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# Evolutionary and Wealth Flows Theories of Fertility: Empirical Tests and New Models

HILLARD KAPLAN

HUMAN FERTILITY VARIES both among and within societies. Total fertility rates have been reported to be over nine births per woman among the Hutterites (Eaton and Mayer 1953) and lower than 1.5 in several European countries (van de Kaa 1987). Even among low-density hunting and gathering societies, completed family sizes vary from just over four (Howell 1979) to almost eight (Hill and Kaplan 1988). In many developing countries and even in the United States, both very high and very low fertility rates occur in different sectors of the same population (Caldwell 1982; Whiteford 1986). An adequate explanatory theory of human fertility ultimately will have to account for this variation. Since the direct and indirect effects of population growth may present the most serious social problems of the next century (the current global population doubling rate is about 41 years: Brown 1990), a robust theory of high and low fertility rates would be of major importance.

A plethora of alternative theoretical approaches to the study of human fertility is derived from different disciplines and schools within disciplines. Among these are the models of quality–quantity tradeoffs and of opportunity costs, developed by the Chicago school of economics (Becker and Lewis 1973; Becker 1981), the taste-preference (Easterlin 1973) and supply-based models of the Pennsylvania school (Easterlin, Pollack, and Wachter 1980), cultural evolutionary approaches that relate fertility to natural selection of culturally transmitted traits (Boyd and Richersen 1985), psychological models of the effects of early childhood family rearing experience (Draper and Harpending 1982), models of female empowerment and resource access (Handwerker 1988), proximate approaches to fertility determination (Bongaarts 1978, 1983; Wood 1990), Caldwell's wealth flows theory (Caldwell 1978, 1982), and parental investment models derived from

evolutionary biology (Blurton Jones 1986; Hawkes and Charnov 1988; Pennington and Harpending 1988; Rogers 1990; Smith and Fretwell 1974). Although much empirical research has been conducted on the basis of these theories, less effort has been directed toward tests among alternative theories, especially those derived from different academic disciplines. The wealth flows and parental investment models offer the opportunity for such a test because they imply directly competing predictions.

The first part of this article presents tests of the competing predictions of these two explanatory theories of human fertility. The second part discusses similarities and differences between evolutionary and wealth flows theories of fertility, and develops a new set of models derived from the logic of evolutionary ecology. The discussion focuses on tradeoffs between fertility and the reproductive value of offspring and between care of, and resource investment in, children. I discuss the new models in terms of the kinds of physiological and psychological mechanisms that may have evolved to solve those tradeoffs and to adjust behavior in response to variable ecological conditions so as to approximate optimal fertility and parental investment. I then consider the empirical predictions those and other evolutionary models generate, focusing on ecological variability in factors affecting optimal birth spacing and investment in the adult income of children. The article concludes with a discussion of the demographic transition and fertility in developed and developing countries. To explain fertility reduction and the small effect of income on fertility in industrialized societies, I propose a hypothesis based upon competitive wage markets and the cumulative nature of human capital.

## Empirical tests of two theories of fertility

The wealth flows theory posits two distinctive human fertility regimes. In the first or "pre-demographic transition" pattern, people express the desire to have many children and average completed fertility exceeds four or five live births. The second, or "post-demographic transition" regime occurs when the demand for children is lower than the potential supply (see Easterlin 1973) and people attempt to limit their fertility to two or three births. Caldwell proposes that the economic value of children and the direction of familial intergenerational wealth flows determine which regime people will follow. When net wealth transfer from children to parents is positive (i.e., subtracting the value of all parental wealth transfers to children from the value of all children's transfers to parents), parents are expected to desire as many children as possible because their wealth will increase as a function of the number of children they produce. Alternatively, when children consume more parental wealth than they provide (negative wealth flow), parents are expected to desire fewer children (albeit some,

because of the direct satisfaction children provide). Caldwell hypothesizes that before modernization, children are net economic assets to parents. Following modernization, fertility is reduced when children cost more to raise than they return. This theory has stimulated numerous studies aimed at explaining the distribution and timing of fertility reduction in developing countries (e.g., Handwerker 1986).

In contrast to wealth flows theory, models of fertility and parental investment derived from evolutionary biology expect that the net flow of resources always will be from parents to offspring, even when fertility is high (Turke 1989). The logic underlying this expectation is that natural selection has produced a preponderance of organisms that are designed to extract resources from the environment and convert those resources into descendants carrying replicas of their genetic material. The theory predicts that, of the existing genetic variants, those genes whose average effects on phenotypes increase the number of descendants accumulate relative to alternatives. Organisms that extract a net gain from their offspring would be able to produce fewer genetic descendants than those that used their own labor and excess energy to produce more viable offspring. This does not mean that under some conditions natural selection could not favor a positive wealth flow from some offspring to parents or from offspring to parents at some ages, but that the overall intergenerational flow of resources will be downward. In addition, the Malthusian logic underlying evolutionary theory suggests that a positive wealth flow from offspring to parents could not be sustained because it would lead to spiraling population growth. Increases in fertility would lead to increased wealth, which, in turn, would permit even greater fertility. In contrast to Caldwell's view, evolutionary theory predicts that the acquisition of wealth will be in the service of reproduction, rather than vice versa.

Opposing predictions from two theories permit one to make empirical tests. However, as a recent debate between Turke (1989) and Fricke (1990) shows, the flow of wealth between parents and children in a high-fertility context has never been directly measured. Caldwell developed his theory in response to what he considered to be poor measurement of intergenerational wealth flows by other scientists, and a great deal of research has been conducted since the theory's publication. Virtually all of these studies have measured intergenerational wealth flow with proxy variables such as time allocation to labor (Cain 1977), children's growth (Nag, White, and Peet 1978; Stinson 1980), informant reports about the economic value of labor (Bulatao and Arnold 1977), or availability of public education (Caldwell 1982).

Small-scale societies with little or no involvement in the monetary economy provide a relatively uncomplicated context for measuring the direction of wealth flows because food is the principal form of wealth. In

order to determine the net economic value of raising children and the life-time direction of wealth flow, I draw on measurements of age-specific food production and consumption<sup>1</sup> in three high-fertility traditional societies in lowland South America. The results are presented below.

### The study populations

There were three study communities:

Until the mid-1970s the *northern Ache* were full-time, nomadic hunter-gatherers in the subtropical forests of eastern Paraguay. During the 1970s all of the individual bands of northern Ache came into peaceful contact with Paraguayan society. During the contact period (1970–78) about half the population died from introduced diseases, and most of the remainder were settled in religious missions where they were taught how to cultivate manioc, sweet potato, corn, and beans. The study reported here was conducted during two field sessions in 1981–82 and 1984–85 by Kim Hill, Kristen Hawkes, A. M. Hurtado, and the author. During the period of study, the Ache practiced a mixed economy, spending about 25 percent of their time on extended hunting-and-gathering treks, foraging as in the past, and 75 percent at the mission with 200 inhabitants where they engaged in horticulture, fishing, hunting, and gathering. The data presented below were collected during the hunting and gathering because the subsistence practices on these treks more closely resembled the Ache's traditional subsistence pattern. Data obtained from reproductive histories of a sample of 174 Ache women indicate that their total fertility rate was 8.15 prior to contact with the society at large;<sup>2</sup> fertility increased in the 1980s following sedentarization (Hill and Hurtado in press).

The second study community, Diamante, consisted of some 200 individuals of mixed, but mostly *Piro*, ancestry in southeastern Peru at the base of the Andes. Having had marginal involvement with the national economy for several generations, the Piro practiced a mixed economy of horticulture (primarily manioc and plantains), shotgun hunting, fishing, gathering, and some wage labor. About 7–10 percent of total food consumed was purchased (about equal to the amount sold). The total fertility rate derived from interviews with 27 women<sup>3</sup> currently living in the community was 8.2. The behavioral data were collected by Michael Alvard and Teslin Phillips under the author's supervision from August 1988 to June 1989, and the demographic data were collected by Alejandro Smith.

The third community, Yomiwato, consisted of 105 *Machiguenga* located in southeastern Peru on a small river in an area protected by the Peruvian government as a national park. Because of park policy, no economic development is allowed and its native inhabitants participate in a highly traditional economy with almost no access to money or wage labor. Their sub-

sistence pattern during the study was based upon swidden horticulture, bow-and-arrow hunting, fishing, and gathering. The total fertility rate derived from interviews with 22 women currently living in the community was 8.1. The data were collected by Kate Kopischke and the author from September 1988 to May 1989.

### **Applicability of the study populations to a test of wealth flows theory**

Caldwell developed the wealth flows theory in response to demographic patterns observed in developing country contexts. These pretransition societies might be described as "peasant" and had much stronger ties with the state society than did the populations considered in this article. As such, it might be argued that hunter-gatherers and forager-horticulturists are inappropriate test cases for the wealth flows theory.

There are three major advantages to conducting a test of Caldwell's theory among small-scale societies with very limited economic interaction with state society and ownership of goods and land. First, the theory is general. It relates fertility levels to the costs of children. If children are a large net economic cost to parents in the societies considered here, we should observe cultural patterns designed to limit fertility. As a corollary, if we observe high fertility and pronatalist views, as is the case among the Ache, Piro, and Machiguenga, the theory predicts that children should be net economic assets to parents. Moreover, if in fact the psychology of fertility decisions is sufficiently different for people in state and nonstate societies, we need an overall theory that predicts those differences.

Second, while none of the study populations is "pristine," their work patterns are a response to economic and group-size conditions that are much closer to those faced by humans throughout most of evolutionary history<sup>4</sup> than is true for the societies for which the wealth flows theory was developed. A basic understanding of the psychology and culture underlying fertility decisions in very small-scale societies may enable us to understand human responses to the conditions of peasantry, modern industrial society, and postindustrial society.

Third, as mentioned above, testing the wealth flows theory is much less complicated in societies where wealth is not stored in land, cattle, money, or other goods. In all three societies examined, food is consumed within a few days of its acquisition or harvesting (usually the same day). Moreover, power differences are small, there is no obvious control over the labor of individuals by persons outside their immediate family, and access to arable land and to hunting-and-gathering locations is essentially free. This allows the investigator to focus on food as a measure of wealth flows without missing major dimensions of economic costs and benefits.

