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EVOLUTIONARY THEORY AND REPRODUCTIVE RESPONSES TO FATHER ABSENCE: IMPLICATIONS OF KIN SELECTION AND THE REPRODUCTIVE RETURNS TO MATING AND PARENTING EFFORT

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INTRODUCTION

Evolutionary theorists are in the business of seeking ultimate explanations for behavior. Ultimate explanations concern why a behavior or trait would have evolved by Darwinian natural or sexual selection and would therefore be adaptive in particular environments. This is in contrast to what is termed proximate explanation, which is usually about more immediate types of motivation, an example being understanding the hormonal underpinnings of a behavior. The topic of father absence due to divorce has not escaped the attention of evolutionary theorists seeking ultimate explanation for its patterns and effects, and the first part of this chapter focuses on a particularly influential ultimate explanation for the pattern of events that appear to be typically associated with father absent household structure. After tracing the history of this evolutionary approach to father absence and showing some empirical evidence for and against it, I move on to how father absence can fit into evolutionary ecological approaches to mating strategies more generally, with a view to improving our understanding of its effects.

Many readers may initially pose the question of why apply evolutionary theory to father absence? One answer is that evolutionary theorists were bound to find father absence interesting because reproductive life-history parameters of children from father-absent homes tend to be affected. Variation in life history parameters, such as age at first reproduction, are known to be major determinants of lifetime reproductive output and of genetic fitness (genetic contribution to future generations). Hence, father absence appears to be associated with the very traits that are the fundamental focus of study for evolutionary research, and due to this, it is likely that researchers working in evolutionary

psychology, anthropology and human biology will continue to try to understand it from an evolutionary perspective.

A THEORY OF CHILDHOOD ENVIRONMENT AND REPRODUCTIVE STRATEGY

Patricia Draper and Henry Harpending sparked the genesis of much of the work on evolution and father absent household structure that has been published since the 1980s. Their 1982 paper posited that children are sensitive to being raised in father absent versus present family structure, and that this feature of early environment kicks off a sequence of developmental effects. The developmental trajectory of those raised in homes with father absence due to divorce culminates in early maturation, sexuality, and first reproduction. This empirical pattern had already been observed (e.g., Whiting 1965), but Draper and Harpending's contribution was to attach evolutionary logic to why the pattern should exist. Their argument can be summarized for male reproductive strategies as follows: males who perceive during childhood that the environmentally appropriate reproductive strategy does not involve forming stable unions will develop behavioral strategies suited to low male parental care mating systems, including intense direct male-male competition for access to females, and aggression. On the other hand, males growing up in mating systems in which they receive and perceive high levels of male parental involvement, will correspondingly develop a high paternal care strategy, and be more interested in being able to secure resources in the long term for sustained parental investment. The corresponding female strategy in high male care systems is to very carefully choose an investing male, being careful not to reproduce in a short-term union.

In high male investment systems both sexes pay mate searching time costs, since all or most reproductive effort will be tied up in a single mate. This is likely to delay first reproduction. When females do not perceive a need for high paternal investment from their mate, there is no need to pay the costs associated with establishing a long term sexual union, and first reproduction may proceed at an early age.

Draper & Harpending refined their model in 1988, but the next major advance for their idea came with the assimilation of attachment theory to their model of developmental strategies. Attachment theory offered a mechanism through which father absent household structure could act on behavior to produce the adaptive outcomes that Draper and Harpending had originally proposed. In a 1991 paper, Jay Belsky, Laurence Steinberg and Patricia Draper introduced the idea of psychological attachment as a key mediator between father absence and reproductive strategy. In their model family context, including father absent or present status, was theorized to cause differences in child-rearing styles. In families with single parenthood, the concomitant stress involved in this situation was expected to lead to harsh and inconsistent parenting. This would lead to insecurely attached children, who in turn would mature rapidly, and engage in early sexual activity in short-term unions. The concept of attachment and its definition had been laid out previously by Bowlby (1969), and others: insecurely attached individuals display aggressive behavior, particularly if male, tend to be anxious and depressed, particularly if female, and see others as uncaring and untrustworthy. As a consequence, insecurely attached individuals experience difficulty in establishing long-term relationships. Belsky's proposition was that the attachment process appropriately

prepares children for the existing 'mating environment' of short-term unions with little paternal investment, or long-term unions with significant male investment. Belsky *et al.* (1991) thus incorporated existing research in psychology to the general argument for adaptive reproductive strategies as a function of family context put forward by Draper & Harpending (1982, 1988). Belsky *et al.* backed up their theory of incipient mating strategies with an impressive number of studies linking the pieces of their argument: that family context is associated with particular child-rearing styles, and that these variables tend to predict attachment and behaviors indicative of reproductive strategy. Readers interested in these studies should refer to Belsky *et al.*'s (1991) paper.

In 1997 I included variables relevant to testing the Draper & Harpending and Belsky, Steinberg & Draper model (which I shall refer to as the 'psychosocial stress' model) in field research on Maya swidden horticulturalists living in Belize, Central America. I felt that it was key that variables such as father absence should be associated with reproductive variables not only in industrialized nations, but also in traditional societies with pre-demographic transition fertility regimes. To test evolutionary hypotheses in traditional societies is one way to get closer to looking at humans living in conditions which would have prevailed during the bulk of human evolution. There was evidence, for example, that father absence leads to early first reproduction in North America and Australia, but it had not, and still has not absolutely, been established that this very fundamental link in the Draper & Harpending and Belsky, Steinberg & Draper model holds in traditional societies. Thus, the research question that I wished to answer in Belize was whether father absence and attachment have similar reproductive

consequences under conditions more similar in important ways to our environment of evolutionary adaptedness (typically abbreviated as EEA). I also had at my disposal some relevant data collected in more than 20 years of research on Ache hunter-gatherers in Eastern Paraguay, by Kim Hill and Magdalena Hurtado. Of course, information gathered from a few modern non-industrialized societies will give us a less than perfect window to our EEA, but the Ache in particular subsist as hunter-gatherers much like humans that existed up until the spread of agriculture.

