DOES OBSERVED FERTILITY MAXIMIZE FITNESS AMONG NEW MEXICAN MEN?

A Test of an Optimality Model and a New Theory of Parental Investment in the Embodied Capital of Offspring

Hillard S. Kaplan, Jane B. Lancaster and Sara E. Johnson
University of New Mexico

John A. Bock
Australian National University

Our objective is to test an optimality model of human fertility that specifies the behavioral requirements for fitness maximization in order *(a)* to determine whether current behavior does maximize fitness and, if not, *(b)* to use the specific nature of the behavioral deviations from fitness maximization towards the development of models of evolved proximate mechanisms that may have maximized fitness in the past but lead to deviations under present conditions. To test the model we use data from a representative sample of 7,107 men living in Albuquerque, New Mexico, between 1990 and 1993. The model we test proposes that low fertility in modern settings maximizes number of grandchildren as a result of a trade-off between parental fertility and next generation fertility. Results do not show the optimization, although the data do reveal a trade-off between parental fertility and offspring education and income.

We propose that two characteristics of modern economies have led to a period of sustained fertility reduction and to a corresponding lack of association between income and fertility. The first is the direct link between costs of investment and wage rates due to the forces of supply and demand for labor in competitive economies. The second is the increasing emphasis on cumulative knowledge, skills, and technologies

Received June 5, 1995; accepted July 11, 1995.

Address all correspondence to Hillard S. Kaplan, Department of Anthropology, University of New Mexico, Albuquerque, NM 87131. E-mail: hkaplan@unm.edu

Human Nature, Vol. 6, No. 4, pp. 325-360. **1045-6767/95/$1.00 + .10**

in the production of resources. Together they produce historically novel conditions. These two features of modern economies may interact with evolved psychological and physiological mechanisms governing fertility and parental investment to produce behavior that maximizes the economic productivity of lineages at the expense of fitness. If cognitive processes evolved to track diminishing returns to parental investment and if physiological processes evolved to regulate fertility in response to nutritional state and patterns of breast feeding, we might expect nonadaptive responses when returns from parental investment do not diminish until extremely high levels are reached. With high economic payoffs from parental investment, people have begun to exercise cognitive regulation of fertility through contraception and family planning practices. Those cognitive processes may *not* have evolved to handle fitness trade-offs between fertility and parental investment.

KEY WORDS: **Male fertility; Fitness; Human capital; Modern low fertility.**

The reduction in fertility accompanying modernization poses a scientific puzzle that has yet to be solved. Despite the fact that the problem has received a great deal of attention by economists, sociologists, demographers, anthropologists, and biologists, no discipline in the social or biological sciences has offered a fully developed and coherent theory of fertility reduction that explains the timing and pattern of fertility reduction in the developed or developing world. The inability to offer an adequate theory raises fundamental questions about the theoretical foundations of those disciplines. For example, although economics has made great strides in explaining consumer behavior, time allocation, and labor force participation through the recognition that the household is a fundamental organizational unit of human action, there is no adequate explanation of why households are mostly composed of men and women who marry and have children. There is no economic theory of why reproductive partnerships form such a fundamental organizational principle in human societies nor of why people have and want children in the first place. The very modest progress of economists in explaining long-, medium-, and short-term trends in fertility highlights this weakness.

Evolutionary biology in its application to human fertility has fared no better. The theoretical core of modern evolutionary biology is that differential reproductive success is the principal driving force determining evolutionary change and stability. A corollary proposition is that competition over the resources for reproduction is the primary determinant of differential reproductive success.[1] Thus, the fact that people in modern, industrial societies obtain access to and utilize more resources than ever before in human history and yet evidence the lowest fertility rates ever recorded presents a particularly critical challenge to evolutionary biology, at least in its application to humans. Vining (1986) has argued that modern human fertility behavior presents strong evidence that evolutionary theory as it is currently understood is incapable of providing adequate answers to the causes of human behavior.

This paper gives the results of an in-depth study of fertility in a representative sample of men from Albuquerque, New Mexico, designed to evaluate the empirical force of Vining's critique. We present a simple three-generation model of optimal fertility based on maximizing number of grandchildren and test it with data from a sample of 7,107 men. Our approach here is to test the optimality model, which specifies the behavioral requirements for fitness maximization, in order *(a)* to determine whether current behavior does maximize fitness and, if not, *(b)* to use the specific nature of the behavioral deviations from fitness maximization in the development of models of evolved proximate mechanisms that may have maximized fitness in the past and lead to deviations under present conditions.

On the basis of largely negative results from these tests, we consider the empirical and theoretical requirements of an adequate theory of human fertility and one possible solution to the problem. We briefly outline a new theory of modern fertility reduction, based on changing returns to human capital investment in the context of competitive labor markets. The paper concludes by discussing the kind of selection on the psychology of decision-making processes that could have produced optimal fertility regulation under traditional conditions and generates nonadaptive low fertility under modern industrial conditions.

A SIMPLE MODEL OF OPTIMAL FERTILITY

Both biological and economic models of optimal fertility are based on the assumption that there is a trade-off between quantity and quality of children (Becker 1981; Easterlin 1987; Lack 1968; Smith and Fretwell 1974). This trade-off is presumed to result from the fact that parents have limited resources they can invest in offspring and that each additional offspring necessarily reduces average investment per offspring. Most biological models operationalize this trade-off as number vs. survival of offspring, but it is also possible that investment affects adult competitiveness of offspring and hence their adult reproductive value as well.

In Figure 1 we present a qualitative model of the trade-off between fertility and parental investment. The model focuses on alternative uses of adult income. By *income*, we mean all time and physical and social resources that adults have at their disposal. It can be thought of as either a flow or rate that varies through time or as the sum (integral) of that flow throughout adulthood. This forms the budget that can be used in alternative ways that will be associated with different outcomes with respect to numbers of descendants in future generations. The fundamental trade-off with respect to parental investment is between ego's reproduction and offspring's reproduction, with the primary assumption being that income invested in one's own reproduction diminishes income that could be invested in offspring's reproduction.

The model also specifies what we considered to be primary ways in which parental investment can be used to enhance offspring's reproduction. First, and most obvious, is through impacts on mortality rates, particularly during the juvenile period. Other things being equal, expected lifetime reproduction per offspring will increase directly with increases in survival rates. Second, income can be invested in the embodied capital of offspring. *Embodied capital* can be defined as a stock of attributes embodied in the soma of an organism which can be converted, either directly or, more commonly, in combination with other forms of capital, into fitness-enhancing commodities. Body mass and complexity as well as skills and knowledge are forms of embodied capital in which individuals can invest, either in themselves or in others. Humans as well as many nonhuman primates (Holekamp and Smale 1991; van Schaik 1989) also appear to invest in "social" capital through aggression, status display, and assistance. Social capital can be thought of as attributes of other individuals that can be converted into fitness-enhancing commodities. Parental investment in the embodied and social capital of

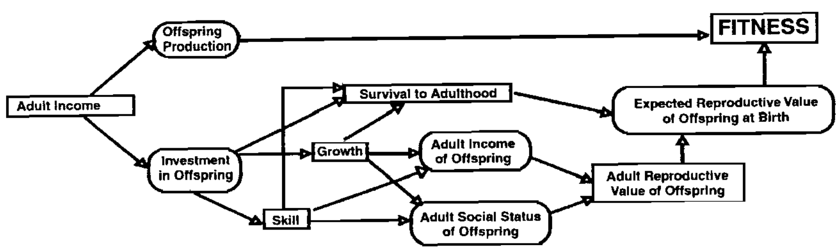

Figure 1. A path model of trade-offs between parental investment and fertility.

offspring can affect the survival,[2] future income, and social status of offspring. The latter two, in turn, form the budget for offspring's investment in own and next-generation reproduction in a recursive process.

This set of causal pathways offers a guide for the investigation of the ecological and individual factors that should affect the investment trade-off between own and offspring's reproduction. Specifically, it focuses on the impacts of physical size, strength, and skill on survival, income, and social status. We have three major steps in the causal pathway. First are the functions that determine the effects of investment of adult income on the survival, size, strength, and skill of offspring. Second is the set of functions that determine the effects of size, strength, and skill on survival, future income, and social status of offspring. Third are the differential impacts of adult income and social status of offspring on their reproduction. The total effects of investments will therefore depend on not only their impacts on the first step but also on the effects of those effects on income and social status and then ultimately on reproduction in the next generation.

The model we attempt to test here simplifies this causal path and operationalizes these trade-offs as completed fertility of parents and reproductive value of offspring,[3] with the outcome measure being number of grandchildren produced (cf. Rogers 1990). Since number of grandchildren is equal to the fertility of parents times the expected or mean lifetime fertility of each offspring produced (i.e., reproductive value at birth),[4] we can represent the fitness function as:

$$G = F_0 F_1 \qquad (1)$$

where G is number of grandchildren, F_0 is the completed fertility of parents, and F_1 is the average completed fertility of children. The variable to be optimized, in order to maximize G, is F_0. The model assumes that the fertility of parents has both direct and indirect effects on fitness. It has a direct positive effect through the number of offspring born but a negative indirect effect through lowering the expected reproductive value of offspring. This is illustrated in Figure 2. To solve for the optimum level of parental fertility, we can find the total derivative of the number of grandchildren in terms of parental fertility, set that derivative equal to zero, and solve for the optimum. Thus we have:

$$0 = \frac{\delta G}{\delta F_0} = \frac{\partial G}{\partial F_0} + \frac{\partial G}{\partial F_1}\frac{\partial F_1}{\partial F_0} \qquad (2)$$

On the right hand side of the equation there are three partial derivatives, the first representing the marginal effects of parental fertility on number of grandchildren, the second the marginal effects of children's fertility on number of grandchildren, and the third the marginal effects of parental fertility on children's fertility (the product of the second and

