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Environmentally Contingent Reproductive Strategies in Mayan and Ache Males

David Waynforth, A. Magdalena Hurtado, and Kim Hill
Department of Anthropology, University of New Mexico, Albuquerque, New Mexico

This research explores male reproductive parameters, particularly the timing of first reproduction, in two traditional populations. Predictions are drawn from theoretical arguments that have their roots in evolutionary psychology and behavioral ecology, and that interpret variation in reproductive outcomes as environmentally contingent adaptations. In both Ache and Mayan samples, father absence, predicted to act as a stressor that causes precocious sexuality and reproduction as well as unstable pair bonds, did not affect the timing of first reproduction in male offspring in the expected way. Father absence in Mayan men, however, was found to be associated with responses to questionnaire items indicating lack of willingness to pay time and energy costs to maintain existing sexual unions. The results suggest that father absence affects male mating strategy, but that strategic differences did not translate into reproductive outcomes in the sample. In the Mayan population, education was associated with early reproduction, more lifetime sex partners, and higher fertility, which was also contrary to the predicted pattern based on a life-history tradeoff approach. Parental resources were associated with earlier reproduction in the Mayan sample, confirming the prediction that restricted resources should delay reproduction. **© 1998 Elsevier Science Inc.**

KEY WORDS: Male reproductive strategy; First reproduction; Environmentally contingent response.

The primary goal of this article is to explore causes of variation in male reproductive strategies in two traditional societies: the Ache of Paraguay, and Mayans living in rural Belize. The specific focus of the first part of the article concerns variation in the timing of age at first reproduction in the presence or absence of certain predictors. They are father absence, economic hardship, education, and family discord. These predictors were chosen in light of

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Address reprint requests and correspondence to: David Waynforth, Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, U.S.A.

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previously established theories linking them to reproductive strategy and are united as theories that view reproductive outcomes as evolved individual responses to variation in environment. These theoretical perspectives then are applied to additional aspects of male reproduction in the Belizean sample only, using data on lifetime number of sex partners, number of offspring produced, and information on willingness to accept time and energy costs to maintain a sexual relationship.

Life-History Theory and the Timing of First Reproduction

Optimality models of reproductive strategies reveal the biological significance of variation in the timing of first reproduction. They indicate that, in general, organisms maximize fitness by diverting energy away from growth to use it for reproductive effort before reaching the theoretical maximum possible adult body size (Roff 1992; Stearns 1992). This is because earlier reproductive maturation leads to a shorter time between generations and a reduced likelihood of death prior to reproducing. The benefits of an early switch from the growing phase to the reproductive phase of the life course have to be balanced against the benefits of continued growth—the main benefit being greater net energy production, which can be channeled into fertility. Hill and Hurtado (1996) tested optimality models of age at menarche in human females and found that Ache, !Kung, and North American women reach menarche (i.e., switch from growth to reproduction) at about the age predicted by optimality models of age at maturation. North American women, chiefly due to high growth rates, had the lowest predicted age at menarche of the three groups. However, North American women, aided by artificial means of birth control, generally do not begin reproduction for many years after reaching sexual maturity. For males there is also a tendency not to begin reproduction at sexual maturity, and this is true not only in societies with easy access to modern birth control, but in traditional populations such as the Ache (Hill and Hurtado 1996). This leaves us with the question of why reproduction is delayed. The theories presented offer adaptive explanations of how individuals vary the timing of first reproduction in response to variation in their social and physical environment. These explanations are by no means an attempt to explain all of the variation in the timing of first reproduction. For example, some of the variation in males is almost certainly a function of variation in male quality, where males who are less attractive to females are likely to have to delay reproduction due to a lack of mating opportunities (see Waynforth and Dunbar 1995 for a discussion of male quality and mating strategies). What the explanations offer are ways in which individual organisms may adjust their life-history trajectories facultatively via adaptations operating on behavior as well as on physiology.

Psychosocial Stress and Age at First Reproduction

Draper and Harpending (1982, 1988) presented a scenario in which offspring adopt a reproductive strategy appropriate for the prevailing environment based on parental behavior. Evidence of effects of rearing environment on reproductive strategy had surfaced nearly two decades earlier (Whiting 1965), but Draper and Harpending

placed such findings within an evolutionary theoretical model. In Draper and Harpending's model, father absence due to temporary sexual unions acts as an indicator that constant male presence and provisioning are not necessary for successful reproduction. For male children, father absence indicates that pursuit of multiple, unstable, sexual unions is more appropriate than the establishment of a single stable pair bond. In such a mating arrangement, males need not pay the time and energy costs that must be paid in any mating system that involves consistent male presence. These costs may range from attainment of a stable career to careful searching for the most appropriate mate (as all or most of an individual's reproductive effort will be tied up in a single mate), and these costs are what may contribute to delayed first reproduction in father-present environments.