## Methods

*Resource production and acquisition* During Ache foraging trips, the women and children generally traveled as a group while men walked alone or in small groups in search of game. To adequately sample Ache food production, one investigator walked with the women and children while another followed individual men. Since men brought virtually all the food they acquired to the main group of women and children, the investigator who remained with the women weighed all food acquired with Homs hanging scales and recorded who acquired it. The weights of foods were then transformed into caloric equivalents using published tables and laboratory analyses of the samples we collected (Hill et al. 1984; Kaplan and Hill 1985a). With this procedure, we summed all calories acquired by every individual on treks and divided it by the number of days sampled to determine the mean amount acquired per day by every individual.

Among the Piro and Machiguenga who lived in settled communities, we employed a modified sampling method. Both communities were subdivided into extended-family clusters of households separated by some minutes' walk from the next cluster. Since it was possible for one person to monitor and weigh all food brought to a cluster, we defined a cluster as a sampling unit. The day was divided into three four-hour sampling frames (morning, midday, and afternoon) and each cluster was sampled equally throughout the day. We also followed individuals away from their homes to determine how much food was eaten away from the community. The allocation of credit for garden products required special consideration. In both communities, most of the forest clearance, planting, and weeding for each garden was performed by a single man with some assistance from other men and, perhaps, a little from his wife. Both men and women harvested crops as needed for immediate consumption about every two to three days. Children performed almost no garden labor with the exception of harvesting. We assigned 50 percent of garden calories acquired to the harvester and 50 percent to the person who cleared, burned, planted, and weeded the garden. This proportional assignment was based on Baksh's data (1984: Table 4.18) on time allocation and work rates in a similar Machiguenga community. He found that harvesting accounts for 46.2 percent of total time spent in agricultural labor.<sup>5</sup>

In addition to the four-hour household samples in Diamante and Yomiwato, we collected data on large game killed by all members of the communities on most days during the field study. We used these data to calculate large game acquisition in lieu of the data from household samples. This was done because large game was killed rarely and the household sampling procedure would have suffered from large sample error. We also collected data on all large communitywide poison-fishing events for the same

reason. The three data sets (household samples, large game, and poison-fishing) were combined in determining total caloric production. The same procedures as employed in the Ache study were used to convert weighed foods to calories acquired per consumer per day. Average daily caloric acquisition for each individual was measured as the sum of the average daily caloric acquisition by that individual from each of the three data sets (i.e., from each of the three food types).

The sampling procedures were not strictly random for logistic reasons. Among the Ache, although we attempted to sample as many groups as possible, our sample consisted solely of those individuals who decided to leave the settlement to forage on wild foods.<sup>6</sup> Data were obtained on 14 foraging trips. The sample includes 840 sample days on 101 Ache children under the age of 18, and 1282 sample days on 94 Ache adults.

Among the Piro and Machiguenga, each cluster was sampled in rotation because a random procedure would sometimes have required two successive samples in the same place, a socially inappropriate length of visitation. However, these deviations from random sampling were not systematically related to age-specific food production and should not affect the validity of the measures of resource flow. The Machiguenga sample includes 790 sample days on 58 individuals under age 18 and 506 sample days on 39 adults. The Piro sample consists of 818 sample days on 84 individuals under age 18 and 489 sample days on 54 adults.

*Food consumption* Since food is eaten out of a common pot among the Machiguenga and Piro and is shared extensively among the Ache, it was not possible to measure individual food consumption directly. Food consumption was estimated by a procedure used by the World Health Organization (1985) and the National Research Council (1989a: Table 3-1; 1989b) for calculating the resting metabolic energy expenditure (REE) of individuals as a function of age, sex, and weight. The REE was determined for every individual in our sample. The average daily food consumption for each individual was then estimated assuming that all food was divided among community members in proportion to their REE. This procedure resulted in estimates of 3087, 3600, and 3827 calories per average adult per day for the Machiguenga, Piro, and Ache, respectively.<sup>7</sup> Each individual's estimated daily caloric consumption was subtracted from the amount he or she actually acquired per day to determine the net deficit or surplus that individual produced.

*Time allocation* For one of the groups, the Machiguenga, time allocation data from the four-hour sample blocks were used to examine the relationship between age, number of descendant kin, and work effort. Every half-hour during the four-hour period, the behavior of each individual in the household cluster was recorded. Those behaviors were either directly



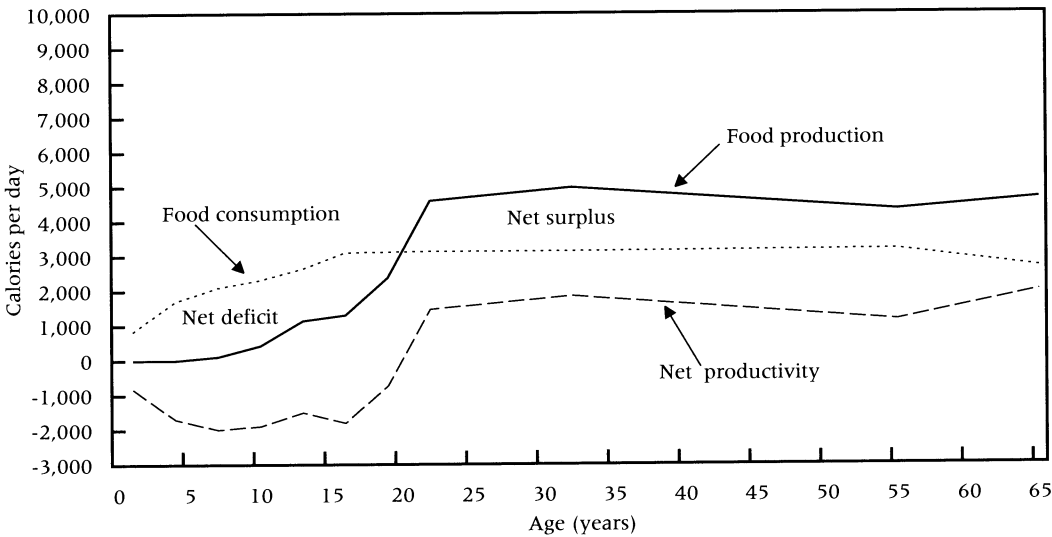
observed or obtained from reports. When individuals left the residential area, they were asked what they were going to do, and when they returned they were questioned about their activities while absent. Reports on the activities of individuals who were absent during the entire four-hour period were obtained from adults who were present and later verified by questioning the absent individual. The mean number of activity records per individual was 156.

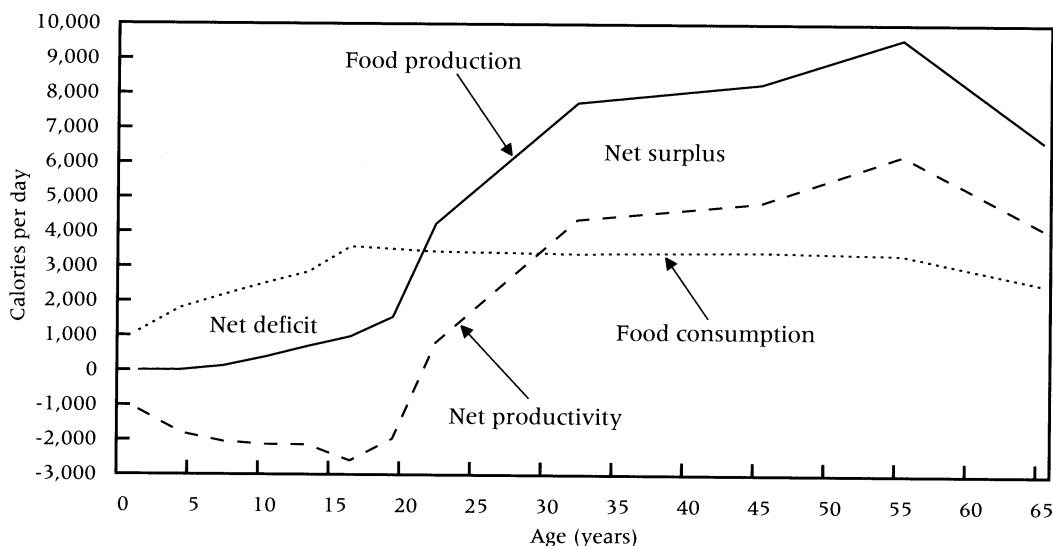
Results

Figures 1–3 summarize the data. They show age-profiles of food production, food consumption, and net productivity, for both sexes combined, for the Machiguenga, Piro, and Ache, respectively.<sup>8</sup> (A more detailed analysis of food production and consumption by age and sex will be published elsewhere.)

The results for the Machiguenga (Figure 1) show that children consumed many more calories than they produced during the period from birth to age 18. The average child under the age of 18 consumed 2120 calories per day but produced only 500 calories, or 24 percent of his or her total caloric consumption. Thus, while the average child consumed close to 14 million calories before age 18, he or she produced only a little over 3 million, yielding a net deficit of 10.5 million calories to be provided by adults. Machiguenga adults, on the other hand, produced some caloric surpluses

**FIGURE 1 Machiguenga food production and consumption by age: Both sexes combined**



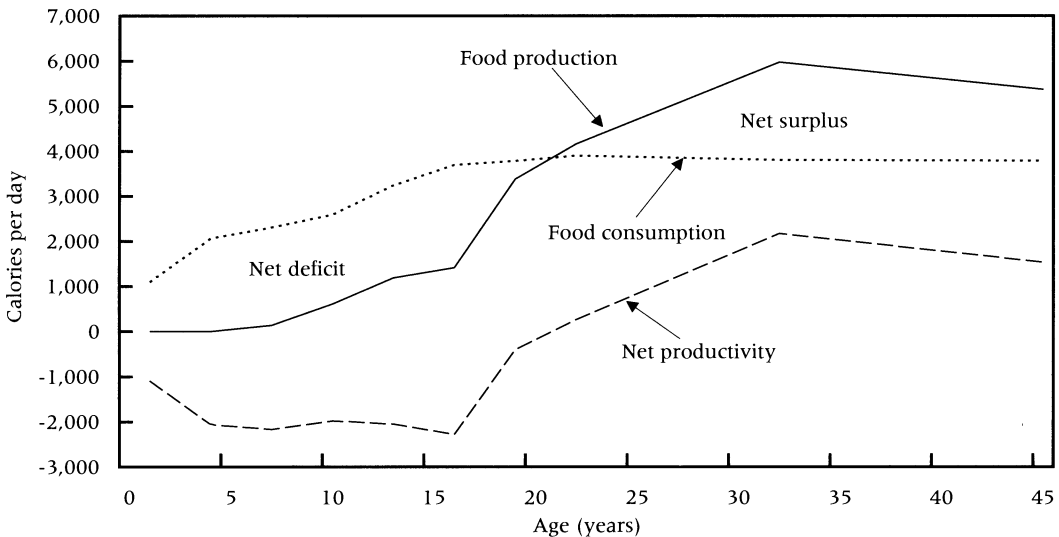
**FIGURE 2 Piro food production and consumption by age: Both sexes combined**

at about age 20 and continued to produce more calories than they consumed into old age. Even after age 60, the average adult produced about 4600 calories but only consumed around 2500.