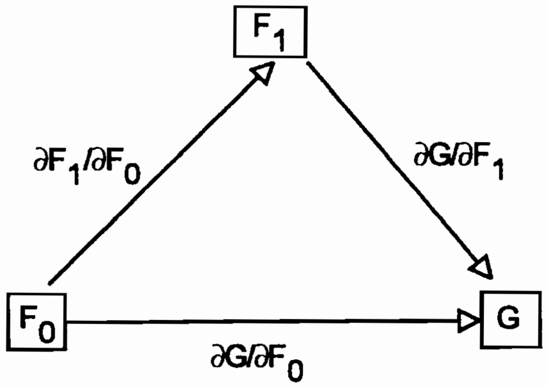

Figure 2. Direct and indirect effects of fertility on fitness.

third term is the indirect effect of parental fertility on number of grandchildren through its negative effect on fertility of children). The model expects the first and second terms to be positive and the third term to be negative. Using equation 1 we can take the partial derivatives of first and second generation fertility on number of grandchildren, respectively, and substitute them into equation 2 to obtain

$$0 = F_0 \frac{\partial F_1}{\partial F_0} + F_1 \tag{3}$$

Solving this equation in terms of fertility in the first generation to obtain its optimum or equilibrium value, we have:

$$F_0^* = -F_1^* \left(\frac{\partial F_1}{\partial F_0} \right)^{-1} \text{ or } \frac{F_1^*}{F_0^*} = -\frac{\partial F_1}{\partial F_0} \tag{4}$$

where the star represents the equilibrium values. This equation has intuitive meaning. Since, at the optimum, the fertility in the second generation must be positive, the partial marginal effect of first-generation fertility on second-generation fertility must be negative in order for there to be a meaningful optimum.[5] If there is no effect (i.e., the partial derivative is equal to zero), infinite fertility (or a corner solution, if first generation fertility is constrained) is expected. Another interpretation of equation 4, obtained by algebraic rearrangement, is that the ratio of children's fertility to parents' fertility must equal the negative of the derivative of the former with respect to the latter. This means that the larger the difference between reproductive value at adulthood and reproductive value at birth (which would be due primarily to pre-adult mortality), the

smaller will be the marginal effect of parental fertility on children's reproductive value at equilibrium. Under modern conditions of low mortality, the ratio of second-generation reproductive value at birth to first-generation reproductive value at adulthood should approach one and the derivative of the former with respect to the latter should approach negative one. This means that at equilibrium each additional child that parents have should decrease each child's fertility by one child.

We test the applicability of this model as a possible solution to the problem of low fertility in modern societies below with data from the sample of Albuquerque men. Those data were collected specifically to test applicability of this model. Men were chosen as study subjects for two reasons. First, the measurement of the relationship between parental investment and income and between income and reproductive outcomes is somewhat more direct for men because of many women's nonmonetized role as a "homemaker" throughout much of this century. Second, the relationship between income and mating opportunities is likely to be stronger for men, and if parental fertility affects children's fertility through effects on mating success, those effects should be easier to detect with men as study subjects.

METHODS

The interview protocol was designed to obtain the following information from each respondent: place and year of birth, ethnicity, education, religion, income, current mate's income, years lived in Albuquerque, number of years he lived with each biological parent, number of half and full siblings, fertility and age of siblings, number and age of biological children, years lived with biological children, number of spouses and women with whom he had children, and number of step and foster children he parented. Information on the respondent's parents' place and year of birth, education, ethnicity, income, and standard of living was also collected.

The Interview Sample

The interview sample of 7,107 men consisted of 2,789 Hispanics,[6] 3,762 Anglos, and 556 others who were interviewed between July 1990 and July 1993. Table 1 presents the composition of the sample by ethnicity and birth cohort.

Potential respondents for the interview were contacted at the Bernalillo County Motor Vehicle Division (MVD), which serves all of

Table 1. The Sample of Albuquerque Men by Birth Cohort

From (≥)	*To* (<)	*Anglos*	*Hispanics*	*Others*	*Total*
1895	1900	3	0	0	3
1900	1905	29	4	0	33
1905	1910	67	12	4	83
1910	1915	234	44	14	292
1915	1920	187	61	12	260
1920	1925	176	78	22	276
1925	1930	208	112	21	341
1930	1935	234	152	30	416
1935	1940	287	188	40	515
1940	1945	419	314	52	785
1945	1950	603	442	71	1116
1950	1955	581	519	113	1213
1955	1960	734	863	177	1774
	Total	3762	2789	556	7107

Albuquerque. All men who appeared to be over 18 years of age were considered eligible for initial screening and were contacted as they received their driver's license photo. If they agreed to the short interview, which took about seven minutes to administer, it was immediately conducted in a private area.

Interviewing men who are renewing or obtaining a driver's license or photo ID at the MVD provides a highly representative sample of the male population. Albuquerque is the largest city in New Mexico with a population in 1990 of 480,577 (U.S. Department of Commerce 1992); approximately 32% of the state's population lives in greater Albuquerque. More than 95% of all New Mexican males over age 20 have a current driver's license (U.S. Department of Transportation 1993), compared with an estimated 93.5% telephone availability for the Albuquerque area (U.S. Department of Commerce 1992). In addition, individuals who do not drive obtain photo IDs from the MVD. Licenses and IDs must each be renewed every four years. By sampling only men who are waiting for license and ID photos, men who visit the MVD more frequently (i.e., those who do not have checking accounts and cannot register vehicles by mail, those who frequently pay fines, those who frequently sell and purchase vehicles, etc.) are not overrepresented in the sample. Groups who are likely to be absent or underrepresented among the licensed drivers include the elderly, disabled, institutionalized, transient, extremely poor, and criminal. These groups are also likely to be underrepresented or uncooperative in most other sampling frames as well.

Evaluation of Sample Bias

The sampling methods employed in this study provided several avenues for evaluating potential biases in the composition of the sample. First, after the first 850 interviews were collected, we compared the demographic characteristics of the sample we obtained with data from other sources such as the census. We examined the age and ethnic distributions of our sample and compared them with data on all male licensed drivers and with census population data for males. There were no significant differences in any of these comparisons. In fact, the ethnic breakdown of the sample obtained at the MVD is almost identical to that obtained from the 1990 Census (Figure 3).

We also examined refusals. About 78% of all men approached agreed to the short interview. One factor that predicted refusals is whether the potential respondent was alone; accompanied men refused 28% of the time whereas men who were alone refused only 18% of the time. No other biases such as age or time of day were detected. Refusals decreased steadily through time because of improved interviewer training.

Following this phase of unbiased sampling, we increased the proportional representation of Hispanics and others by not interviewing

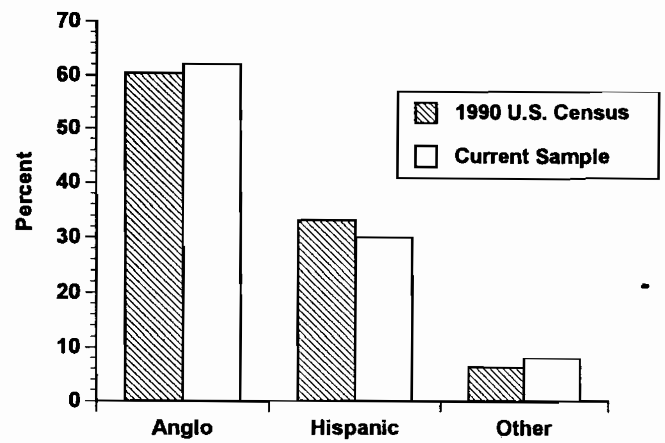

Figure 3. Comparison of U. S. census data for 1990 for Albuquerque males over age 20 with data from the study sample of men (1990–1993) (U.S. Census of Population and Housing, New Mexico, 1991a,b,c).

Anglos on about 20% of sample days. In this way, we obtained a sample that was 53% Anglo, 39% Hispanics, and 8% other ethnicities.

DESCRIPTIVE RESULTS

Data on the fertility of Albuquerque men are presented in Figures 4 and 5. Figure 4a shows the mean completed fertility of five-year cohorts of men born between 1900 and 1960 among white (Anglo) and Hispanic men, respectively. (*Anglo* is a term used in the Southwest to identify all white, non-Hispanic males regardless of ethnicity and religion. It does not imply Anglo-Saxon extraction.) The cohort labeled 1920 includes all men born before 1920, with the oldest man in our sample born in 1897. The men born after 1945 may not yet have completed their fertility (although our analysis showed that more than 90% of men completed their reproduction by age 45, at least in the older cohorts for which we have data). These results show clear effects of both cohort and ethnicity on reproduction. White male fertility is low for men born in the early part of the century (many of whom reproduced during the Great Depression) and increases to a maximum for men born between 1935 and 1940. This peak corresponds to the baby boom. Among Hispanics, reproduction is highest for men born before 1935 and decreases thereafter, possibly representing a later demographic transition for Hispanics and, hence, relatively little impact of the baby boom on their fertility.

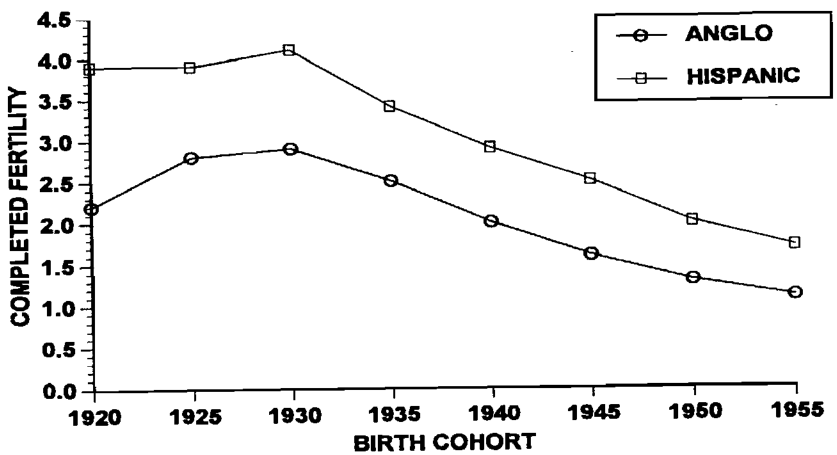

Figure 4a. Completed fertility by ethnicity and birth cohort.