Belsky et al. (1991) and Belsky (1997) built upon Draper and Harpending's thesis by realizing that father absence is likely to be only one of several conditions in the family environment that children may use in the formation of their own reproductive strategies. They added the idea that marital discord and unstable employment would be likely to have the same effect as father absence. Belsky thus presented a more general model of family context and reproductive strategy, which I refer to as the psychosocial stress model. The underlying hypothesis is the same as Draper and Harpending's: parents respond to the environment by adopting parenting styles that shape their offspring's reproductive strategies to suit that environment. Belsky's model can be summarized as follows: stressors in the family environment, including father absence, marital discord, and limited resources, lead to harsh, unaffectionate, inconsistent parenting. This results in male children who are aggressive, opportunistic, and mistrustful of others and of relationships with others. These children will in turn have more rapid sexual maturation, engage in sexual activity at an earlier age, and have offspring at earlier ages in unstable unions.

Substantial empirical support for Belsky's hypothesis has been found for females, but fewer studies have documented differences in male reproductive strategies as a function of rearing environment (Kim et al. 1997). This may be in part because fewer researchers have studied males, although theoretical reasons why males should not show identical responses to stressful circumstances have been forwarded by Weisfeld and Billings (1988), Maccoby (1991), and Surbey (1998). Surbey argues that because males invest less in offspring and, hence, pay lower fitness costs for reproductive mistakes, they should be less sensitive to environmental conditions. However, one recent study found support for early male reproductive maturation under conditions of family stress (Kim et al. 1997). The data analyzed here test whether father absence due to marital breakup leads to earlier reproduction in Ache hunter-gatherer males and in a predominantly Mayan population in rural Belize. The Belizean data additionally contain information on how often subjects' parents or guardians argued, struck each other, and struck the subject, as measures of stress in the family environment.

Resources and the Timing of First Reproduction

The psychosocial stress model of reproductive strategy formation considers lack of financial resources among those stressors that encourage precocious sexuality and reproduction. However, despite the fact that low or uncertain resources undoubtedly

cause psychosocial stress, the weight of the evidence indicates that restricted resources are associated with later first reproduction in humans (Hajnal 1965; for a discussion of resources and reproduction in humans see MacDonald 1997) and in other animals (Bercovitch and Strum 1993; Milagres et al. 1979; also see Hill and Hurtado 1996). There are a number of potential reasons for this pattern, and among them are the physiological effects of restricted food intake on reproductive functioning, and that males must often obtain resources to be chosen by females in mate choice. For the Belizean sample in this research, data on ego's and ego's parents' financial resources are analyzed with the expectation that men from poorer families and with lower income themselves will show delayed first reproduction.

MacDonald (1997) presents evidence that upward social mobility is associated with late first reproduction, low fertility, and high parental investment in historical data on human populations. Although MacDonald does not assert that this response is adaptive behavior, from a life-history perspective it seems very reasonable, because competing for resources often may involve expending time and energy in activities that increase competitive ability at the expense of time spent directly on reproductive effort. An example of this tradeoff involving current versus future reproduction is time investment in education, and it has been shown for U.S. data that men who invest more in education tend to delay reproduction until after the completion of their educational trajectory (Waynforth et al. 1996; for detailed theoretical models of education and reproduction see Kaplan 1996). Pursuit of education means that individuals forgo immediate resource gain in favor of working towards future opportunities for higher resource returns. The fitness benefit to investment in education is an increased total budget for reproduction, i.e., investment in education can be thought of in exactly the same way as investment in physical growth in optimality models of the timing of first reproduction. The situation in rural Belize reflected in the data, in which over half of the males have abandoned subsistence agriculture in favor of participation in the paid work force, may represent the beginning of a trend of pursuit of upward social mobility through education. The prediction that can be made is that men who have reached higher levels of education will delay reproduction in favor of competing for resources, in order to secure a higher budget for reproduction.

Like the psychosocial stress model, this economic model predicts that resources will be positively associated with the timing of first birth as resources are expected to have been gained at the expense of early reproductive effort. If indeed the observed pattern turns out to be that those with fewer resources on average have earlier reproduction, then it is likely that either this model or the psychosocial stress model, or both, is correct for predicting the timing of reproduction in the Belizean sample.

Psychosocial Stress, Resources, Education, and Other Reproductive Variables

The Belizean data contain additional information relevant to the theories presented. In this section, data on lifetime number of sex partners, number of offspring produced, and reports of behavior in relationships are considered.

The psychosocial stress hypothesis provides predictions not only about the timing of the onset of sexual activity and reproduction, but on other aspects of variation in reproductive behavior stemming from experiences during ontogeny. As stated previously, father-absent males should have more unstable mateships and be less psychologically oriented towards seeking a stable sexual union. These predictions are tested using data on lifetime number of sex partners and self-reported data on willingness to pay time and opportunity costs to maintain a sexual relationship.

