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**FATHERING AMONG THE TSIMANE OF BOLIVIA:
A TEST OF THE PROPOSED GOALS OF PATERNAL CARE**

BY

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DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

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DEDICATION

*To my father, for always entertaining my questions and
nurturing my inquisitiveness.*

*And to my mother, for believing in me enough to let me to
choose my own path, despite how much it sometimes went
against your better maternal instincts.*

*No amount of gratitude could ever reflect my sincere
appreciation.*

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ABSTRACT

Human males are quite exceptional in the levels of investment they provide to their children, yet variation across and within populations indicate that men are not blindly driven by paternal love. Researchers have proposed numerous models that outline different pathways through which men can receive benefits from paternal care. The ultimate goal of this exercise is to explain why human males enjoy such greater returns to the behavior than other primates, as well as account for its variation within humans. In this dissertation I test predictions produced by three of these models by exploring the fathering behaviors of the Tsimane of central Bolivia.

Traditional evolutionary theory tells us that men invest in their children because they have a vested interest in their well-being—if a man’s descendents fail to reproduce, then that man’s fitness is no different than if he had no descendents at all. This argument forms the basis for what I refer to as the Paternal Provisioning Model, which holds that men invest in their children because of the direct benefits they receive by increasing the

fitness of their offspring. Many researchers, however, have noted that a man's ability and willingness to invest in offspring are highly valued by women and that the offering of paternal care is often succeeded by the winning or continuation of sexual access to the mother, providing a pathway through which paternal care can lead not only to greater offspring fitness but greater fertility as well. Some have even contended that the mating benefits conferred through this pathway (termed the Mating Effort Model) provide the main motivation for paternal care. Finally, the Tolerated Theft Model suggests that men specifically target resources that are widely shared and consequently cannot be directed to their children. The proponents of this argument contend that men target these resources because of the mating benefits derived from displaying the skill required to acquire them and the social benefits from their extensive redistribution.

I explore these models by first testing if men alter their parental behavior with respect to variation in the proposed benefits within unions. Specifically, I explore the question: do men deliver paternal care in a way that maximizes its effect on the well-being of their children or on the ability to maintain access to their spouses' fertility. I then test for differences between the fitness outcomes of children with and without fathers to determine if Tsimane men can have a positive impact on the welfare of their children.

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CHAPTER 1: INTRODUCTION

Fathers have long received scant attention compared to their female counterparts. Mother's Day was declared a national holiday in 1914, but fathers would have to wait another 52 years to have their own day officially recognized. Disenfranchised fathers have been so frequently overlooked in custodial disputes that they have formed lobby organizations such as the American Coalition for Fathers and Children, including 43 affiliates in 20 states (American Coalition for Fathers and Children (n.d.)). These inequalities are reasonable considering that mothers are the ones that spend more time with the children, nurse them as infants and actually go through the process of labor. But compared to other mammals and particularly to other great apes, it is the human father that truly stands out. The provisioning, protection, and direct care that human fathers offer truly make them a rarity. Although paternal care is more prevalent in the primate taxon than in other mammalian groups (Clutton-Brock 1991, Kleiman and Malcolm 1981), no other great ape has ever shown the level of male involvement that is found in all human cultures the world over. But despite its ubiquity, there exists great variation in the intensity and frequency of paternal care between and within populations and through time for individuals (see Draper and Harpending 1988, Hewlett 1992c). The research presented here explores potential explanations of this variation through the investigation of male parental behavior among the Tsimane of Central Bolivia.

Traditional evolutionary theory tells us that men invest in their children because they have a vested interest in their well being—if a man's descendents fail to reproduce, then that man's fitness is no different than if he had no descendents at all. This argument holds that men invest in their children specifically to increase the children's fitness and

that they forgo alternative mating opportunities and the ability to enhance the number of their offspring in order to raise a smaller progeny of higher quality children. More recently, however, researchers have realized that the offering of paternal care is often succeeded by the winning or continuation of sexual access to the mother, providing a pathway through which paternal care can lead not only to greater offspring fitness but greater fertility as well (Smuts and Gubernick 1992, van Schaik and Paul 1996). When these benefits are realized through the provisioning of non-biological offspring, we refer to it as step-parentage—a practice which is considered as mating effort among evolutionists (Daly and Wilson 1998, Lancaster and Kaplan 2000, Rohwer 1986, Rohwer, Herron, and Daly 1999). If men are unrelated to the children, they cannot derive any direct fitness benefits from increasing their quality, but can enjoy the indirect benefits derived from winning the favor of the children's mother. Some researchers have hypothesized that these mating benefits may also play an important role in driving men's parental behavior towards *biological* offspring as well (Blurton Jones et al. 2000, Freeman-Gallant 1998, van Schaik and Paul 1996). The fact that men tend to invest less in biological children of previous marriages than those of current marriages has been attributed to the loss of these mating benefits once a marriage dissolves (Anderson, Kaplan, and Lancaster 1999). Given that men appear to alter paternal investment based on the presence or absence of these mating benefits, it can then be asked: do men alter their parental behavior in response to factors that mediate these mating benefits *within* a union? And do these factors better account for men's parental behavior than those expected if men were truly concerned with increasing offspring fitness?

LIFE HISTORY THEORY

Men's parental decisions must be considered within the context of the entire option set they have available to them. A decision to invest time or resources into one venture means that it will not be available for some other. These constraints, or trade-offs, play a central role in the subset of biology known as life history theory. This field aims to explain variation in reproductive strategies across and within taxa, particularly focusing on biological decisions such as size at birth, age at maturity, age-specific reproductive investment, number and quality of offspring, and the length of life (Roff 1992, Stearns 1992). Classical life history theory typically employs an optimality approach to explore these fitness decisions, which involves defining the parameters of a problem (how fitness is defined, how variation in traits affect fitness, etc.) and then determining which strategy maximizes fitness (Stearns 2000).

Fundamental Trade-offs in Life History

Living organisms are typically faced with two fundamental life history trade-offs (Kaplan and Lancaster 2003). The first of these is between current and future reproduction. The latter half of this trade-off is sometimes represented as growth, condition, or survivorship, but the effect of these measures on fitness can only come through their effects on future reproduction. An organism can increase its future fertility rate by investing in growth, skill or maintenance, but must do so at the expense of investing in current reproduction; indeed this trade-off is often referred to as that between somatic effort and reproductive effort (Anderson 1999, Hirshfield and Tinkle 1975). Organisms typically have a juvenile stage during which they do not reproduce and only

begin to do so when their size permits a fertility rate great enough to make reproduction more worth-while than continued growth. Once reproduction has commenced, iteroparous species must continue to decide how much energy to invest in current reproduction versus maintenance and survivorship.

The second fundamental trade-off is that between the quantity and quality of offspring. Given that an organism has determined how much energy to invest in reproduction, it must then decide amongst how many offspring it wishes divide that allocation. It could produce a large number of low-quality offspring or a small number of higher-quality offspring. The optimal decision often depends on a suite of environmental, social and phylogenetic parameters and is expected to maximize the number of offspring that survive to reproduce themselves (Smith and Fretwell 1974), or the number of grand-offspring if fertility affects the reproductive value of offspring (Kaplan et al. 1995, Rogers 1990). Because males and females employ such disparate reproductive strategies (Trivers 1972), this trade-off presents itself to each of them differently. Among mammalian females, this trade-off relates to decisions concerning size of neonates (Smith and Fretwell 1974), weaning (Ylonen, Horne, and Luukkonen 2004), inter-birth intervals (Blurton Jones 1986, Hill and Hurtado 1996) and completed family size (Kaplan 1996, Kaplan et al. 1995, Mappes and Koskela 2004). To males, who essentially have limitless reproductive potential, the trade-off presents itself as one between mating effort and parental effort, which are discussed below.

Mating Effort versus Parental Effort in Males

In his germinal paper, Trivers (1972) provided a cogent explanation for why one sex usually engages in greater mate competition than the other; it is an argument that has been built upon and honed by others (Emlen and Oring 1977, Maynard Smith 1977). Given initial disparities in overall levels of parental investment (see Parker, Baker, and Smith 1972 for an explanation of these disparities), individuals of the lesser-investing sex (usually males) typically experience higher potential reproductive rates and are therefore more likely to be available for reproduction at any given time. This results in their being over-represented in the breeding population, and hence greater competition among them as they must vie over a smaller number of the opposite sex (Clutton-Brock and Vincent 1991, Emlen and Oring 1977). Because mammalian females gestate and nurse offspring, their potential reproductive rates are usually much lower than males; theoretically, a male's potential reproductive rate is simply as long as the period between copulations. Males thus have an opportunity to increase their reproductive success by winning the fertility of multiple females, whereas females typically experience no increase in fertility through having multiple male partners (Bateman 1948). This ever-present potential to win more fertility leads males to engage in higher levels of mating effort (total investment in increasing future fertility) than females (Low 1978, Trivers 1972).