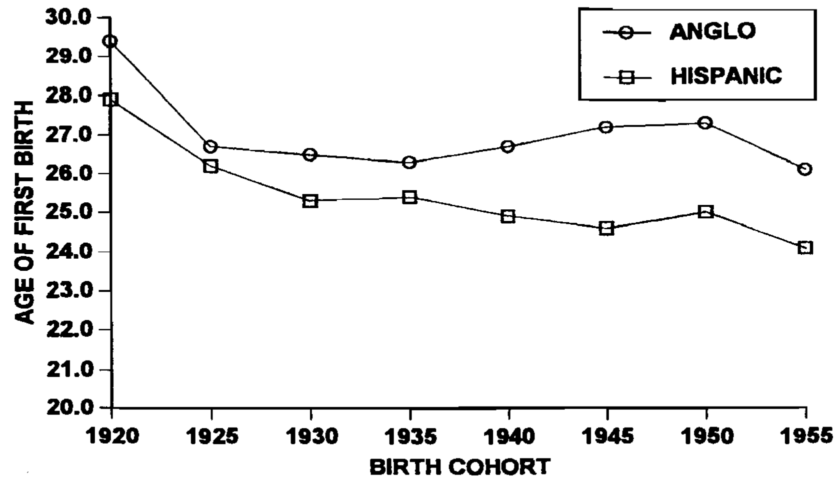

Figure 4b. Age at first birth by ethnicity and birth cohort.

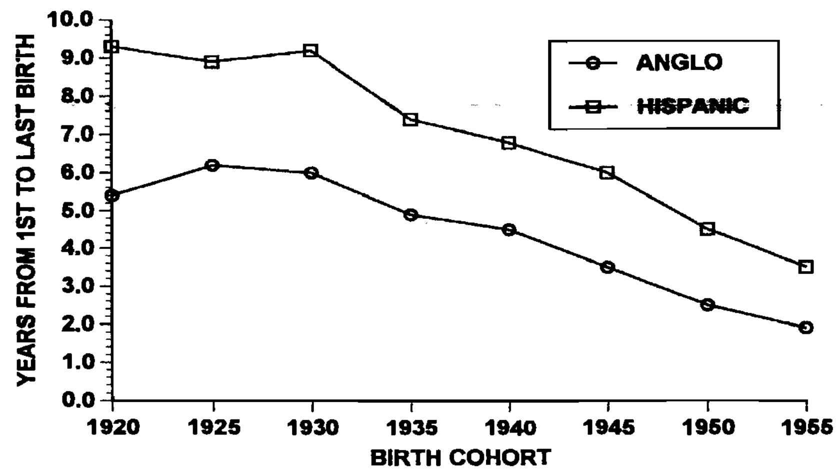

Figure 4c. Reproductive span by ethnicity and cohort.

Thus there is a clear interaction effect of ethnicity and cohort on reproductive performance. These effects are all significant at a level of $p < 0.0001$. Figures 4b and 4c show the effects of cohort and ethnicity on age at first birth and total years of reproduction. These figures mirror the results on completed fertility. Cohort/ethnicity classes with high completed fertility reproduce earlier and have a longer span between first and last births than those with lower completed fertility.

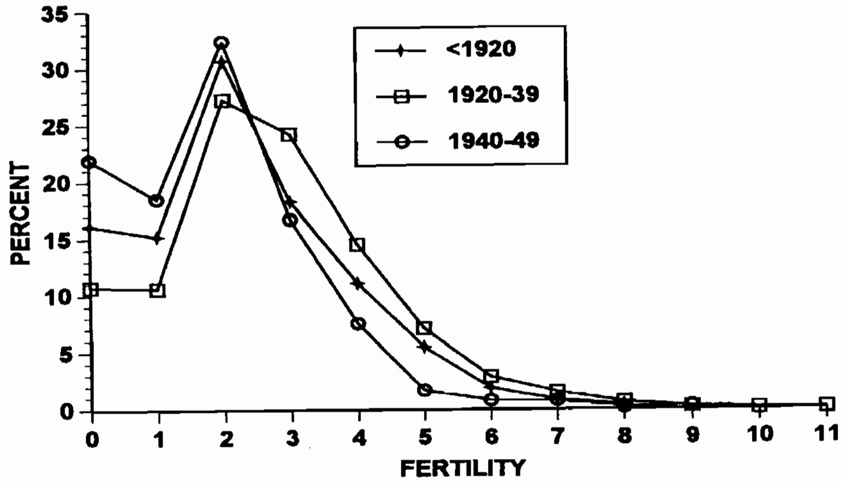

Figure 5a. Frequency distribution of Anglo fertility by birth period.

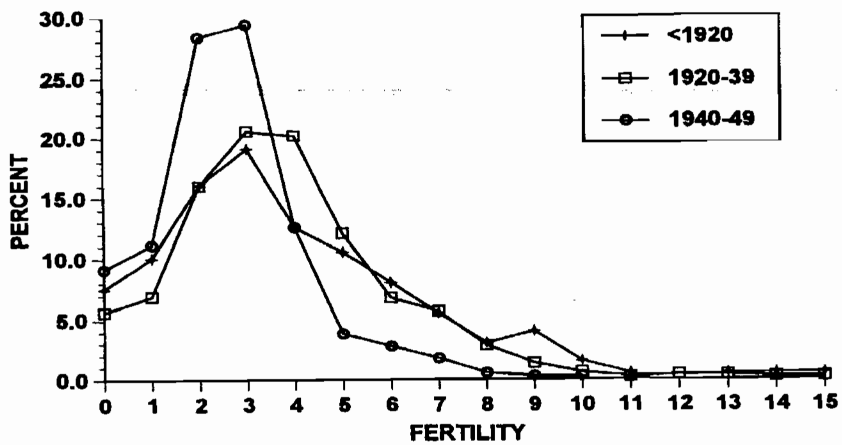

Figure 5b. Frequency distribution of Hispanic fertility by birth period.

Figures 5a and 5b show the frequency distribution of completed fertility among different cohort/ethnicity cells. For Anglo men, there is a clear peak in the frequency distribution at two children, especially for men born before 1920 and men born between 1940 and 1945 (men born after 1945 are omitted because many may not yet have completed their fertility). For men born between 1920 and 1939 (those who reproduced during the baby boom), we see a much greater frequency of men with

three children. Hispanics show a peak frequency of three, with a greater variance for men born before 1920.

Thus, for the model we presented above to be applicable, optimum fertility for maximizing number of grandchildren should be close to two for Anglos and between three and four for Hispanics. However, caution should be exercised here because of the possibility of what is referred to as "phenotypic correlation" or "selection bias" by biologists and economists, respectively. In brief the problem results from the fact that independent variables, such as fertility, which are presumed to affect some outcome variable, such as survival or children's adult income, are themselves choice or endogenous variables. Since levels of endogenous independent variables are not randomly assigned to individuals, statistical models designed to estimate their effects on outcome variables can lead to biased estimates of the "true" effects. For example, there may be variation among men in the optimum level of fertility; men with greater access to resources may be able to produce more children and therefore should have a higher optimum than those with fewer resources. This possibility is illustrated in Figures 6a and 6b. Figure 6a illustrates a single global optimum for the population, whereas Figure 6b illustrates heterogeneous optima for men with differential access to resources. If Figure 6b characterizes modern American men, we might be unable to detect the hypothesized intergenerational trade-off in reproductive value. We might find a positive correlation between fertility in the first and second generations because men with more resources or men from ethnicity/cohort classes that could support more children would have both higher fertility and higher offspring's fertility. Therefore, we must disaggregate the data by income, cohort, and ethnicity to test for such a possibility.

TESTS OF THE MODEL'S APPLICABILITY

The Association between Children and Grandchildren

To determine if a particular level of first-generation fertility maximized number of grandchildren, polynomial regressions of number of grandchildren on number of children were run for the whole sample and by ethnicity, cohort, and income quartile. If number of grandchildren peaks at some intermediate level of fertility as depicted in the above figures, a second-order polynomial regression should yield a

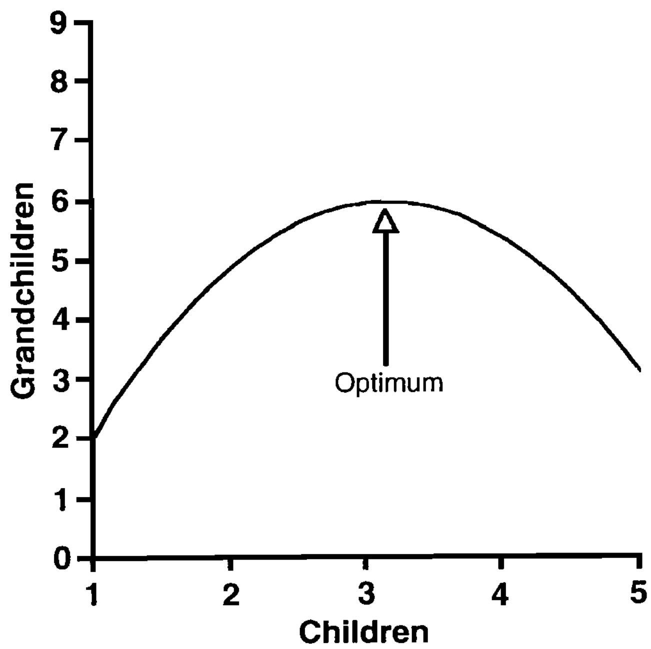

Figure 6a. Optimizing fertility.

positive linear term and a negative squared term. The full model we tested included the respondent's father's number of grandchildren as the dependent variable and father's number of children, father's number of children squared, ethnicity, cohort, father's income, and all two-way interaction terms as predictor variables. This model was then reduced to include only significant effects. This analysis included all men for whom all siblings were at least 45 years of age (or would have been 45 at the time of the interview but had died earlier) with known reproductive histories. This yielded a sample of 4,066 men (respondents' fathers) with complete sets of grandchildren.