FATHER ABSENCE AND REPRODUCTIVE STRATEGY IN THE MAYA AND ACHE

The study populations

Those studying evolution and human behavior often assume for the sake of convenience that we evolved in a *single* environment type or EEA. The Ache and Maya environments, if they represent something approximating our EEA, are dramatically different social environments in many ways. Although they both have fertility regimes typical of societies that have not undergone industrialization, as well as relatively high morbidity and child mortality rates, they differ substantially in marital patterns. Ache marriages, which are almost always monogamous, tend not to be enduring. On average, Ache men marry nine times in their lifetime (Hill & Hurtado 1996). In contrast, in the Mayan sample few men married more than once. Both the Ache and Maya have experienced change due to contact with other groups. The Ache since contact with the outside world during the 1970s have ceased existing solely as hunter-gatherers, and are now settled on permanent reservations. The Maya of Western Belize have been in contact with other

groups for well over 100 years. Many inhabitants of my study site are descendants of refugees from the Yucatan in Mexico, or from highland Guatemala, and still maintain their separate Mayan languages. Both the Ache and Maya have had sustained contact with Christian missionaries. In Belize evangelical missionaries from North America have been particularly persistent in their attempts to convert Maya. The effect of efforts of missionaries on Ache and Mayan mating systems is difficult to determine. Ache marriages since settlement on reservations have become more enduring (Hill & Hurtado 1996). It is unlikely that the Mayan general pattern of lifetime monogamous marriage represents a recent change. Whatever changes have occurred in the Ache and Maya in recent decades, for the Maya there is a high social value placed on father involvement with their children, and on stable family relations. The Ache data analyzed here show a high rate of father absent household structure, and the social importance of father presence is almost certainly much lower than in the Maya.

Father absence and age at first reproduction in the Maya and Ache

Analysis of Ache and Mayan men's age at first reproduction was initially reported in Waynforth, Hurtado & Hill (1998). The analyses presented here include these results and expand on them. Data on the age at first birth of Ache women and their father absence status (due to marital separation) have not previously been reported. These data are included to back up the data on men and to make a general case for the effect that father absence will tend to have on the timing of first reproduction: women's reproductive strategies will not be considered in detail in this chapter. This is not because they are not

interesting, but because there are differences in the implications of father absence on female reproductive strategies which deserve a paper in their own right.

Father absence had to be measured quite differently for the two populations. For the Maya, it was collected as the number of years that the subject's biological father resided in the subject's household, up until age 18. Cases in which the father was not present due to his death were omitted from all analyses, since the effects of father absence due to death may not be the same as for father absence due to marital dissolution (e.g., Hetherington 1972). For the Ache, the data collection methods made it impossible to obtain the number of years of father presence in the same way. Instead, the proportion of children that the father had with the subject's mother was calculated for male subjects. For example, if the father only had children with the subject's mother, the proportion equals 1, and lower values indicate that the father had children with more women. For female subjects, the proportion of the mother's children that she had with the subject's father was used. The resulting variable represents not only whether the subject was raised in the absence of their biological father, but also indicates the reproductive strategy of the subject's same sex parent, i.e., it gives a measure of how many of the same sex parent's marriages ended, not just whether the marriage to the subject's other biological parent ended. So, it turns out that this limitation in the Ache database with regard to measuring father absence can be viewed as a particularly interesting test of the psychosocial stress theory, because it comes closer to testing whether children respond closely to the reproductive strategies of their same sex parents.

Calculating ages at first birth for Ache was also methodologically problematic. Birth dates are known for all Ache born after 1976, but prior to Hill and Hurtado's record keeping, ages had to be determined by using 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: p120). A system of birth records and certificates for the Maya was originally established by British colonial authorities, and most men in the Mayan sample had records of and/or knew the year in which they and their children were born, although by no means all births are recorded by the government.

As originally reported in Waynforth, Hurtado and Hill (1998), for Mayan men, the number of years of father presence in the subject's household was significantly negatively associated with age at first birth, with birth year controlled for in the time-to-event statistical model (Gamma LIFEREG estimate = -0.012, Chi-squared = 4.46, *df* = 1, p = 0.03, n = 50). The statistical test used took account of the fact that not everyone in the sample had experienced the outcome variable, first birth or fatherhood. For a detailed description of time-to-event modeling, and when it is appropriate to apply it, see Collett (1994). This result was counter to the prediction, which was that father absence would lead to early first reproduction. For Ache men, the result was non-significantly in the same direction (estimate = -0.08, Chi-squared = 1.56, *df* = 1, p = 0.21, n = 272). Again, birth year was controlled for in the regression model to partial out any shifts through time in age at first reproduction. To avoid bias towards fathers with fewer children appearing to have more stable marriages simply because they had fewer children, the total number

of children that the father had was also controlled for in the statistical model of Ache age at first reproduction.