As discussed above, however, investment in increasing the number of offspring often comes at the expense of offspring quality. Individuals are thus faced with the problem of optimally balancing levels of mating effort with those of parental effort (total investment in offspring quality). Because female mammals are at the very least obligated to nurse the young until they are weaned, they typically provide the majority of all other

forms of parental care as well (van Schaik and Paul 1996) (indeed, in all major taxa that exhibit parental care, females are more commonly the main caretakers) (Clutton-Brock 1991, Ridley 1978, Tallamy 1984). Males take active roles in the parenting of offspring in only 5% of mammalian species (Clutton-Brock 1991), with their participation being most common and most intense within monogamous species (Clutton-Brock and Harvey 1976, Smuts and Gubernick 1992).

In primates, male care is more prevalent, occurring in roughly 40% of the genera (Kleiman and Malcolm 1981). It is found across a wide range of mating and social systems, including single-male, multi-female species such as the mountain gorilla (Fossey 1979), and multi-male, multi-female species such as the olive baboon (Smuts 1985) and rhesus macaque (Breuggeman 1973), but the most intense examples of male care are found among the monogamous and polyandrous new world monkeys. Among the titis, owl monkeys and callitrichids, of Central and South America, males play an important role in carrying and protecting the infants. These infants are usually of greater proportional weight than offspring of other primate species and commonly born in pairs among the callitrichids (van Schaik and Dunbar 1990, van Schaik and Paul 1996, Whitten 1987, Wright 1984), resulting in a greater overall burden of dependency and hence the opportunity for male care to make a difference. Indeed, the callitrichids are one of the only primate groups in which paternal provisioning of offspring is common (Kleiman and Malcolm 1981).

Factors Influencing the Payoffs to Parental and Mating Effort

A male's optimal division of reproductive effort into parental and mating effort depends on a suite of factors that influence the returns to each. From a cross-species perspective, males are expected to engage in paternal care if the proportion of offspring that survive to reproductive age under bi-parental care multiplied by the probability of paternity is greater than the proportion that survive under uniparental care multiplied by the proportional increase in fertility of the non-caring male (Maynard Smith 1977). We can transform this calculation to an instantaneous time scale: males should parentally invest in existing children if the resulting marginal increase in the summed reproductive values of these children (multiplied by probability of paternity) is greater than the marginal increase (if investing in mating effort) in the number of children a man can expect to sire with other females multiplied by the reproductive value of a child at birth (this reproductive value will be contingent upon other factors, such the male's future investments in the child, availability and willingness of other potential caretakers to provide care, etc.). From this, we can derive the main factors that mediate this trade-off. These include the ability of the father to increase the reproductive value of his children, the probability of paternity, and the returns to seeking additional mates (Clutton-Brock 1991, Geary 2000).

Paternal Care Effectiveness

There exists much variation in the ability of males to increase offspring success as well as in the opportunity to do so. Among mammals, paternal care effectiveness often depends on how well a female can successfully rear offspring given the ecological setting

and developmental requirements of infants. Given female lactation and the proximity it requires, male care may provide little additional increase to offspring quality. Similarly, across human populations, there is great variation in women's access to resources and their ability to successfully rear children on their own (Lancaster 1989). Female contribution to the diet is positively associated with levels of polygyny cross-culturally, supposedly because the need of paternal provisioning is lower, thereby allowing men to have multiple wives (or women to pursue already-married men) (Low 1990, Marlowe 2003b). Similarly, women in cultures that have high measures of female "empowerment" (indexed by their income, political and professional representation) were found to place less importance on the earnings of potential mates (Eagly and Wood 1999).

In many circumstances, however, male care can prove very important and occasionally even necessary for offspring survival and well-being. This often occurs when trying circumstances relegate uniparental care insufficient. Male care can prove valuable as a source of supplemental provisioning for species that inhabit arduous feeding niches (Clutton-Brock 1991). Similarly, higher predation or infanticide risk may provide an opportunity for males to increase the fitness of their offspring by acting as family guards (Buchan et al. 2003, Hurtado and Hill 1992, Kleiman and Malcolm 1981, van Schaik and Dunbar 1990). Altriciality is often associated with greater offspring need and has been argued to be associated with greater paternal investment (Clutton-Brock 1991, Garber and Leigh 1997), although such altriciality may have originated as a subsequent co-adaptation to pre-existing bi-paternal care (Ah-King and Tullberg 2000). Progeny size also strongly determines levels of offspring need and can have a large impact on the returns to parental investment as well (Hames 1992, Westneat 1988).

Finally, males can often cooperate with females to attain high levels of complementarity. Complementarity refers to increasing marginal returns to investment in relation to the investment of the other caregiver (Kaplan and Lancaster 2003). More simply stated, it means that the combined efficiency of male and female care is greater than the sum of their productivities if acting as single parents. This most often occurs when provisioning and direct care are both important to offspring success but cannot effectively be performed simultaneously (Ember and Ember 1979, Hurtado et al. 1992, Kaplan and Lancaster 2003, Lancaster and Lancaster 1980, Marlowe 2003b, Shetty et al. 1991). For instance, offspring that cannot safely be cached or that require constant thermoregulation often inhibit foraging in many bird species, requiring parents to take turns fulfilling the roles. High levels of complementarity can also be reached when the pair can more effectively forage as a team, such as that found among the the net-hunting Aka foragers, in which the wife beats the ground to scare prey into the nets held by the husband (Hewlett 1992c, also see Ruttenberg 2004 for primate example).

Paternity Certainty

Any benefit that an offspring receives through paternal care is translated to the father's fitness through the coefficient of probability of paternity. This particularly presents a problem for males of internally fertilizing species who are never fully aware of the exact timing of female ovulation (Perrone and Zaret 1979, Trivers 1972). The existence of discriminate infanticide of unrelated infants in many species is testament to males' awareness of this problem (Bogges 1979, Hrdy 1979, Packer and Pusey 1983). Studies have shown that even males within large multi-male, multi-female groups with

high levels of promiscuity are cognizant of paternity (Anderson 1992, Buchan et al. 2003).

Among humans, ethical concerns have limited studies concerning the accuracy of men's predictions of paternity, but there is some evidence that their perceptions have an impact on parental behavior in the predicted direction (Apicella and Marlowe 2004). The consistently observed differences between fathers' treatment of biological children and step-children point to at the very least a dichotomous understanding of the fitness problem. Relative to biological children, fathers are more likely to abuse step-children (Daly and Wilson 1985), murder them (*ibid.*), spend less time interacting with them (Marlowe 1999b), interact agonistically with them when they do (Flinn 1988b), less effectively supervise them (Tooley et al. 2005), and invest less resources in them (Anderson, Kaplan, and Lancaster 1999). Paternity certainty, however, is unlike the other two factors (paternal care effectiveness and the returns to mating effort) in its role in the determination of the optimal reproductive strategy. Although the phylogenetic constraints of internal fertilization and other requirements such as extended absences associated with animal husbandry or external warfare limit a man's ability to control his wife's fertility, variation in paternity certainty is far less dependent on exogenous factors. If paternal care is indeed an effective strategy, men can take efforts to ensure paternity through mate guarding or appealing to female choice (Buss 1988, Flinn 1988a), meaning that it may just as well be a result of the relationship between the other two factors.

Returns to Mating Effort

The returns to mating effort depend on a male's ability to win the fertility of potential mates and therefore are subject primarily to the availability of reproductively active females. The dispersion of sexually receptive females through space and time can have large impacts on males' reproductive strategies. Wide spatial disbursement of females limits a male's mating success by increasing transit time between potential mates and often precludes the monopolization of multiple females (Emlen and Oring 1977, Rutberg 1983, van Schaik and van Hoof 1983). Similarly, the synchronization of ovulation among females often impedes male attempts to win the fertility of multiple females (Dunbar 2000, Eberle and Kappeler 2001).

Within populations, variation in competitiveness in male-male contests as well as in the ability to attract females mediate intra-specific returns to mating effort. For males of species in which females can easily be defended, the outcomes of male-male contests can sharply determine their reproductive success, such as among elephant seals in which 100% of a season's offspring can be sired by less than a third of the male population (Fabiani et al. 2004). In human history, men who have been able to control access to women through the coercive power they hold over other men have long enjoyed greater numbers of sexual partners and higher reproductive success (Betzig 1992, Betzig 1982, Chagnon 1988). When female reproduction is not strictly controlled, however, men can appeal to female-choice to win fertility. Many factors are associated with a man's attractiveness as both a long-term and short-term partner to women, influencing his returns to pursuing such relationships (Buss 1989, Buss and Schmitt 1993). Researchers

have consistently found that more attractive and athletic men report more sexual partners than their less desirable counterparts (Thornhill and Gangestad 1994, Waynforth 1998).

Evidence of a Trade-off

In order for the relationship between mating and parental effort to accurately be described as a trade-off, the two must be mutually prohibitive of one another and therefore negatively correlated (given a constant income). The degree to which one type of effort prohibits the other varies greatly across species, environments and situations and is often considered to be a variable itself in the ultimate determination of the optimal strategy. Parental effort does not always hinder a male's ability to acquire extra fertility and, as will be shown in detail below, can actually aid in its acquisition. Many forms of parental care and mating effort, however, are unambiguously exclusive. Investment in a family (brood, clutch, litter, etc.) after the death or desertion of a mate must greatly impede one's ability to seek a new partner. Similarly, any investment in the pursuit of extra-pair copulations is clear investment away from the well-being of one's existing progeny.

