice variables is investment in offspring survival. Following the same reasoning, each additional unit of investment in offspring survival will cost b, because it must be given to each of b offspring. Again proportional increases in survival produce proportional increases in fitness, thus the proportional impact on fitness of an increase in investment in survival will be:

$$\frac{d(W)}{W} = \frac{\frac{\partial s_\alpha^1}{\partial i_s^0}\, d(i_s^0)}{s_\alpha^1 b^0}. \qquad \text{(A4)}$$

If, given a set of investments in fertility, survival and adult income of offspring, this effect is greater than the effect of a unit of investment in fertility, it will pay to invest more in offspring survival. This should continue until the fitness effects were equal, or until

$$\frac{1}{p} = \frac{1}{(k^0 + i_s^0 + i_t^0)} = \frac{1}{s_\alpha^1}\frac{\partial s_\alpha^1}{\partial i_s^0}. \qquad \text{(A5)}$$

Notice that b cancels on both sides of the equality. When this equality is satisfied and if the parent were given an extra unit of income to spend, she would be indifferent to spending it on fertility or offspring survival. Again, a proportional change in income, regardless of how it was spent, would generate a proportional change in fitness.

The same reasoning applies to income invested in the adult income of offspring. A unit increase in investment in the adult income of each offspring will cost b. The effect of this investment will be to increase the income for investment in the next generation. Offspring, as adults, will face the same choices that their parents did. They can invest in fertility, offspring survival or next generation income. The same equilibrium conditions will apply and each proportional increase in income must yield a proportional increase in fitness. Thus, the rather formidable equation that calculates the multigenerational effects of investment in offspring income can be ignored and we have

$$\frac{1}{I^1}\frac{\partial I^1}{\partial i_t^0} = \frac{1}{(k^0 + i_s^0 + i_t^0)} = \frac{1}{s_\alpha^1}\frac{\partial s_\alpha^1}{\partial i_s^0}.$$

(A6, eq. (3) in text)

The key to this result is the assumptive ability of parents to replicate the production process to yield as many offspring as their income allows. Thus even though investments in survival and adult income will be eventually characterized by diminishing returns to scale, investments in fertility will not. Therefore in this model there are no diminishing returns to income.

Part II

Following the above derivation of the two-generational model, we can log transform equation (4) and then combine it with equation (5) to obtain the discrete-time, two-generational Lagrangian function of log fitness,

$$\begin{aligned}\underset{b^0, i^0_{p,x}, i^0_{e,x}}{\text{MAX}}\ \mathrm{L} &= \ln(b^0) + \ln(I^1) + \sum_0^{\alpha-1} \ln(p_x^1)\\ &\quad + \lambda\left(I^0 - b^0 \cdot \left(k^0 + \sum_0^{\alpha} (i_{p,x}^0 + i_{e,x}^0) \cdot s_x^1\right)\right),\\ &\qquad \{x | x \in 0,1,2 \ldots \alpha - 1\}, \qquad \text{(A7)}\end{aligned}$$

where superscripts distinguish the parental generation (0) from the offspring generation (1), and the entire term multiplied by λ is the budget constraint. This model yields the following equilibrium conditions:

$$0 = \frac{\partial L}{\partial b^0} = \frac{1}{b^0} - \lambda\left(k^0 + \sum_0^{\alpha-1} (i_{p,x}^0 + i_{e,x}^0) \cdot s_x^1\right)$$

$$0 = \frac{\partial L}{\partial i_{p,x}^0} = \frac{1}{p_x^1} \cdot \frac{\partial p_x^1}{\partial i_{p,x}^0} - \lambda(b^0 \cdot s_x^1) \quad \{x | x \in 0,1,2 \ldots \alpha - 1\}$$

$$0 = \frac{\partial L}{\partial i_{e,x}^0} = \frac{1}{I^1} \cdot \frac{\partial i^1}{\partial E_\alpha^1} \cdot \frac{\partial e_x^1}{\partial i_{e,x}^0} - \lambda(b^0 \cdot s_x^1)\ \{x | x \in 0,1,2 \ldots \alpha - 1\}.$$

To examine the allocation of reproductive investments we can compare the equilibrium conditions for fertility, investment in age-specific survival and adult income. Eliminating λ and rearranging results in

$$\frac{s_x^1}{\left(k^0 + \sum_0^{\alpha-1} (i_{p,x}^0 + i_{e,x}^0) \cdot s_x^1\right)} = \frac{1}{p_x^1}\frac{\partial p_x^1}{\partial i_{p,x}^0} = \frac{\partial e_x^1}{\partial i_{e,x}^0}\frac{\partial i^1}{\partial E^1}\frac{1}{I^1},\ \{x | x \in 0,1,2 \ldots \alpha - 1\}.$$

(A8, eq. (6) in text)