For Ache women, a similar pattern emerged: the more men that female subjects' mothers had children with, the later the subject tended to have her first child (LIFEREG estimate = -0.16, Chi-squared = 12.00, *df* = 1, p = 0.0005). The statistical model included three control variables, the total number of children that the mother had, the subject's birth year (see above for explanations), and the mother's age at first birth, as an attempt to partial out genetically heritable effects. Figure 1 graphically displays the tendency for father absent women to have later ages at first birth. To produce this graph, women whose mothers never had children with men other than the subject's father were compared with those whose mother had children with two or more men. What Figure 1 shows is that a higher proportion of father present women experience first birth in their teens and early twenties. By age 24, equal proportions of father absent and present women have had a child. The SAS LIFETEST analysis used to generate Figure 1 revealed that the difference between the two groups is statistically significant over the early reproductive years (Wilcoxon Chi-squared = 6.33, *df* = 1, p = 0.02, n = 199).

Also of interest in the model of Ache women's first birth, women's ages at first birth were not significantly associated with their mothers' ages at first birth (LIFEREG estimate = -0.01, Chi-squared = 0.27, *df* = 1, p = 0.61). It has been argued that most of the variance in age at first reproduction can be explained by genetic factors (Marshall and Tanner 1986). In the Ache case, genetic influences appear to have no effect.

FATHER ABSENCE, MATING AND PARENTAL ORIENTATION IN MAYAN MEN

Father absence, while not showing an association with early first reproduction, was consistent with the psychosocial stress model when data on Mayan men's self-reported willingness to maintain sexual relationships were analyzed (Waynforth, Hurtado and Hill 1998). Before going on to further discussion of the above findings on the timing of first reproduction, I will present this and other analyses of Mayan men's reproductive strategies that are associated with father absent rearing, so that the entire pattern of findings can be evaluated together.

The sample of Mayan men were asked to rate their own performance of a number of activities related to the maintenance of sexual relationships with women. Since the psychosocial stress model predicts that father absent individuals will show preference for short-term sexual unions without extensive continued paternal support of children, the prediction was that men would show a lack of effort toward maintenance of marriage or sexual relationships with women in general. The variables contributing to the self rated measure were constructed using responses to the following questions about men's behavior in 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. Responses were given on a Likert type scale according to how much subjects felt that they actually did each of the things listed, and were collapsed into a single variable using Principal Components

Analysis (for more detail see Waynforth, Hurtado and Hill 1998). Men who had experienced more years of father absence assessed their relationship maintenance effort as being lower than that of father present men (in a regression model with age controlled for, beta = 0.19, T = 2.50, p = 0.02).

In order to expand upon the analyses shown in Waynforth, Hurtado and Hill (1998), similar methods to those applied above were used to assess men's orientation towards paternal care, in both its financial and direct care forms. The questions asked of men were: I stay home to be with my children whenever I can; I do not go to work when I have a sick child at home; it is important that my children attend school above the primary school level; it is worthwhile to pay for private schooling. Again, responses to these questions were recorded on a seven point Likert scale according to how strongly the subject felt about each question, and they were they reduced to a single variable using Principal Components Analysis. The first Principal Component, representing the overall rate of performance or rating of the importance of the paternal orientation questions, was significantly associated with father absence in the predicted way in a one-tailed test: father absent men reported less orientation towards valuing paternal contribution (in an age controlled linear regression model, Beta = 0.12 , T = 1.69, p = 0.04, n = 50).

FATHER ABSENCE AND FACIAL TESTOSTERONE CUES IN MAYAN MEN

The success of father absence as a predictor of self-rated lack of orientation towards paternal care and relationship maintenance led me to seek corroborative evidence from the Mayan men's database. Testosterone appears to be associated, among other things,

with many of the male behaviors predicted to be causally related to father absent rearing in the psychosocial stress model. Booth and Dabbs (1993) found that men with higher testosterone levels were more likely to separate and divorce their wives. High testosterone levels are also associated with indicators of high mating effort, such as more frequent thoughts about sex (Udry 1988), and more sex partners (Udry 1988; Dabbs and Morris 1990).

Several masculine features of male faces indicate the presence of testosterone during development. Evidence of the link between testosterone and masculine facial architecture can be seen in a particularly interesting experimental study, which used boys who showed no signs of puberty at age 14 or older. The boys were assigned to a treatment group or a control group. The treatment group was given regular low doses of testosterone. At the end of the experiment, the boys who had received testosterone showed more masculinized facial architecture than the control group (Verdonck et al. 1999). For the Mayan sample of men, two masculine features that can be easily measured from frontal facial photographs, cheekbone prominence and mandibular robusticity, were recorded and added together to create a measure of facial testosterone. Cheekbone prominence was measured as the width of the face at its widest point minus the width of the face at the mouth, divided by face height. Mandibular robusticity was measured as chin length: the distance from the bottom of the lower lip and the tip of the chin, again, divided by face height. All distances were measured in pixels using Scion Image software.

The result of the analysis of Mayan men's facial testosterone cues were consistent with the self-rated relationship maintenance and paternal orientation patterns: father absent men had significantly larger facial testosterone cues (in an age controlled regression model, Beta = -0.004, T = -2.10, p = 0.041).

AN EVALUATION OF THE PSYCHOSOCIAL STRESS MODEL

To summarize so far, we found that counter to expectations, in Mayan men and Ache women, father absence was associated with later, rather than earlier, reproduction. Yet, consistent with the psychosocial stress model, father absent Mayan men were less oriented towards maintaining their sexual relationships and parenting, and had larger facial testosterone cues.

In industrialized societies, father absent household structure or family stress usually results in early ages at first birth and/or early reproductive maturation (e.g., Kim et al. 1997; Surbey 1990; Moffitt et al. 1990; Jones et al. 1972). However, the Ache and Mayan findings on father absence strongly suggest that in conditions more like those in which humans evolved, early maturation and reproduction cannot be an adaptive response to father absence, because the pattern simply appears not to exist in small scale non-industrialized groups.