Empirical data has supported the contention that the two types of effort present a tradeoff, evidenced by the changes in levels of investment in opposite directions as the returns to the two strategies vary. Komdeur et al. (2002) found that the experimental increase of clutch sizes in European starlings would cause males to increase incubation time at the expense of time spent in mating effort activities. Reducing the clutch size led to the opposite pattern. Conversely, fairy martin males in breeding colonies with higher proportions of fertile females spent less time incubating (Magrath and Elgar 1997).

Marlowe (1999a) has suggested that such an effect occurs among the Hadza of Tanzania, where both the absolute number of women of fertile age and the ratio of females to males in camp were negatively associated with men's time spent in proximity to and engaged with children. Waynforth (1999a) found that more attractive Mayan men spend less time in nepotistic activities and marginally more time in mating effort activities, presumably because of the higher returns to mating effort that their attractiveness conferred. Furthermore, there appears to be a general life history trend in men that is characterized by greater investment in mating effort as young adults and then a switch to a more parental-effort intensive strategy as their progeny grows and they have more offspring to invest in (Gray et al. 2002, Wood and Hill 2000, Chapter 4, this volume).

PATERNAL PROVISIONING MODEL

Given the theoretical framework outlined above, we can now ask: What aspects of humans' adaptive niche cause human males to experience higher payoffs to parental investment than those provided to males of other primate species? Humans' adaptive strategy is characterized by a number of exceptional aspects that set them apart from other primates (see Flinn, Geary, and Ward 2005), and any particular trait must be viewed within the complex whole of this strategy. Given this caveat, the focus of this work is the parental behavior of men and it will therefore hold the central place in any theoretical or hypothesis formation here within. The direction of phylogenetic causality between the various facets of the human adaptive strategy, or their chronological order, cannot always be determined and must not be incorrectly inferred from the hypothesized

relationships among these features. Indeed, many features can only function in tandem with others and most likely co-evolved simultaneously. Therefore, the role of men's parental behavior within the adaptive strategy of *extant* humans will be explored below, and discussion of causality and chronology will be avoided unless supporting paleoanthropological evidence exists.

Offspring Need: Altriciality and Size of Progeny

As argued above, greater offspring need confers to men more opportunity to increase offspring fitness through investment. This need is heavily augmented in humans on both the individual level of demands per child and in total progeny need involving the demands of the total number of dependent children at any given time. Human offspring can be considered altricial in two respects—firstly, they are born extremely helpless (Trevathan 1987) and secondly, they proceed to mature at a delayed rate compared to other primates (Dean et al. 2001, Hawkes, O'Connell, and Blurton Jones 1997, Kaplan et al. 2000).

Infant altriciality in humans is usually attributed to the trade-off between intelligence and bipedalism (Flinn, Geary, and Ward 2005, Martin 1983). The female pelvis is constrained by locomotor requirements and therefore cannot accommodate the passage of a precocial infant with a fully developed brain. Female pelvis dimensions in hominins are not very different from those of australopithecines, despite having a brain nearly twice as large (Begun and Walker 1993). This has resulted in human females giving birth to cognitively underdeveloped infants that lack the ability to grasp on to their mothers (which is also hindered by a lack of fur) and yet require near constant protection

and contact (Blurton Jones 1972, Ross 2001). Infants compensate for this cognitive altriciality by a prolonged period of rapid postpartum brain development (Leigh 2001) that requires a constant flow of lipid rich nutrients (Robson 2004). This places a new mother with a helpless infant who simultaneously requires near constant care *and* large quantities of breast milk. Although the invention of the baby sling has partially alleviated the problem of protecting the infant while obtaining enough food to produce sufficient breast milk, infants still pose a great burden to a foraging mother (and the chronology of altriciality, hairlessness and the invention of the baby sling is still in question (see Falk 2004)). Despite the elevated nutritional demand of new mothers and the decreased foraging efficiency, human mothers of infants do not increase foraging time like many non-human primate mothers do, but actually *decrease* time spent in foraging (Hurtado et al. 1992, Lancaster et al. 2000). Among the Hadza of Tanzania, this critical infancy period is exactly the time that fathers target more reliable, calorie-rich resources (Marlowe 2003a), suggesting that this hardship provides a great opportunity for male care to make a large impact.

The helplessness of newborns clearly creates a great strain on women's productive capabilities. As the children mature and become less needy of mother's protection, they continue to be dependent on kin for food and guidance for a remarkably long period of time. Although there exists much cross cultural variation, most children are unable to fully meet their own caloric demands until their mid-teens to early-twenties (Kaplan and Lancaster 2003). Numerous reasons have been offered to account for this extension of the juvenile period, including the need for an extended period of learning foraging techniques (Kaplan et al. 2000), or social skills (Bogin 1997, Flinn, Geary, and

Ward 2005), or simply an extended period of development permitted by the independent extension of the lifespan (Hawkes, O'Connell, and Blurton Jones 1997). Regardless of the initial impetus for its extension, the prolonged juvenile period provides males with the opportunity to increase offspring fitness for a number of years.

This prolonged juvenile period is associated with the uniquely human phase of childhood, a period during which offspring are weaned, yet still sexually immature and mostly dependent on others for sustenance. The establishment of this phase facilitated prolonged development while maintaining of high rates of fertility, as families became comprised of multiple offspring of varying levels of development and dependence. Typically, large progeny sizes are associated with low-investing species, as lower investment per offspring allows for the production of greater numbers of offspring. But given high payoffs to investment, animals that produce multiple offspring usually increase investment with progeny size (Erikstad and Tveraa 1995, Komdeur, Wiersma, and Magrath 2002, Koskela et al. 2000, Sikes 1995, Thomson, Monaghan, and Furness 1998). Like many resources, parental investment provides diminishing returns to its recipients. This means that after the first unit of investment, continued investment in greater numbers of offspring confers higher returns, as there are more utility curves to climb.

Essentially, this logic implies that the fitness benefits to men's care are mainly in the form of increased offspring fitness, and that the returns to such care are greater in humans partly because of greater offspring need. This would indicate that men should therefore mediate levels of investment based on variation in this need:

Paternal Provisioning Hypothesis 1

Men should provide parental investment in relation to the need of their children.

Complementarity

As noted above, complementarity refers to the synergistic increase in efficiency that parents can experience by cooperating in investment, and often occurs in bird species in which the constant direct care that is required is not conducive to the acquisition of resources needed to provision the offspring. As just argued however, human infants are particularly inhibitive of effective foraging, as they are unable to cling to the mother, and yet need near constant care and contact and must be provisioned for an extended period of time. This problem has been solved by a division of labor between the sexes (Brown 1970, Lancaster and Lancaster 1980, Murdock 1949). Women typically specialize in childcare and tasks conducive to it, such as collecting, less-labor intensive garden labor, food processing and household tasks. Men have specialized in riskier and more labor intensive activities that would not be possible while caring for an infant such as hunting, most fishing, large animal herding, intensive garden labor and defense/warfare.

Hunting in particular has been emphasized as being important to raising the level of complementarity, as hunted game often constitutes a substantial portion of the diet (ranging from 12 to 86% of calories (Hill 1982)), including much needed macronutrients (Hill 1988), and yet hunting is particularly incompatible with child care. This incompatibility is mainly due to the risk involved with capturing wild prey, the extended periods of travel involved, and the intensive and prolonged training required to become proficient at it (Kaplan and Lancaster 2003). Indeed, the extremely high level of skill

required to be a successful hunter often results in peak return rates not being reached until the 40's, long after peak strength has been reached (Gurven n.d., Kaplan et al. 2000, Walker and Hill 2002). Similarly, the execution of skill-intensive female tasks, such as extractive foraging and childcare, is facilitated by the longer and more frequent training that specialization confers.

Based on this logic, men are expected to provide investment in a way that increases women's productivity, maximizing the functioning of the marital unit:

Paternal Provisioning Hypothesis 2

Men should provide investment in a way that maximizes the efficiency of the marital unit.

Pair-bonds

Although the research presented here does not specifically explore the functional benefits of pair-bonding, it is important to note that such reproductive relationships are very important in facilitating paternal investment. With regards to the logic of the Paternal Provisioning Model, pair-bonds facilitate paternal investment by allowing men to invest in multiple children (progeny size) in which they have high confidence of having sired (paternity confidence), as well as the ability to cooperate with the female partner to enjoy elevated returns (complementarity). In addition to progeny size increasing the need for investment, it allows more biological descendents to enjoy the benefits of non-depreciable care, or care in which the benefits to the recipients do not decline with the number of recipients. This includes such investments as family defense, house construction and even provisioning to an extent. Finally, by maintaining a single

reproductive relationship, parents enjoy greater efficiency brought about by congruent relatedness to the offspring and hence similar goals. Because of the fact that humans have multiple dependents, reproducing with sequential partners can often lead to conflicts of interest with regards to the division of resources between step- and biological children (Kaplan and Lancaster 2003).