The analysis shows that number of children is, by far, the strongest predictor of variance in number of grandchildren. It alone accounts for 57% of the total variance in number of grandchildren. Although, in a polynomial regression, the partial p-value of number of children squared is significant at the 0.0001 level, adding it to the model only changes the percentage of variance explained by 0.1% (Table 2). Moreover, the parameter estimate is just barely positive at .07. Adding cohort, ethnicity, and parental wealth along with interaction effects only increases the variance explained to 59%. The linearity of the relationship of children

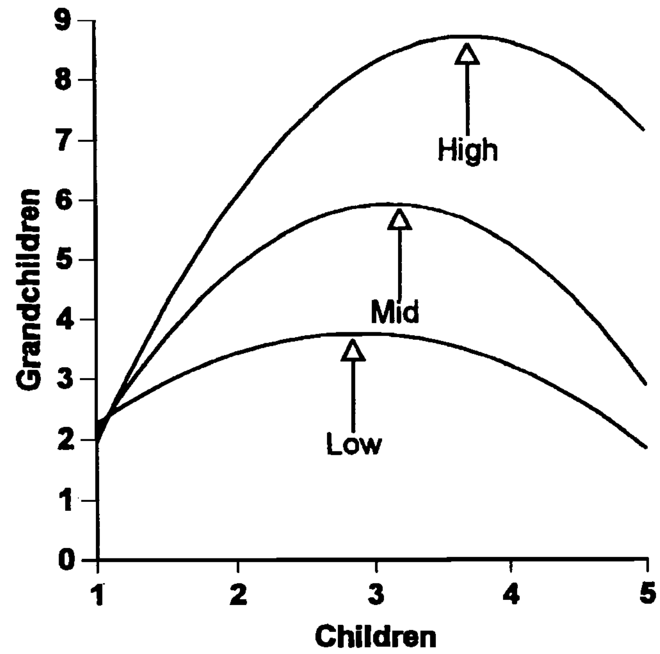

Figure 6b. Phenotypic variation in optimum fertility.

to grandchildren is striking (see Figure 7a). Even though the relationship is fit with a polynomial equation, the line is virtually straight for both Anglos and Hispanics. The lines bend slightly upward at high levels of fertility, due to a slight tendency for the children of men who had large families to have large families themselves.

A simplified model was also run for each ethnicity cohort cell and for each quartile of father's income, stratified by ethnicity. There was no evidence of a negative squared term in the data sets disaggregated by ethnicity and income. In fact, the second-order polynomial term for parental fertility was either nonsignificant or just marginally positive. Again, within each of the eight ethnicity and income cells, number of children accounts for about 50% of the variance in number of grandchildren. In no case was there evidence of an optimum at an intermediate level of first-generation fertility. In all cases maximum fertility was associated with maximum number of grandchildren.

Another way to examine this relationship is with regression of the respondent's number of children on his father's number of children (see Figure 7b). Here again we find no evidence of a trade-off when only males are considered. In no case and in no region of the domain of

Table 2. Regression Models of Number of Grandchildren on Predictor Variables

Variables in Model	df	*T*†	*Partial p <*	*Parameter Estimate*	*Standardized Parameter Estimate*
SIMPLE LINEAR MODEL					
($N = 4065$, $F = 5403$, $p < 0.0001$, $R^2 = 0.57$)					
Intercept	1	−5.3	0.0001	−0.97 (0.18)	0
Number of Children	1	73.5	0.0001	2.48 (0.03)	0.76
REDUCED POLYNOMIAL MODEL					
($N = 4065$, $F = 2707$, $p < 0.0001$, $R^2 = 0.571$)					
Intercept	1	−1.5	0.13	−0.44 (0.29)	0
Number of Children	1	20.19	0.0001	2.23 (0.11)	0.68
(Number of Children)^2	1	2.36	0.02	0.02 (0.01)	0.08
FULL POLYNOMIAL MODEL WITHOUT INTERACTION TERMS					
($N = 3692$, $F = 537$, $p < 0.0001$, $R^2 = 0.59$)					
Intercept	1	0.81	0.42	0.36 (0.44)	0
Number of Children	1	17.36	0.0001	2.04 (0.12)	0.62
(Number of Children)^2	1	2.73	0.006	0.02 (0.009)	0.10
Hispanic	1	8.82	0.0001	2.16 (0.24)	0.11
Other	1	2.11	0.035	0.88 (0.41)	0.02
Father born 1860–1869	1	−2.07	0.038	−2.32 (1.12)	−0.02
Father born 1870–1879	1	−1.43	0.15	−0.77 (0.54)	−0.02
Father born 1880–1889	1	1.81	0.07	0.63 (0.35)	0.02
Father born 1890–1899	1	5.56	0.0001	1.78 (0.32)	0.06
Father born 1910–1919	1	−4.31	0.0001	−1.04 (0.24)	−0.05
Father's Income	1	−2.86	0.004	−0.42 (0.14)	−0.03

† *T* for parameter = 0

Note: Ethnicity and father's cohort were treated as indicator or dummy variables. Ethnicity was coded as Anglo, Hispanic, and other, and respondents' fathers were assigned to ten-year birth cohorts from 1860 to 1919. Parameter estimates for Hispanics and others are comparisons using Anglos as the base. Parameter estimates for father's birth cohort are comparisons using the 1900–1909 cohort as a base. Father's income is estimated on the basis of the average income for his profession in 1980 dollars in units of $10,000 based on data from the U.S. Census. The number in parentheses next to the parameter estimate is the standard error of the estimate.

father's number of children do we find a negative relationship between father's children and respondent's children. The slope of the relationship is not significantly different from zero for all cohort, ethnicity, and income cells. As stated above in the presentation of the model, this means that maximal fertility is favored and there is no maximum to the function that relates first-generation fertility to fitness.

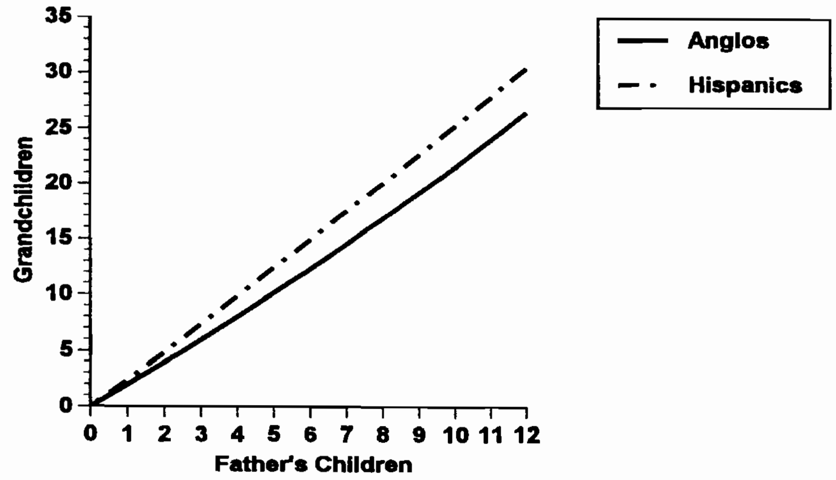

Figure 7a. The effect of number of children on number of grandchildren: Second-order polynomial regression.

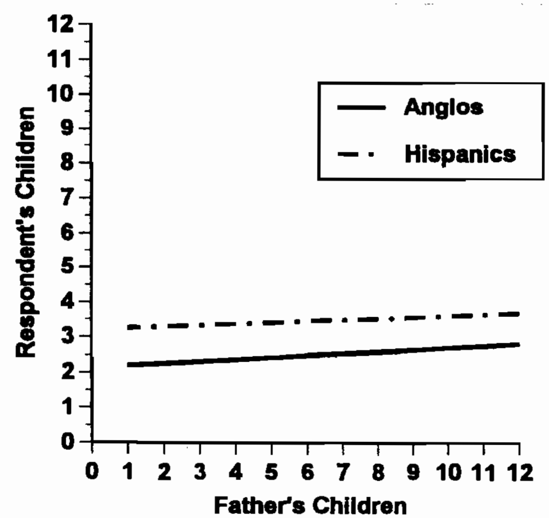

Figure 7b. The effect of number of father's children on number of respondent's children.

Testing the Intermediate Relationships in the Proposed Causal Pathway

In this section we examine the effects of parental wealth and fertility on educational attainment and income. In addition to those predictor variables, the age to which the respondent was raised by both parents is used as another indicator of total parental investment received (e.g., if parents divorced, separated, or died before the respondent reached adulthood, the variable "age raised" reflects the age at which biparental rearing ceased). The model tested includes years of education as the dependent or criterion variable and ethnicity, year of birth, year of birth squared, father's income, father's income squared, age raised, age raised squared, total sibship size, and interaction effects as predictor variables. The squared terms were included to capture nonlinear effects. Table 3a presents only significant effects as the final model. As predicted by the path model (Figure 1), all measures of parental investment affect years of education in the predicted direction. Father's income and the age at which biparental care ended both positively affect years of education. The size of the respondent's sibship negatively affects years of education.[7] This result clearly shows that when analysis controls for the effects of other factors, such as cohort, ethnicity, and income, first-generation fertility is negatively associated with educational attainment.

The next model we tested used the same predictor variables but substituted respondent's income as the criterion variable. Again we found the predicted effects. Age raised and father's income both affect respondent's income positively whereas parental fertility affects it negatively. These results are presented in Table 3b.

Table 3a. Reduced Regression Model of Effects of Parental Investment on Years of Education ($N = 5509$, $F = 181$, $p < 0.0001$, $R^2 = 0.21$)

Variables in Model	df	*T*†	*Partial p* <	*Parameter Estimate*	*Standardized Parameter Estimate*
Intercept	1	36.09	0.0001	10.96 (0.3)	0
Hispanic	1	−18.15	0.0001	−1.71 (0.09)	−0.25
Other	1	−2.04	0.04	−0.31 (0.15)	−0.03
Year of Birth	1	10.69	0.0001	0.14 (0.01)	0.63
(Year of Birth)^2	1	−9.9	0.0001	−0.002 (0.0002)	−0.59
Father's Income	1	16.07	0.0001	0.87 (0.05)	0.2
Size of Ego's Sibship	1	−11.96	0.0001	−0.18 (0.02)	−0.15
Age Raised	1	4.71	0.0001	0.08 (0.02)	0.14
(Age Raised)^2	1	−2.41	0.02	−0.001 (0.0005)	−0.07

See Table 2 for details on variable measurements and parameter estimates.