If men with more education achieve a higher budget for reproduction through the financial rewards of education, and this budget is subsequently applied to fertility, then it follows that more educated men should have higher fertility. It is, on the contrary, well documented that maternal education is associated with fertility reduction in industrializing economies (Das Gupta 1987; LeVine et al. 1991). Unfortunately, the emphasis in demography has tended to be placed solely on maternal education rather than paternal education, but LeVine's research contains data on males suggesting that male and female educational attainment have similar effects.

There may be specific circumstances that result in fertility reduction in industrializing economies, and Kaplan (1996) presents an argument that, in competitive labor markets, education should be associated with lowered fertility, as parents should invest in offspring quality at the expense of offspring quantity under these conditions. Competitive labor markets produce some occupations with high returns, which require more schooling, and parents increase investment in a smaller number of offspring so that their offspring are able to receive very high returns to their labor. It is likely that both the levels of parental investment required and the resource holding potential that can be produced in offspring are out of the range found in subsistence level economies. If parents adjust parental effort in response to the fact that returns to investment do not diminish even at high levels of parental investment rather than responding to absolute returns, this could result in fitness maximization in traditional societies and lower than optimal fertility in industrialized nations. An alternate explanation has been put forward by Kessler and Boone (1996), who argue using computer simulations that reduced fertility is a strategy used by wealthy individuals to reduce the probability of lineage extinction in population bottlenecks (such as famines). There is therefore some theoretical basis to predict that more educated Belizean men will, on average, have fewer offspring if the conditions stated previously do indeed exist. The data allow some evaluation of whether parents increasingly are investing in offspring quality, and whether educational attainment predicts higher income (i.e., whether rural Belize has a competitve labor market economy). These evaluations are presented along with the analysis of education and fertility.

Summary of Predictions

1. Father absence, acting as a psychosocial stressor, will be associated with early first reproduction.
2. Stress in the rearing environment, manifesting itself as parental arguing, hitting each other, and hitting of the subject, will be associated with early first reproduction.

3. Low personal and parental income will be associated with delayed first reproduction.
4. High educational attainment will be associated with delayed reproduction.
5. Psychosocial stress will be associated with a greater number of lifetime sex partners and a decreased willingness to maintain sexual relationships.
6. Higher educational attainment will be associated with reduced fertility.

METHODS

The Ache Sample

Data on father absence and the timing of first birth for 271 Ache men were provided by Kim Hill and Magdalena Hurtado, and detailed descriptions of the population and data collection methods can be found in their monograph (Hill and Hurtado 1996). The Ache lived until the 1980s as hunter-gatherers in the forests of eastern Paraguay. During the 1980s, they began to settle in permanent reservations, although they continue to forage in the forest as well as practicing slash-and-burn agriculture and raising domestic livestock. Most Ache marriages are monogamous, although polygyny is not uncommon during the transition to a new marriage, and polyandry has been known to occur (Hill and Hurtado 1996: 229). Marital dissolution is commonplace and most frequently occurs early on in the relationship. Before settlement, the probability of divorce during the first year of marriage was about 61% (Hill and Hurtado 1996: 246). These high rates of dissolution reflect a flexible mating system in which individuals freely switch marital partners. This pattern has now shifted towards more permanent unions in the reservations, perhaps in part due to the influence of missionaries.

Ache Variables

Father absence. Data on the number of years the biological father of a child resided with his mother cannot be obtained for the Ache. Instead, the data consist of the proportion of offspring that the subject's father had with his mother. If the father only had offspring with the subject's mother, the proportion equals 1, and lower values indicate that the father had offspring with multiple women. The Ache data thus provide an indicator of father absence, which is also an indicator of male reproductive strategy and, hence, may be particularly suitable for testing the idea that offspring model their reproductive strategies on those of their (same sex) parents. In statistical analyses, cases where there was father absence due to death were omitted.

Age at first reproduction. Births to Ache that occurred between 1977 and 1996 were recorded during regular field trips by Hill and Hurtado. The age of anyone born before this time was determined through use of relative age lists (for a detailed description of this method and of the difficulties involved in achieving accurate age estimates in an illiterate population, see Hill and Hurtado 1996: 120).

The Belizean Sample

The Belizean study subjects were 56 males between the ages of 18 and 75, recruited from two villages in western Belize. The villages, San Antonio and Cristo Rey, lie about 5 miles apart on an unpaved road that was built in the early 1980s, before which access to the nearest sizable town was by canoe and took about 20 minutes to the closer of the two villages. Sixty-three percent of the subjects identified themselves as Mayan; the majority of whom were Yucateca Maya. Of the remaining men, 34% were Mayan through one parent only or were Mestizo, and 3% belonged to other ethnic groups.