Non-promiscuous Mating Effort

In addition to the benefits of pair-bonding listed above, the securing of the future fertility of a woman and cooperating with her to raise the children produced within the union can reduce the opportunity costs to paternal investment. Traditionally, paternal investment has been viewed as an investment away from mating effort, an investment away from increasing the number of offspring and towards increasing the quality of existing offspring (Trivers 1972). However, within a union, male parental investment can also facilitate mate investment (it's much easier for a man to find meat to give to his wife if he is already trying to find meat for his children) as well as alleviate the need for female labor. Indeed, in a survey of 10 foraging societies for which there was sufficient data, Kaplan et al. (2001) found that after subtracting their own consumption, men provide an average of 97% of the calories to offspring, and women only the remaining 3%. When a man and woman's fertility are tied, reducing the costs to female reproduction can enhance the fertility of both partners.

It has been argued that optimal investment levels per child are robust across all incomes, meaning that an increase in total income (e.g. the addition of male investment) would simply result in an optimal strategy of more offspring with the same level of

investment per offspring (Smith and Fretwell 1974). This means that any male investment should allow women to allocate more to producing further offspring, and therefore has a component that can be conceptualized as a form of mating effort within the union (total investment in increasing future fertility). Gwynne (1984) argued that such male investment that reduces the cost of female reproduction and hence increases female fertility (and the male's fertility if he is the mate) should be termed non-promiscuous mating effort in order to distinguish it from the traditional promiscuous mating effort in which men vie for additional fertilizations.

Simply stated, male investment in the family can increase the fertility of the pair-bond through the direct provisioning of the wife and by permitting her to increase allocations to future reproduction. This is particularly true for humans, whose offspring require elevated levels of investment. This is perhaps why Marlowe (2001) found that women in populations in which males contributed more to the diet have significantly higher total fertility rates. Thus, when a man considers whether to invest in increasing future fertility through allocations to extra-pair mating effort or to invest in increasing the fitness of his offspring through in-pair parental effort, he must also include in his calculation these benefits derived from non-promiscuous mating effort.

Effect of Father Presence on Child Well-being

The logic of the Smith and Fretwell (1974) model implies that a deserted mother should compensate for her husband's loss by increasing her own investment per child at the expense of her future fertility. This alone may suggest that no fitness differences should be observed between fatherless children and those raised within a complete

family. There are three reasons, however, that this may not hold true. Firstly, the Paternal Provisioning Model holds that the complementarity between the husband and wife results in an effectiveness that exceeds that of the combined total of the investments if given individually. This means that the allocation decisions concerning parental investment versus alternative needs would more heavily favor investment within a pair-bond due to greater returns, resulting in a greater total investment per child. Secondly, some forms of male care may not be substitutable by female care. For instance, mothers may be less adept at protecting their children against certain threats, acquiring meat or imparting male-oriented skills to sons, regardless of their level of investment. And finally, a deserted woman would have previously been pursuing a reproductive strategy based on the presupposition of continued male support, resulting in a fertility rate that would be greater than the optimum given no other support. Because dependency loads vary with the age of the child, this could leave her with a progeny whose needs exceed that which she can provide.

Anthropologists started studying the impact of fathers on their children's well-being in traditional settings relatively recently (Blurton Jones et al. 2000, Flinn 1988b, Flinn 1992, Hewlett 1992c, Hurtado and Hill 1992). In one survey, the effect of father presence was found to range from no effect to a proportional increase in child survivorship of 62% in the four populations studied, although some sample sizes were extremely small (Blurton Jones et al. 2000, Hurtado and Hill 1992). Although child survivorship was used to assess the effect of fathers on child well-being, completed fertility would be a more accurate measure, as fathers may be able to not only increase the probability of a child living to adulthood, but the child's fertility in adulthood as well.

In at least one traditional society, father presence was found to have a positive effect on the later reproductive rates of children (Flinn 1988b). In modern contexts, in addition to father presence reducing mortality (Gaudino, Jenkins, and Rochat 1999), it also appears to increase their social competitiveness by enhancing psychological well-being (Adams, Milner, and Schrepf 1984, Beaty 1995, Flouri and Buchanan 2003) and academic achievement (Anderson, Kaplan, and Lancaster 1999, Lancaster and Kaplan 2000, Mulkey, Crain, and Harrington 1992). This leads to the third Paternal Provisioning hypothesis:

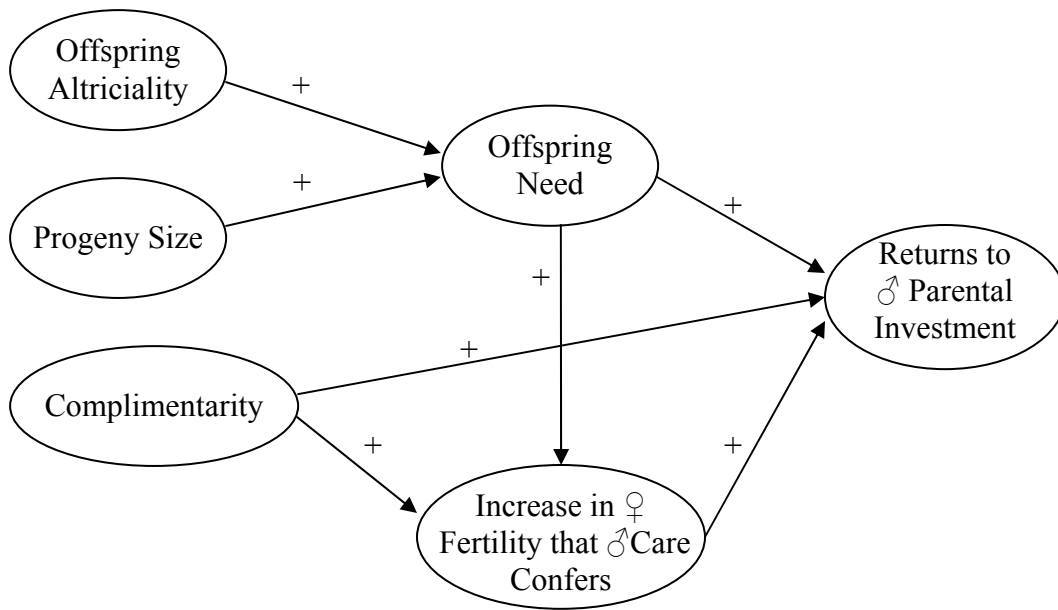
Paternal Provisioning Hypothesis 3

Children of fatherless homes should exhibit lower fitness outcomes than children raised within complete families.

Summary

The Paternal Provisioning Model postulates that men engage in elevated levels of parental investment because of the greater ability to enhance offspring success afforded by the increased progeny need and the high levels of complementarity enjoyed from cooperating with mothers. Additionally, because the rearing of human offspring is so costly, men's investments reduce the reproduction costs of women, increasing the fertility of the pair-bond (Figure 1.1).

Figure 1.1 Paternal Provisioning Model.



ALTERNATIVE MODELS

Some researchers have expressed doubt concerning the ability of the Paternal Provisioning Model to fully explain men's parental behavior (Anderson, Kaplan, and Lancaster 1999, Blurton Jones et al. 2000, Hawkes 1993b, van Schaik and Paul 1996). Some have noted that the offering of paternal care is often followed by the winning or continuation of sexual access to the mother, providing another pathway through which paternal care can lead to increased fertility. Additionally, a few researchers actually contend that men do not invest in their children at all. They argue that men target resources that are widely shared and that men have no control over their redistribution, disabling them from any investment. These arguments and their associated models are described below.

Mating Effort Model

Primatologists noted that males in many paternally investing primate species direct care and resources to unrelated offspring, a practice that could not possibly provide returns through the traditional pathways. The principal explanation for paternal care in primates has traditionally been that it is a true form of parental investment (similar to that argued by the Paternal Provisioning Model for humans), in which males sacrifice future fertility in order to increase the survivorship and quality of offspring they are likely to have sired (Kleiman and Malcolm 1981, Taub and Mehlman 1991, van Schaik and Paul 1996). For many cases, this interpretation is clearly valid. Among gelada baboons, a deposed harem leader will often remain in his old group and actively protect his offspring, though he rarely mates (Dunbar 1984). Chacma baboon males vary the frequency of infant carrying based on the probability of paternity (Anderson 1992). Savannah baboons support biological offspring in disputes more frequently than unrelated juveniles, even if they mated with the unrelated juvenile's mother during its conception (Buchan et al. 2003). And dominant males of many species will often be much more tolerant of infants born during their reign (van Schaik and Paul 1996).