Table 3b. Regression Model of Effects of Parental Investment on Income ($N = 5034$, $F = 92.7$, $p < 0.0001$, $R^2 = 0.13$)

Variables in Model	df	*T*†	*Partial p* <	*Parameter Estimate*	*Standardized Parameter Estimate*
Intercept	1	9.74	0.0001	23718 (2434)	0
Hispanic	1	−9.91	0.0001	−7288 (735)	−0.14
Other	1	−2.22	0.03	−2581 (1164)	−0.03
Year of Birth	1	7.38	0.0001	779 (106)	0.48
(Year of Birth)^2	1	−10.53	0.0001	−15 (1)	−0.68
Father's Income	1	9.52	0.0001	4011 (421)	0.13
Size of Ego's Sibship	1	−5.53	0.0001	−659 (119)	−0.08
Age Raised	1	3.66	0.0003	496 (136)	0.12
(Age Raised)^2	1	−3.43	0.0006	−13 (4)	−0.11

See Table 2 for details on variable measurements and parameter estimates.

The next steps in the proposed causal pathway are that income and education affect attractiveness to mates, and that attractiveness to mates and income both affect fertility. While we do not test for the effects of attractiveness to mates here, we do conduct the ultimate test concerning the relationship between income and fertility. It is here that the model breaks down.

In Figures 8a and 8b completed fertility as a function of income is presented for three different age groups and for Anglos and Hispanics, respectively. Income is divided into both cohort- and ethnically adjusted percentile scores. Use of adjusted scores was necessary because Hispanic and Anglo incomes tended to differ by about 25%, and middle-aged men born between 1920 and 1940 had significantly higher incomes than

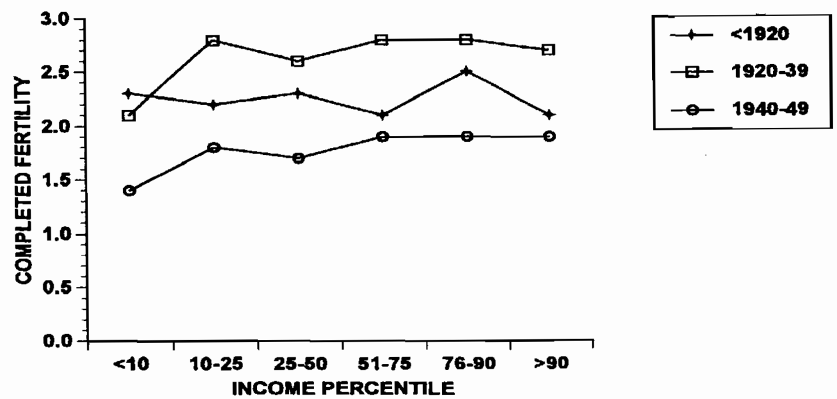

Figure 8a. Completed fertility for Anglo men by income and birth period.

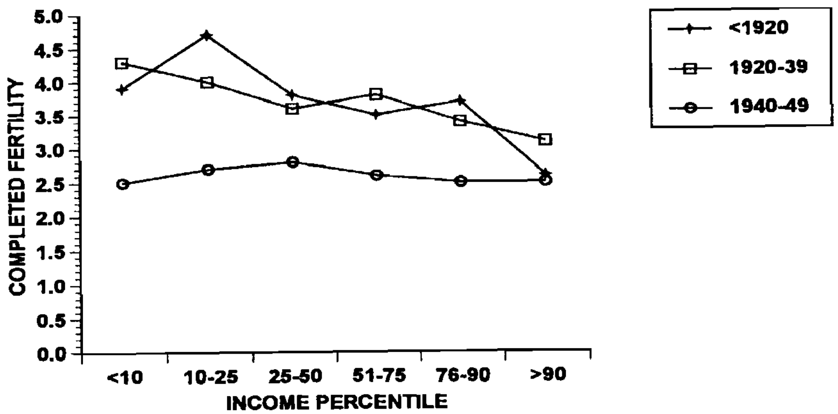

Figure 8b. Completed fertility for Hispanic men by income and birth period.

older and younger men. The first class represents the lowest 10% of earners; the second includes the tenth to twenty-fifth percentiles; the third, the twenty-sixth to fiftieth percentiles; the fourth, the fifty-first to seventy-fifth percentiles; the fifth, the seventy-sixth to ninetieth percentiles; and the sixth, those earning above the ninetieth percentile. The results show virtually no effect of income on fertility, either positive or negative. Among Anglos, there is a tendency for income to affect fertility positively for the group of men born between 1940 and 1949. This result may be due to the fact that age, income growth, and fertility are confounded for men in their forties. Another possibility, of course, is that income does positively affect fertility for this group.

Among Hispanics, there is a small negative effect of income on fertility in the earlier cohorts and no effect in the 1940–1949 group. The negative effect on the fertility of men born earlier in this century may reflect a later demographic transition among Hispanics than among Anglos. It is often reported that wealthier and more educated individuals are the first to reduce fertility in response to modern conditions, followed by poorer and less educated individuals in subsequent years. If Anglos completed the demographic transition prior to the years sampled in this study, we would not detect this timing. If Hispanics were in the process of passing through the demographic transition during this century, we may be seeing this effect in the earlier cohorts. In any case, there is no evidence of the strong positive effect of income on fertility required by the trade-off model.

IMPLICATIONS FOR A GENERAL THEORY OF HUMAN FERTILITY

Taken together, these results present a clear picture. A trade-off model in which parents regulate fertility to maximize number of grandchildren produced does not characterize the behavior of modern fertility. The data show that first-generation fertility has no negative effect on second-generation fertility and that, in the absence of such a trade-off, number of grandchildren would be maximized by maximizing first-generation fertility (at least in the domain of zero to twelve children) in the context of twentieth-century reproduction in the United States. Most people, however, have two children. Moreover, income had little or no effect on completed fertility, especially among Anglos. Ethnicity and cohort effects were powerful. Cohort/ethnicity cells with high average fertility tended to show high fertility across all income classes and vice versa for cells with low fertility.

These results are consistent with the findings of earlier studies (e.g., Irons 1990, 1993, 1995; Lam 1986; Perusse 1993; Retherford 1993; Vining 1986; but see Simons 1974 for data suggesting a positive correlation among wealth and fertility within socioeconomic groups). Studies of traditional small-scale societies suggest that fertility may be optimized to maximize the production of descendants over the long run (e.g., Blurton Jones and Sibly 1978 and Blurton Jones 1986 for the !Kung in Botswana, but see Hill and Hurtado 1995 for disconfirmation among the Ache). In addition, it appears that fertility and wealth are positively correlated in most small-scale societies (see Borgerhoff Mulder 1992; Cronk 1991; and Irons 1995 for reviews) and in many state societies (Betzig 1986). The abrupt change in the association between wealth and fertility that historically occurs at the same time fertility is reduced (Retherford 1993) requires explanation.

In addition to explaining these facts about fertility in modern industrial nations, any satisfactory theory of human fertility must also be capable of explaining other facts. It must generate empirically robust predictions about the pattern of variability in fertility among traditional small-scale societies. For example, it must be able to account for the fact that prior to recent contact with whites, Ache hunter-gatherers throughout this century exhibited total fertility rates of more than eight children (Hill and Hurtado 1995), and !Kung hunter-gatherers only achieved rates of about four and a half (Howell 1979). The theory would also have to explain the pattern and pace of fertility reduction in response to modernization. It would have to generate predictions about the timing of fertility change and the demographic composition of groups reducing fertility in historical European populations. It must also explain current fertility patterns in the developing world. It must make predictions about those sectors of the population that are not lowering fertility, as well as those that are. All of these patterns must be accounted for in the development and testing of a model of human reproductive decision-making.

To be adequate, the theory must specify both the factors people take into account in "deciding" how many children to have and the specific socioecological and personal factors that interact with those psychological and physiological processes to generate variable fertility outcomes. In our view, a satisfactory theory would also have to explain how those decision-making processes could have evolved by natural selection. The theory must specify the evolutionary historical conditions that could have selected for the characteristics of those processes. It is not sufficient to "explain" low modern fertility with the argument that humans are experiencing novel conditions to which their evolved psychological mechanisms respond nonadaptively. An explanatory theory must specify exactly what has changed, why those changes result in low fertility, and what kinds of selection would have produced the suite of proximate mechanisms governing human fertility decisions.

There have been several attempts to specify exactly what is novel. Barkow and Burley (1980) suggest that the change is due to increasing control over fertility decisions by women. Lancaster (Lancaster and Lancaster 1987; Lancaster in press) suggests that parents increase investment in children and reduce their total number in order to enhance their competitiveness on the marriage market. Turke (1989) suggests that the breakdown of extended family ties owing to the mobility required by modern job markets both increases the costs of childrearing and allows people to focus on production of a few high-quality children. Perusse (1993) suggests that contraception and socially imposed monogamy causes the link between wealth and reproduction to be severed, even though the link between wealth and men's sexual access to women remains strong. Irons (1983) offers a view similar to that of Perusse with additional consideration of the more proximate goals that human psychology is designed to pursue. Each of these hypotheses has merits and is likely to be part of a final explanation. In the following section, we offer a new approach that builds on some of those ideas but attempts to explain why people favor contraception and small family size as a function of the payoffs from parental investment in modern skills-based labor markets. In our view, improved technologies of contraception and control over fertility are an effect of the desire to reduce family size rather than vice versa.[8]

APPLICATION TO MODERN FERTILITY AND SKILLS-BASED LABOR MARKETS

In this section we present an overview of a more general theory of fertility and parental investments developed elsewhere (Kaplan 1994a) and a specific application of that theory to modern fertility. We extend the quantity-quality trade-off model developed initially by Lack (1954) and then more formally by Smith and Fretwell (1974) to include the alternative allocations of parental investment depicted in Figure 1. The basic models imagine that parental investment consists of two types: investments in offspring survival and investment in the adult productivity or income of offspring (see Kaplan 1994b for more detailed presentation of these models). By productivity, we mean the efficiency of time allocated to producing resources, care of children, and all other fitness-enhancing activities. The productivity of parents forms the budget constraint for investment—that is, parents can only invest what they can produce with their time. With this formulation, fertility and parental investment are related because total fertility can be no greater than the total income or productivity of parents allocated to reproduction divided by the average or expected investment in each child. This leads to the multigenerational recursion depicted in Figure 9.