The traditional mode of subsistence is slash-and-burn agriculture (known as *milpa*), although only 48% of the sample still engaged in milpa. The remainder of the men primarily performed paid work. The paid occupations represented vary from manual labor, such as logging and employment in large-scale agriculture, to work in the tourism industry and government work. It was also common to make some income through ownership of small village stores selling food and household items. Most men, regardless of occupation, spent at least some time hunting wild game.

The population of the two villages together totaled about 1,500 individuals according to Belize 1991 census figures. Subjects were recruited by the following method: the villages were divided into groupings of approximately ten houses based on geographical proximity, and then within each grouping of ten houses one was selected. If no adult males were home, a time to return was arranged with other family members. If the man was not home at the arranged interview time, another house in the grouping was selected. This method yielded a total of 56 interviewed men, residing in every part of the two villages. Given that the sex ratio in Belize is 1.03 males to each female and that 43% of the population is under 15 years of age (1997 CIA World Facts), this means that approximately 15% of the adult male population of the villages was sampled. Of the 58 men approached for interview, two refused to participate in the study. Interviews lasted between 1 and 3 hours, although sometimes considerably more time was spent with subjects than was taken to complete the interview. At the end of each interview, the subject was paid the equivalent of US $5.

In contrast to the Ache, the Belizean sample displayed low rates of father absence due to marital dissolution: 84% of the 56 men in the sample grew up in homes with their fathers present for their entire childhood. Among these Mayans, family unity and stability are highly valued, although it is unclear how different the typical family environment and values were prior to contact with missionaries.

Belizean Variables

Father absence. For the Belizean sample, the data on father absence consist of the number of years that the father was present in the home, up until the subject reached age 18. As with the Ache data, cases where there was father absence due to death were omitted in statistical analyses.

Lifetime number of sex partners. This information was obtained via private interview. The estimate excludes prostitutes. A cross-check of the data on lifetime number of sex partners was performed for subjects for whom a close male friend or brother was available who claimed to know the subject's sexual history. Sixteen subjects consented to this cross-check, and the same number of sex partners was reported for the subject in 11 of the 16 cases (69%). In all five cases where there was a discrepancy, the subject reported fewer sex partners than the friend/brother reported for him. Four of the subjects later admitted to the extra sex partners, and one claimed that his friend/brother was wrong (and so his original estimate was used).

Parents' arguing, physical fighting, and striking of subject. This consists of the subject's reports of how often during childhood (up to 18 years of age) each of these three events occurred typically in a year, on a scale of 1 to 5 where 1 = never and 5 = more than once per week.

Age at first reproduction. This is the subject's age when his first child was born. Unlike the Ache, all of the Belizean sample were literate to some degree and knew the year of their own birth and the age of their oldest child.

Income. This is the 1996 cash income from all sources, in Belizean dollars (two Belizean dollars equal one U.S. dollar). Subjects' income is useful only insofar as it probably is related to income in the past, prior to reproduction. Parents' income was collected as a categorical variable coded on a six-point scale.

Educational attainment. This is scored as a categorical variable that ranges from 1 to 5 according to educational landmarks reached (graduation from primary, secondary, and high school). In some analyses it is coded as a binary variable with a value of zero if the subject did not graduate from primary school and a value of one if he reached secondary school or further.

Number of offspring. This is the total number of children that the subject believes he has fathered. In almost all cases these children are by a current or former wife.

Willingness to maintain sexual relationships. This variable measures likely marital or relationship stability and is constructed from six interview items, which are responses on a seven-point Likert-type scale to the following questions about behavior in sexual relationships: I frequently promise commitment or marriage; I try to be sensitive to her needs; I stay home to care for her when she is ill; I sacrifice spending time with my friends to be with her; I frequently run errands for my partner; I frequently do what she wants me to do rather than what I want to do. One variable is created from the six items using principal components analysis in SAS, and the first principal component is used in the data analysis, which can be viewed as the overall rate of performance of the above activities.

RESULTS

Father Absence in the Ache

Figure 1 shows that 50% of Ache men whose parents survived until the subject was at least 18 had fathered a child by age 26. Men for whom one or both parents died were omitted because parental absence due to death may have different consequences for offspring reproductive strategies than father absence due to divorce or separation (Hetherington 1972). More descriptive statistics on father absence, marriage, and reproduction are listed in Table 1, in which Ache and Belizean men are compared for these parameters.

(1) Father absence will be associated with early first reproduction. For Ache males, paternal reproductive strategy, as evidenced by the proportion of the subject's father's children who were fathered with the subject's mother, was not significantly associated with age at first birth (estimate $= -0.08$, $\chi^2 = 1.56$, $df = 1$, $p = 0.21$). Because the age at first reproduction variable contained right-censoring (i.e., not all of the subjects had fathered a child), statistical analysis was performed using time-to-event modeling designed to handle censoring (the LIFEREG procedure in SAS). The event in this case is fatherhood, and this procedure uses information on the current age of right-censored individuals so that results are not biased by these cases

Figure 1. Age at first birth for 272 Ache and 50 Belizean men. Cases where a parent died before the subject reached the age of 18 have been deleted. Lines are 5-year moving averages.