Despite these examples, many researchers realized that not all paternal behavior served as parental care, as much investment was provided to juveniles that could not have been sired by the male caretaker (Smuts and Gubernick 1992, Snowdon and Suomi 1982, van Schaik and Paul 1996). This type of behavior was interpreted as a form of mating effort—males attempting to win future matings from females by caring for their offspring, regardless of paternity. This interpretation of particular types of paternal care

has also appeared in the animal literature for various species of insects (Simmons and Parker 1989), fish (Kraak and Van den Berghe 1992), and birds (Freeman-Gallant 1998, Rohwer, Herron, and Daly 1999). In humans, this takes the form of step-parentage—a relationship that differs in many ways from that of a biological father/offspring dyad. Step-parental care clearly distinguishes itself from biological parental care by the amount and quality of investment (see above section on Paternity Certainty) and its elements of design: men alter their behavior based on whether the care will be witnessed by the mother (Anderson 1999, Flinn 1988b), and interact more frequently with step-offspring before they marry the mother than after they are married (Flinn 1992). Although step-parentage had long been understood as mating effort, its prevalence among primates led some researchers to consider the mating benefits derived from the behavior as the possible cause of biological male parental care as well.

Male Care as Mating Effort in Humans

Because male investment can increase offspring success as well as female fertility, women highly value the ability and willingness to invest in men (Buss 1989, La Cerra 1994). The offering of male parental investment, therefore, is often associated with the winning or continuation of access to a female's fertility, resulting in a pathway through which paternal investment can increase not only the quality of offspring, but the quantity of future fertility to which a male has access, and therefore can be considered as a form of true mating effort (Anderson, Kaplan, and Lancaster 1999, Rohwer, Herron, and Daly 1999, Smuts and Gubernick 1992, van Schaik and Paul 1996). This is different from the non-promiscuous mating effort aspect of paternal care discussed above, in

which men's care allows women to allocate more energy to fertility, thereby increasing their own fertility. In that scenario, men and women's goals are thought to be tied and mutually sought, resulting in a cooperation that maximizes the production of the marital unit. The mating effort model suggests more of a conflict between men and women's goals, in which men offer the paternal care because it is what women demand in exchange for access to their fertility. A man's parental behavior therefore increases his number of offspring not by increasing the future fertility of his wife but by improving the probability of winning and maintaining access to it.

There is some evidence that men's magnanimity towards children can win over potential mates and improve the probability of keeping them. La Cerra (1994) found that women reacted favorably to pictures of men positively interacting with an infant and negatively to men ignoring an infant, while men were indifferent to such contextual factors. Within marriages in Western populations, women are more likely to list a lack of economic support or financial problems as a cause of divorce (Goode 1956, Kitson 1992, Levinger 1966), indicating that levels of investment do play a role in women's decisions to desert. Similarly, in a cross-cultural survey, inadequate support was listed as a legitimate cause for divorce by women in significantly more populations than it was by men (Betzig 1989).

Few evolutionists would dispute that increased access to fertility is the principal fitness benefit to step-parental investment, but could this fitness pathway also prove important to parental investment in biological children as well? Since men and women benefit equally from any enhancement of fitness in their shared offspring, it may seem implausible that the main fitness benefits that men receive from investment would be

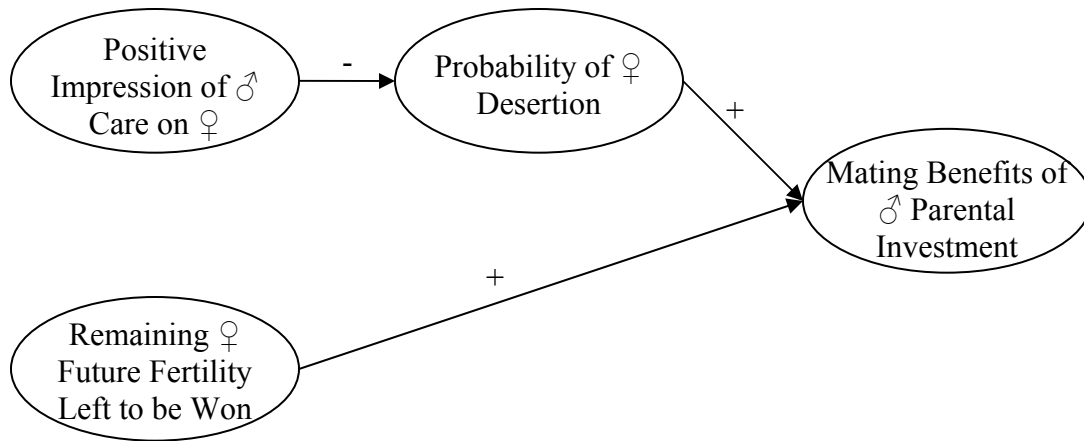
different from that of women. If, however, bi-parental care is conceptualized as a collective action problem, in which both parents benefit equally from the increasing of offspring fitness, but the costs are incurred only by the one investing, then this may hold true (Anderson 1999). When a man brings meat back to his children, both he and his wife benefit from the increased health that that meat confers to their children, but it is the male that pays the cost of acquiring the meat and suffers the opportunity cost from not being able to invest that meat elsewhere. Both partners therefore benefit most if the children are provisioned by the other parent (this assumes that male and female care are substitutive as opposed to complementary as argued before). Given this, women should prefer men to allocate more to familial investment than would be optimal for them given no risk of wife desertion, providing an opportunity for men to barter such increased investment for continued access to wives' fertility.

Nuptial gifts offered by many male insects can offer an illustrative example. If we imagine an insect population with a male biased operational sex ratio (which is usually the case), in which males are forced to compete for the females who are in shorter supply, then males may be able to increase their competitiveness by offering nuptial gifts. It would be best for males if the females would simply accept them without having to offer a gift and if the females would simply acquire all of the nutrients on their own, allowing the males to allocate more energy to seeking additional mates. Despite the fact that females may invest the energy acquired from these gifts into reproduction, resulting in higher quality eggs (or more of them), the benefit to the male from this small increase in offspring quality may be superseded by that derived from actually winning access to the female's fertility in the first place (Simmons and Parker 1989, Thornhill 1976). In

humans, part of the fitness benefits from men's parental care may be derived through the same pathway. Some researchers go so far as to argue that the mating benefits from men's care are the *main* fitness benefits provided by such care (van Schaik and Paul 1996). This would only be true if the addition of men's care had little impact on offspring quality (i.e. women were fully capable of rearing them on their own) and women strongly based mating decisions on levels of men's investment.

Some evidence points to the fact that men augment levels of care to biological children in relation to female preferences. Anderson et al. (1999) found that men invested more resources and time in biological children of current mates than in biological children of previous mates. They argued that this was due to the fact that investments to in-pair biological children provided benefits from both increasing offspring quality and the probability of maintaining access to the wife's fertility, whereas investing in biological children of previous unions involved no such mating benefits. Given that men appear to bias their investment in relation to the absence or presence of these mating benefits, they may also bias their investments in relation to the variation of these benefits *within* unions. They should therefore be more likely to provide investment within a union when it more effectively accomplishes its proposed goal: when it has a greater negative impact on the probability of a wife's desertion, and when this reduction results in maintaining access to greater fertility. Figure 1.2 displays this pathway, which leads to the two hypotheses below.

Figure 1.2 Mating Effort Model.



Mating Effort Hypothesis 1

Men should provide parental investment in relation to the impact that such investment has on wives' perceptions of them.

Mating Effort Hypothesis 2

Men should provide parental investment in relation to the reproductive value of the wife.

Tolerated Theft Model

Although the previous two models have attempted to explain men's parental investment, it is important to note that some researchers have argued that within foraging populations (and perhaps by extension, our evolutionary past), it simply does not exist.

The proponents of this model contend that men in foraging societies target resources that are widely shared and that they are unable to direct the flow of these resources to their family, thereby disabling them from investing (Hawkes 1991, Hawkes, O'Connell, and Blurton Jones 2001b). Much of the research that initiated the formation of this model focused on the Hadza of Tanzania, among whom the researchers claim that grandmothers and not husbands are the ones subsidizing women's fertility (Hawkes, O'Connell, and Blurton Jones 1989, Hawkes, O'Connell, and Blurton Jones 1997), although the extremely small sample sizes of these studies (less than 10 post-menopausal women) greatly limit their generalizability, even to that of the greater Hadza population.

In most foraging groups, men tend to target large resources, such as game animals, that provide much more variable returns and are shared more extensively (Hawkes, O'Connell, and Blurton Jones 2001a, Hawkes, O'Connell, and Blurton Jones 2001b, Kaplan and Hill 1985). Hawkes (1993b) argued that the distribution of these resources (particularly of large packages) is better accounted for by a model referred to as "tolerated theft" (Blurton Jones 1984). This model holds that the cost of defending certain foods from other consumers is often greater than the benefit it would provide to the acquirer, resulting in the acquirer "willingly" relinquishing the resource to others. In other words, the distribution is not directed by the acquirer, but by the consumers, who are often more numerous and who may have a greater incentive to win the resource. This leaves the acquirer with a share no greater than that of everyone else. Men are therefore relegated powerless to efficiently invest in their children, as any resources they acquire will only reach their children as an incidental result of this distribution pattern. The adherents to this argument contend that men forgo more profitable resources that are less

extensively shared (and hence the ability to invest in their children) in order to target more variable, larger packages, as a means of displaying skill to potential mates or obtaining social benefits through the subsequent sharing of large packages (Bleige Bird, Smith, and Bird 2001, Hawkes and Bleige Bird 2002).

