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Chapter 2

Paternal Effect on Offspring Survivorship among Ache and Hiwi Hunter-Gatherers: Implications for Modeling Pair-Bond Stability

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The effects of father absence on child morbidity and mortality constitute an area of considerable interest in the medical and social sciences (Desai 1970; Franklin and Vial 1981; Marchione 1980; Brown 1973; Lancaster 1988 and references therein; Epenshade 1979; Daly and Wilson 1985; Berklov and Sklar 1976; Jason et al. 1983; Golding et al. 1986; Skjaerven and Irgens 1988). The few studies that have been conducted indicate that there are large differences in the effects of father absence on child survivorship across societies. In some populations the absence of fathers leads to a decrease in child health while in others paternal abandonment may lead to an increase or to no change in the health of offspring (see Lancaster 1988). For example, some studies show that in modern economies with well-developed health care systems child survivorship is negatively affected by the absence of fathers (e.g., Sweden, see Skjaerven and Irgens 1988), while in less developed countries child survivorship is sometimes positively associated with father absence (e.g., Dominican Republic, Brown 1973). Interestingly, this high variation in paternal effects on child health across human populations is paralleled by a rich diversity in human mating systems.

In recent years, anthropologists specializing in human behavioral ecology have become increasingly interested in the relationship between mortality in offspring and the differential distribution of parental care and male and female mating strategies (Draper and Harpending 1982; Kaplan and Hill 1985a; Harpending and Draper 1986; Pennington and

Harpending 1988; Borgerhoff Mulder 1988; Hewlett 1988). Child mortality is of particular interest in human behavioral ecology because it is an important component of reproductive success or biological fitness.

In this chapter we report preliminary analyses of the relationship between father absence and child mortality in two groups of hunter-gatherers: the Ache of Eastern Paraguay and the Hiwi of Southwestern Venezuela. We also present a preliminary model of the relationship between *paternal effectiveness in reducing child mortality* and marital pair-bond stability. The comparative analysis of Ache and Hiwi foragers is particularly revealing due to extreme differences in the socioecologies of these two hunting and gathering societies.

Even though we focus primarily on the anthropological literature on mating systems, it is important to note that a number of more sophisticated and comprehensive models of male and female desertion of mates have been proposed by biologists (see Trivers 1972; Maynard Smith and Ridpath 1972; Maynard Smith 1977; Parker and McNair 1978; Murray 1984, 1985; Brown 1987). Due to the primarily anthropological focus of this introduction to comparative research on Ache and Hiwi mating systems, we will not incorporate these more exhaustive models in this chapter. There is nevertheless considerable overlap between the causal components considered in our analyses and in the behavioral ecology literature on mating systems (Trivers 1972; Maynard Smith and Ridpath 1972; Maynard Smith 1977; Parker and McNair 1978; Murray 1984, 1985; Brown 1987).

THEORY

A key aspect of human mating systems is male reproductive strategies. Modern evolutionary theory allows us to generate useful general predictions regarding the conditions under which fathers might be expected to allocate most of their resources into raising few offspring with one spouse, and the conditions under which they might be expected to invest heavily in obtaining mates instead of providing paternal care. However, the predictions are at present too general and difficult to translate into rigorous hypothesis testing because adequate data collection on most variables of interest minimally requires frequent sampling over the entire life span of subjects.

Males among sexually reproducing organisms have three general alternatives for investment of time and energy: improving their own survivorship and growth (somatic investment), obtaining copulations (mating investment—*MI*), and increasing offspring survivorship (parental investment—*PI*).¹ Since somatic investment is mainly important be-

cause of its long-term effects on both mating and parenting success, we can focus primarily on the way total fitness is affected by a male's decisions concerning resource allocation to parenting versus mating investment. The total amount of resources (i.e., time, energy, food, wealth, etc.) that males have available to invest in parenting or mating is finite such that investment in parental care is expected to compete with investment in securing many mates. On average, natural selection is expected to favor individuals who allocate investment in mating and parenting in ways that yield a higher number of surviving offspring than the number that could be potentially produced via alternative allocations of mating and parenting investment.

Harpending and Draper's (1986) theoretical work on pair-bond stability in humans is an important step toward specifying conditions under which human males might prefer to invest most of their time and resources in parenting, or conversely, invest mainly in obtaining matings (see also Kleiman and Malcolm 1981; Lovejoy 1981). They have proposed a pair-bond stability model describing how differences in the effects of paternal abandonment on child survivorship across socioecologies may explain men's preference for stable monogamous unions over the frequent desertion of their mates and vice versa. Specifically, they propose that in societies in which father absence results in significantly lower offspring survivorship, pair-bond stability will be high. At the other extreme, higher divorce rates will be favored in situations where the presence of fathers in the households has a negligible or negative effect on the survivorship of their offspring.

The hypothesized relationship between the effects of paternal investment on offspring survival and resultant pair-bond stability in a given socioecological context is a function of the fitness gains associated with an additional unit of paternal investment versus an additional unit of mating investment. When an additional unit of paternal care yields less of a fitness increase than would an equal investment in obtaining copulations, males are expected to seek matings rather than continue to invest in offspring. Under extreme conditions where paternal investment does not increase offspring survivorship, it is expected that males will direct all of their resources into mating. On the other hand, some conditions may favor high parental investment, which should often lead to high pair-bond stability. This is because high levels of paternal investment probably preclude frequent male desertion of mates since father's ability to increase child survivorship probably occurs along several dimensions that require continual presence and much of an individual's time, energy, and resources (i.e., human fathers simultaneously protect their children from harm by conspecifics or predators, feed and teach their children valuable social, economic, and other skills, and provision

and protect mates such that they can be more effective mothers in turn). Consequently, under conditions in which fathers can positively affect child survivorship, it is expected that high levels of marital stability will result in highest fitness.