For Mayan men, the disadvantage of late first fatherhood leads to lower lifetime reproductive success: in a statistical model predicting offspring number (with age and age

squared controlled for), age at first fatherhood was strongly associated with lower fertility (Beta = -0.28, T = -7.00, p = 0.0001).

The findings regarding the timing of first reproduction seem to suggest that the psychosocial stress model is inadequate. Indeed, recent research indicates a move away from this model, and a focus instead, on attachment rather than father absence (e.g., Belsky 1998; Chisholm 1999). This may be because father absence can be viewed as a predictor of attachment rather than an important causal variable in its own right. Whether or not father absence can be viewed as a root cause of incipient reproductive strategies, any theory that predicts reproductive strategies as mechanistic responses to rearing conditions faces a problem. The problem is simply this: individuals that can respond reproductively to the current conditions that they face would out-reproduce individuals tracked from childhood (through experience) to model their reproductive strategy on that of their parents. To maximize reproductive success, individuals should determine their reproductive strategy using their own personal situation or characteristics. Associations between father absent rearing and reproductive strategy may only occur because father absence creates a common or typical situation that these individuals face when formulating their reproductive strategies. The question then becomes, what exactly constitutes this particular situation, and what would be the fitness maximizing approach to it? In the next sections of this chapter these questions are considered.

AN EVOLUTIONARY ECOLOGICAL APPROACH TO FATHER ABSENCE

The psychosocial stress model assumed that being oriented towards short-term mating produces the highest fitness returns in environments with low existing pair-bond stability. Evolutionary ecologists typically pay a great deal of attention to theoretical and actual fitness consequences of behavior, and I will use this approach to pay careful attention to how fitness and mating strategies might vary according to father absence status.

Questions relevant to reproductive strategy decisions and father absence have in the past been addressed as mate-desertion versus parental care problems (e.g., Hurtado and Hill 1992; Parker and McNair 1978; Trivers 1972). This body of theory generally predicts that male reproductive decisions should be governed by the fitness payoffs to parental care and mating effort. If men receive high fitness returns to paternal care (in the form of improved offspring survival and competitiveness at maturity), and at the same time, low benefits to attempting to seek new mating opportunities, then marital stability should be high. Conversely, when the male parenting contribution makes little difference to offspring survival, and new mating opportunities are relatively easy to attain, marital stability should tend to be low (Hill and Hurtado, 1992). However, even if the returns to male parental investment are very high, as they appear to be in the Ache, the optimal male mating strategy can still involve a high emphasis on mating effort, and as a consequence, marital instability, if the returns to mating effort are also high (i.e., sexual access to new partners is relatively easy) (Hurtado and Hill 1992). The important message from this is that to predict mating strategy, the returns to other opportunities have to be considered simultaneously.

To apply a simple evolutionary ecological theoretical approach to the decisions of offspring who are the product of stable or unstable (father absent) unions, the conditions created by father absent rearing that are relevant to offspring reproductive decisions need to be considered. Here, I focus on two likely conditions: that the children of father absent homes face the mating market with fewer economic resources on average than children from father present homes; and that father absent children tend to be raised in homes in which they are less closely genetically related to the other family members in the home. As in the above models, the fitness returns to two types of behavior will be considered: mating effort and parenting effort, but one additional route to increasing fitness will be added, which is investment in existing genetic kin.

FATHER ABSENCE AND INVESTMENT IN KIN

For humans living in the industrialized world, in which extended kin networks tend to be broken up geographically due to migration patterns, it can be difficult to even imagine the importance that kin can play in the lives of those living in less mobile, small scale societies. In the Maya, there is a tendency for male sib groups to maintain close relationships during adulthood, and it is common to find them setting up households in close proximity to one another, and to find them helping each other with agricultural tasks. Perhaps not surprisingly, the number of brothers that a man has positively influences fertility. Figure 2 shows the relationship between number of brothers and offspring number for the sample of 56 Mayan men. Since age and age squared have a large influence on fitness in any model predicting offspring number using men aged 18

and up, Figure 2 displays offspring number with age and age squared effects partialled out. The wide age range of the subjects additionally produced a non-normal distribution for offspring number, which was modeled statistically by fitting a Poisson model. In a regression model predicting offspring number with age, age squared, and number of brothers, the estimate for number of brothers was 0.08, Chi-squared = 4.01, p = 0.046).

Divorce or male desertion in Mayan households tends to result in one of three outcomes: The mother will remarry, particularly if she is still young; the mother will remain unmarried and attach herself to a male-headed household (almost always a parent or other relative); or, less commonly, she will adopt out her children to increase her chances of remarriage. All of these situations tend to mean that father absent children are raised in homes in which they are less closely genetically related to others in their household. This reduces the benefits to cooperating with household members, as cooperating with step-brothers or sisters, half sibs, or cousins will have lower, or no genetic benefit. Thus, the potential for contributing to inclusive fitness through relatives (Hamilton, 1964) cannot be fully realized for father absent individuals, and on top of this, fewer close kin will be present to help contribute to the fitness of those who are father absent. As a consequence, it may be optimal for father absent individuals to be less oriented to investing in family, and more oriented towards being independent from the family group that raised them.

There is some evidence that the degree of genetic relatedness within households has some importance. Jankowiak and Diderich (2000) studied family solidarity in a polygamous Mormon community in the United States. Polygamy created a predominance of

households containing both full and half siblings. Within these households, full siblings reported that they felt more affectual solidarity, were more likely to state willingness to lend money to full siblings over half siblings, and preferred full siblings to half siblings as baby sitters to infants.