Recent research, however, has countered the claim that acquirers are entirely at the mercy of hungry mobs. Acquirers seem to have varying levels of control over the distribution of resources across many populations, with the families and kin of acquirers often receiving greater shares (Gurven 2004, Hames 2000). Additionally, men target many resources that are not widely shared. Marlowe (2003a) found that Hadza men specifically target these resources when their wives have newborns and most need their support. In response to a request for supporting evidence for the above model (referred to here as the Tolerated Theft Model), Hawkes (1993a) actually found that men's daily hunting capture rates were correlated with the wife and children's weight gain, although in a subsequent analysis it was argued that this was due to better hunters being married to more proficient gatherers (Hawkes, O'Connell, and Blurton Jones 2001b).

If men are choosing to target resources that inhibit direct provisioning of children, then an alternative explanation is needed for pair-bonding. Hawkes, Rogers and Charnov. (1995) utilized simulation models to show that, given an environment in which males have the possibility of investing in parental care, mate guarding, and seeking additional matings, males often invest very little in parental care unless the gains from the other activities saturate quickly. Additionally, the returns to seeking additional matings (i.e. the operational sex ratio) seems to be a better predictor of divorce rates across populations than does the effect of paternal presence on the survivorship of children,

although tests have only been performed using four populations (Blurton Jones et al. 2000). These researchers postulated that pair-bonding evolved because the monopolization of a single woman's fertility provided greater fertility benefits than the costly competitive game of pursuing sequential short-term relationships. This idea is reminiscent of earlier hypotheses in which pair-bonding is envisaged as a game-theoretic solution to male contests, perhaps driven by the greater need for male-male cooperation within humans' unique foraging niche (Alexander 1987, Betzig 1986, Deacon 1997).

In its most extreme form, the Tolerated Theft Model argues that men simply do not provision their children and that they specifically target resources that cannot be invested in their family, presumably because the social returns to acquiring them is greater than those conferred through paternal provisioning. This model, however, has only been employed to explain the parental behavior of men in foraging groups, in which food sharing is often quite extensive. Among horticultural populations, such as the Tsimane, in which predictable, easy-to-acquire plant goods play a larger role, sharing of resources is less widespread (Gurven 2004), and tolerated theft poses less of a problem to well-intentioned fathers and perhaps fewer returns to status-seeking hunters. Showing that men in these populations are able and willing to provision their children would be evidence that men have at least a facultative interest in offspring well-being. This could be tested by comparing children with and without fathers. If fathers truly have no impact on the amount of resources available to their children, then children whose fathers have died or are absent due to divorce should exhibit no differences in measures that are most closely associated with caloric intake: growth and morbidity.

Tolerated Theft Hypothesis 1

Children of fatherless homes should exhibit lower growth and higher morbidity than children raised within complete families.

SUMMARY AND LAYOUT OF DISSERTATION

Three potential benefits from male care have been proposed: increasing offspring quality, increasing mate's fertility (and hence one's own) and increasing access to mate's fertility. The Paternal Provisioning Model suggests that the first two combine to produce the most important pathway through which benefits are realized, while the Mating Effort Model emphasizes the third, and the Tolerated Theft Model argues that men do not invest in their children. Six hypotheses have been derived from the models to test whether men do invest in their children, and if so, if the benefits accrued from increasing offspring quality and wife fertility and/or increasing the probability of maintaining access to the wife's fertility mediate men's parental behavior.

The main body of this dissertation will focus on the testing of the hypotheses laid out in this chapter using various methods and manifest measures of the latent variables found within each hypothesis. Specifically, situations in which the models produce opposing predictions were sought in order to determine which model best accounts for men's parental behavior.

After a brief introduction to the Tsimane in Chapter 2, Chapter 3 explores the effect of the wife presence on men's direct parental care. The first Mating Effort and Paternal Provisioning Hypotheses produce opposing predictions concerning the effect of the wife's presence. The Paternal Provisioning Model predicts that men should be more

likely to provide care when it is most needed, or when the mother is not present to provide the care. The Mating Effort Model, however, predicts that men should be more likely to provide care when it has the greatest positive impact on the wife's perceptions of them and when this leads to the securing of more fertility. Men should therefore provide care when the wife is present to view the care, and this effect should be greater for men with wives of greater reproductive values.

In Chapter 4, I investigate the timing of men's extra-marital sexual behavior to test the Paternal Provisioning Hypothesis 1 and Mating Effort Hypotheses 1 and 2. As previously argued, the pursuit of extra-marital affairs represents a clear investment away from the family. According to the Paternal Provisioning Model, such behavior should decrease in frequency as the size and consequent need of a man's progeny grows—as family need increases, so too should the returns to investing in his family, and consequently, investments in pursuits that do not benefit his family should therefore decrease. The Mating Effort Model, however, predicts that men, concerned with the fertility they risk losing, should act most nobly, and refrain from pursuing extra-marital relationships, when they have wives of higher reproductive value. Since the number of children increases through time in a marriage, during which the reproductive value of the wife decreases, the two pathways again produce opposing predictions.

Chapter 5 tests the third Paternal Provisioning Hypothesis and the Tolerated Theft Hypothesis, concerning the effects of the presence of fathers, by exploring the fitness outcomes of individuals that are being raised or were raised with and without fathers. This chapter tests for differences in the survivorship, morbidity, growth, and fertility of children from these two groups. The Paternal Provisioning Model predicts that fatherless

children will experience lower fitness outcomes due to reduced provisioning and care, whereas the Tolerated Theft Model holds that fathers have no impact on the availability of resources to children, and that there should therefore be no differences between the two groups in measures most associated with caloric intake, such as growth or morbidity.

Finally, Chapter 6 summarizes the results of the previous chapters and provides a comprehensive evaluation of the different models. I also review potential avenues for future research that could shed further light on the subject.

CHAPTER 2: STUDY POPULATION: THE TSIMANE OF CENTRAL BOLIVIA

INTRODUCTION

The research for this dissertation was conducted among the Tsimane of the Beni region of central Bolivia. There are approximately 7,000 Tsimane residing in the lowland rain forests and savannas that extend from the foothills of the Andes to the savannas of Moxos (VAIPO 1998). Throughout this riverine environment, the Tsimane make a living through swidden agriculture, hunting, fishing, gathering, and occasional wage labor. Their population is organized into communities generally ranging from 8 to 100 households (30 to 450 individuals) that vary considerably in river access, surrounding game densities and access to market goods. There also exists great variation in the extent of integration into the larger Bolivian society and economy among the Tsimane, continuously increasing with proximity to towns. Most Tsimane are still monolingual in their native tongue, although up to 30 villages now house schools where students learn to read and write in both Tsimane and Spanish. The Tsimane are tentatively making small steps towards acculturation but appear hesitant due to a desire to maintain a social identity and an omnipresent mistrust of Bolivian nationals.

HISTORY

The Tsimane were first encountered by Westerners as early as the 16th century, as Spanish Conquistadors explored the area; Jesuit missionaries followed shortly thereafter. By 1744, there existed 26 Jesuit missions in the area surrounding the Tsimane territory

(Chicchón 1992). The sixth of these to be settled was San Francisco de Borja in 1693, which at the time of its inception, housed more than 3,000 Tsimane. This mission would later become the city of San Borja, the largest town in the area and the main market center for modern Tsimane. Despite these successes, the Jesuits encountered great difficulties in their attempt to permanently settle the Tsimane and were ultimately expelled from the region in 1767. Some have argued that those original Tsimane who did decide to settle with the Jesuits eventually developed into a closely related but distinct group now known as the Mosetene (Aldazábal 1988). Two other Catholic missions were later established, but were abandoned in the 19th century due to a smallpox epidemic and the murder of a priest (Ellis and Gonzalo 1998).

The next establishment to have a large impact on the lives of the Tsimane was that of the Misión Fatima in 1953 (originally located near San Borja, but relocated further upriver in 1955 to the Río Chimanés tributary) (Reyes-Garcia 2001). Two priests unsuccessfully attempted to change the Tsimane into cattle ranchers and commercial growers of cocoa and coffee. Today, the only lasting impact remains in the village of Misión Fatima along the Río Chimanés, where community members tend large communal fields of rice, look over a small herd of cattle, and attend mass every Sunday in a seemingly out-of-place church adorned with stained glass windows.

The evangelical New Tribes Mission has also been working with the Tsimane since the 1950's, perhaps with greater success. Having conducted a thorough linguistic study of the Tsimane language, including the development of an orthography and the creation of exhaustive dictionaries, the missionaries translated the Bible into the indigenous language. Today, they operate from a center called Horeb, located 3

kilometers from San Borja, where they broadcast Christian radio programs in Tsimane and offer basic medical services. They also organize the training of the local Tsimane school teachers, allowing the mission to simultaneously impart seminary instruction. Despite the growing presence of the missionaries, most Tsimane appear to view Christianity with some casualness, evidenced by the frequent low attendance at sermons, rare discussion of the topic, and widespread acceptance of polygyny.