Results for the Piro (Figure 2) parallel the Machiguenga data. The average child consumed about 2300 calories per day and produced only 370, for a net daily deficit of 1970 calories. For the first 18 years of life, children cost about 13 million calories in excess of what they provided. Piro adults were also quite productive into old age. The average adult over age 60 produced some 6600 calories but consumed only around 2500.

The Ache did not differ substantially from the Piro and Machiguenga (Figure 3). On average, children consumed 2500 calories and acquired about 560 calories, or about 22 percent of the total. For the period from birth to age 18, the net deficit for children was about 13 million calories. Women produced fewer calories than they consumed at all ages, but men produced more than they consumed until about age 60. Old men (over age 60) in our sample produced an average of only 800 calories per day even though they probably consumed quite a bit more.<sup>9</sup>

The developmental trends differed between sexes and among groups. Among the Machiguenga, girls' food production exceeded that of boys from age 6 to about age 20, after which males outproduced females. Girls helped their mothers with the harvesting and processing of garden products, while boys spent considerable time traveling in play groups, shooting small lizards with miniature bows and arrows. Boys acquired more meat than girls throughout adolescence. Since meat acquisition is much more time inten-

**FIGURE 3 Ache food production and consumption by age: Both sexes combined**

NOTE: Data for the Ache are limited to persons aged 45 or younger because our sample of women older than 45 is too small to yield meaningful results.

sive than harvesting garden products, girls may not be cheaper to raise than boys. There is also evidence of developmental change during adulthood among men. Men between ages 20 and 40 acquired the most meat. Men over age 50 hunted less and spent more time clearing and weeding gardens. For this reason, the caloric production of old men was high, even though they acquired little meat.

Among the Piro, the effects of age and sex on food production among adults were almost identical with those among the Machiguenga. There is no evidence, however, that girls outproduced boys in childhood and adolescence. Among the Ache, girls acquired more food than boys until about age 18. Again, boys spent more time in play and acquiring hunting skills, while girls were more directly productive in gathering fruits. However, since meat and honey accounted for some 80 percent of the total calories eaten by the Ache, adult males outproduced females by a margin of about five to one. In addition, the reduction in hunting productivity associated with aging rendered old men (60 and older) less productive than their counterparts among the Piro and Machiguenga horticulturists.

The Machiguenga data set also permitted additional analyses that are the most direct tests of the alternative hypotheses regarding human fertility. For adults between ages 18 and 40, total caloric production was regressed on number of dependent children and sex of producer. Males produced more than females, and food production was positively related to

the number of biological children ( $n = 24$ ,  $r^2 = .40$ ,  $p = .0036$ ; standardized coefficient for sex = .489, partial  $p = .009$ , standardized coefficient for number of children = .36, partial  $p = .047$ ). The results were even more telling for the old-age security hypothesis. For adults over age 40, total food production was regressed on number of grandchildren (which correlated with number of adult children at .998; sex was not significantly related to food production for this group). Again, older individuals' food production was positively correlated with both number of grandchildren ( $n = 13$ ,  $p = .03$ ) and number of adult children ( $p = .049$ ).

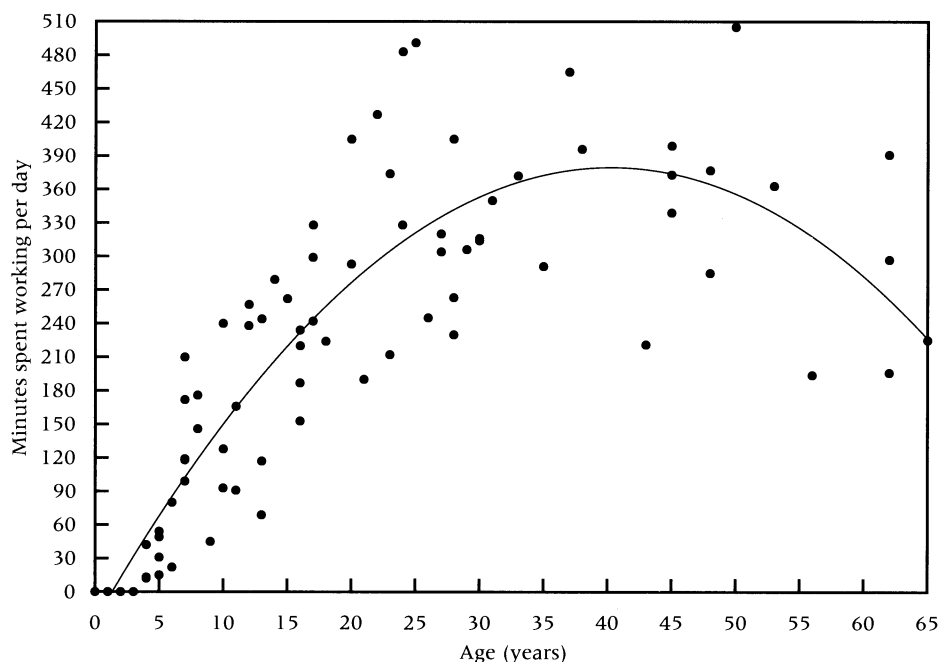
The time allocation data among the Machiguenga revealed similar trends. Total work time (including time spent in foraging, gardening, processing and cooking food, child care, manufacture and repair of tools, clothing, and houses, and other miscellaneous work) was regressed on number of children and number of grandchildren for adults aged 18–40 and over 40, respectively. Number of children is positively correlated with total time spent working for men aged 18–40 ( $n = 13$ ,  $r^2 = .38$ ,  $p = .02$ ), but not for women ( $n = 11$ ,  $p = .34$ ). Although total work time was not related to number of grandchildren for adults over age 40, garden labor, the most energy-intensive work, was strongly associated with number of grandchildren ( $n = 13$ ,  $r^2 = .67$ ,  $p = .0006$ ).

Figure 4 shows the relationship between age and work effort throughout the life course. The fitted curve is given by  $y = -21.62 + 19.55x - 0.24x^2$  ( $r^2 = .80$ ,  $p < .0001$ ,  $n = 87$ ), where  $y$  is work time in minutes and  $x$  is age. Work effort peaks at about age 40, when most adults are having their first grandchildren as well as caring for several dependent children of their own. Although work effort declines in old age, even the oldest adults work more than adolescents.

Children work less than three hours per day until they reach age 15. Much of their "work" is difficult to distinguish from play. Most foraging time (which averages 30 minutes a day for 6–10-year-olds, 70 minutes a day for 11–14-year-olds, and 100 minutes a day for 14–15-year-olds) is spent play-hunting. Child care does not exceed an average of 15 minutes per day for any age below 15 years. The same is true of gardening activities with the exception of 14–15-year-olds, who average about 20 minutes per day. Children aged 6–13 years spend about 20–30 minutes per day processing food; the average for the two girls in the 14–15-year age class, however, was 70 minutes a day.

## Discussion

Our results have negative implications for Caldwell's wealth flows hypothesis. The data from all three groups show that even though children were very costly to raise, fertility was high. In fact, children provided only about 20–25 percent of their caloric consumption before age 18. At the age when

**FIGURE 4** Time spent at all types of work by age among the Machiguenga

they began to produce more than they consumed, most already had children of their own. Postreproductive adults produced much more than they consumed, and helped support their grandchildren. Net wealth flows were downward in all three groups even though their fertility was high.

Rather than support the theory that parents in traditional societies have many children in order to reap economic benefits (especially in old age), these data suggest that parents desire children despite their economic cost and that the labor of postreproductive individuals and adults with few dependents supports this high fertility. To illustrate this, consider a hypothetical Machiguenga couple with husband and wife both being between 30 and 40 years of age with three living children, a boy aged 4, a girl aged 8, and a boy aged 12. According to the food production and consumption data underlying Figure 1, the daily deficit for the whole family would be 2160 calories. This deficit must be balanced, at least in part, by the surplus production of other adults with fewer dependents, otherwise the adults could not maintain weight and the children could not grow. The same calculation for Ache families would yield a net deficit of 2800 calories, and Piro couples would have a surplus of about 2580 calories. Young Piro adults, on the other hand, often have two or three children before they themselves

produce more calories than they consume. During this time, older adults support them and their young children. Data from other societies in Africa (Hawkes, Blurton Jones, and O'Connell 1989) and Asia (Nag, White, and Peet 1978) also show that old people work very hard, possibly indicating that a life history pattern in which people experience reduced fertility in old age and support the rearing of grandchildren may be a fundamental human adaptation. Even if menopause cannot be explained by investment in grandchildren (see Hill and Hurtado 1991; Rogers 1993), selection for increased longevity following reproduction could be due to the ability of grandparents to support the rearing of grandchildren. This may be unique to humans.