A prediction testable with the Mayan men's database is whether father absent men spend more time away from the individuals in the family home in which they were raised, as well as the children of all those with whom they were raised as siblings (i.e., their nephews and nieces). The time-use data for Mayan men were collected retrospectively from interviews. Men were asked to remember in detail the last day when they did not work. Non-working days were chosen to maximize the amount of choice that men would be able to exert over their time-use decisions. Some men had not recently taken a day off at the time of interview, and were asked instead to recall their time-use on the day within the previous two weeks on which they worked the least. Men were asked to report in one hour blocks, both their activity and who they were with, beginning with times for which they were the most certain of their activity.

Retrospectively gathered time-use data are convenient to collect, but less than ideal to analyze due to the problem of recall bias. This was minimized by never asking men to remember activities more than two weeks prior to interview. A second problem with the methods employed is that time-use on only one day was recorded. These methodological deficiencies are likely to decrease the probability of finding any significant statistical relationship between time-use and any predictor, although these time-use data confirmed

a predicted negative association between Mayan men's physical attractiveness and time spent with family (Waynforth 1999).

The maximum reported amount of time spent with kin was 15 hours (out of a 24 hour period), and the minimum and mode was zero. In a Poisson regression model, father absence (recorded as number of years of father presence in the home) was significantly associated with time spent with kin: Estimate = 0.06, Chi-squared = 4.77, *df* = 1, p = 0.03, n = 50. Number of siblings was controlled for in the model, although father absent men did not grow up with fewer siblings (defined as full, half and step siblings) on average. The regression estimate for sibling number was 0.09, Chi-squared = 25.55, *df* = 1, p = 0.0001, n = 50. It is difficult to know how much of this effect is driven by the fact that men who had more siblings were simply more likely to encounter a sibling, and hence spend time with them.

Those from father absent homes were predicted not to spend as much time with kin, as on average, they are less related to those individuals with whom they were raised. Father absent Mayan men's time use appears to be optimal in that it reflects an orientation away from kin, but the question of what exactly father absent men should be doing with their time instead remains. Next, mating and parental effort will be considered.

FATHER ABSENCE, MATING AND PARENTING EFFORT

Mating effort should, in part, be based on the availability of mating opportunities. These can come in the form of short term sexual relationships in which no extended resource

flow to the woman is expected, or long-term relationships with extended paternal care. The fitness returns to seeking short-term relationships may not differ greatly between men who were raised father absent and those raised father present if women tend not to be seeking resources from short-term mates. This is because it is more likely that women's greatest gain from short-term mating comes in the form of high quality male genetic contribution to offspring. Genetic quality may be read by women via physically attractive facial and body characteristics, and there is evidence that the physical attractiveness of potential mates is of primary importance to women in the short-term mating context (Buss and Schmitt 1993; Gangestad and Simpson 1990). The utility of mating with physically attractive men may be that offspring produced will have superior disease resistance. Consistent with this, research by Gangestad (1993) showed a tendency cross-culturally for physical attractiveness to be more important in mate choice in pathogen prevalent regions of the world.

There appears to be no evidence linking low physical attractiveness and father absence. In the Mayan sample, father absent men did not have fewer (or more) lifetime sex partners than father present men (Waynforth, Hurtado and Hill 1998), and they also did not differ in facial attractiveness ratings, or another component of male physical attractiveness, fluctuating asymmetry (for facial attractiveness, in an age controlled model, Beta = 0.02, T = 0.05, p = 0.60; for fluctuating asymmetry, Beta = -0.00, T = -0.02, p = 0.99). However, as shown above, father absent men did differ in the degree of testosterone influence on their facial structure. Some researchers have found that men with highly developed facial testosterone cues are preferred by women (Cunningham et

al. 1990?), while others have found a preference for the opposite, i.e., feminized male faces (e.g., Perrett et al. 1998; Rhodes 2000). At this point, it cannot be concluded that large facial testosterone cues either particularly attractive or unattractive to women. One unresolved problem is that although Perrett et al. (1998) and Rhodes (2000) found that women rated computer manipulated photos of men with masculine facial features less attractive, it is not known whether women would in practice mate with these men, and perhaps seek long-term relationships with men with feminized features (who might provide more paternal care). For the present argument, it appears that father absent men will face little disadvantage in the context of accessing short-term mates, and what disadvantage they might have could be compensated for if their adult testosterone levels are also higher, leading them to be motivated to seek more short-term sex partners (see above argument).

In seeking long-term sexual relationships, there is substantial evidence that women focus extensively on male resource provisioning ability (e.g., Buss 1989; Weiderman 1993; Waynforth and Dunbar 1995). At the same time, there is firm evidence that those from father absent homes have worse economic outcomes, including school performance (e.g., Keith and Finlay, 1988). Levels of direct and financial paternal involvement, which are lower in father absent households, are generally associated with lowered educational attainment (e.g., Amato, 1998). It therefore can be concluded that father absent men will have less to offer women in the context of long-term mating, indeed, father absent men may often have difficulty finding a long term mate at all. In the Mayan data, there is a marginally statistically significant association between current income and whether men

have ever been married (Logistic regression, 1-tailed p = 0.035). Given that the income data consist of income in only the year prior to interview, any effect is surprising. Current income was not significantly associated with extra-marital sex partner number (in an age controlled Poisson regression model, estimate = 0.04, Chi-squared = 2.28, *df* = 1, p = 0.14). Income was associated with offspring number (see Figure 3): in an age and age squared controlled Poisson regression model, estimate = 0.05, Chi-squared = 8.55, *df* = 1, p = 0.004). These results are consistent with income having a greater impact on fitness in long-term relationships than in short-term relationships, as well as possible difficulty in marrying without resources to offer. The highly significant effect of resources on fertility may stem from early marriage for wealthier men, as well as marriage to women with greater reproductive potential. The missing link in the Mayan data is between father absence and income: income in a single year was not associated with father absence (Waynforth, Hurtado and Hill 1998). Father absence probably has a stronger effect on income for young men, and the Mayan data unfortunately do not provide enough cases to show this. Nevertheless, as evidenced by late first reproduction in father absent Mayan men, and research in other societies consistently showing economic and educational disadvantages to those from father absent homes, father absences implies disadvantages in mate acquisition and ability to produce competitive offspring through long-term paternal care.