Perhaps the greatest impact of the New Tribes Mission resulted from the assistance they offered in the establishment of the Gran Consejo Chiman in 1989 (Ellis and Gonzalo 1998). The Gran Consejo acts as the Tsimane population's governing body, enforcing rules, settling disputes, organizing cooperative enterprises, and dealing directly with the Bolivian government and logging groups.

HABITAT AND SUBSISTANCE

The majority of the Tsimane reside in the subtropical rainforests and savannas along the Maniqui River System. Seasonality is most notably marked by precipitation, with the rainy season lasting from December to March and the dry season from June to September (CIDDEBENI 1990). The average annual temperature is 26° Celsius (78.8° Fahrenheit). The forests are crossed by many rivers and creeks containing numerous species of fish that can reach sizes of 30 kg. The forests themselves house a wide variety of flora and fauna as well as relatively fertile soils along the rivers.

The Tsimane clear and burn fields during the dry season, usually ranging from 0.1 to 1.0 hectares in size (\bar{X} =0.350 hectares, n=49 fields), although fields often reach much larger sizes in communities that are closer to San Borja where cash-cropping is more

common. Although the Tsimane cultivate upwards of 80 species of plants (Piland 1991), the bulk of the caloric contribution can be attributed to rice, plantains, yucca and corn (yucca and corn are mostly consumed in the form of chicha, a fermented drink). Each family maintains a number of fields in various stages of cultivation. Rice and/or corn are usually the first to be planted, followed by yucca, plantains, and other minor cultigens.

Fish often form an important part of the Tsimane diet, although this varies with access to major rivers. The Tsimane employ various tactics to acquire fish, including hook and line, bow and arrow, and the use of weirs and poison during communal barbasco events. The most commonly caught fish is the sábalo or “vonej”, a medium-sized spine-filled fish that can only be taken using bow and arrow.

Hunting also plays a varyingly important role, depending on the game densities surrounding each community; those near San Borja have experienced the sharpest declines. The most important species by total biomass harvested include (in descending order) collared peccary, Brazilian tapir, grey-brocket deer, howler monkey, agouti paca, white-faced capuchin monkey, and coati (Gurven n.d.). Hunting expeditions normally consist of 1 to 3 men, usually related, traveling a few kilometers in the areas surrounding their community. The trips typically last a number of hours, depending on the success of the hunt. Occasionally, larger parties, often including women and children, will depart on multi-day hunting, fishing, and gathering treks. Shotguns are the current weapon of choice for Tsimane hunters, although they will resort to hunting with bow and arrow if they are without a working firearm or ammunition. Access to such weaponry is heavily dependent on trade avenues that often close in the wet season for interior villages and in

the dry season for river villages. The use of hunting dogs is also common but varies by targeted game species, availability and personal preference.

Reliance on gathered foods fluctuates throughout the year as different fruits come into season, although foraged foods rarely constitute significant proportions of daily caloric intakes.

Recently, dependence on market goods has significantly increased in communities that have direct access to San Borja or are frequented by roving merchants peddling their goods from canoes. The most popular market goods include sugar, flour, salt, vegetable oil, and pasta. Incomes are earned mostly by younger men who work for loggers and merchants for US\$4 to US\$5 per day. Men will typically work wage labor for a few days at a time, although some occasionally leave for a number of weeks, leaving their wives and children dependent on related families until their return. A second important source of income is earned through the manufacture of jatata roof panels—considered to be the longest lasting and most rain-proof thatch panels in the region, and the consistent covering of many homes and buildings in San Borja and surrounding towns. The small jatata leaves must be collected on long foraging trips and attached one-by-one to one-meter long bamboo sticks. Each panel takes approximately 30 minutes to manufacture and nets roughly US\$0.30. Jatata production is less lucrative than wage labor, but once the leaves are gathered, the labor requires little physical effort and can be performed by individuals of all ages.

MARRIAGE, REPRODUCTION, DIVISION OF LABOR

Day-to-day life centers mainly around the household cluster, a grouping of several houses typically consisting of a single extended family. Upon marriage, a couple will usually build their own house near the wife's family where they will live for two to three years. Although there is no institutionalized bride service, during this time, the husband is expected to work with affilial male relatives in typical cooperative tasks, as well as maintain fields, fish and hunt. After a period of time, most families move closer to the relatives of the husband, although some stay with the wife's relatives, and still others venture into new areas. Tsimane residential patterns are driven just as much by opportunity as they are by convention.

Marriages among the Tsimane are very stable with roughly 20% of marriages ending in divorce (n=76 marriages). The median age of marriage for men is 21 and for women 16.5 (n=77 men, 59 women). Polygyny is widely accepted, but only 6% of men (5 of 83 men age 21 and over) were married to more than one woman at the time of our research. Such polygyny is nearly universally sororal. Men usually begin searching for a spouse in their late teens. The preferred arrangement is with a cross cousin, although any woman of an appropriate age that is not a parallel relative is suitable. The pursuit of a wife often leads men to visit other distant communities, although this can sometimes be accomplished during wage-labor expeditions. Men also frequently pursue women for casual relations, which they refer to with the common term "wowodye". Pre-marital sex among the Tsimane may not be as common as it is in Western contexts, but men still report an average of 1.4 sexual partners prior to their first marriage (n=34 men). Once a man finds a suitable partner, he must approach the family and engage in a courtship

period that often lasts one to two weeks, during which time the suitor attempts to convince the woman and her parents of his merit. Men court an average of just over two women before they find a match that is suitable to all parties ($\bar{X}=2.14$, $n=37$). The Tsimane do not commemorate weddings with formal ceremonies, but consider a pair to be married when they sleep together in the same house.

Divorce, although rare, is most common in the first year, resulting in some confusion concerning whether such unions are formal marriages or simply failed extended courtships. Of those who continue on, the timing of the first birth averages two years after marriage. Within marriages, inter-birth intervals average approximately two and a half years, resulting in a total fertility rate of 6.5 for women (6.9 for men, the difference most likely being due to sample error) (Gurven, Kaplan, and Winking 2004). Approximately four-fifths of children born live to the age of 15. The highest risk of mortality is endured in the first year of life during which 7.5% of all live-born infants die ($n=837$). The most common causes of infant mortality include respiratory illnesses, diarrhea, perinatal complications and infanticide. By the age of ten, mortality rates stabilize at around 1%.

Men and women's chores are well defined within the household unit and are often exclusive. Women are for the most part solely responsible for childcare, food processing, and washing clothes. Fathers spend very little time in the direct care of their children, although they do provide occasional assistance and are frequently named as the primary teachers for numerous skills. Men are also typically the sole income earners and are responsible for the acquisition of game and fish. Both men and women tend to their common fields, with men felling trees and often clearing the underbrush and women

weeding and harvesting the crops. Both sexes take part in the planting of new crops. Although men and women spend roughly equal amounts of time manufacturing items, their respective areas of expertise overlap very little. Women manufacture nearly all woven items, including marico bags, floor mats, fans and baskets. Men, on the other hand, work mostly with wood, making bows, arrows, canoes, and houses. Men and women spend approximately equal amounts of time in the manufacture of jatata.

CURRENT SITUATION

Today's Tsimane population is divided between areas that have been formally protected as indigenous territories and those that have been opened to logging interests (Ellis and Gonzalo 1998). The Tsimane territory proper (Territorio Indígena Chimane) extends from approximately 50 km north of San Borja to 100 km south of the town along the Maniqui River, encompassing over 300,000 hectares (CIDDEBENI 2001). Parcels of comparable size have been protected to the east and west of the formal Tsimane territory (Territorio Indígena Pilon Lajas and Territorio Indígena Multiétnico), that also hold numerous Tsimane settlements as well as those of neighboring indigenous groups.

A number of Tsimane settlements are located within areas that have been ceded to logging interests. The Tsimane have long had a tumultuous relationship with logging groups. At first glance, the relationship may appear to be one of mere exploitation, but in actuality, it is quite complex and often characterized by mutual dependence and mutual distrust. While most Tsimane hold negative opinions of the loggers and their presence, the industry remains one of the only constant sources of income for the Tsimane, and there is no stigma associated with working for them.

The Bolivian population growth and sprawl is also threatening the Tsimane and their territory as colonists encroach on their native lands. This is most evident near San Borja and to the west of the town along the Yucumo-Rurrenabaque road. The areas of greatest agricultural potential have been taken by colonists, as the Tsimane have no documented entitlement to the land outside of the formal territories (Ellis and Gonzalo 1998). Most Tsimane villages, however, are remote enough that they are in no risk of encroachment in the immediate future.

For the majority of Tsimane, access to modern health care and social services is extremely limited. Health care expenses are covered by the Bolivian government for pregnant women and infants, but the journey to the San Borja hospital often requires many days of travel and is impractical for most. Recently, immunization teams have begun traversing the rivers in an attempt to vaccinate all children against the most common tropical infectious diseases. These efforts appear to be having an appreciable impact, as Tsimane mortality rates for infants and the elderly have dropped in the last decade. The infant mortality rate remains nearly one and a half times that of the greater Bolivian population, however, and nearly 12 times as high as the United States rate (CIA 2004).