Some objections to these conclusions could be raised. It is possible, for instance, that the procedure used to estimate caloric consumption overestimated the food eaten by children. Since the procedure did not adjust for energy expenditure due to activity, children's food consumption would have been overestimated if adults were much more active than children. Also, if some individuals, such as adult males, have preferential access to food and consume more as a result, the estimates might not reflect true consumption. However, sharing is very egalitarian in each of the groups. Among the Piro and Machiguenga, women and children tend to eat from one pot and men from another. But women serve the dishes with little male supervision and children appear to eat freely. Among the Ache, sharing is band-wide and much attention is paid to equality of shares (see Kaplan and Hill 1985a for a detailed discussion of Ache food sharing). Children receive their shares through their parents, but our informal observations suggest that children receive preferential treatment when food is scarce.

Moreover, the estimates of caloric consumption used here do not differ substantially from National Research Council recommendations for very active children. For example, NRC recommendations for the average Machiguenga child would be 2030 calories per day<sup>10</sup> compared with the 2110 calories generated by the estimation procedure used here. While the activity data for children in these groups have yet to be analyzed, they appear to be much more active than American children and are exposed to a very high disease and parasite load.<sup>11</sup> Nevertheless, even if this procedure overestimated children's caloric consumption by 30 percent, correcting for this error would only raise children's food production to 30–35 percent of the calories they consumed.

It is also possible that the caloric production of children was underestimated. The attribution of 50 percent credit to the gardener and 50 percent to the harvester for garden products acquired by the Machiguenga and Piro may have been incorrect. However, since felling large trees and weeding are almost certainly the most energy-intensive activities in slash-and-burn horticulture, 50 percent credit to the harvester may be too high, over-

estimating the productivity of children. Among the Ache, the change from a lifestyle based solely on hunting and gathering to a mix of horticulture and foraging may have rendered children less effective as foragers than children in the past. Ache informants report, though, that prior to peaceful contact with other cultures, boys began to kill animals regularly only after ages 15–16.

Other objections might be raised regarding the use of calories as a measure of the economic value of children. Differences in the nutrient content of foods acquired by different age and sex classes could have a considerable impact on economic costs and benefits. Meat appears to be a limiting resource among traditional Amazonian peoples, and garden products, particularly manioc, are often in abundant supply (see Hames and Vickers 1983 for a collection of such reports). This is probably the case here. Adjusting for the fat and protein content of foods would make children even more expensive to raise, but would also lower the value of the labor of older people.

Children do other chores, such as cleaning, bringing water, and caring for other children. Although data on these activities have yet to be analyzed for all three groups, adult women and men appear to spend much more time in domestic chores than do children. Virtually all firewood is acquired by adult women in all three groups. The only individuals observed to engage in building and repairing houses were adult men and women. Although children were frequently sent for water, those trips rarely lasted more than five minutes because village sites and foraging camps were located along water courses. The data from the Machiguenga presented above show that children spend little time in productive and domestic labor.

In fact, it is likely that this analysis underestimates the cost of children because it does not include parents' time spent in child care. Observations of Machiguenga children under the age of 6 revealed that the primary caretaker was the child's mother 61 percent of the time, other adults 25 percent of the time, and children only 14 percent of the time. Among the Ache, children under 4 years are in tactile contact with their mothers more than 80 percent of the time. Even if older children do help parents with the care of younger siblings, any time that parents dedicate to child care is an extra cost of parenting that must be added to the costs of provisioning calculated here.

Caldwell (1982) proposes that a principal economic benefit provided by children is the increase in status and power associated with large families. As children become adults, large sibships may increase parental influence in the community. The political benefits of high fertility were not examined in this study, but, as argued earlier, these three societies do not exhibit high levels of social stratification or differential access to resources. This is why the regressions of adult work effort and food production on

number of children and grandchildren are so revealing. Neither hunting territory nor arable land is a limited resource for any of the groups. They are surrounded by large tracts of forest. Individuals choose an area they wish to clear, cut down the trees, and make a garden. A new patch is chosen when the soil is no longer fertile. Hunting is also characterized by free access. Therefore children cannot be the vehicle of resource access. Resource production is completely determined by individual variation in time allocation and the productivity of time. If older people are working harder as a result of their number of grandchildren (and hence of their adult children), it cannot be because they have greater access to resources or because they are storing wealth (as almost none is stored); it must be because they are responding to greater payoffs to (demands on) their productivity.

Caldwell (1982) also suggests that a large number of surviving children may ensure that parents will have someone to care for them if they do not die before they become frail. The Machiguenga data showed that adults with dependent children produce more food and work longer hours as the number of children increases. The same is true of older adults, who increase food production and time in garden labor as the number of grandchildren increases. If this is the case, parents and grandparents work very hard through most of their adulthood and middle age to "pay" for that security. While it is true that people do become frail and nonproductive in very old age, suicide and "euthanasia" are reported frequently among the Ache and Machiguenga as causes of death among the frail. When people become too weak to work, death often follows quickly.

In these three societies, in short, the overall flow of wealth appears to be downward from parents to children and from grandparents to grandchildren.

## **Toward a general theory of human fertility and implications for empirical research**

There is a fundamental similarity between Caldwell's wealth flows theory of fertility and models derived from evolutionary biology. Both posit that socioecological variability in the costs of rearing children partially determines completed family size. The principal differences between the two theoretical approaches lie in their conceptualization of the determinants of children's costs and of the factors that shape the underlying psychophysiology of fertility. Caldwell's theory treats the costs of children as an exogenous variable that is itself determined by social factors outside the scope of the model. It assumes that humans are primarily consumers of satisfaction-inducing goods and that they will increase their fertility when children positively affect wealth. The effect of children on parental wealth is determined by exogenous variables such as social attitudes and laws re-



garding child labor, availability of education, and economic resources. The theory does not attempt to explain culturally variable patterns of parental investment in children and the social attitudes and policies associated with them.

Life history models derived from evolutionary theory differ in two important ways from the wealth flows theory. First, they posit that, in part, the costs of rearing children are determined endogenously. Second, evolutionary models assume that the ultimate utility governing behavior is biological fitness. A basic theoretical premise is that individuals face tradeoffs in the allocation of resources. Through time invested in work, individuals acquire resources that can be invested either in their own consumption ("somatic investment" in evolutionary jargon) or in the production and consumption of offspring ("reproductive investment"). In life history models, the tradeoff between somatic and reproductive investment can also be understood as a tradeoff between future and current reproduction because somatic investment in health, growth, and social status is expected to translate into higher levels of reproductive investment later in life. Additionally, given a fixed budget of time and economic resources that are allocated to reproduction, a second major investment tradeoff is between offspring quality and offspring number. Investments in child quality subtract from resources available for investment in child number, and vice versa. As Becker and Lewis (1973) point out in an independently derived economic version of this theory, each unit of investment in child quality makes a unit increase in child quantity more expensive, and vice versa. The expectation of evolutionary theory is that natural selection acts on the joint outcome of investments in offspring number and offspring quality, favoring those variants that are associated with the most genetic descendants in subsequent generations.

The outcomes associated with different investment allocations are expected to vary with exogenous environmental conditions. Under conditions in which the impacts of parental investment on offspring quality diminish rapidly with increased investment, high fertility and low investment in quality are expected. Alternatively, in environments where relatively longer or more intensive investment continues to increase offspring quality, expected fertility would be lower (Pennington and Harpending 1988).

For species that rely heavily on learning and developmental adjustments to environmental conditions, the theory predicts that individuals will possess psychological and physiological mechanisms that allow them to perceive variation in the benefits of parental investment and to adjust fertility and the timing and intensity of parental investment accordingly. Parents who either invest too little in offspring, such that they suffer high rates of mortality, or invest too much, at the expense of extra fertility, will leave fewer descendants than individuals who invest optimally.

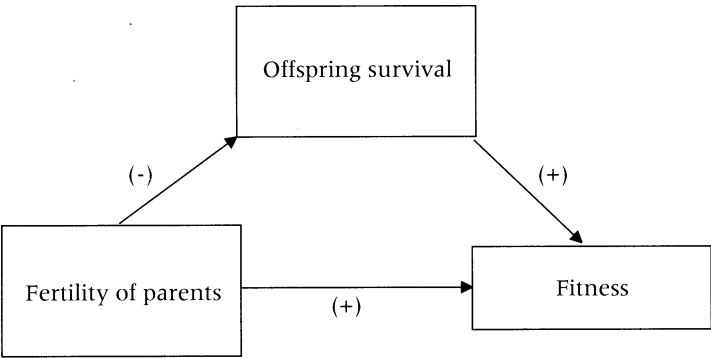
This perspective directs attention to the effects of fertility on child outcomes. Define fitness ( $w$ ) as the total number of offspring of a representative individual who survive to reproduce, that is,  $w = vs$ , where  $v$  is total fertility over the reproductive ages and  $s$  is the proportion surviving to reproductive age.<sup>12</sup> If the proportion surviving is a negative function of fertility (i.e.,  $ds/dv < 0$ ) because parental investment must be divided among more offspring, maximizing adult fertility may not maximize fitness. Fitness has a direct positive effect through number of children and an indirect negative effect through its impact on the survival of children. These causal routes are illustrated in Figure 5.