The pair-bond stability model is a useful starting point for identifying specific socioecological conditions that might be expected to affect the fitness payoffs of paternal abandonment and the fitness payoffs of paternal care. These two variables are probably independently affected by aspects of the physical and social environment in important ways. The payoff to mating investment, for example, is likely to be affected by the adult sex ratio and female fertility (Harpending and Draper 1986). In contexts characterized by an abundant number of females with high fertility, there are many opportunities for a temporarily mated male to produce more offspring with other unencumbered females. On the other hand, paternal care-independent and care-dependent causes of child mortality may represent important determinants of the fitness payoffs to paternal care. High child mortality due to paternal care-independent causes (e.g., some infectious diseases) favors abandonment because there is little fathers can do to reduce child mortality. However, when child mortality is primarily due to paternal care-dependent factors (e.g., protection from conspecifics, nutritional deficiencies), stable monogamous unions may be favored (Harpending and Draper, 1986:46).

In summary, the simple model of pair-bond stability described above assumes that male fitness is a function of two important components, male parental and mating investment and their respective payoffs, such that:

$$F_m = (MI) \times (M) + (PI) \times (P) \quad (1)$$

where F_m = fitness of males

MI = investment of resources in obtaining copulations
(mating investment)

M = fitness payoff per unit of mating investment (MI)

PI = investment of resources to effect offspring survival
(parental investment)

P = fitness payoff per unit of paternal investment (PI)

and that pair-bond stability is directly proportional to PI/MI .

Thus, if the left side of Equation (1) is to be maximized, it is argued that the level of pair-bond stability can be predicted by the relative size of the M and P components in the formula. When M stays relatively constant,

the model suggests that changes in the payoff to paternal investment (P) can be used to predict pair-bond stability. Increases in P should lead to increases in PI , and complementary, inevitable reductions in the mating investment component (MI). Thus, if pair-bond stability is a function of PI/MI , increased payoffs to parenting will lead to increased pair-bond stability. When specific socioecological factors are taken into account it becomes apparent that the size of the M and the P components are in turn determined by subsistence opportunities, disease ecology, female fertility, group composition, and other such factors.

BACKGROUND

The Ache² are a native population of Paraguay who until recently were full-time foragers (Hill and Hurtado 1989). By the end of the 1970s, four distinct macrogroups of Ache had made contact with local Paraguayans and government officials. At contact, three of these groups were rather small with 35–65 individuals each. The remaining group, the Northern Ache, however, were more numerous with approximately 600 individuals just prior to contact. Recall by informants suggests that the median size of a band was 48 people; the range on a given day was 3 to 160. The Northern Ache, who are the focus of this study, made peaceful contact between 1971 and 1978 and subsequently settled as part-time agricultural farmers in several reservations (Hill and Hurtado 1989).

The Northern Ache traditionally foraged in an area approximately 18,500 km², between 54–56° west and 24–25° south. This area is drained to the west by the Paraguay River and to the East by the Parana River. It is characterized by rolling hills covered with tropical forest vegetation and grasslands surrounded by stands of palms. The Ache hunt and gather primarily in the forest. Precipitation in Eastern Paraguay is highly unpredictable from month to month and from year to year. The mean annual precipitation is approximately 1600 mm. Temperature changes predictably across seasons with mean low temperatures ranging from approximately 10°C in the cold season to 20°C in the warm season.

Descriptions and analyses of foraging behavior (Hawkes et al. 1982; Hill 1987), hunting (Hill and Hawkes 1983; Kaplan and Hill 1985b), food sharing (Kaplan et al. 1984), men's and women's time allocation (Hill et al. 1985; Hurtado et al. 1985) and child development (Kaplan and Dove 1986) among Ache hunter-gatherers have been published over the past decade.

The Hiwi are hunter-gatherers of Southwestern Venezuela. They live in the extremely seasonal neotropical savannas of the Orinoco River

Basin where a larger population of closely related Guahibo-speaking populations reside. Although all the Guahibo-speaking populations refer to themselves as "Hiwi," here the term Hiwi is used exclusively to refer to the hunting and gathering bands of the Guahibo population, as no other adequate label is available. The local criollo populations use the term "Cuiva," which has strong derogatory connotations.

The Hiwi territory is confined to the drainages of the upper Cinaruco, Capanaparo, Ariporo, Agua Clara, and Meta Rivers. The main territory of the Venezuelan Hiwi is confined to areas contiguous to the Cinaruco River (see Hurtado and Hill 1990b).

Close to 90% of the precipitation falls during the months of May–November followed by an intervening period of severe moisture stress between January and March. During these dry months, monthly precipitation averages fall below 25 mm (Hurtado and Hill 1990) and often there is no rain in January and February. The ecological consequence of this rainfall regime is marked fluctuations in the temporal and spatial distribution, the biomass, and productivity of plants and animals. In the past, the Hiwi coped with these fluctuations by moving as much as 150 km from one food patch to another over a huge range that included three river drainages in Venezuela and Colombia. This transhumancy has recently been greatly constrained by the presence of military forces in the area, and by cattle ranching.

Changes in temperatures across seasons are less drastic than fluctuations in precipitation. Temperatures range between an average daily maximum of 37.7°C in March to an average daily minimum of 19°C in December (Hurtado and Hill 1990).

The population size of the Venezuelan and Colombian Hiwi hunter-gatherers is approximately 800 individuals (Hurtado and Hill 1987). Venezuelan and Colombian Hiwi bands visit one another primarily during the dry season when nocturnal traveling across savannas is less arduous than in the wet season. The size of the Venezuelan Hiwi population was 290 individuals in 1988 (Hurtado and Hill 1990b). These 290 individuals form two semipermanent residential bands. The bands form very large camps including all members of the band during much of the year, but also break up into smaller bush camps for periods of up to 4 weeks at a time. The two residential settlements are located near the Cinaruco river within a 4-hour walk of each other on a reserve bounded by two rivers and an incipient cattle ranch: 12,058 hectares set aside in 1971 by presidential decree.

The larger band (188 individuals) is settled in the middle of a dry savanna next to the local indian services office. We studied the more isolated, smaller band (102 individuals) that lives in the gallery forest along the Cinaruco River. Its central place has been moved several times over the past 20 years.