Those models generate analytical results that depend on the relationships between investments and outcomes (i.e., child survival and adult productivity of children). In the simplest case where the impacts of parental investment on offspring outcomes depend on neither parental qualities nor offspring number, an extended version of the Smith-Fretwell results are obtained. Under those conditions optimum levels of

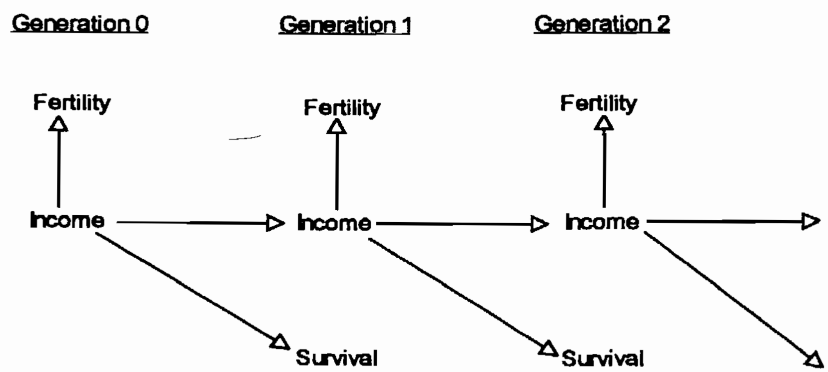

Figure 9. Multigenerational recursion for fitness effects of parental investment.

investment in offspring survival and productivity do not vary with parental income, and both fertility and fitness increase linearly with parental income.[9] Optimum investments occur at the point at which the proportional effects of investments on survival and adult productivity of offspring equal one another, and are equal to the proportion of an additional offspring that a unit of investment in fertility would produce. Additionally, meaningful optima are obtained only when investments in both fitness components yield diminishing returns to scale. Figure 10, adapted from Rogers and Blurton Jones (1992), shows that optimum

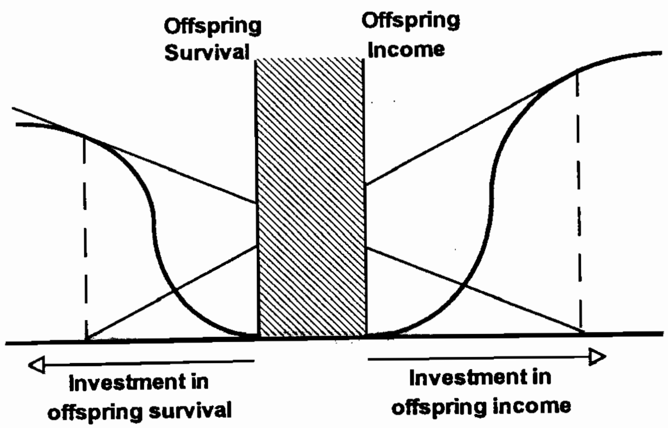

Figure 10. This figure models optimal investment when there are three separable costs to producing offspring: the fixed costs of producing an offspring (stippled area), investments in offspring survival, and investments in increasing the offspring's adult income. The model assumes that adults have limited income and that expenditures on offspring cannot exceed total income allocated to reproduction. Fertility is then determined by dividing income allocated to reproduction by the sum of these three cost components per offspring. The S-shaped curves depict the relationship between investments and outcomes for offspring survival and fertility, respectively. The straight lines, which proceed from the x-axis through the point at which they are tangent to the S-shaped curves, represent the average benefits of producing offspring survival and income, respectively, at the optimum (the rise is equal to the outcome level and the run is equal to the sum of fixed costs, investments in offspring survival, and investments to increase offspring's income). Long-term fitness is maximized when investments in offspring survival (read from right to left) and investments in offspring income (read from left to right) occur where the dashed lines intersect the x-axis; at those levels of investment the slope of the average benefit line equals marginal benefits (the instantaneous slopes of the S-shaped curves). This figure is adapted from a more general model by Rogers and Blurton Jones (1992).

investment in each quality component (dashed lines) occurs when the marginal effects of an additional unit of investment are equal to average effects (including fixed costs of producing an offspring and investments in both quality components). Thus, factors that increase investment in one component tend to increase investments in the other component (see Rogers and Blurton Jones 1992 for a related discussion). Finally, an interesting implication of the analysis is that maximizing the expected adult income of offspring at birth is equivalent to maximizing long-term fitness.

The following is one concrete scenario for understanding the means by which allocations to offspring quantity and quality are achieved in traditional human societies. The total food available to families depends upon both the work effort and efficiency of parents and children of different ages as well as inputs and demands from other families. Cultural norms and family decisions about how much children of different ages should work and at what tasks are likely to depend upon ecological variability in the dangers associated with different activities, the effects of strength and skill on productivity, and opportunities for investment in learning that will affect adult productivity. Available food is then shared among family members in accord with the age- and sex-specific impacts of food on health, growth, and fat storage. Mothers' decisions and cultural norms regarding breast feeding and the introduction of weaning foods should be sensitive to their effects on the health and growth of infants at different ages in relation to local and individual conditions (Lee, Majluf, and Gordon 1991; Vitzthum 1994). The supply of food to women and the rate of breast feeding then affect the secretion of reproductive hormones that regulate ovulation and implantation. In this sense, optimal allocations would be achieved by a combination of cognitive/cultural and hormonal mechanisms. Investments in survival and offspring productivity would be determined by cognitive analysis of their effects on children of different ages (with cultural norms representing stored knowledge of those effects), whereas fertility would be the outcome of food intake rates and breast-feeding practices affecting hormonal regulation of the reproductive cycle. This would mean that people would possess cognitive mechanisms for the analysis of the effects of investments of offspring outcomes and physiological mechanisms for fertility regulation.

Can such models also predict the pattern of low, income-unaffected fertility found in the sample of Albuquerque men? The models suggest that two conditions must be met to generate that pattern. First, low fertility requires that diminishing returns from parental investment per offspring must occur at much higher levels proportional to total parental income. Second, lack of income effects on fertility require that optimal levels of parental investment increase with parental income. We propose that skills- and education-based competitive labor markets characteristic of modern industrial and postindustrial societies produce these two conditions.

There are qualitative differences between subsistence production and modern competitive labor markets in the relationship between investments in human capital and productivity. In subsistence-based economies the relationship between skills and productivity depends upon the activity. For example, successful agricultural production requires differing degrees of knowledge of weather, soil, and pests, depending upon the local ecology. Some function with eventually diminishing returns will likely characterize the relationship between productivity and human capital. In those economies, optimal levels of investment will be determined by the diminishing impacts on productivity of further investments. However, competitive labor markets will tend to produce wage structures that equalize the present value of costs of investments with the earnings (see Becker 1975 for a detailed presentation of this argument). To illustrate this, imagine that some jobs require a high school education and other jobs require a college degree. If all individuals are alike in aptitude and the costs of financing education, the wages will equilibrate the supply and demand for workers of each type when the wage difference between the two types of jobs exactly compensates more educated workers for the costs of the investment in education—including both direct and opportunity costs associated with foregone income. If parents were to finance those costs, they would face an essentially linear relationship between investments in offspring education and offspring income as adults through the range of job types and education requirements in the labor market. In fact, if there is a significant time lag between increases in demand for higher levels of education (as would be the case with growing technology) and growth in the supply of more educated workers, returns from investments could exhibit increasing returns to scale (see Figure 11). Without diminishing returns from investments, fertility could be driven to minimal levels because low fertility would be associated with the highest expected total income of adult descendants.

A second feature of modern job markets is that wages are closely associated with the quality and quantity of formal education received. We propose that higher-earning parents tend, on average, to have higher rates of return on investments in children's education. Consider inputs of parents' time. There is significant evidence that the nature of parent-child interaction varies with the educational level of parents (Hart and Risley 1995; Hoff-Ginsberg and Tardif 1995). This probably

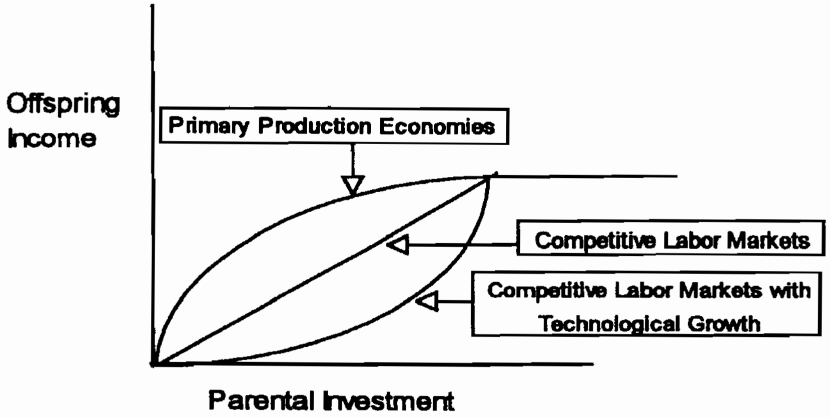

Figure 11. Relationship between parental investment and offspring income as a function of the economy.

means the skills and behavior patterns that result from parental time inputs are associated with the capital embodied in parents. By the time children enter the public education system there are clear differences among them in school-related skills, and those differences are related to socioeconomic status. In addition, the rate at which a child learns may depend on the knowledge and skills he or she already possesses. Much of the education offered in schools is based upon the premise that knowledge is cumulative (Cromer 1993). Basic skills are acquired first, and those skills are used as a foundation for the acquisition of the next set of skills. By implication, the impact of the child's time inputs depends upon skills already in place. The same is likely to be true of later monetary investments in children's education (both the choice of which neighborhood to live in and support for higher education). The children of higher-earning parents (who themselves tend to be more educated) may be able to take greater advantage of advanced curricula in better-funded public schools and universities because of their relatively enriched home environment. If this is true, it would imply that higher-earning parents tend to invest more in each child. If the effect were strong enough, those higher levels of investments could equalize fertility across income strata (since higher income would be balanced by greater investment per offspring).