Optimal fertility,  $\bar{v}$ , the level of  $v$  that maximizes fitness, is found by setting  $dw/dv$ , the total derivative of fitness with respect to fertility, to zero:

$$dw/dv = v(ds/dv) + s = 0,$$

giving  $\bar{v} = -s/(ds/dv)$ . Figure 6 shows a simple example, where the relationship between actual fertility and child survival is specified by  $s = a - bv^2$ , with  $a = 0.8$  and  $b = 0.008$ . (This is the dashed line in the figure.) The fitness isoclines,  $sv = 1, 2, 3, \dots$ , represent possible combinations of fertility and survival that yield equal numbers of total surviving offspring. The point at which the broken line is tangent to the highest isocline is the optimal fertility level. With the above specification, this level is  $\bar{v} = (a/3b)^{1/2} = 5.77$ . Points to the left and right of the optimum yield lower numbers of surviving children. The expectation is that observed variation in human fertility patterns across and within societies will be associated with ecologi-

**FIGURE 5** Direct and indirect effects of fertility on fitness



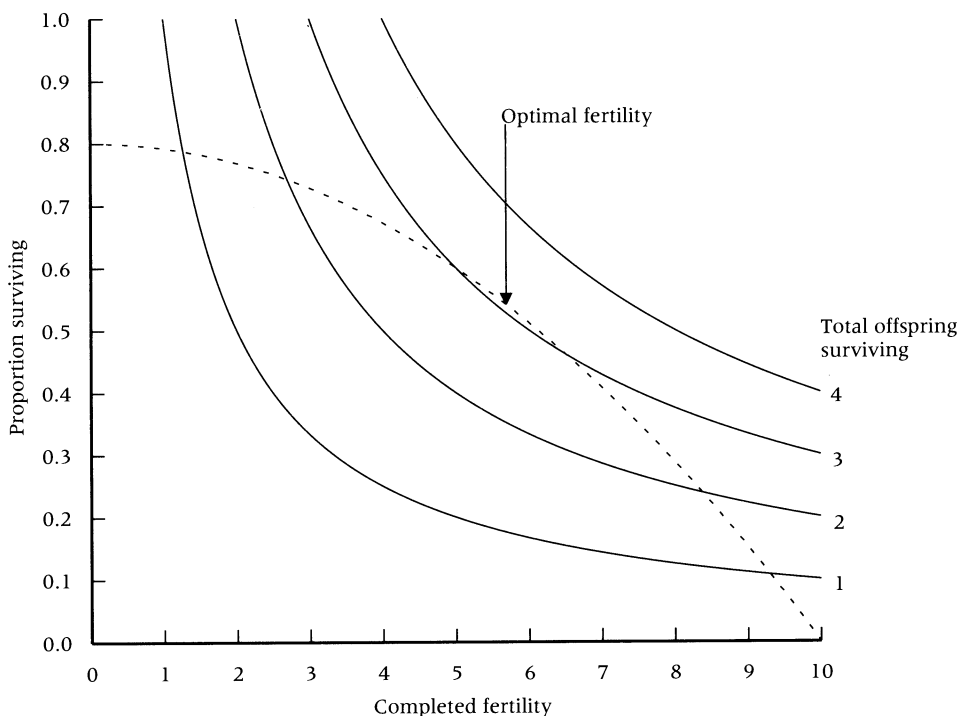
NOTE: The figure depicts the relevant causal pathways in a static optimality model of fertility. In a dynamic model, survival would also affect fertility because the death of a child could lead to a shortening of time to next birth (as is often the case empirically).

cal variation in the optimum point as a function of differential relationships between fertility levels and child survival.

Figure 6 illustrates how the optimal fertility level depends upon the nature of the relationship between fertility and child survival. That relationship itself should be determined by exogenous factors such as mortality risks, the age-specific effects of parental provisioning, the impact of direct care on survival, and other factors discussed in greater detail below. Thus the optimum should be ecologically and individually variable.

The data presented here, however, suggest that this simple model does not address several fundamental aspects of human reproductive behavior. First, third-generation effects appear to be important in many traditional societies because grandparents provision grandchildren. This may mean that fertility in the first generation may affect not only survival in the second but also fertility in the second and survival in the third (see Rogers 1990). Thus it may be necessary to measure fitness in terms of third-generation (or longer) effects. Models including those effects are likely to predict lower

**FIGURE 6** Fitness isoclines and optimal fertility



NOTE: Broken line shows relationship between actual fertility ( $v$ ) and child survival ( $s$ ). See text for specification. Fitness isoclines are given by  $w = sv = 1, 2, 3, \dots$

optimum rates of fertility than the one-generational model that maximizes number of surviving children.

Second, the model does not take into account the timing of fertility and parental investment. The data presented here illustrate that the demands children place on parental resources vary with age. Since human parents do not stop provisioning older children when the next child is born, the demands increase as families grow. This means that it may be necessary to model fertility dynamically in terms of optimal interbirth intervals. Presumably, as Blurton Jones (1986) has suggested, the optimal interval between births should increase with the number of dependent children parents must provision. In addition, to understand the timing of births it will probably be necessary to distinguish the direct care components of parental investment (e.g., protection, training, emotional support) from the economic resources parents invest in children. Here again, parents face a tradeoff: time invested in care subtracts from time available for productive work, and vice versa.

If we imagine that people have a fixed time budget for parental effort, we can model the allocation of that time in terms of the amount invested acquiring resources through labor and the amount invested in direct child care.<sup>13</sup> Parental effort invested in work produces resources (which may be invested in existing children or in the production of the next child) at a given wage or return rate. Thus parents can trade off time spent in care against resources at a ratio set by the wage or return rate.

The expected reproductive value of each child, which is the product of its expected probability of survival to adulthood times its expected fertility as an adult, may be thought of as its expected future genetic contribution to the next generation.<sup>14</sup> For each child at a given age, its probability of surviving to reproductive age and its fertility as an adult should be functions of both resources invested in it and direct care. The shape of those functions should depend on its age, other individual characteristics, and local socioecology, but should always be increasing.

Given the assumption that natural selection tends to optimize tradeoffs in investment allocations, the expectation is that over their lifetime parents will attempt to maximize the sum of the reproductive values of their children through the optimal allocation of their investment budgets and by optimizing their fertility regime at each point in time. Thus the optimization problem for investment at any point in time is to maximize the sum, subject to the parental budget constraint.

A mathematical analysis of these tradeoffs (not presented here but available from the author on request) yields some further insights. At equilibrium when investments are optimally distributed, care will have a bigger effect than resources on one fitness component (offspring survival to adulthood or offspring fertility as an adult) and the opposite will be true of their

relative effects on the other component. This is due to the tradeoff between time spent in care and time spent acquiring resources to invest in children. This means that the difference between the marginal effects of care and resources on survival is equal to the marginal effect on survival of an increase in the proportion of total parental investment that is allocated to care. An analogous statement may be made regarding the difference between the marginal effects of resources and care on expected adult fertility of offspring who reach reproductive age. It also means that the difference between the marginal effects of care and resources on survival divided by the difference between their effects on fertility will equal the equilibrium value of offspring survival to adulthood divided by the equilibrium value of offspring fertility as an adult. (This is due to the tradeoff between investing in survival to reproductive age and adult fertility of offspring.)

A fundamental result is that at equilibrium the marginal effects of care and of time spent acquiring resources on both survival and fertility must all be equal, both for a given offspring and across offspring.

Since offspring reproductive value is only partially determined by parental investment, we can examine the effects of exogenous changes in survival and fertility on optimum investment allocations. For example, an exogenous increase in survival, holding all else constant, should lead to a relative increase in investment in the adult fertility of offspring and a relative decrease in investment in survival. The equilibrium condition requires that an increase in the proportion of juvenile survival to adult fertility of offspring must be accompanied by an increase in the proportion of the marginal effects of parental investment on survival to its marginal effects on fertility. This increased proportion would occur at a higher level of investment in fertility and a correspondingly lower level of investment in survival, if, as is likely, the impacts of parental investment on fertility and survival are characterized by diminishing returns. This result is due to the interaction of offspring survival and fertility in determining fitness, and, in general, favors intermediate values of investment in each.

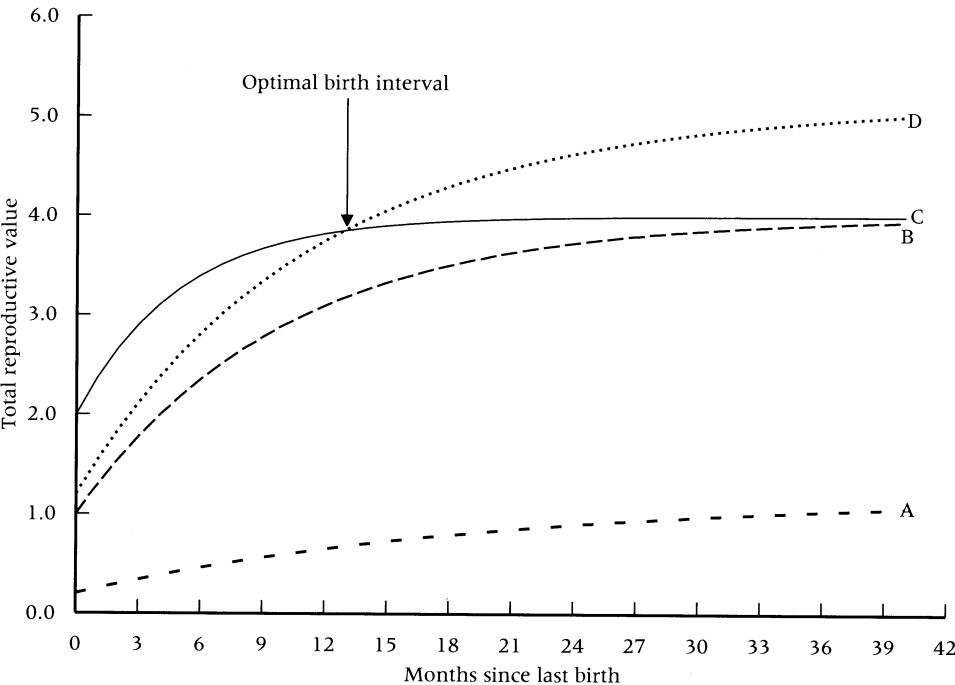
We may also consider the effects of changes in the wage/return rates on optimal investment allocations. Increases in wage rates, holding all else constant, should result in increased investment of resources in offspring for analogous reasons. When wage rates increase, holding all else constant, a smaller marginal effect of resources on offspring reproductive value will meet the equilibrium condition. However, this does not necessarily imply that the relative investment of *time* allocated to acquiring resources to *time* allocated to care should increase. Since increases in wage rates result in a larger total budget for parental investment, its effect on time allocation to work relative to care should depend on the functions that relate care and resources to survival and adult fertility. If the total marginal effect of resources on offspring reproductive value diminishes more quickly with

amount of resources invested than does the total marginal effect of care, we might find an increased investment of time in care with an increase in wage rate, even though the absolute amount of resources invested increases.

Given that the allocation of care and resources can be optimized to maximize the expected reproductive values of children, the next problem is to optimize the birth interval between each child. In this case, the tradeoff is between the decrease in the reproductive values of existing children through investment in the next child and the increase in the reproductive value of the parent provided by the next child. Interbirth interval is optimized when the difference between the sum of the reproductive values of existing children without an additional competitor for investment and that same sum with another competitor is equal to the reproductive value of the newborn. This is illustrated graphically in Figure 7.