Socioecological Differences in Paternal Care-Dependent Child Mortality

Obtaining adequate measures of the difference in the relative contribution of paternal care-dependent and care-independent child mortality between societies is methodologically challenging. To date we can only guess about how the Ache and Hiwi population might differ along these lines. Food consumption among the Ache is high relative to the Hiwi (Hill et al. 1984; Hurtado and Hill 1987), and the food sharing pattern of the Ache generally ensures that no individual undergoes severe nutritional stress (Kaplan et al. 1984). The forest environment of Ache foragers appears to contain more insect pests and dangerous animals than the grassland savanna of Venezuela. Ache foragers also live in new uncleared forest camps each day whereas the Hiwi inhabit well cleared permanent villages during much of the year. Consequently, in the Ache case careful monitoring of children is crucial to child survivorship. However, this is probably a more important determinant of maternal care than paternal care strategies (Hurtado 1985; Hurtado et al. 1985; Hurtado and Hill 1990a). Ache men spend relatively little time holding, playing, grooming, or carrying their children and spend most of the day hunting or in other activities. Men tend to take care of infants and children when their wives leave camp for water, firewood, or to gather food, and usually do very little childcare when the children's mother is in camp (see Hill 1983).

Among the Ache, fathers appear to play a more important role in protecting their offspring from the infanticidal/homicidal attacks of conspecific adult males (Hill 1990). The positive effects of men's hunting ability on child survivorship that we have previously reported (Kaplan and Hill 1985a) may be due in part to the better treatment that the children of good hunters receive from the other men in the band than to the food that fathers share with their offspring (Kaplan and Hill 1985b).

In contrast, among the Hiwi food consumption levels are relatively low, and paternal food provisioning seems to be a key determinant of child survivorship, particularly during long seasons of food scarcity when men hunt and gather close to 90% of the food consumed (Hurtado and Hill 1990b). This paternal provisioning may be crucial for breaking the cycle of frequent microbial intestinal disease bouts associated with increasing levels of malnutrition, and ultimately death. It is our impression that gut infections and diarrhea are much more common and serious health hazards to Hiwi children than they are for Ache children (Hurtado et al. 1988). Unlike Ache fathers, Hiwi men spend considerable amounts of time taking care of their children (unpublished data). Men frequently hold infants and carefully monitor older children when women engage in food processing activities, manufacturing, and forag-

ing. Nevertheless, Hiwi fathers do not spend as much time taking care of the young as do women on average. Preliminary analyses suggest that paternal food provisioning probably has a greater effect on child survivorship than does this kind of direct paternal care. Among the Hiwi, men whose caloric return rates per hour spent searching and acquiring food is higher than the median for all hunters have more surviving offspring than hunters whose rates fall below the median (unpublished data).

In summary, even though paternal care-dependent causes of child mortality appear to be important in both Ache and Hiwi society, the types of care required from fathers to prevent death in offspring are very different. Ache fathers may influence their children's long-term health to a great extent by building alliances via hunting partnerships with other men, whereas Hiwi fathers may gain more from putting much of their time and energy into making sure that their own children consume a reasonably sufficient and constant diet across all seasons of the year.

Socioecological Differences in Mating Opportunities

The neotropical forests of Eastern Paraguay and the llanos (savannas) of Venezuela and Colombia are very different habitats. Seasonal fluctuations in rainfall and food availability are more extreme for the Hiwi of Venezuela than for the Ache of Paraguay. Thus, while foraging opportunities change dramatically across the year for Hiwi foragers, they are fairly constant for the Ache year round (see Hill et al. 1984; Hurtado and Hill 1990). In the Ache environment, foods of different types are relatively evenly distributed across time and space. Even though single meat and vegetable resources can be patchily distributed and differ in availability across the year, their distribution in time and space overlaps considerably across a vast territory with very low population density (Hill et al. 1984). In contrast, the Hiwi environment is extremely patchy with plant and animal resources found in discrete clumps mainly along river banks and streams or in transitory areas between the gallery forest and the savanna (Hurtado and Hill 1988; Hurtado and Hill 1990b). There are few areas that have the preferred combination of abundant root and fruit patches, as well as lagoons with rich supplies of fish, capybara, alligators, and turtles in the dry season and effective population densities are high.

Associated with differences in forest cover and seasonality we find large differences in the social systems of Ache and Hiwi hunter-gatherers. While territorial defense plays a minor role in Ache society, it seems to constitute a major factor in the distribution, size, and warfare patterns of Hiwi bands. Hiwi territories appear to be discrete with well-

defined boundaries. Bands seem to have exclusive rights to these territories, with violations poorly tolerated.

Low levels of territorial defense and amicable interband relations among the Ache facilitate considerable movement of individuals across bands and increases the pool of mates for individuals of marriageable age. Even though the Ache live in small bands ranging in size between 7 and 30 individuals, movement across bands in combination with a total population size of approximately 600 individuals increases the mating opportunities that are open to men. An unmarried Ache man can always find a potential female mating partner by simply visiting each foraging band in turn. In contrast, the Hiwi population with a total size of approximately 800 individuals is extremely endogamous. Marriage across bands occurs rarely and visiting is often dangerous or impossible. Consequently, the mating pool is considerably smaller for individuals of marriageable age at any given point in time among the Hiwi than is the case for the Ache.

Low seasonal fluctuations in food supply and higher levels of protein and caloric consumption may be responsible for higher female fertility rates among the Ache than among the Hiwi. This difference in the socioecologies of Hiwi and Ache foragers also affects the difference in the number of potential mating partners for males of the two groups. The Ache have a high fertility population with a positive growth rate and a very young population age structure (Hill 1990). This disproportionately inflates the number of individuals in the younger age groups with respect to older age groups. The size of the younger female cohorts will in turn affect the number of potential female partners that are available to men in the population because females become incorporated into the mating system several years before males. The Hiwi on the other hand are characterized by low fertility with a negative population growth rate (Hurtado and Hill 1987), a relatively old population age structure, and fewer mating opportunities available to men than is the case for the Ache.