These two features of modern economies may interact with evolved psychological and physiological mechanisms governing fertility and parental investment to produce behavior that maximizes the economic productivity of lineages at the expense of fitness. If cognitive processes evolved to track diminishing returns from parental investment and if physiological processes evolved to regulate fertility in response to nutritional state and patterns of breast feeding, we might expect nonadaptive responses when returns on parental investment do not diminish until extremely high levels are reached. With high economic payoffs from parental investment, people have begun to exercise cognitive regulation of fertility through contraception and family planning practices. Those cognitive processes might not have evolved to handle fitness trade-offs between fertility and parental investment (see Irons 1983 for a related view). From a psychological perspective, parents may be trading off child quantity against the child's economic well-being. In the past this suite of proximate mechanisms, combined with physiological regulation of fertility, may have closely approximated fitness maximization even though it does not in the context of education-based, competitive labor markets.

These propositions generate a series of predictions, some of which have direct application to social policy. First, the principal effect of parental income on parental investment should be due to the education-based capital embodied in parents. Therefore, within each economic stratum, better-educated parents should invest more in each child and should have lower fertility. Holding parental skills, intelligence, and knowledge constant, income should be positively associated with fertility (since optimal levels of investment should be constant, higher income allows for increased child quantity). Second, more academically able children should receive higher levels of investment (especially school-related investment) than less able children, even within families (see Becker and Tomes 1976 for a similar argument). Third, levels of investment at different stages of the child's development should be positively correlated with one another, contingent on the child's progress. The quantity and quality of early investments should positively affect early educational performance, which in turn should positively affect later investments.

If these hypotheses are correct, they might explain the patterns of class mobility and ethnic differences in achievement in the United States. Intergenerational correlations in income and scholastic achievement would be the result of associations between parental capital and both the quality of early parental time inputs and the level of total investment during development. Stable ethnic differences, even in the face of equal access to high-quality public education, could result from the above associations. Ethnic groups whose members entered this country with lower levels of academic skills (or who were prevented from obtaining those skills) may persistently experience lower levels of

achievement over the generations, even without prejudice and social obstacles for educational achievement.

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

A similar line of reasoning can be applied to international differences in scholastic achievement. In less-developed countries both parents and teachers have lower average levels of education-based capital. For each year children spend in school, they will learn less than their counterparts in a more developed country. This would lower the rate of return on investment in children's education and, therefore, tend to cause a decrease in parental support for schooling, further augmenting the difference. Such a pattern could generate persistent global variance in investments in human capital. Firms with knowledge-intensive production technologies would preferentially locate where human capital is the least expensive to acquire, lowering the demand for educated workers in less-developed countries and further lowering the payoffs from investment in education. Becker et al. (1990) were the first to present this argument, although our derivation was independent.

This would imply that lowered fertility in the developing world requires increased return rates on investment in embodied capital. It also suggests that development programs must compensate for the low education of parents and the poor quality of school systems, and that increased efficiency of human capital production may be the key to increasing educational achievement and attracting knowledge-based jobs to less-developed countries. Development programs that facilitate the transfer to less-developed countries of educational technology designed both to increase rates of knowledge acquisition and to upgrade teacher knowledge would have a significant payoff. The availability of inexpensive computers and educational software should enhance the viability of such development programs.

SUMMARY

This paper asks the question: Can a psychology that evolved by natural selection acting on trade-offs between fertility and adult income of offspring, interacting with specifiable environmental conditions, produce the observed low pattern of fertility at all socioeconomic levels in modern industrial societies exemplified by our data from the Albuquerque Men Project? We propose that two characteristics of modern economies have led to a period of sustained fertility reduction and to a corresponding lack of association between income and fertility. The first characteristic is the direct link between costs of investment and wage rates owing to the forces of supply and demand for labor in competitive economies. The second is the increasing emphasis on cumulative knowledge, skills, and technologies in the production of resources. These two characteristics may together produce two historically novel conditions: (1) investments in offspring's ability to produce income have nondecreasing (i.e., constant or increasing) returns to scale, and (2) embodied capital of parents is positively associated with returns on investment in embodied capital of children.

But is this response adaptive in the fitness-maximizing sense? The fitness cost is lost fertility, and the benefit is stored in increasing capital accrual in descendants. Since the poor in the Albuquerque Men study do

not have lower fertility than those with higher incomes, and since those with very high fertility (more than ten children) slow no decreases in fertility in the next generation (Kaplan et al. 1995 and this paper), the costs may be greater than the benefits, at least over the short term. Whether descendants of high investors will ever take the profits from their increased capital through increased fertility and disinvestment, or whether descendants of low investors eventually will be unable to reproduce, remain open questions.

This paper has combined the theory of evolution by natural selection with economic models of allocation of limited resources. The theoretical approach we propose here requires further development, but the data show that a new theory is required. Testing the direct predictions of the models we propose here will help determine the productivity of the approach.

A preliminary presentation of this data was published in R. I. M. Dunbar, ed., *Human Reproduction Decisions: Biological and Social Perspectives.* New York: St. Martin's Press, 1995. Support for the research project, "Male Fertility and Parenting in New Mexico," began with two seed grants from the University of New Mexico's Biomedical Research Grants Program, 1988 and 1989, and one from the University of New Mexico Research Allocations Committee, 1988. Further seed money as well as interim funding came from the William T. Grant Foundation (#89130589 and #91130501). The major support for the project came from the National Science Foundation from 1990 to 1993 (#BNS-9011723 and #DBS-911552). Both National Science Foundation grants included Research Experience for Undergraduates supplements.

The authors would like to thank Robin Dunbar, Bill Irons, Robin Smith Jacobvitz, Alan Rogers, and Phil Szydlowski for helpful comments on drafts of this paper as well as the many undergraduate and graduate students at the University of New Mexico who worked on the Albuquerque Men project in interviewing, coding, data entry, office management, and data management and analysis. They would also like to thank Ted Bergstrom, Erik Charnov, Phil Ganderton, Steve Gangestad, Kristen Hawkes, Kim Hill, Nick Blurton Jones, David Lam, and Robert Willis for stimulating discussions about the theory of fertility.

Hillard S. Kaplan is an Associate Professor of Anthropology at the University of New Mexico. His earlier research and publications focused on food sharing, time allocation, parental investment, and reproductive strategies among Ache hunter-gatherers in Paraguay, Machiguenga and Piro forager-horticulturalists in Peru, and villagers of several ethnicities in Botswana. New research and theory concern fertility, parental investment, and mating strategies in developed and developing nations. This research formulates a new theory of reproductive decision-making and the demographic transition, integrating human capital and parental investment theory in a synthesis of economic and evolutionary approaches.

Jane B. Lancaster is a Professor of Anthropology at the University of New Mexico. Her research and publications are on human reproductive biology and behavior, especially human parental investment; women's reproductive biology of pregnancy, lactation, and

child-spacing; and male fertility and investment in children. Current research with Hillard S. Kaplan is on male life history strategies among a large sample of men in New Mexico. She has coedited three books on human parental investment: *School-Age Pregnancy and Parenthood* (with B. Hamburg), *Parenting across the Life Span* (with J. Altmann, A. Rossi, and L. Sherrod), and *Offspring Abuse and Neglect* (with R. Gelles). She is scientific editor of a quarterly journal, *Human Nature: An Interdisciplinary, Biosocial Perspective* published by Aldine de Gruyter. She is also a council member of the newly formed Human Behavior and Evolution Society.

John A. Bock is Andrew W. Mellon Post-Doctoral Fellow in Epidemiology and Population Health at the National Centre for Epidemiology and Population Health, The Australian National University. His research focuses on the allocation of parental investment and the determinants of children's activities, integrating aspects of economic and evolutionary theory. He has ongoing field research with Bantu and Bushmen agro-pastoralists and forager-horticulturalists in the Okavango Delta, Botswana. He is also collaborating with Lancaster and Kaplan on the determinants of progeny distribution and homosexuality among New Mexican men.

Sara E. Johnson is a Ph.D. candidate at the University of New Mexico. Her major research trajectory focuses on trade-offs in life history characters. Her research experience includes participation in a study of variation in growth and development among children in a multi-ethnic community in the Okavango Delta, Botswana, in addition to her dissertation work on individual variation in growth and mortality among juvenile baboons. She is collaborating with Lancaster and Kaplan on the association between survival and fertility among Albuquerque men.

NOTES

1. It is also the case that resistance to disease and predation are primary determinants of reproductive success. However, disease and predation may also be viewed from the perspective of competition for the resources for reproduction. Potential hosts and prey are subject to selection to prevent other organisms from capturing the energy they have stored in their soma, and selection also operates on characteristics that enable predators and pathogens to acquire energy from them.

2. For the purpose of simplicity, this pathway is not shown in Figure 1.

3. In most biological and demographic models, fertility is generally defined as a rate, often as daughters produced per unit time (e.g., Charnov 1993; Rogers 1993; Stearns 1992). In the case of modern industrial societies with "parity-dependent" fertility and very low adult mortality rates prior to the end of the reproductive period (Henry 1961), completed lifetime fertility is probably a more useful measure.

4. Reproductive value at birth is defined as

$$V_0 = \int_{\infty}^{0} l_x m_x e^{-rx}$$

where l_x is the probability of surviving to age x, m_x is the instantaneous fertility rate at age x, and r is the instantaneous population growth rate.

5. The second derivative test shows exactly this.

6. Individuals were offered the opportunity to conduct the interview in Spanish, but all of our potential interviewees felt comfortable with an English interview.

7. The variable "years of education" is measured in terms of the highest degree the respondent achieved rather than in terms of the actual number of years he spent in school. For example, high school graduates were assigned 12 years of schooling, recipients of bachelor's degrees 16 years, etc.

8. This is true of Turke's (1989) argument as well. However, his approach focuses on the loss of assistance from kin in childrearing and the costs of cultural success in modern society, whereas ours emphasizes the changing payoffs of parental investment.

9. Slightly different results are obtained if the effects of parental investment increase or decrease with offspring number, as would be the case if older children assist in the socialization of younger children (positive economies of scale) or there were crowding effects (diseconomies of scale).

REFERENCES

Barkow, J. H., and N. Burley
1980 Human Fertility, Evolutionary Biology, and the Demographic Transition. *Ethology and Sociobiology* 1:163–180.