If each interval between successive children is optimized from first reproduction to last, total fertility will then be optimized. The age of last re-

**FIGURE 7 Optimal birth intervals**



A: Reproductive value of  $(n+1)$ th child at birth  
B: Sum of reproductive values of existing  $n$  children given that an  $(n+1)$ th child is born  
C: Sum of reproductive values of existing  $n$  children  
D: A + B  
Birth interval is optimized when C = D

production should occur when bearing an additional child decreases the sum of the reproductive values of children. This model assumes that early reproduction does not lower subsequent fertility through increased mortality of the parent or through effects on the budget constraint, but those effects should be incorporated in further elaborations of the model (cf. Charnov and Krebs 1974). The model shows why survival can also affect fertility. If an infant dies, there are  $n-1$  children. If it was worth producing another child when the last baby was born, the death of that baby should lead to immediate resumption of fecundity, given that all of the other children would then be older as well.

### **Physiological and psychological mechanisms underlying fertility and parental investment**

The dual dynamic optimization problem proposed in this analysis (i.e., optimal allocation of time and resources in children and optimal timing and number of children) is complex. Determining the shapes of the age- and environment-specific functions that relate time and resources to the reproductive value of children is a daunting task. This is true both for the scientist and for the parent, who must "know" them to determine the optimal allocation of time and resources. It is likely that people use some simplifying "rules of thumb" to approximate those solutions. Attention must be paid to plausible kinds of physiological and psychological mechanisms that could: (1) have arisen through the action of natural selection; (2) approximate the optimal solutions to these problems; and (3) generate the specific pattern of fertility variation found among and within human societies across time and space.

Some of the physiological mechanisms underlying fertility are becoming better understood. The duration of intensive breastfeeding has been shown to be associated with length of the interbirth interval (e.g., Bongaarts 1983; Campbell and Wood 1988; Wood 1990), although the relationship is apparently complex (Lesthaeghe 1987; Vitzhum 1989; Panter-Brick 1991). Nutrition and work have also been shown to relate to reproductive physiological function and to fecundity (Delgado et al. 1978; Ellison, Peacock, and Lager 1989; Huffman et al. 1987; Hurtado et al. 1992; Lewis et al. 1991; Lunn et al. 1984). This area of research should produce some definitive results in the near future. The next step will be to integrate this understanding of mechanisms with an explanatory framework for understanding why those mechanisms evolved to perform they way they do.

The psychological mechanisms underlying fertility decisions are even less well understood. For example, we know very little about the psychological mechanisms underlying how long women breastfeed, whether they use birth control when it is available, the length of the postpartum sexual

taboo, and the frequency of marital and nonmarital intercourse. Although the study of knowledge, attitudes, and practice (KAP) is well developed in world fertility studies, those studies have not provided an understanding of why there are cultural differences and why there is individual variation within societies in each of those three areas. Although, as scholars in different disciplines have suggested (e.g., Easterlin 1973; Boyd and Richersen 1985), it is likely that the attitudes and behavior affecting fertility are determined by some combination of imitating cultural models and individual adjustments to current conditions, we do not know how alternative models come to predominate in populations nor how individual adjustments are made.

It is not hard to imagine that women might adjust the rate at which they introduce supplemental foods, the timing of nursing, and their involvement with sex to evaluations of their youngest child's development and physical condition. In general, between 30 percent and 50 percent of babies born in traditional societies without access to modern medicine die before adulthood. Thus there is ample opportunity to observe many infant and child deaths and the events leading up to them. The impacts of reduced care on sickly babies and the age at which most children would not be too adversely affected by the birth of the next child should be both directly observable and the subject of much cultural lore that guides women's behavior.

The human pattern of providing resources for children well into adolescence and often into adulthood may present a more difficult problem for analysis. The models discussed above focus on the tradeoff between utilizing resources for producing additional children and the reproductive value of those children. The impacts of parental provisioning on the adult fertility of children should be harder for parents to assess because of the delayed nature of the effects. In the context of hunting-and-gathering societies and small-scale horticulturists, the decision should concern the work effort parents require of children. Why are parents often lax in disciplining children and require little in the way of productive work from them (Draper and Cashdan 1988)? Do foragers assess the probable returns from child labor, the rate of substitution between their labor and that of their children, and the payoffs to play and other activities in which children engage? If so, how are they assessed, by whom, and to what extent do imitation and cultural copying predominate in the population? Do peasants and landowners in agricultural societies assess the availability of land, the distribution of wealth, and the impacts of fertility on adult outcomes of offspring in adjusting patterns of inheritance, onset of reproduction, and total fertility? Again, if so, how, and by whom? The same questions may be asked about returns from education, parental investment, and fertility in modern industrial contexts. The critical requirement of the models discussed above is



mechanisms by which limited time and resources can be optimally allocated in relation to changing marginal returns so as to maximize a single currency, fitness.

The assumption that those mechanisms exist is a working hypothesis in model building. However, it also guides the search for the kinds of psychological mechanisms we might expect to find. Given that available evidence suggests that the domestication of animals and plants began about 10,000 years ago, the greater part of hominid evolution occurred in the context of a simple food-gathering lifestyle. We need to investigate the kinds of psychological and physiological mechanisms underlying fertility and parental investment decisions that would have evolved under those conditions. Available evidence suggests that hunting-and-gathering groups tend to be small, composed largely of kin, and that there is little in the way of wealth and power differentials. Yet, in spite of those similarities, there is also evidence of considerable ecological diversity in subsistence patterns and associated social relationships. We do not know the extent to which the human brain and its associated psychological processes are specialized to those conditions and the extent to which they are sufficiently flexible to respond to novel conditions. This issue becomes critical when we consider behavior in peasant and modern industrial contexts. If behavior in modern contexts systematically deviates from expectations derived from fitness-maximizing models, we need to determine the specific features of human psychology and of contemporary socioeconomic conditions that are responsible for those deviations (see Turke 1990; Tooby 1990; Perusse 1993; Kaplan 1993 for more in-depth discussions of this issue).

Moreover, abundant evidence points to regional and cross-cultural variation in norms and practices regarding breastfeeding, postpartum sexual abstinence, timing of marriage, nonmarital sexual activity, and other behaviors that affect fertility rates. It is clear that men and women do not "reinvent" such behaviors individually, solely on the basis of trial-and-error learning (see Boyd and Richerson 1985). People rely, at least to some extent, on accumulated knowledge and on existing responses to problems in investment decisions. Thus there is room for historical forces and the processes of cultural transmission to exert an impact on reproduction and parental investment. In fact, it is when the outcomes of behavior are difficult to assess, as seems to be the case with the effects of parental investment on adult outcomes, that cultural copying becomes increasingly useful (Boyd and Richerson 1985).

This discussion suggests that we need an integrated understanding of the physiological and psychological mechanisms and of the cultural processes underlying varying fertility outcomes. For example, since the physiological pathways that relate breastfeeding to fecundity probably evolved under conditions in which females had some control over the length of breastfeeding, it will be difficult to understand the adaptive significance of

those pathways without a clear understanding of the psychological and cultural processes that govern maternal decisions concerning breastfeeding. Since long-term investment in offspring after weaning is a fundamental characteristic of the human species, it is likely that mechanisms governing birth spacing respond to the length and intensity of investment. This is a rich area for future investigation.

### **Empirical predictions derived from an evolutionary perspective on fertility and parental investment**

Although the direct application of the above model awaits measurement of the relevant parameters, its formalization assists in specifying the information we need to test it and leads to a number of qualitative predictions. We focus here on two impacts of parental investment: (1) survival to reproductive age and (2) adult fertility of offspring.

*Parental care and child survival* The impacts of direct care on child survival are almost certainly greatest when children are very young. In none of the three societies studied here do children develop significant awareness of environmental hazards until they are over two and a half years of age (see Kaplan and Dove 1987 for results of developmental tests with Ache children). In fact, when they begin to explore their environment in the second year of life, they are at great risk of such accidents as falling into the fire and puncture wounds, and can require even greater maternal vigilance than newborns. One reason why most societies do not have birth intervals resembling the Hutterite pattern of around one year may be that the human developmental program is based on intensive maternal supervision until children learn to talk and have a significant awareness of the dangers posed by their environment.

The relationship between parental care and child survival is likely to vary by ecological circumstances. If the critical factor determining the optimum length of interbirth intervals is the impact of reduced care on the child who will be displaced from the breast by the newborn, a significant component of the variation in average birth intervals across and within societies should be explainable in terms of factors affecting the value of varying lengths of intensive maternal care (see Blurton Jones 1986; Blurton Jones, Hawkes, and O'Connell 1989; Borgerhoff Mulder 1992; and Low 1993 for related discussions). Significant differences across environments are likely in health risks to children and in the improvements in those environments people invest in. Nomadic peoples are likely to invest the least in improvements because the future benefits are of shorter duration. Variation in danger to infants and young children related both to the environment and to investments in improving it should be associated with differences between foragers and farmers, and among foragers and farmers, respectively, in infant carrying (Lee 1979; Blurton Jones 1986), the use of

sibling caretakers (Borgerhoff Mulder 1992; Borgerhoff Mulder and Milton 1985; Draper and Cashdan 1988), maternal food production (Hurtado et al. 1992), and fertility (Blurton Jones, Hawkes, and O'Connell 1989).

There is some suggestive evidence of this effect among the Ache. When the Ache forage nomadically in the forest, they move camp daily and do not create safe places for children to explore and play. As a result, mothers closely guard young children and rarely allow them to be cared for by siblings or other adults. Children under age 3 spend over 90 percent of the time in tactile contact with their mothers. However, at the permanent agricultural village where they now spend most of their time, areas in and around houses are cleared and children spend significantly less time in tactile contact with their mothers (Kaplan and Dove 1987). Consistent with those behavior changes, the interval between births also has decreased from a mean of 3.2 years when the Ache were full-time nomadic foragers to a mean of 2.5 at the settlement (Hill and Hurtado in press; Hill and Kaplan 1988; see Hawkes, Blurton Jones, and O'Connell 1989 for similar suggestions concerning !Kung and Hadza foragers). Of course there are many other possible causes of the change in fertility such as differences in workloads, availability of weaning foods, and increased medical care.