Lastly, differences in the availability of reproductive-age females between the Hiwi and the Ache population is exacerbated by differences in the adult sex ratio for each population. Among the Hiwi, mating opportunities available to males are greatly reduced by a high male-biased sex ratio from birth through middle age. This is due in part to high female infanticide rates apparently caused by women's strong preference for sons over daughters (Hurtado and Hill 1987). The Ache, in contrast, show a male-biased sex ratio in the junior age grades, but a relatively even sex ratio in most adult categories (see Table 1).

Differences in levels of mating opportunities between Ache and Hiwi bands permeate other aspects of social organization in interesting ways.

While there is little segregation in space by sex among the Ache, interactions among nonspouses in the Hiwi community are quite restricted. Ache men and women who are not married to each other are frequently seen having long private conversations or spending time together in tactile contact even in public. Among the Hiwi mixed sex interaction among unmarried individuals is almost completely absent and tactile contact between unmarried adults of different sexes has never been observed. In addition, when Hiwi men and women that are not married to one another converse, they face opposite directions and speak in a loud voice, so that their conversation may be overheard by all band members. Married couples, on the other hand, do not follow these behavioral restrictions and spend considerable amounts of time in close proximity to one another and converse privately for hours at a time facing each other.

Differences in levels of mating opportunities between the Ache and the Hiwi occur alongside marked contrasts in marital stability. While serial monogamy and extra marital promiscuity is very common among the Ache, stable lifetime monogamous unions with almost no extramarital copulation is the normative mating pattern among the Hiwi.

The differences in mating systems are reflected in the roles of Ache and Hiwi fathers. Even though men do almost all the hunting in both societies, the Ache share most of the meat they acquire outside the nuclear family (Kaplan et al. 1984). Ache men not only acquire food for their spouses and children but also for all other individuals that are in their residential band. This food sharing is associated with high levels of male-male cooperation in hunting as opposed to cooperation among spouses. In contrast, Hiwi men share most of the meat and other foods they acquire with their spouse and offspring only (Lyles et al. 1990), and spouse cooperation in foraging activities is commonly observed. In addition, while Ache men specialize almost exclusively in hunting throughout the year, Hiwi men not only do all the hunting but also gather most of the fruit consumed during the late dry/early wet season, and do considerable amounts of childcare in the late wet season when women gather large amounts of tubers (Hurtado and Hill 1990a). Thus, while in the former season, husbands free their wives from strenuous foraging activities, in the latter season they free them from the burden of having to care for small infants and children during food collecting trips. Women, in turn, very frequently accompany their husbands on hunting outings. Even though the women do not kill prey, they help their husbands with the paddling and steering of canoes while they shoot game along the river bank. In summary, economic and other kinds of cooperation between spouses appears to be more common among the Hiwi than among the Ache.

METHODS

The data presented in this paper were collected over a period of 10 years by Hill and Hurtado. A demographic interview developed by Hill in 1981 is the main source of data in this study. The same interview was used in both the Ache and Hiwi populations, however, interviews with Ache individuals were conducted without the help of translators whereas among the Hiwi, it was necessary to use a bilingual (Hiwi/Spanish) informant. The investigators have not yet developed the necessary language skills to carry out complicated interviews without assistance.

The interviews are designed to record the following reproductive experiences of all men and women in the population: live births of own children, names of an individual's mates over the course of a lifetime, and dates of divorce, dates and causes of death for children, dates of death or divorce for each child's parents, and a large number of other variables not relevant to this study. Individuals were also asked the same questions about their deceased and living siblings. Reproductive events and their outcomes were recorded for each ego in chronological order and coded for computer analyses.

The Ache data set for this study consists of information on 832 births provided by 161 reproductive histories of individual women. The Hiwi data set is substantially smaller with information on 135 births recorded in 23 reproductive history interviews. The methodology used to determine the dates of birth and death, or divorce of all individuals mentioned in interviews is quite elaborate and thoroughly described in Hill (1990). Here it is sufficient to mention that most dates were assigned based on information provided by relative age lists and known calendar dates and reference to previously dated events.

This method to determine ages in combination with questions concerning causes of death and the survival/marital status of fathers provided the necessary information to measure child mortality by age, and as a function of the marital and survivorship status of father, as well as population-level divorce rates and female total fertility rates. Standard life table analyses were used to estimate the survivorship rates of children to different ages, l_x , as a function of characteristics of their parents' marriage or father's death. Pearson and Mantel-Haenszel χ^2 tests for statistical significance and one-tailed probability values less than or equal to 0.05 were used to test alternatives against null hypotheses.

Because the Ache have gradually become settled agricultural farmers in the past two decades, we report only precontact, retrospective demographic data. Thus, the Ache data set is censored at 1970, the last year that all Ache individuals lived as uncontacted hunter-gatherers. In contrast, we analyzed the entire Hiwi data set, which represents the

precontact and postcontact periods. This is because the Hiwi have maintained an almost intact foraging economy in spite of considerable exposure to outsiders since the late 1950s.

RESULTS

The Ache before Contact

The Effects of Father's Death on Child Survivorship. Among Ache hunter-gatherers, the probability of child survivorship tends to be lower when father dies than when father lives. This is true for all children up to 10 years of age at which point paternal mortality ceases to have an effect on child survivorship ($n = 294$ births; Figure 1). However, in our sample, this difference is statistically significant only in the 1- to 5-year interval [Pearson's $\chi^2 = 44.2$, p (one-tailed) = 0.04] with children without fathers experiencing a risk of death 2.6 times higher than children with fathers. In all the other intervals, there is no statistically significant effect, primarily due to high mortality for all children in the first interval and a very small paternal effect in later intervals [0-1 year Pearson's $\chi^2 = 0.83$, $p = 0.49$; 5-10 year Pearson's $\chi^2 = 2.36$, p (one-tailed) = 0.1149]. The effect of father's death on child survivorship is, however, highly significant when all age strata are examined [Mantel-Haenszel $\chi^2 = 4.48$, p (one-tailed) = 0.017].