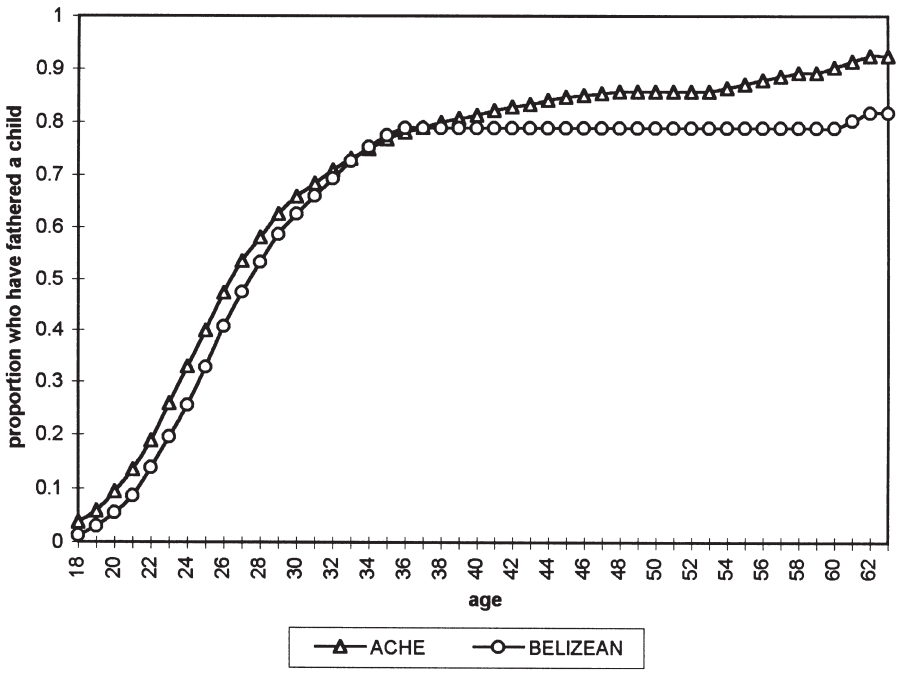

Table 1. Descriptive Statistics Comparing Marriage and Family Patterns in Ache and Belizean Men

	Mayan		Ache	
	Mean	Range	Mean	Range
Proportion of children the father had with the child's mother	N/A		0.75	0.08–1
Years of father's presence	15.8	1–18	N/A	
Lifetime number of marriages	1.05[a]	0–2	9.00[b]	0–23
No. of children fathered	8.10[a]	0–17	6.40[b]	0–13

Notes. [a]For men over age 40.

[b]From Hill and Hurtado (1996). Offspring number is for men over 50, and marriage data are for men over 40 in 1990.

(Collett 1994). Two other variables were statistically controlled for in the regression model: birth year, to partial out any shifts through time in age at first reproduction; and the total number of children that the father had, to control for bias towards fathers with fewer offspring appearing more monogamous simply because they have few children.

The Belizean Sample

As can be seen in Figure 1, Belizean and Ache men show similar patterns in the timing of first birth, with 50% of the Belizean sample fathering a child by age 27, only 1 year later than Ache men. Descriptive statistics for variables analyzed in the Belizean sample are listed in Table 2.

(1) Father absence will be associated with early first reproduction. For Belizean males, the number of years of father presence was significantly associated with age at first birth (Table 3), but in the opposite direction to that predicted: father absence due to marital dissolution was associated with delayed first birth. Age was partialled out in all models predicting age at first birth for the Belizean sample, as it was highly associated with age at first reproduction (Gamma LIFEREG estimate for age run without any other predictors = 0.008, $\chi^2 = 13.18$, $df = 1$, $p = 0.0003$). This means that older men tended to be older at first reproduction, i.e., successive cohorts have been reproducing earlier in recent decades.

Given the low incidence of father absence due to marital dissolution in the Belizean sample, it is particularly important to establish that its effect on age at first re-

Table 2. Descriptive Statistics for Belizean Men

Variable	Mean	Range
Educational attainment	2.44	1–5
Family resources	2.42	1–4
Income	4,330	0–16,000
Frequency parents hit each other	1.16	1–3
Frequency parents argued	1.92	1–4
Frequency parents struck subject	1.61	1–4
Lifetime sex partners	1.84	0–7