In addition to ecological factors affecting the value of direct care of children, exogenous environmental factors affecting the wage rate of women (defined broadly to mean the rate at which resources are produced per time spent working) should affect the costs of direct care, and hence birth intervals. Increases in wage rates for women raise the opportunity costs of child care and tend to favor greater investment in resource production; this tends to produce lower fertility in modern industrial contexts (Mincer 1963; Becker 1981). On the other hand, the ratio of men's wage rates to women's should be positively related to women's time allocation to child care and hence to higher fertility in modern contexts (Becker 1981). It should be mentioned, however, that an increase in the value of women's labor does not invariably lead to lowered fertility. For example, working-class women in eighteenth-century France were more likely to use wetnurses when they were involved in family businesses, and such women appeared to have increased fertility as a result (Hrdy 1992 citing data from Garden 1970).

In general, the composition of residential groups and the time allocation of nonreproductive individuals (older people and children) should affect the availability of alternative caretakers for children (Borgerhoff Mulder 1992; Turke 1988; see Hrdy 1992 for a full treatment of delegated mothering). When women can effectively substitute their direct care with the care of others, they should be able to dedicate more time to resource production and to shorten interbirth intervals. A more common pattern, however, appears to be subsidizing child care with shared food (Hames 1988; Hawkes, Blurton Jones, and O'Connell 1989; Hurtado et al. 1992). Preliminary analysis of all three data sets discussed here shows that parents do not increase

productivity calorie-for-calorie in relation to the net food requirements of their children. In fact, young families and large families do not meet their caloric needs with their own production and are supported by older people and individuals with few dependents. In addition, some individuals are exceptionally high producers and share the resources they acquire with other families. For example, one Machiguenga man acquired about 45 percent of the total meat eaten in the community of Yomiwato. The provisioning of children, either directly or indirectly, by individuals other than their biological parents should affect age at first reproduction, interbirth intervals, and total fertility. In these three societies, it allows young adults to reproduce when they are still dependent upon their parents for resources, allows families to have multiple dependent children they cannot support, and allows mothers of young infants to work little and to engage in intensive care of infants (Hurtado et al. 1992).

Such aid greatly complicates the development of adequate models of fertility. The models and the data presented here suggest that most human groups should exhibit parity-sensitive fertility. They suggest that we must reevaluate the evidence upon which the distinction between natural and controlled fertility (Henry 1961) is based. It is generally agreed that parity-sensitive fertility becomes prevalent in Europe only in the mid to late nineteenth century (see Coale and Treadway 1986 for a detailed discussion). Most peasant societies are characterized as "natural fertility" regimes. The separation of parity-sensitive and natural fertility regimes is based on age-specific fertility profiles. A standard natural fertility schedule is used as a basis for comparison, and deviations toward a greater proportion of births at younger ages and a smaller proportion at older ages are used to infer parity-specific fertility control (Coale and Treadway 1986).

The data presented here suggest that demands on parental resources increase with each child, at least until the oldest child is almost an adult. The models suggest that interbirth intervals should be sensitive to that increase. Since the standard natural fertility schedule itself exhibits declining fertility with age, conformity with that schedule does not necessarily indicate insensitivity to parity. Moreover, since more-fertile women who experience higher offspring survival may be healthier and better off economically, cross-sectional tests relating birth intervals to number of living children or to parity prior to the interval may not detect parity-specific fertility or reproductive tradeoffs (see Hill and Hurtado in press for lack of evidence of tradeoffs). If costs do increase with number of surviving children, resource sharing and assistance in care should attenuate the effects of parity. We should expect that, other things being equal, fertility will be increasingly parity-sensitive the greater the economic and social self-reliance of parents.

*Parental investment and adult reproductive value* Consideration of the impact of parental investment on the adult fertility of offspring implies an additional set of qualitative predictions. Variation in the timing and inten-

sity of resource provisioning by parents should reflect the costs and benefits of substituting child labor for adult work. Therefore the rate at which children's productivity (i.e., resources produced per unit of labor) approaches adult productivity will affect the proportion of time adults and children work, and the proportion of total resources that children provide for themselves as a function of age. This suggests that the importance of strength and learned skills in the efficiency of production of local resources should affect developmental trends in children's productivity. When stationary resources such as gardens and naturally occurring plant foods and insects are located close to home, children's productivity should increase (see Blurton Jones, Hawkes, and O'Connell 1989). So too should children's labor when harvest size increases with the number of unskilled laborers. When the diet or the principal sources of monetary income are derived more from resources that require strength or learned skills, however, children should depend upon parents longer, and parents should be able to raise fewer children.

The cost of labor to children should also affect their self-sufficiency. Two kinds of costs may be important. Direct risks to children's health such as increases in the probability of accidents and illness due to productive labor are one kind. Delayed effects and opportunity costs in terms of training and skill acquisition are another. If engaging in productive labor prevents children from learning skills that will greatly increase their productivity as adults, we might expect children to devote more time to skill acquisition and to be less self-sufficient. This may be the case in foraging societies where the acquisition of hunting skill requires years of nonproductive play, and in modern industrialized societies where earnings increase with time spent in school. Under those conditions parents, by provisioning children, may influence their reproductive value by increasing their earnings as adults, which, in turn, would affect their budget for reproduction. Alternatively, if, as may be the case among peasants in developing countries and among the underclass throughout the world, parents can do little to provide children with the resources necessary to remain in the education system for long periods, we might expect higher fertility and lower parental investment per offspring. Finally, if children's labor is both productive and provides training opportunities for skill development, we might expect children to work hard and parents to achieve high fertility. This may be true among many pastoralists, horticulturists, and peasant agriculturists.

### **The human capital theory of fertility in developed and developing countries**

It does not appear that people in modern industrialized countries are maximizing fitness with the low fertility they exhibit. Recent analyses of US data (Kaplan et al. in press; Mueller nd) show that people with the highest fertility have the most grandchildren and that the modal fertility of two chil-

dren is not associated with the highest fitness. Why do most people choose to have two, or at most three children when they would have so many more grandchildren if they had larger families? In addition, many studies suggest that individuals with more wealth do not translate that wealth into higher fitness (e.g., Vining 1986; Kaplan et al. in press; Perusse 1993). We must be able to explain why people of very different incomes have converged on the same fertility rates.

The theoretical approach and the models presented here imply directions for hypothesis formulation. The models suggest that if parents elect to have two or three children, their assessment must be that the care and resources diverted to a third or fourth child would worsen outcomes for the first two children sufficiently to motivate cessation of reproduction. If this is correct, it suggests the need to focus on cues parents use for assessing outcomes and on the conditions that change the function relating parental investment to those cues.

Data from England from 1550 to the mid-nineteenth century indicate that marital fertility rates were rather stable; however, marriage rates themselves varied markedly, with an average of about 50 percent of reproductive-age women being married (Wilson and Woods 1991). These comparatively low marriage rates may have been caused by population growth and a resultant scarcity of land. The principal means by which people acquired the resources necessary to establish a family were inheritance and the capture of land through military exploits (see, for example, Boone 1986). Scarcity of land was associated with biased inheritance patterns in which one or two children received the majority of the inheritance and the remainder were forced to fend for themselves and often to enter nonreproductive roles in the clergy, the military, or domestic service (Boone 1988; Lesthaeghe and Wilson 1986). Apparently, setting up one or two children with sufficient capital resources to start a family and investing little in the remaining children produced a more attractive result than intermediate amounts of investment in each.

The industrial revolution, which itself may be seen as a response to these demographic and economic conditions, appears to have had several simultaneous effects on fertility. As the demand for labor began to approach its supply, more individuals could earn enough to support children. Parents faced an additional tradeoff: the market demand for child labor increased, but at the same time competition in wage markets may have raised the value of parental investment and delayed entry into labor markets (i.e., investment in human capital). Through parental support, children could delay entry into the labor force and receive education and training that increased their final wages.

The standard theoretical result of general equilibrium theory in competitive economies is that workers are paid according to their marginal product (i.e., the increase in revenues they provide to the firm) (see, however,

Frank 1985 for a critique of this result). The theory of investment in human capital (e.g., Becker 1975) predicts that people will invest in training to the point where the marginal returns on lifetime income from additional investment equal the marginal cost. Those costs are expected to rise with age because of reduced years in the work force available to reap the advantages of higher wages and because, as skill increases, each additional year of investment is more costly in terms of lost wages.

The impact of skills and knowledge (i.e., human capital) on marginal product is likely to be a direct function of the technology of production (Willis 1982). Prior to large-scale industrial production, the impact of human capital on production is likely to have diminished at much lower levels. Lindert (1986) estimates that in England the overall share of national income attributable to human capital increased from 15 percent in 1967 to 52 percent in 1972–73. In agrarian/ranching societies, limitation of physical capital (land and livestock) probably placed greater constraints on production than did human capital.

Consideration of the cumulative nature of human capital stock accrual may help us understand some of the seeming contradictions associated with modern fertility.<sup>15</sup> The acquisition of many skills is dependent upon the base of precedent skills on which they are built. This is especially true of mathematics, but also seems to be true of skills associated with reading and writing. This suggests that the skills parents have may form part of the base from which children draw their skills.

This observation has several implications. First, the value of investing resources in children's education may depend directly on the time parents dedicate to their children, if success at school, particularly at higher levels, depends upon the base children receive from parents. Second, the payoffs to investments in the higher education of children may be greater for parents who themselves are more educated (and hence, other things being equal, earn more).

Taking these two implications together, a third emerges concerning small or no income effects on fertility rates in developed countries. Because of the positive association between human capital and earnings, richer parents tend to possess more human capital. This should increase the payoff both to time spent on children and to resources invested in them. Thus, the extra income of richer parents may be balanced by increased optimal levels of investment in offspring, so as to yield no net fertility effect.