The Effects of Divorce on Child Survivorship. Similarly, parental divorce within the first year of life and in subsequent 5-year intervals also leads to higher child mortality than when no parental divorce is experienced ($n = 292$ births; Figure 2). Again, at age 10 and beyond, the marital status of parents appears to have little impact on subsequent survivorship. Between birth and 1 year of age, the effect of divorce on child survivorship is highly significant [Pearson's $\chi^2 = 13$, p (one-tailed) = 0.0001]. In this age interval, children who experience parental divorce are 2.6 times more likely to die than children who do not get divorced. In the 1- to 5-year interval the effects of divorce are also significant [Pearson's $\chi^2 = 5.8$, p (one-tailed) = 0.007] with children of divorce parents being 2.9 times more likely to die than children whose parents stay together. Not surprisingly, the effect of divorce on child survivorship is highly significant when all age strata are examined [Mantel-Haenszel $\chi^2 = 10.2$, p (one-tailed) = 0.0007].

Parental divorce leads to increases in mortality from certain causes but not others (Figure 3). When the analyses is stratified by cause of death, it was found that children who experience parental divorce between birth

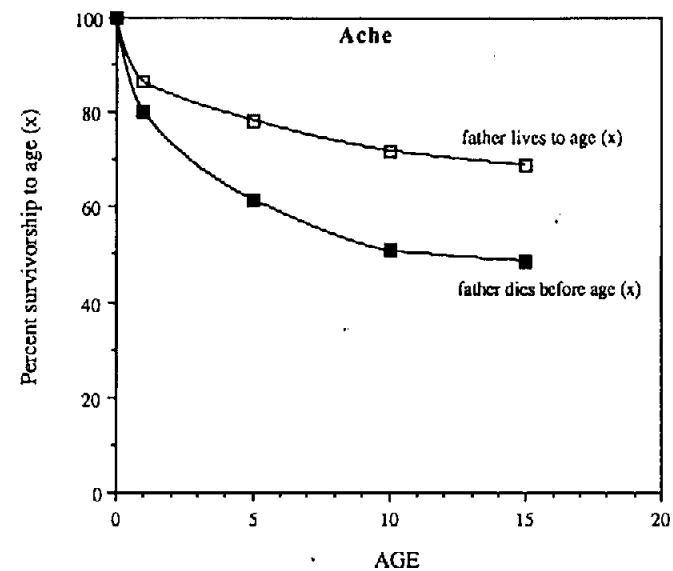


Figure 1. Percent of children who survive to a specified age as a function of whether their father lives until they reach that age or dies before they reach that age. This is equivalent to the l_x calculation in demographic analyses and calculated as the product of age specific probabilities of survival (p_x) through each age interval as a function of whether father does or does not survive to the end of that interval. Probability of survival through an interval $p_x =$ number of children who survive an interval/number of children who enter an interval.

and 1 year of age are more frequently victims of sickness, homicide, and capture in raiding by Paraguayans than children whose parents stay together [Pearson's $\chi^2 = 3.8$, p (one-tailed) = 0.0021; Pearson's $\chi^2 = 7.7$, p (one-tailed) = 0.0055; and Pearson's $\chi^2 = 8.9$, p (one-tailed) = 0.0028, respectively]. Children whose parents were divorced before their first birthday were not more likely to die at birth or from accidental causes. In later age strata, only differences in mortality due to illness reach statistical significance [1-5 years Pearson's $\chi^2 = 7.3$, p (one-tailed) = 0.0003], although mortality rates from homicide and capture in warfare are consistently higher in children whose parents are divorced. When all age strata are combined the effect of parental divorce on the probability of death from sickness, homicide, and capture in warfare are all statistically significant [Mantel-Haenszel $\chi^2 = 2.98$, p (one-tailed) = 0.042; Mantel-Haenszel $\chi^2 = 3.1$, p (one-tailed) = 0.04; and Mantel-Haenszel $\chi^2 = 3$, p (one-tailed) = 0.042, respectively]. Thus children whose

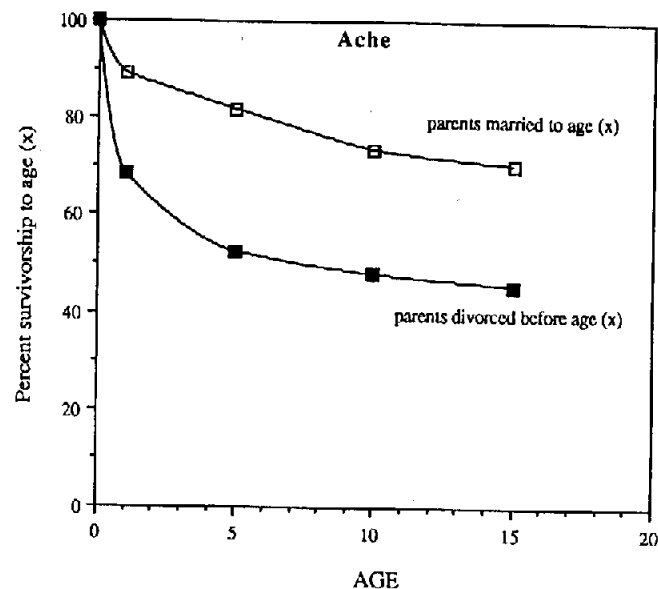


Figure 2. Percent of children who survive to a specified age as a function of whether or not their parents stay married until they reach that age (calculated as described for figure 1).

parents get divorced are more vulnerable to sickness, homicide, and capture in warfare, but not to accidental causes of death.

Pair-Bond Stability. In addition to a very high effect of father absence on child mortality, the Ache show very high levels of pair-bond instability. A small sample of postreproductive women report an average of 12.1 spouses to date ($SD = 4.3, n = 8$). The number of spouses a woman has had increases as a function of age throughout her reproductive years (Figure 4). It is therefore not at all surprising that 25% of all Ache children ever born grew up with a divorced parent. Paternal losses due to death by the time children reach 15 years of age are experienced at a lower rate (20%) (Figure 5).