The above argument contends that men from father absent homes may not get the chance to choose a strategy that involves focusing on paternal care of their children. When they do get the chance, their reduced education and earning capacity may reduce the fitness

returns to high investment in their offspring, relative to the potential gains to seeking new mating opportunities. A problem with the idea that father absent, resource poor men should focus more on short term mating than father present men, because father absent men receive lower returns to paternal care, is that it assumes that men with resources will maximize their fitness through parenting effort, as appears to be the case for the Maya. This is not necessarily true for all societies: in the Ache it appears that resources have a larger effect on fitness via mating effort than via paternal care (Hill and Hurtado 1996). It is therefore unlikely that there is a universally valid fitness maximizing response to father absent rearing, and the conditions particular to every society will have to be considered to make a prediction in each context. A second issue is that women may assess male genetic quality partly through their resource acquisition ability. Indeed, resource acquisition ability and other markers of genetic quality may typically be positively correlated with one another. In the Mayan sample, fluctuating asymmetry was correlated with income in the expected direction despite the availability of only a single year's data on income (Pearson $r = -0.15$, $p = 0.26$). However, father absence may constitute a special case in which resource level and attractiveness do not correlate strongly: As I have argued, father absence restricts the resource acquisition ability of young men without affecting their physical attractiveness, i.e., these men are not poor because they carry 'bad' genes.

Summary

In attempting to clarify the likely returns to important fitness influencing behavior in men (kin investment, mating and parenting), we have seen how father absent men's optimal strategy might be to focus on short term mating, because they get lower returns to

nepotistic effort, lower returns to paternal investment if they can access a woman for a long-term relationship, but probably not lower returns to short-term mating effort. This argument is consistent with father absent Mayan men's orientation towards mating effort, and away from spending time with their kin group. Their larger testosterone cues may reflect preparation for a strategy consisting largely of mating effort, and the fact that they reproduce later on average than father present men could just reflect disadvantage in competing for access to long-term mates. Since almost all of men's reported children came from long-term unions, it is hardly surprising that the data would show late ages at first fatherhood for father absent men.

RISK AND FATHER ABSENT REPRODUCTIVE STRATEGIES

I have tried to show how father absence can affect the relative fitness returns to men's set of behavioral options, and in turn affect their optimal reproductive strategy. There are additional possible evolutionary adaptations which may simultaneously operate on reproductive timing decisions, and be related to father absence. Chisholm (1999a; 1999b) has explored the possibility that mortality hazard influences the decision about whether to reproduce now versus later. Life-history theorists have studied the effects of survivorship on the timing of first reproduction in animals. For example, if chemicals produced by predators are introduced into a tank containing *Daphnia* (a freshwater invertebrate), they will reproduce earlier (Stibor 1992). This is because in high mortality conditions, early reproduction tends to be favored by natural selection, since any benefits of waiting to reproduce have to be weighed against the probability of survival to reproductive age (for a concise explanation of life-history theory and first reproduction, see Hill and Hurtado

1996, p27). Some aspects of human reproduction seem to be consistent with this life-history theoretical perspective: In industrialized nations, mortality rates tend to vary by neighborhood. Analysis of Chicago neighborhoods showed high rates of early childbearing in neighborhoods with high mortality (Wilson and Daly 1997). Chisholm (1999a) found that female university students who believed that they would die young, had earlier ages at first sex. Father absence may become involved as an issue because early reproduction might also entail not waiting to obtain a long-term mate.

There are, however, problems with this line of research which need addressing in future work. For example, it is not known whether individuals at risk of dying young or who believe that they will die young, are in this mortality risk category because they selected a mating strategy that puts them at risk, rather than because mortality hazard drove their mating decisions.

FATHER ABSENCE AND OPTIMAL FEMALE REPRODUCTIVE STRATEGIES

I have focused on optimal male reproductive strategies here, in part because the Mayan men's database allowed a number of qualitative tests of male optimal reproductive strategy under father absent versus present conditions. For women, some of the same predictions should hold: women from father absent homes should, like men, be less oriented towards nepotistic effort, and should become oriented away from the home in which they were raised in favor of their own reproductive effort. For women, however, focusing on achieving successive short-term matings cannot have the same degree of reproductive benefit, since women are constrained by high minimal time and energy costs

for each child that they produce (Bateman 1948). Father absence may in some ways put women into situations in which they cannot secure long-term male investment. This can be easily envisioned in industrialized societies, in which the economic disadvantages of father absence might put young women into a neighborhood or mating pool with few men who plan on long-term parental investment. In this scenario, women need not pay the time and energy costs associated with seeking out a long-term mate, and would tend to reproduce early, much as Draper and Harpending (1982) originally theorized. In traditional societies, the resource disadvantage from father absence may lead to nutritional and other social stress that could delay menarche and first reproduction (for a summary of stress and first reproduction see Wasser and Barash 1983). The result reported here for Ache women's first reproduction may be explained as stress induced reproductive suppression.