Without taking such effects into account, the models presented above (like other evolutionary models of parental investment) imply that (1) optimal parental investment does not depend upon income; and (2) adult reproductive value is a positive linear function of adult income. If, in the past, income linearly predicted adult reproductive value, psychological mechanisms that adjusted fertility and parental investment to the adult in-

come of offspring (rather than to reproductive value, *per se*) could have maximized fitness and may have evolved through natural selection. Thus human psychology may be designed to maximize the sum of the energetic resources garnered by descendants. Perhaps the critical novel element in modern society is the combination of increased importance of human capital in determining income and a positive relationship between parents' human capital and optimal investment in offspring to maximize the sum of their incomes. If this is correct, parents may be accurately adjusting investment in response to cues that no longer predict offspring reproductive value.

A fourth implication is that differences between the developed and developing worlds may be explained by the cumulative nature of human capital. This theory suggests that in addition to the availability and cost of contraception, three factors should affect fertility reduction in the developing world: (1) production opportunities that require high levels of accrued human capital; (2) access to education; and (3) the cost of education. With respect to the first factor, growth in production opportunities and women's access to them may be especially critical. Without growth in jobs that require high levels of human capital, parents with low levels of accrued capital may not find it worthwhile to reduce fertility, because their children would be outcompeted by the children of parents with higher stocks of capital. If women have access to those productive opportunities, both the opportunity costs and the benefits of childcare will be greater, favoring lower fertility. The costs of training, in terms of lost child labor, fees, and parental time, must be high enough to favor reduced fertility, but low enough that training is feasible for poor people.

A fifth implication is that competition in wage markets and cumulative human capital acquisition may positively feed back on one another. As the supply of individuals with a given stock of human capital increases, the associated wage rate of jobs requiring that level of human capital should drop. The level at which the effect of human capital on wage rates decelerates may rise as the stock of capital increases.<sup>16</sup>

### Unique features of evolutionary models and implications for empirical tests

Many of the predictions and some of the reasoning discussed here have been derived independently from very different theoretical perspectives. Many functional models share the prediction that fertility responds to the technology of production, the productivity of child labor, and juvenile mortality, and is resource-limited. The distinctive feature of current evolutionary models is their reliance on a single outcome currency, biological fitness. This reliance has a number of important implications.



First, it focuses attention on competition between reproductive alternatives within populations. In contrast, many functional theories within demography, history, and anthropology propose that humans adopt fertility patterns that maintain an equilibrium between population and resources (see, for example, Coale 1986; Hayden 1986; Harris and Ross 1987). Cultural patterns of fertility control are viewed as adaptations to maintain that equilibrium. If mortality rates drop or food supply decreases, people compensate with reductions in fertility. This view is now disfavored by evolutionary biologists. Because variants that increase their genetic representation in future generations relative to alternatives become more prevalent through time, altruistic individuals who curtail reproduction in order to maintain equilibrium with resources will be outcompeted by individuals who turn a disproportionate share of the resource base into their own genetic progeny. Explanations based upon population advantage in terms of equilibrium with the environment have been shown to be theoretically and empirically inadequate (see Williams 1966 and Trivers 1985, for discussions). For this reason, explanations of low population growth rates among hunter-gatherers as an adaptation to avoid overexploiting resources (Hayden 1986; Harris and Ross 1987) are suspect, as are models of demographic transition as an equilibrium response to lower mortality (see van de Walle 1986 for a discussion). The models presented here rely on very different mechanisms for explaining the relationship between resource accrual, mortality, and fertility (i.e., payoffs to parental investment and limited budgets for investment). Moreover, evolutionary biologists expect populations to overexploit resources when it is individually advantageous to do so and to experience Malthusian checks as a result.

Another implication is that evolutionary models view the psychological processes governing satisfaction, decision, and action as the result of a history of natural selection through the differential representation of genetic variants. This focuses attention on descendants and outcomes for descendants. In contrast, most rational models, including those of the new home economists (Becker 1981; Becker and Barro 1988; Becker, Murphy, and Tamura 1990) and of Caldwell (1982) and Handwerker (1988, 1993), propose that investments in children are governed by their effects on parental satisfaction, either because children increase parental wealth or because positive outcomes for children provide pleasure for parents. The concepts of utility and satisfaction are quite flexible, and ultimately they are compatible with almost any set of behavioral results. The more rigid requirements of evolutionary models make them inherently more falsifiable. In fact, it is likely that the low fertility behavior and high adult consumption levels characteristic of modern industrial society will not be explained by models of current fitness maximization. However, the robustness of the theory of natural selection in explaining organic evolution demands that

an adequate explanation of human reproduction confront the effects of natural selection.

## Conclusion

Although more data are necessary to determine whether net intergenerational wealth flow is downward in all societies, it should come as no surprise that under most conditions, humans, like all other known organisms, invest in, rather than exploit, their offspring. We clearly need theories that are grounded in our general understanding of the biology of living organisms while also being capable of predicting the pattern of variability in human fertility. An adequate general theory of fertility requires: (1) a theory of parental investment consistent with our understanding of the effect of natural selection on life histories; (2) the specification of a set of proximate physiological and psychological mechanisms that could have evolved under traditional conditions in a hunting-and-gathering life; and (3) empirical adequacy for explaining variability in fertility levels across traditional societies, historical changes in marriage patterns and fertility levels in complex state societies, fertility reduction in the industrial era and short-term fluctuations in those fertility levels, and the pattern of fertility reduction and nonreduction in the developing world.

Such a theory will require a synthesis of data and theory that have emerged from biology, anthropology, sociology, demography, history, economics, and psychology. Those disciplines offer a plethora of theoretical approaches to the study of human fertility. These alternatives, when compared one against the other, share some common predictions, offer some unique and competing predictions, and, in some cases, are complementary. Research designed to evaluate those alternatives within single studies is clearly needed. The study of human fertility could serve as a paradigm for interdisciplinary cross-fertilization, theory development, and empirical test.

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## Notes

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1 Although a longitudinal sample of food production and consumption through the life

course would be ideal, it is of course unfeasible. This is a cross-sectional sample that is being used to approximate life course changes and is subject to ambiguous interpretation of cohort effects. The age pattern of work in a cross-sectional sample confounds developmental effects with historical change. This problem is especially serious in societies undergoing rapid social change, as are the Ache and Piro and, to a lesser extent, the Machiguenga. Informant reports about work patterns in the past, however, do not reveal cognizance of major changes in the age pattern of work.

2 Data on the women's sisters who died were included in the sample. Thus our measure is a total fertility rate rather than completed family size. The two measures yield very similar estimates, though.

3 This is a small cross-sectional sample, and the sample sizes for the later ages become quite small. The estimates of total fertility rates for the Piro and the Machiguenga may not be reliable for the purposes of cross-cultural comparison. However, analysis of data from independent samples of the reproductive histories of the informants' mothers revealed almost the same figure, suggesting both that the estimates are reliable and that there has been little change in fertility patterns.

4 Clearly, the evolution of our species and its ancestral lines occurred under a wide range of ecological circumstances, most of which were quite different from the tropical forests of Amazonia. We do not know the sensitivity of child labor patterns to local ecology among foraging groups. Nevertheless, forager and forager-horticultural societies share characteristics in terms of the scale of production, the lack of ownership of land, the activities involved in subsistence, the accumulation of wealth, and distribution of and access to power that are different from those of state and peasant societies.

5 Changes in these percentages primarily affect the proportions acquired by adult men and women, respectively (higher percentage credit to the harvester increases women's and decreases men's food production). Children harvested only small amounts of food, and these figures may actually overestimate children's food production because children

frequently did not process the food they harvested and they sometimes were given full harvesting credit for tubers they transported even though their mothers actually dug them out (i.e., because the digging was not observed).

6 A comparable sample at the settlement would be quite useful and should have been collected.

7 This method assumes that effort expended in activity is the same for all age/sex classes and is insensitive to differences in work effort. This procedure may overestimate the food consumption of children and underestimate consumption by adults.

8 Since the number of days sampled varied across individuals and since within-individual variation in food production across days is greater than among-individual variation in mean food production within age/sex cohorts, the data on food production are presented as means for the entire cohort (total food produced divided by total days sampled) rather than as the mean of the individual means across days. This smoothes out the developmental trends but does not alter the overall results substantially.

9 About 28 percent of Ache ever born reach age 60 years; this is about half those that reach age 20 (Hill and Hurtado forthcoming).

10 This figure was obtained by extrapolating from the formula ( $BME \times 2.25$ ) used for very active adults ( $BME$  = basal metabolic expenditure).

11 Unpublished analyses of Piro and Machiguenga stool specimens indicated that the average child was infested with more than four species of intestinal parasites. It is likely, however, that Ache children's food consumption was overestimated to some extent because adult men were so much more active than women and children.

12 The intrinsic rate of increase,  $r$ , is a more accurate definition of fitness because it relates age-specific mortality and fertility schedules to the rate of increase of alleles through time. In the discrete time form, it can be obtained by solving Lotka's equation for  $r$ :

$$1 = \sum_{x=1}^{\omega} l_x m_x e^{-r(x+1)}$$

where  $\omega$  is age at last reproduction,  $l_x$  is the probability of surviving to age  $x$ , and  $m_x$  is fertility at age  $x$ . The model presented here focuses on survival to adulthood and total fertility, ignoring such factors as generation time, because doing so simplifies presentation and directs our attention to a principal tradeoff faced by parents in investment decisions.

13 This assumes that the division of time between parental effort and the time they allocate to themselves (including maintenance, financial support, leisure, pursuit of status and mating opportunities, etc.) is fixed and outside the scope of the model.

14 More technically, reproductive value at birth should be defined in continuous form as:

$$\int_0^{\omega} l_x m_x e^{-rx} dx$$

where  $\omega$  is age at last reproduction,  $l_x$  is the probability of surviving to age  $x$ ,  $m_x$  is fertility

at age  $x$ , and  $r$  is the population growth rate. I choose to simplify this expression in the text as survival to adulthood times fertility as an adult because it captures the essence of the parental tradeoff.

15 See Becker and Tomes 1986; Becker and Barro 1988; and Becker, Murphy, and Tamura 1990 for similar discussions. I only discovered their papers after having written this section.

16 Becker, Murphy, and Tamura 1990 offer an elegant set of models suggesting that to the extent that new technologies of production are built on accumulated knowledge, there may be greater marginal effects of human capital on income as the overall stock of human capital increases. They use those models to explain lower equilibrium levels of investment in human capital in developing countries.

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