Hiwi Hunter-Gatherers

The Effects of Father's Death and Parental Divorce. Due to small sample sizes, we were unable to stratify statistical analyses of child mortality among the Hiwi by divorce status of parents and father's death, and by

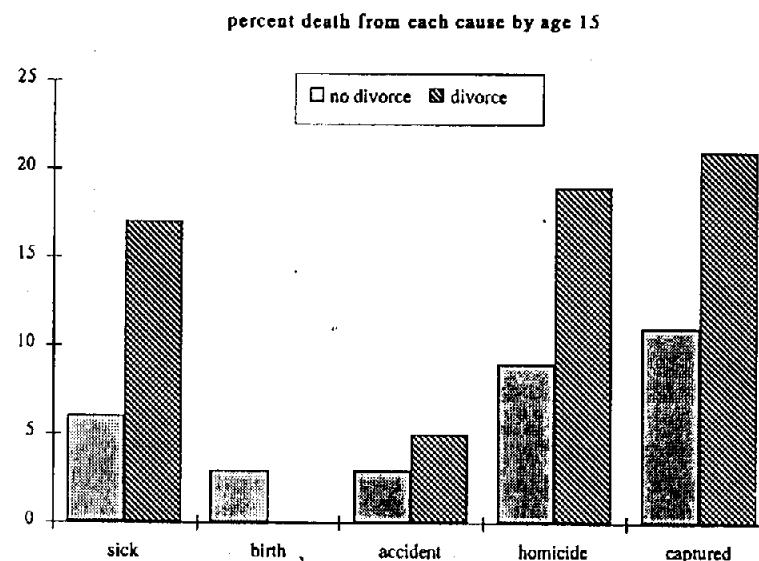


Figure 3. Percent of children ever born who die from each of five causes before the age of 15 years depending on whether their parents stay married until they reach their 15th birthday, or divorce before that time. Causes of death are: died from sickness; died at birth; died in an accident; was a victim of infanticide/homicide; and captured in warfare. The ultimate fate of children captured in warfare is generally unknown.

cause of child's death and age group. Consequently, in this data set, "father absence" is operationalized as both divorce and father's death. All analyses are limited to a single age interval: from birth to 5 years.

Analyses show that father's death and divorce have less of an effect on child mortality in the Hiwi than in the Ache population. Between birth and 5 years of age, Hiwi children whose fathers die and whose parents divorce are only 1.1 times more likely to die than children whose fathers live and stay married. This difference is not statistically significant at the 0.05 level [Pearson's $\chi^2 = 2.2, p$ (one-tailed) = 0.08; $n = 107$ births].

Pair-Bond Stability. Interestingly, only 8% of Hiwi children in our sample experienced the dissolution of their parents' marriage by the time they reached 5 years of age. The comparative rate for the Ache is considerably higher (17%). In contrast to the Ache women, Hiwi women report an average of only 1.7 husbands by the end of their reproductive careers ($n = 23$ women).

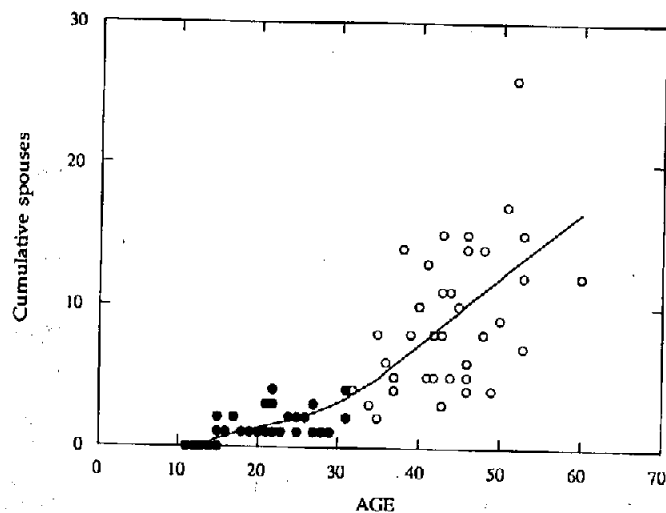


Figure 4. Cumulative number of spouses reported by women who were alive in 1990. Solid circles represent those born after 1960 whose marriages all occurred on reservations.

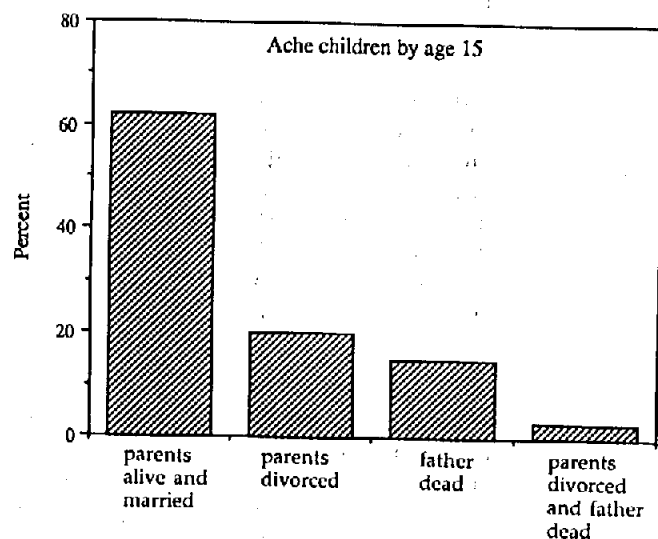


Figure 5. Probability of different family outcomes by the age of 15 for Ache children.

DISCUSSION

In the anthropological literature it has been proposed that under conditions where father presence has a strong positive effect on child survivorship, long-term stable monogamous unions will be favored over less stable marriages while paternal abandonment is expected to be common under conditions where father presence has no effect or has a negative effect on the survivorship of offspring. The findings of this study run contrary to these expectations. Even though father absence has a strong negative effect on child survivorship among the Ache, pair-bonds are highly unstable in this group of hunter-gatherers. In contrast, father absence appears to have a very small impact on child survivorship among the Hiwi, and yet pair-bonds in this group are quite stable.

Thus, our data do not support the model proposing that parents are more likely to stay married when father absence makes a big difference in child survivorship. This can either mean that the hypothesized relationship is invalid, or that the conditions under which we might expect the relationship to be significant have not been adequately specified in the anthropological literature (but see Maynard Smith 1977; Murray 1984).