SUMMARY, CONCLUSIONS AND FUTURE DIRECTIONS

The development of the psychosocial stress model of father absence and the timing of first reproduction marked the beginning of the application of evolutionary theory to father absence in humans, and became very influential, particularly in the field of evolutionary psychology. The results reported here suggest that patterns in age at first reproduction in traditional societies do not fit the model (for another criticism of the psychosocial stress model, see Geary 2000), but instead, father absence may simply create a difficult set of conditions for fitness maximization that individuals try to overcome through adjusting the allocation of their reproductive effort. By examining potential consequences from father absence for three components of fitness: kin help, mating effort, and parenting effort,

more realistic predictions about fitness maximization as a function of father absence than had been identified in the psychosocial stress model could be made. Since individuals in households that have split up due to marital dissolution tend to be less closely genetically related to each other, it was predicted that father absent individuals would be less oriented towards those reared with them, and would focus instead on their own reproductive effort. The time use of Mayan men was consistent with this prediction: men from father absent homes spent less time with the family in which they were raised.

The Belizean Mayan mating system is one in which long-term sexual relationships predominate, and short term partners are also obtainable, although not to the extent that they are in many other societies, the Ache, for example. Resources had a large effect on marital fertility, but less of an effect on the number of sex partners that men reported outside of marriage. Since raising children successfully entails long-term commitment of resources, it seemed plausible that long-term mating effort with paternal care might yield lower net fitness gain for father absent men, as these men will likely have received lower parental investment, and be disadvantaged in their ability to acquire resources. Due to the fact that father absence might not affect the returns to short-term mating effort as much as it does long-term mating effort (or by aiding existing genetic kin), father absent men were hypothesized to focus on short-term mating effort. In Mayan men, this appeared to be the case: father absent men self-reported less orientation towards the maintenance of sexual relationships, and less paternal orientation. They also had larger facial testosterone cues, suggesting physiological adaptedness to short-term mating.

Despite father absent Mayan men's orientation towards short-term mating appearing to be optimal, the optimal allocation of effort is likely to depend on aspects of the environment in any given society. For example, father present men's optimal strategy could be to focus on mating effort if resources do not affect offspring survival or competitiveness to a great extent. This makes universal predictions about reproductive strategies as function of father absence impossible.

The inadequacy of the psychosocial stress model for predicting reproductive strategies as a function of father absence does not preclude an important role for psychosocial stress as a concept relevant to reproductive decisions, and it may genuinely be causally related to early first reproduction in modern conditions. Volatile family relations and inconsistent parenting might indicate limited parental investment, and force children to focus away from the nuclear family and towards their own reproductive choices. Future studies which take into account the fitness consequences of mating strategies as a function of psychosocial stress may provide a more fruitful approach to the study of evolution and stress induced mating strategies.

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FIGURE 1 Father absence due to marital dissolution and Ache women's ages at first birth, stratified by whether or not women's mothers ever had children with more than one man.

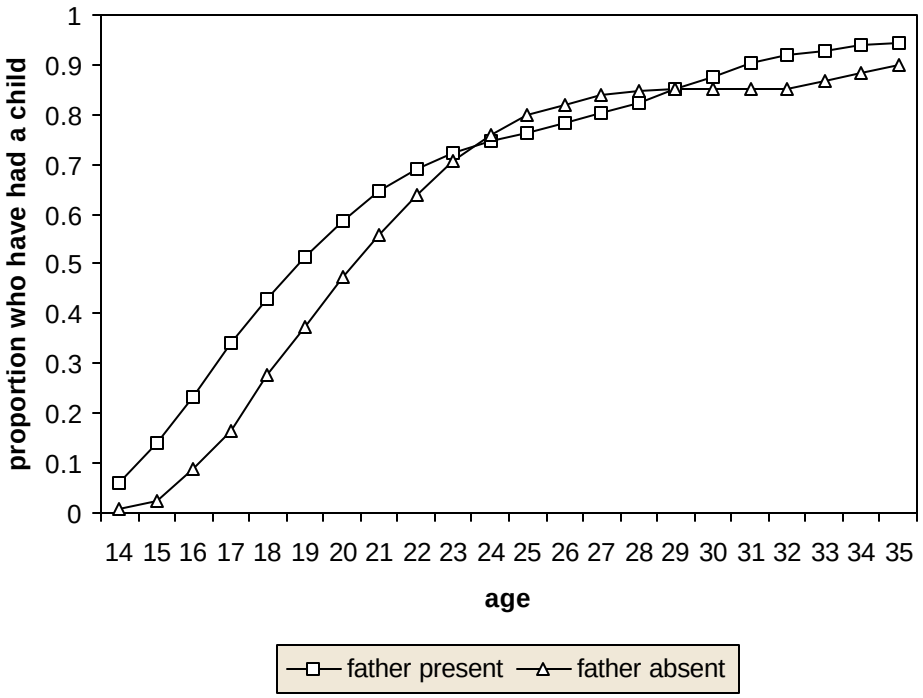


FIGURE 2. Number of brothers and offspring number for 56 Mayan men. Offspring number is expressed as standardized residuals to partial out age and age squared effects. Line is a least squares regression line.