Table 3. Predictors of Age at First Birth for Belizean Sample

Variable	Prediction	Estimate	χ^2	p	Error distribution
Years of father presence	+	−0.012	4.46	0.03	Gamma
Educational attainment	+	−0.15	6.98	0.01	Gamma
Family resources	−	−0.15	3.98	0.05	Log Logistic
Income	−	−0.001	0.04	0.99	Gamma
Frequency parents hit each other	−	−0.06	1.47	0.23	Gamma
Frequency parents argued	−	−0.03	1.68	0.19	Gamma
Frequency parents struck subject	−	−0.08	1.88	0.17	Log Logistic

Note. Estimates are LIFEREG estimates. Error distribution choice was made by minimizing the −2LogL. In cases where the −2LogL was not significantly different for two or more models, the distributional assumption providing the lowest p values for the outcome variables was used. Each variable was run separately in a model with subjects' age controlled for.

production is not merely an artifact of one or a few statistical outliers. Of the nine father-absent cases, three reproduced earlier than the father-present mean of 26 years, and six reproduced later, or were censored close to or above the mean. Part of the statistical significance additionally results from the fact that the father-absent men who were older at first reproduction on the whole experienced more total years without the father in the home.

(2) Stress in the rearing environment will be associated with early first reproduction. None of the variables representing stress in the family environment was significantly associated with age at first reproduction, although all three of the estimates were in the predicted direction (Table 3).

(3) Low income and parental income will be associated with delayed first reproduction. Parental resources were associated with age at first reproduction in the predicted direction (Table 3), but the subject's own income was not significantly related to first reproduction.

(4) High educational attainment will be associated with delayed reproduction. Educational attainment was significantly associated with age at first reproduction, but in the opposite direction to the prediction. Figure 2 displays this result with education treated as a binary variable. Estimates were obtained using the LIFETEST procedure in SAS, which provides analysis of time-to-event data with censoring stratified by the values of a predictor variable. Figure 2 shows that not only did the more educated group reproduce earlier, but that the pattern of censorship was unequal: men who had completed primary school were more likely to have fathered a child (87% of men who completed primary school had fathered a child vs. 71% of those who did not complete primary school).

(5) Psychosocial stress will be associated with a greater number of lifetime sex partners and a decreased willingness to maintain sexual relationships. Table 4 shows statistical results for relationships between the explanatory variables and number of lifetime sex partners for the Belizean sample. The analyses were performed using Poisson regression in the GENMOD procedure in SAS. Data on sex

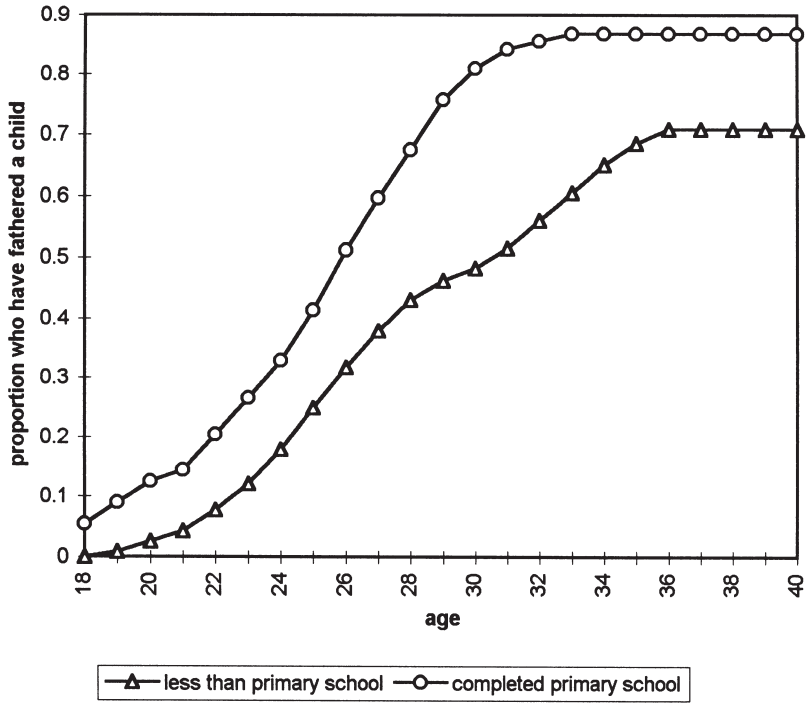

Figure 2. Age at first birth for Belizean men stratified by whether or not subjects completed primary school.

partner number and on offspring number tend not to be normally distributed in general (Hill and Hurtado 1996: 286), especially when they do not represent completed reproductive histories. They therefore violate a key distributional assumption required for standard linear regression. Poisson regression is appropriate for data consisting of a count through time, and the sex partner and offspring number data fit a Poisson distribution more closely than they fit the normal distribution. Although it is rare to see offspring number modeled using Poisson regression, this method has long been used for this purpose in exactly the circumstances seen here, i.e., when the data do not consist of completed reproductive histories (Aitchison 1955; Singh 1963). In each analysis, age and age-squared were controlled for, as both were statistically significant. None of the psychosocial stress measures were found to be significantly associated with sex partner number (Table 4). Income was marginally significantly positively related to sex partner number, and educational attainment was positively associated with sex partner number.