Problems with the Current Formulation of the Pair-Bond Stability Model

The simplest formulation of the pair-bond stability model as proposed by Harpending and Draper (1986) and described in the introduction implicitly assumes that

1. The payoffs to mating investment in various societies are all approximately equal.
2. Paternal effects on child survivorship lead to an increase or decrease in the amount of paternal investment (*PI*) that males provide to offspring.
3. The amount of investment that males put into mating (*MI*) is a complementary response to the amount of paternal investment because investment in parenting and mating requires mutually exclusive use of time and resources.
4. Increasing levels of parental investment lead to an increase in pair-bond stability and decreasing levels of parental investment lead to a decrease in pair-bond stability.

Under these assumptions, if Equation (1) roughly captures the components of male fitness, and if fitness is to be maximized, it does appear

that increased paternal effects on child survivorship should lead to higher pair-bond stability.

We would like to examine one obvious difficulty with these assumptions, namely, that the first assumption is almost certainly invalid. As the model is theoretically derived and expressed in Equation (1), payoff to paternal investment is not the only independent variable in the model. Nevertheless, for the sake of simplification, payoffs from mating investment have been treated as invariant in the simplest predictions about pair-bond stability (Harpending and Draper 1986). While we sympathize with the attempt to simplify the model and make straightforward testable predictions, we believe that it is more likely that the payoffs from mating investment and paternal investment are both determined by socioecological factors that are independent of one another and that the payoffs from mating and paternal investment are both important independent determinants of pair-bond stability.

When two independent variables such as mating and paternal investment payoffs independently participate in the causal pathway of an outcome, they frequently interact on the dependent variable (in this case, pair-bond stability). Interaction occurs when the magnitude of the effect of one independent variable on a dependent variable changes according to the values of the second variable and vice versa (see Neter et al. 1985). With respect to the problem of pair-bond stability, this means that the amount of variance in pair-bond stability in a system that is explained by paternal investment payoffs may change depending on the level of mating investment payoffs. Considering the possibility of interaction effects allows us to examine and specify the conditions under which a univariate relationship is likely to be present, absent, weak, or strong at different levels of other independent factors.

Ache and Hiwi group composition data allow us to illustrate the potential problems of interaction between the two independent variables (P and M) and pair-bond stability. The Ache and Hiwi not only vary in paternal effects on child survivorship but also on the number of mating opportunities that are open to males at any one point in time. One very crude estimate of potential differences in the mating opportunities open to males across these two groups is the ratio of females of reproductive age to reproductive adult males in the population. This ratio is determined by mortality and fertility schedules characterizing a population at different points in time and the age-specific sex ratios in the population. This ratio of females per male of reproductive age is higher in the precontact Ache population (1.13) than in the Hiwi population (0.72) over the past 30 years (see Table 1): Ache men appear to have experienced a social situation where there has been higher availability of potential fecund mating partners than seems to be the case for Hiwi men.

Table 1. Calculation of the Parenting/Mating Index

Parameter	1970 (precontact)	
	ACHE	HIWI
a Number of females 15–40 years of age	122	18
b Number of males 20–55 years of age	108	25
c Female/male ratio ($= a/b$)	1.13	0.72
d Female total fertility rate	7.8	5.4
M Fertility units per male ($= c \times d$)	8.8	3.9
e Child survivorship with father	0.86	0.57
f Child survivorship without father	0.53	0.52
P Relative increase in child survivorship with father and without father ($= e/f$)	1.6	1.1
I Parenting/mating index ($= P/M \times 100$)	18.2	28.2

It is therefore possible that the relationship between paternal effectiveness and pair-bond stability is tempered by the relatively higher levels of mating opportunities that are open to Ache men. At high levels of mating opportunities the steepness of the slope defined by the relationship between paternal effects on child survivorship and marital stability may be lower than at low levels of mating opportunities for men (see Figure 6). Consequently, in the Ache system, the fitness benefits to be gained from changing mates frequently may be considerably higher than the payoffs associated with investing in one mate and her offspring only, even though paternal abandonment leads to high offspring mortality.

In contrast, low levels of mating opportunities may create the necessary conditions for the effects of father absence on child survivorship to strongly influence levels of marital stability. In this situation, any difference in child survivorship might select for high levels of pair-bond stability. Hence, in this hypothetical example, the Ache represent point D in Figure 6 while the Hiwi represent point A.

It is evident that to adequately test this interaction hypothesis we would need data on several societies with high, medium, and low levels of mating opportunities and high, medium, and low levels of paternal effects on child survivorship. The information on the Ache and the Hiwi provides only two extreme points in a much larger comparative data set.

Qualitative Predictions about Pair-Bond Stability Using a Simple Model

Faced with sparse comparative data, we can at least attempt to evaluate the potential explanatory value of the simple model described in the introduction, through qualitative means. In this model we adhere to

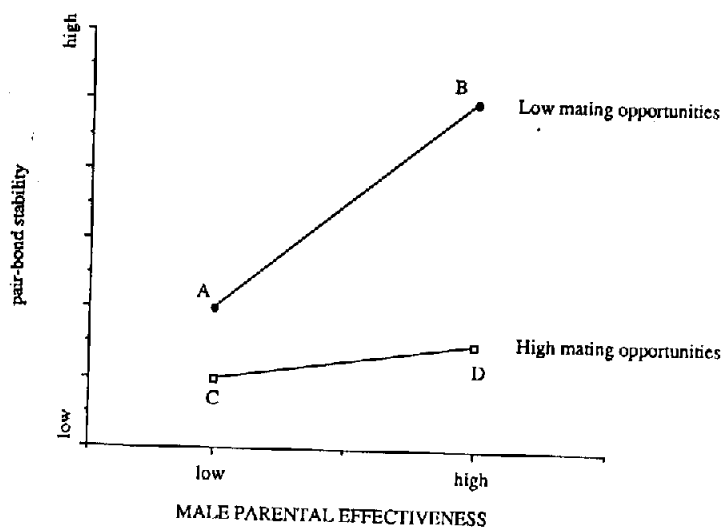


Figure 6. A hypothetical model describing the relationship between male parental effectiveness (increase in survivorship as a function of father's parental investment) and pair-bond stability as a function of the level of mating opportunities. In the model there is an interaction effect between father effectiveness and mating opportunities such that father effectiveness only is a strong determinant of pair-bond stability when mating opportunities are low.

assumptions 2-4 in the previous section, and to the simple formulation of male fitness as expressed in Equation (1). We can then estimate the relative differences in the payoffs from parenting versus mating investment for the Ache and the Hiwi to assess the prediction that pair-bond stability should be higher when the relative payoffs to parenting versus mating are higher. A measurement of the potential parenting versus mating investment payoffs given certain relevant parameters is possible with our demographic data and is shown in Table 1.