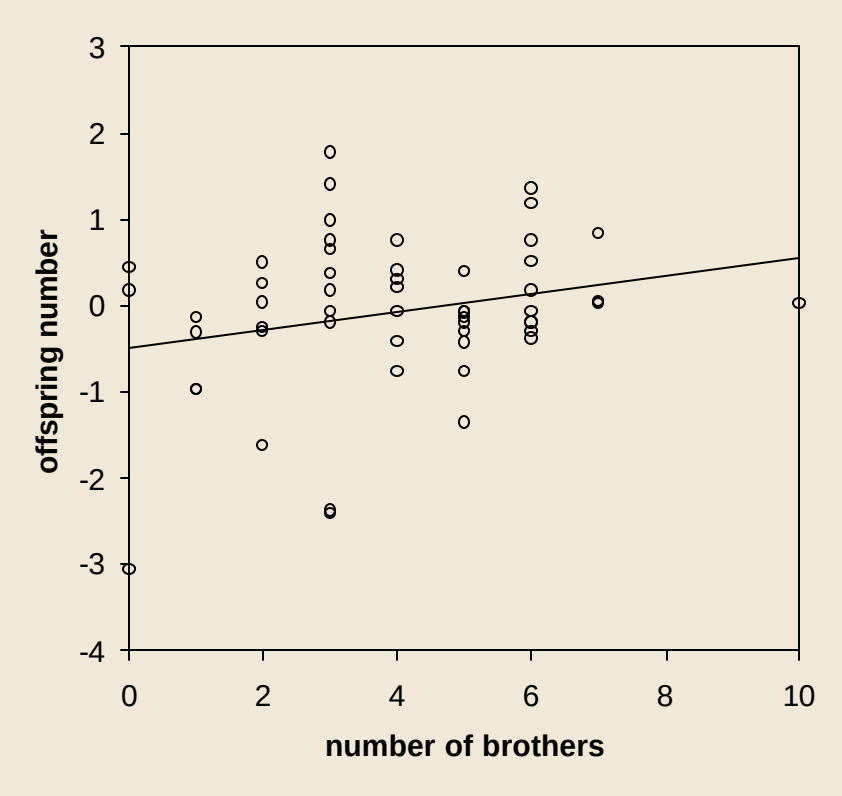
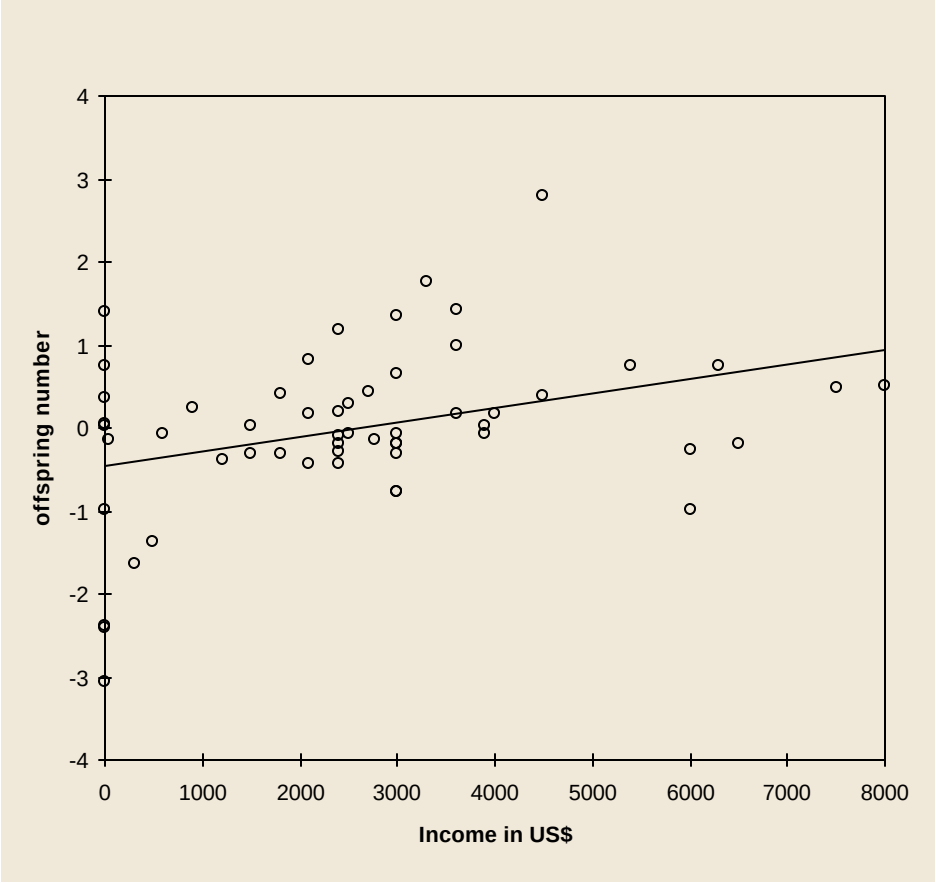


FIGURE 3. 1996 income (in US dollars) and offspring number for 56 Mayan men. Off Offspring number is expressed as standardized residuals to partial out age and age squared effects. Line is a least squares regression line.



D. Waynforth, Evolutionary Theory and Reproductive Responses to Father Absence: Implications of Kin Selection and the Reproductive Returns to Mating and Parenting Effort. S.C. Josephson, Fathering as Reproductive Investment. Part V: I. Garfinkel, Father Involvement: Economic Perspectives. P. England, N. Folbre, Involving Dads: Parental Bargaining and Family Well-Being. W. Sigle-Rushton, I. Garfinkel, The Effects of Welfare, Child Support, and Labor Markets on Father Involvement? J.W. Graham, A.H. Beller, Nonresident Fathers and Their Children: Child Support and Visitation From an Economic Pers Drawing on concepts from modern evolutionary theory, and particularly Trivers's (1974) parental investment theory, Draper and Harpending (1982) argued that early experience "sets" the reproductive strategy that individuals will follow in later life.Â father-present households anticipate the opposite and thus defer sexual activity once they reach biological maturity and seek to establish and maintain enduring, close, heterosexual relationships.Â Whereas Draper and Harpending restricted their focus to father absence, we contend that byÂ In other words, a disproportionate amount of reproductive effort will be allocated toward the individual's growth and development and mating rather than toward parenting.