Willingness to pay time and opportunity costs to maintain a sexual relationship was significantly related to years of father presence (Table 5). The eigenvalue for the first principal component was 3.25, and for the second was 0.90. The first principal component accounted for 54% of the total variance, and it weighted each item approximately equally, with slightly lower loadings on trying to be sensitive to my partner's needs, and sacrificing spending time with my friends to be with her, than

Table 4. Predictors of Lifetime Number of Sex Partners for the Belizean Sample

Variable	Estimate	χ^2	*p*
Years of father presence	−0.03	0.66	0.42
Educational attainment	0.33	5.17	0.02
Family resources	0.10	0.66	0.42
Income	0.00	3.12	0.08
Frequency parents hit each other	−0.19	0.76	0.38
Frequency parents argued	−0.04	0.13	0.71
Frequency parents struck subject	−0.01	0.02	0.09

Note. Estimates are Poisson regression estimates. Each predictor was run separately in a model with age and age-squared controlled for.

on the other four items. The results of the principal components analysis suggest that the first principal component, representing paying time and energy costs to maintain a relationship, is an adequate summary of the data.

One of the family violence measures was also marginally significantly associated with willingness to maintain a relationship: the frequency with which the subject was struck by his parents. Age was statistically controlled for in these analyses, and there was a significant tendency for older men to be less willing to pay time and opportunity costs to maintain a sexual relationship.

(6) Higher educational attainment will be associated with reduced fertility. Higher educational attainment was associated with more offspring born to men, rather than fewer as was predicted: Poisson regression estimate = 0.21, $\chi^2 = 4.11$, $p = 0.043$. Figure 3 displays number of offspring fathered by age. This result indicates that the younger men in the sample with fewer children were not more educated than individuals of their own age with more children. This result would make sense if education does not provide high enough returns to justify high investment in offspring education, yet education predicts income in the sample (controlling for age, beta = 1662, $T = 2.16$, $p = 0.035$). In addition to this, it appears that parents were increasingly investing in educational opportunities for their offspring, because age strongly predicts educational attainment (beta = −0.023, $T = -3.9$, $p = 0.0003$). The results indicate that these men were operating within a skills-based market economy, and that parents were increasingly investing in offspring quality. Yet, despite these necessary conditions being in place, men were not reducing their fertility.

Table 5. Predictors of willingness to pay time and opportunity costs to maintain a relationship, for Belizean men. Age is controlled for in each model.

Variable	β	T	adjusted r^2	*p*
Years of father presence	0.19	2.50	0.14	0.02
Educational attainment	−0.33	−0.96	0.11	0.34
Family resources	0.14	0.45	0.07	0.65
Income	−0.01	−1.17	0.10	0.25
Frequency parents hit each other	−0.18	−0.34	0.07	0.74
Frequency parents argued	−0.20	−0.85	0.08	0.40
Frequency parents struck subject	−0.51	−1.82	0.13	0.07

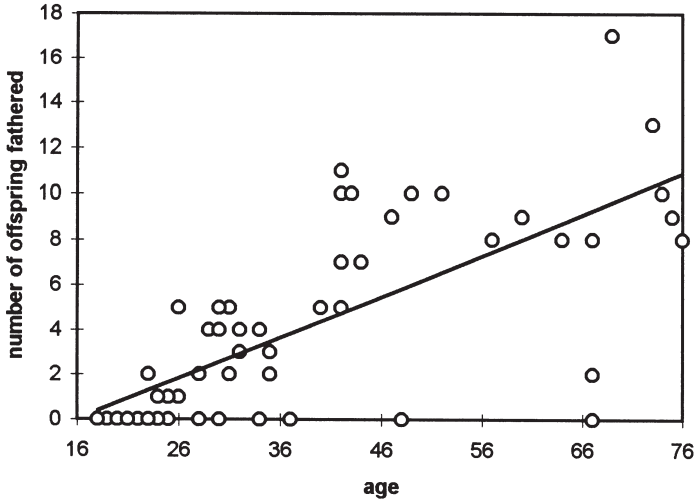

Figure 3. Number of offspring fathered by age in the Belizean sample. The line is a least-squares regression line.