Using demographic data we calculate a "parenting/mating index" and estimate this parameter for different societies as follows:

$$I = \text{parenting/mating index} = P/M \times 100$$

$$P = \text{payoff to parental investment}$$

$$M = \text{payoff to mating investment}$$

where P is estimated as
$$P = \frac{\text{offspring survivorship to adulthood with father}}{\text{offspring survivorship without father}}$$

and M is estimated as
$$M = \frac{\text{number reproductive females} \times (\text{total fertility rate})}{\text{number of reproductive males}}$$

Thus, an estimate of potential male mating investment payoffs can be calculated by multiplying the ratio of reproductive females per male times the total female fertility rate (see Table 1). This number represents the fertility increment potential for a male if he could sire the average number of children given that he obtains access to an average share of females in the population. We term this estimate of the mating payoff "fertility units per male." The estimate of paternal investment payoff, or P , that we use is based on the reported difference in survivorship for children whose fathers stay with their mothers or abandon them.⁴ Finally, the ratio of the relative risk of survivorship to fertility units per male can be used to estimate the relative payoffs of parenting to mating investment in a group. We have labeled this measurement the "parenting/mating index."

Among the Ache, the parenting/mating index is lower (18.2) than the Hiwi index (28.2) (Table 1). This is primarily due to the fact that both the ratio of reproductive age females to adult males (1.3) and the female total fertility rate (7.8) are higher among the Ache than among the Hiwi (0.72 and 5.4, respectively). Thus, the number of "fertility units per male" is considerably higher among the Ache (8.8) than among the Hiwi (3.9). Consequently, even though the relative increase in survivorship for offspring in father-present versus father-absent families is higher among the Ache (1.6) than among the Hiwi (1.1), it is not sufficiently high to make the parenting/mating index higher for the Ache than for the Hiwi. Using the parenting/mating index numbers as a guide, we might expect pair-bond stability to be higher in the Hiwi than in the Ache, just as we observe. Unfortunately, this model does not allow us to make quantitative predictions about how much higher the divorce rate should be among the Ache.

The quantitative estimates of male mating opportunities and potential payoffs from mating investment presented above are particularly useful because they are independent measurements of the levels of marital instability that we are trying to explain. This is an important issue to address since it can be easily argued that one reason why mating opportunities are so high among the Ache is *because of* high divorce rates, which produce many potential sexual partners, rather than vice versa. This circularity can be avoided in our model because neither the age structure of the population nor female fertility rates are necessarily determined by divorce rates.

In summary, the age structure of the Ache population and high female fertility may greatly increase the fitness payoffs associated with male mating investment relative to payoffs associated with paternal investment relative to the Hiwi population. The socioecological conditions necessary to favor pair-bond *instability* appear to be met in the

Ache population while the opposite seems to be the case among the Hiwi.

The model we have presented here generates some interesting hypotheses worthy of future investigation. Levels of mating opportunities not only vary across societies, but are also likely to vary across categories of men within societies. The model predicts that individual differences in the effects of father absence on child survivorship should be a stronger predictor of marital stability among men who have fewer mating opportunities than among men who have more mating opportunities.

CONCLUSION

Analyses of the fitness outcomes of paternal abandonment and its marital correlates among Ache and Hiwi hunter-gatherers suggest that the effect of father absence on child mortality is only one of several component causes of pair-bond stability. Another important component in determining marriage patterns is the fitness payoff that males can gain by investing time and energy into having more than one mating partner. Data analyses suggest that among the Ache father absence has a negative effect on child survivorship and nevertheless pair-bonds are highly unstable. In contrast, among the Hiwi father absence has a relatively small effect on child survivorship and yet most marriages last a lifetime. Previous models have proposed that positive paternal effects on child survivorship should be correlated with high levels of marital stability and vice versa but our data do not meet these predictions. Instead we propose that the interacting effects of levels of mating opportunities and paternal effect on marital stability need to be considered.

This attempt to develop a multivariate model of pair-bond stability requires considerable theoretical improvement. It nevertheless points to the present scarcity of adequate multivariate models, and for the need to incorporate the exhaustive and universal models proposed by behavioral ecologists, in studies of human mating systems and human behavior in general (see Maynard Smith and Ridpath 1972; Maynard Smith 1977; Parker and McNair 1978; Murray 1984, 1985; Brown 1987). Multivariate analyses can be extremely useful in the study of complex relationships between socioecological variables, fitness, and human behavior. The utility of single variable models for explaining human behavioral patterns is likely to be extremely limited and should be invoked only when supported by strong theoretical inference.

NOTES

1. In theory parental investment includes any investment that increases the survivorship or mating success of offspring at the cost of the parent's ability to invest in other offspring (Trivers 1972). We have chosen to ignore effects on offspring mating success in this chapter to simplify the models presented.
2. The ethnographic present for the Ache is the precontact period. The ethnographic present for the Hiwi is both the precontact and postcontact periods.
3. We chose age categories based on data concerning the age span over which males and females normally reproduce. Since few Hiwi women reproduce beyond age 40, we chose that as our cutoff point even though many Ache women reproduce beyond that age.
4. In theory, paternal effectiveness should be measured based on the effect of divorce, not father death, since we are modeling the behavioral decision about whether to abandon a pair-bond, not whether or not to die.

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