Barnett, W. S.
1985 *The Perry Preschool Program and Its Long-Term Effects: A Benefit-Cost Analysis.* Early Childhood Policy Papers No. 2. Ypsilanti, Michigan: High/Scope Educational Research Foundation.

Becker, G. S.
1975 *Human Capital*, second ed. New York: Columbia University Press.
1981 *A Treatise on the Family.* Cambridge, Massachusetts: Harvard University Press.

Becker, G. S., and N. Tomes
1976 Child Endowments and the Quantity and Quality of Children. *Journal of Political Economy* 84:s143–s163.

Becker, G. S., K. M. Murphy, and R. Tamura
1990 Human Capital, Fertility and Economic Growth. *Journal of Political Economy* 98:s12–s37.

Betzig, L. L.
1986 *Despotism and Differential Reproduction: A Darwinian View of History.* Hawthorne, New York: Aldine.

Blurton Jones, N. G.
1986 Bushman Birth Spacing: A Test for Optimal Interbirth Intervals. *Ethology and Sociobiology* 7:91–105.

Blurton Jones, N. G., and R. M. Sibly
1978 Testing Adaptiveness of Culturally Determined Behavior: Do Bushman Women Maximize Their Reproductive Success by Spacing Births Widely

and Foraging Seldom? In *Human Behavior and Adaptation,* N. G. Blurton Jones and V. Reynolds, eds. Pp. 135–157. London: Taylor and Francis.

Borgerhoff Mulder, M.
1992 Reproductive Decisions. In *Evolutionary Ecology and Human Behavior,* E. A. Smith and B. Winterhalder, eds. Pp. 339–374. Hawthorne, New York: Aldine de Gruyter.

Charnov, E.
1993 *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology.* New York: Oxford University Press.

Consortium for Longitudinal Studies
1983 *As the Twig Is Bent: Lasting Effects of Preschool Programs.* Hillsdale, New Jersey: Erlbaum.

Cromer, A.
1993 *Uncommon Sense: The Heretical Nature of Science.* New York: Oxford.

Cronk, L.
1991 Human Behavioral Ecology. *Annual Reviews in Anthropology* 20:25–53.

Easterlin, R. A.
1987 *Birth and Fortune: The Impact of Numbers on Personal Welfare,* second ed. Chicago: University of Chicago Press.

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

Henry, L.
1961 Some Data on Natural Fertility. *Eugenics Quarterly* 8:81–91.

Hill, K., and A. M. Hurtado
1995 *Ache Life History: The Ecology and Demography of a Foraging People.* Hawthorne, New York: Aldine de Gruyter.

Hoff-Ginsberg, E., and T. Tardif
1995 Socioeconomic Status and Parenting. In *The Handbook of Parenting,* vol. 2, M. Bornstein, ed. Hillsdale, New Jersey: Erlbaum.

Holekamp, K. E., and L. Smale
1991 Dominance Acquisition during Mammalian Social Development: The Inheritance of Maternal Rank. *American Zoologist* 31:306–317.

Hood, J.
1992 *Caveat Emptor: The Head Start Scam.* Policy Analysis No. 187. Washington, D.C.: Cato Institute.

Howell, N.
1979 *Demography of the Dobe !Kung.* New York: Academic Press.

Irons, W.
1983 Human Female Reproductive Strategies. In *Social Behavior of Female Vertebrates,* S. K. Wasser, ed. Pp. 169–213. New York: Academic Press.
1990 Let's Make Our Perspectives Broader Rather Than Narrower: A Comment on Turke's "Which Humans Behave Adaptively, and Why Does It Matter?" and on the So-called DA-DP Debate. *Ethology and Sociobiology* 11:361–375.

1993 Monogamy, Contraception, and the Cultural and Reproductive Success Hypothesis. *Behavior and Brain Sciences* 16:295–296.
1995 Cultural and Reproductive Success in Traditional Societies. Ms. in author's possession, Department of Anthropology, Northwestern University, Evanston, Illinois.

Kaplan, H.
1994a Evolutionary and Wealth Flows Theories of Fertility: Empirical Tests and New Models. *Population and Development Review* 20:753–791.
1994b A Theory of Human Parental Investment and Fertility. Ms. in author's possession, Department of Anthropology, University of New Mexico, Albuquerque.

Kaplan, H. S., J. B. Lancaster, J. A. Bock, and S. E. Johnson
1995 Fertility and Fitness among Albuquerque Men: A Competitive Labour Market Theory. In *Human Reproductive Decisions: Biological and Social Perspectives,* R. I. M. Dunbar, ed. Pp. 96–136. New York: St. Martin's Press.

Lack, D.
1954 *The Natural Regulation of Animal Numbers.* Oxford: Oxford University Press.
1968 *Ecological Adaptations for Breeding in Birds.* London: Methuen.

Lam, D.
1986 The Dynamics of Population Growth, Differential Fertility, and Inequality. *American Economic Review* 76:1103–1116.

Lancaster, J. B.
in press An Evolutionary History of Human Reproductive Strategies and the Status of Women in Relation to Population Growth and Social Stratification. In *Evolution and Feminism,* P. A. Gowaty, ed. New York: Chapman and Hall.

Lancaster, J. B., and C. S. Lancaster
1987 The Watershed: Change in Parental-Investment and Family-Formation Strategies in the Course of Human Evolution. In *Parenting across the Life Span: Biosocial Dimensions,* J. B. Lancaster, J. Altmann, A. S. Rossi, and L. R. Sherrod, eds. Pp. 187–205. Hawthorne, New York: Aldine de Gruyter.

Lee, P. C., P. Majluf, and I. J. Gordon
1991 Growth, Weaning and Maternal Investment from a Comparative Perspective. Journal of Zoology (London) 225:99–114.

Perusse, D.
1993 Cultural and Reproductive Success in Industrial Societies: Testing the Relationship at the Proximate and Ultimate Levels (with comments). *Brain and Behavioral Sciences* 16:267–323.

Retherford, R. D.
1993 Demographic Transition and the Evolution of Intelligence: Theory and Evidence. Ms. in author's possession, East-West Center, Honolulu, Hawaii.

Rogers, A. R.
1990 Evolutionary Economics of Human Reproduction. *Ethology and Sociobiology* 11:479–495.
1993 Why Menopause? *Evolutionary Ecology* 7:406–420.

Rogers, A. R., and N. G. Blurton Jones
1992 Allocation of Parental Care. Ms. in authors' possession, Department of Anthropology, University of Utah, Salt Lake City.

Schweinhart, L. J., H. V. Barnes, and D. P. Weikart
1993 *Significant Benefits: The High/Scope Perry Preschool Study through Age 27.* Monographs of the High/Scope Education Research Foundation, No. 10. Ypsilanti, Michigan: High/Scope Press.

Simons, J. L.
1974 *The Effects of Income on Fertility.* Chapel Hill, North Carolina: Carolina Populations Center.

Smith, C. C., and S. D. Fretwell
1974 The Optimal Balance between Size and Number of Offspring. *American Naturalist* 108:499–506.

Stearns, S. C.
1992 *The Evolution of Life Histories.* New York: Oxford University Press.

Turke, P. W.
1989 Evolution and the Demand for Children. *Population and Development Review* 15:61–90.

U. S. Department of Commerce
1992 U. S. Census of Population: General Population Characteristics: New Mexico. Washington, D.C.: Bureau of the Census.

U. S. Census of Population and Housing, New Mexico
1991a Summary Tape File 1, New Mexico (1990). Washington, D.C.: Bureau of the Census.
1991b Summary Tape File 3, New Mexico (1990). Washington, D.C.: Bureau of the Census.
1991c CP-1-33, Table 54, Pg. 82. Washington, D.C.: Government Printing Office.

U. S. Department of Transportation, Federal Highway Administration.
1993 Highway statistics 1987. TD2.22.991. Washington, D.C.: U.S. Government Printing Office.

van Schaik, C. P.
1989 The Ecology of Social Relationships amongst Female Primates. In *Comparative Socioecology,* V. Standen and R. A. Foley, eds. Pp. 195–218. Oxford: Blackwell.

Vining, D. R.
1986 Social versus Reproductive Success: The Central Theoretical Problem of Human Sociobiology. *Behavioral and Brain Sciences* 9:167–260.

Vitzthum, V.
1994 Comparative Study of Breastfeeding Structure and Its Relation to Human Reproductive Ecology. *Yearbook of Physical Anthropology* 37:307–349.

Zigler, E., and S. J. Styfco
1994 Head Start: Criticisms in a Constructive Context. *American Psychologist* 49:127–132.

MATERNAL ENCOURAGEMENT IN NONHUMAN PRIMATES AND THE QUESTION OF ANIMAL TEACHING

Dario Maestripieri
Emory University

Most putative cases of teaching in nonhuman animals involve parent-offspring interactions. The interpretation of these cases, particularly with regard to the cognitive processes involved, is controversial. Qualitative and quantitative observations made in nonhuman primates suggest that, in some species, mothers encourage their infants' independent locomotion and that encouragement can be considered a form of instruction. In macaques, experience in raising previous offspring accounts in part for variability between mothers in propensity to encourage infant motor skills. Parsimony suggests that the cognitive mechanisms underlying maternal encouragement of infant locomotion in primates as well as some other putative cases of animal teaching may involve first-order intentionality (i.e., goal-directed behavior) and not higher cognitive processes such as attribution of knowledge/ignorance or perspective-taking. Encouragement of infant independent locomotion early in life may have benefits to mothers later on, in terms of reduction of costs of infant carrying, earlier infant weaning, and increased probability of reproduction in the mating season. The elementary forms of teaching observed in nonhuman primates may have played an important role in the origin and evolution of human culture.

KEY WORDS: **Cognitive mechanisms; Experience; Mother-infant interactions; Nonhuman Primates; Reproductive consequences; Teaching.**

Received May 31, 1995; accepted June 20, 1995.

Address all correspondence to Dario Maestripieri, Yerkes Regional Primate Research Center, Emory University, 2409 Taylor Lane, Lawrenceville, GA 30243.

Human Nature, Vol. 6, No. 4, pp. 361-378. **1045-6767/95/$1.00 + .10**