DISCUSSION

The Ache and Belizean data show no suggestion of a negative relationship between father absence due to marital dissolution and age at first reproduction. For both samples, the direction of the relationship was opposite to the expectation generated from psychosocial stress theory. In the Belizean sample, it was significantly positively associated with age at first reproduction. Given the small sample size of father-absent Belizean men, the significance of this association should be regarded with caution. On the other hand, it is not difficult to imagine confounders that may cause father absence to have the opposite effect to the one predicted. It is possible, for example, that reduced parental investment that results from father absence in turn results in reduced ability to acquire mates or resources, and this delays reproduction. There is, however, no evidence of this in the Belizean data, because father absence was not significantly associated with the educational attainment or the 1996 income of the subjects (multiple regression estimates with age partialled out: predicting educational attainment: beta = 0.018, $T = 0.84$, $p = 0.4$; predicting 1996 income: beta = 16.02, $T = 0.13$, $p = 0.9$). Nevertheless, it appears that father-absent males were somehow disadvantaged in obtaining mates or marriage. It should be noted that this result does not necessarily show that the psychosocial stress model is incorrect, only that other factors swamp any possible negative effects of father absence on the reproduction of male offspring.

The Ache result is particularly interesting, because the sample size is large and contains a much higher incidence of father absence. The Ache data may, however, contain sample bias capable of obscuring any relationship between father absence and reproductive outcomes. This potential bias concerns the occurrence of infanticide and neglect of a man's offspring when he leaves his spouse. Hill and Hurtado

(1996: 164) directly observed serious neglect of children recently abandoned by their fathers. They also received anecdotal evidence of infanticide due to paternal abandonment. Prior to settlement on reservations, Hill and Hurtado (1996: 452) found parental divorce to be a significant predictor of increased child mortality. This evidence indicates that father-absent Ache have died at higher rates during childhood and, thus, are under-represented in this sample.

Measures of family stress and violence were unsuccessful in predicting age at first reproduction, and none of the psychosocial stress indicators predicted lifetime number of sex partners (assumed to be a sign of instability in sexual relationships and low paternal investment).

On the other hand, support for the psychosocial stress model of reproductive strategy formation was found in the data on willingness to pay time and opportunity costs to maintain a sexual relationship. The finding that father absence was associated with less willingness to pay costs to maintain a relationship should be viewed with some caution given the small number of observed father-absent cases. However, the result is interesting because, combined with analysis of the findings above, it suggests that father absence does indeed shape offspring reproductive strategy, but that individual differences in strategy do not necessarily translate into the reproductive goals that they may be designed to achieve.

The patchy support found for the psychosocial stress model may lend credence to arguments by Surbey (1998) and others that male reproduction is less sensitive to stressful circumstances than is female reproduction. These results combined with those of Kim et al. (1997) do indicate, however, that males show some reproductive response to stress.

Fewer family resources, as expected, predicted later first reproduction for Belizean men. The factors mediating this relationship cannot be determined from the data, but are likely to be related to female choice of men from wealthier families.

The predictions that educational attainment would cause delayed reproduction and reduced fertility were not upheld, because the strongest relationships discovered were that more educated men reproduced earlier, had more sex partners, and had more offspring than less educated men. For age at first birth, this probably indicates that these men did not face a tradeoff between effort spent in education and in competition for resources, and reproductive effort. The result appears to be a simple relationship in which men with more resources and education found themselves desired as sex partners and as husbands and, therefore, tended to reproduce early.

The interpretation that men were not facing a significant tradeoff between effort spent in education and reproductive effort makes sense if investment in education tends to occur significantly prior to reproduction. This certainly appears to be the case, because, on average, the men in the sample left education at age 14 (the range was from no education up to completion of high school at age 18). On the other hand, data from another Central American population show a (nonsignificant) increase in age at marriage and age at first birth for women at similar levels of completed education (LeVine et al. 1991).

The increase in fertility as a function of education implies that educated parents did not decrease fertility to invest more heavily in offspring quality. It is possible

that this is because the population was sampled before the predicted reproductive effects of transition to a skills-based market economy had a chance to manifest themselves.

These results also may contain sample bias if the most educated, financially successful men tend to leave the village permanently to pursue opportunities in larger towns and cities. Unfortunately, no data were collected to assess whether successful men leave the community at higher rates, and such bias still would not explain adequately the observed pattern in the men who remain in the community.

Age proved to be a highly significant predictor of reproductive outcomes, although no theory was presented to predict age effects. Age was particularly powerful as a predictor of age at first reproduction in the Belizean sample, and this shift through time from later to earlier first reproduction may be a result of the decreasing isolation of the communities causing increased marriage opportunities for men.

In conclusion, the theoretical model presented to explain why education may lead individuals to reduce fertility rather than increase it as a function of the increased resources accrued via education was not supported. In the Belizean sample, education was associated directly with lower ages at first birth and higher fertility. It is also interesting to note that in Figure 3, the plot of offspring number by age, there are no apparent signs of demographic transition, and it remains to be seen whether the first individuals to reduce fertility will be the most educated. Parental resources had an effect on age at first reproduction, probably because men from poor families were disadvantaged in female mate choice.

Psychosocial stress theory, although it proved unsuccessful at predicting reproductive outcomes, predicted reproductive strategy orientation towards low investment in long-term sexual unions. This finding is apparently the first of its type for a traditional population.

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