Like many indigenous populations, the Tsimane find themselves caught between two worlds, both offering unique facets of security, comforts and hopes. Although the Tsimane have maintained their cultural identity and succeeded in preventing the total outright usurpation of their native territory, the direction of the recent trend has clearly been towards greater acculturation, something the Tsimane greet with great ambivalence. The first cultural elements to be adopted by indigenous populations are most often the

most technologically pragmatic—machetes, shotguns, metal pots. Many of the Tsimane, however, particularly the younger men, have begun adopting Western articles that have no practical utility, only the ability to display status. These items include radios, bright shoes and clothing, watches whose owners may or may not be able to read them, glasses of random prescription, and many others. The fact that the Tsimane youth are looking to Bolivian nationals and Western culture to define status may point to changing attitudes and values, perhaps brought on by ever improving and available technology, or more frequent and immersive contact with the colonizing population. Fortunately for the Tsimane, they have had a long enough history of interaction and cultural resistance to have already established the appropriate political and economic infrastructures to ensure the continuation of their culture, their social identity, and their way of life for some time to come.

RELATION TO RESEARCH

Various aspects of the Tsimane population and their behavioral and cultural patterns facilitated the realization of the reported research, while others clearly presented challenges. The sheer population size of the Tsimane people provided substantial power to the tests, while their fairly economically uncomplicated ways of life and utilization of uniform strategies allowed for more straightforward investigation and meaningful comparison. The openness of their social environment, their candidness and lack of conversational taboos greatly facilitated the collection of observational and interview data. Finally, the greater similarity of their environment to that of our ancestral history freed the study from the novel conditions of modern environments that often cause

previously adaptive strategies to lead to lower fitness outcomes. On the other hand, the remarkable stability of marital unions resulted in relatively few step-relationships, which precluded statistically powerful comparisons between aspects of step- and biological relationships.

CHAPTER 3: EFFECT OF WIFE'S PRESENCE ON MEN'S PARENTAL BEHAVIOR

INTRODUCTION

As argued in Chapter 1, the delivery of paternal care may be mediated by two frequently competing fitness pathways, as it can confer benefits by increasing both the quality of children as well as access to fertility. This chapter will test predictions derived from these pathways by exploring direct paternal behavior in relation to the location and behaviors of the wife and other caretakers.

Parental care is often conceptually divided into direct and indirect care. In the animal literature, direct parental care is defined as care that has an immediate influence on the offspring's survivorship or overall fitness and includes activities such as carrying, playing and feeding (Kleiman and Malcolm 1981). Indirect parental care encompasses activities that improve offspring fitness through secondary and often incidental effects. The guarding of a territory or resources, for instance, may not have an immediate impact on a male's offspring and may be performed regardless of their presence, but the offspring nevertheless benefit from the behavior. In the human literature, offspring provisioning by males has traditionally been categorized as indirect care, although the immediacy of its impact on offspring fitness, as well as its independence of offspring presence, can be argued (Hewlett 1992a, Marlowe 1999a). Direct care in humans is mostly limited to those activities that involve direct interaction, such as holding, comforting, and playing.

Direct parental care is overwhelmingly provided by mothers (Babchuck, Hames, and Thompson 1985, Hames 1992). Even the much heralded fathers of the Aka pygmies of Central Africa, who were observed holding their newborn infants an astounding 22% of their time while in forest camps, engage in infant holding less than half as frequent than mothers while in camp, and even less so when non-camp locales are included (Hewlett 1992c). Tsimane fathers are rather typical of traditional populations, engaging in very little direct care. For adults under the age of 45, men spend 1.9% of their time in camp holding children and 4.4% providing some form of direct care. Women, on the other hand, spend 19.5% of time in camp holding children and 31.2% of time providing care (holding, $\chi^2=391.925$, $p<0.001$; all care, $\chi^2=607.481$, $p<0.001$). A number of studies have explored the cross-cultural variation in direct father involvement and have found many factors to be associated with it. It is reasonable to assume that direct care varies with factors that are also associated with overall levels of paternal investment, mainly the ability of men to enhance offspring fitness (positive) and the returns to seeking additional matings (negative) (Blurton Jones et al. 2000, Draper and Harpending 1988, Lancaster and Kaplan 1992). Additionally, there are factors that are specifically associated with levels of intimacy in the father-child bond, regardless of overall levels of investment. Katz and Konner (1981) found that measures of emotional warmth and physical proximity between fathers and children were lower in agricultural and pastoral societies compared to foraging societies and are negatively associated with the frequency of warfare and polygyny within a population.

Despite the rarity of male direct care among the Tsimane, such care is invaluable for the testing of the proposed hypotheses for the same reasons that it has been used in

countless other studies: it is unambiguous and conspicuous investment from the caretaker to the care-receiver and may represent a better reflection of intent than other measures of paternal investment since it is often essential for offspring success, relatively uncostly, and more equally performed by all men than other productive tasks. In other words, individuals may vary in ability to obtain resources, secure social allies and the like, resulting in differences in levels of paternal investment due to variation in ability, not intent, but few factors influence a man's ability to provide direct care to his children when he is in their presence.

The study of direct paternal care also proves valuable because the paternal provisioning pathway and the mating effort pathway produce contradictory predictions concerning the effect of an audience on men's decisions to provide such care. The paternal provisioning pathway suggests that such care should be allocated on a basis of need; it is argued below this need is greatest when the father is left alone with children. According to the mating effort pathway, however, such care provides the greatest benefits when it has a positive impact on the wife's impression of the husband and therefore decreases the probability of her desertion. This would imply that men should bias their care to when the wife is *present* and is able observe it. Below, the logic of these predictions and others pertaining to the delivery of male care is laid out within the context of the hypotheses formulated in Chapter 1.

HYPOTHESES AND PREDICTIONS

Paternal Provisioning Hypothesis 1: Men should provide care in relation to the need of children

If men are truly concerned with increasing the quality of their offspring, then men should be more likely to deliver care when there is a greater need for it, as this affects the effectiveness of the care. One factor greatly influencing the need for care is the presence of the mother, the primary caretaker (Trivers 1972). The need for care is not only dependent on the state of the child, but on the amount of care that others are willing and able to provide (Hill and Hurtado 1997). When a child is already being tended or at least being supervised by the mother or some other caretaker, there may be little that an additional person's care could offer. Men are therefore expected to be more likely to provide direct care to a child when the mother is not present.

Paternal Provisioning Hypothesis 2: Men should provide care in a manner that maximizes efficiency of pair-bond

The husband and wife function not only as a reproductive unit, but also as an economic one. The paternal provisioning pathway postulates that the cooperative union experiences an economy of scale, in which the efficiency of a man and woman's combined effort equals more than the mere sum of their individual productivities. This is due in part to the facilitation of specialization, allowing for more intensive and longer periods of training in sex-specific tasks, and consequently higher return rates (Kaplan et al. 2000, Walker and Hill 2002). A second factor is the ability to engage in simultaneous activities that are often prohibitive of one another and therefore temporally exclusive for

a lone individual such as laborious foraging practices and childcare (Brown 1970, Hurtado et al. 1992, Lancaster and Lancaster 1980, Marlowe 2003a, Murdock 1949).

The direct care of children is typically the realm of women (engaging in it nearly seven times as frequently as men among the Tsimane), who are able to nurse infants and often begin practicing childcare at early ages with younger siblings. If the pair-bond optimizes efficiency, then tasks should, all else being equal, be assigned to the respective specialist. If, however, the specialist is preoccupied with an alternative productive task (or is not present) when his or her specialized services are required, the other partner's sub-standard performance then becomes the most effective and can stand in as a substitute. This is the situation frequently parodied by cinema and television with higher-income earning wives that go off to work leaving the inept fathers to take care of the children.

Based on this logic, mothers should be more able to engage in tasks away from the children when the fathers are available for supervision. It is during this period of supervision that men are expected to provide higher levels of direct care as argued above. When both the mother and father are in camp with children, male care should allow mothers to more easily engage in alternative tasks. This effect of men's care has already been shown to exist among the Aka pygmies (Hewlett 1992b), and anecdotally referenced elsewhere (Hurtado and Hill 1992).

Mating Effort Hypothesis 1: Men should provide care in relation to the impact of the delivery of care on the wife's perception of them

The mating effort pathway suggests that men should provide care when it most effectively improves the caregiver's reputation in the eyes of his wife, or more specifically, when it decreases the probability of her desertion. Clearly, the wife's knowledge of such care is necessary for it to effect her impression of him. If she is unaware of the care, her impression remains unchanged, and the benefits conferred through the mating effort pathway would totally be lost.

For this study, the wife's knowledge of care will be operationalized as the wife's presence during the delivery of care. Although a man's wife may know when he is supervising the children, even when she is away, she cannot be fully aware of his exact behavior during her absence. There are many levels of the intensity of parental supervision, many of which are beyond that needed to assure the safety of children, and men should reserve those that involve the greatest effort, such as holding, playing or comforting, for times in which the wife can observe them.

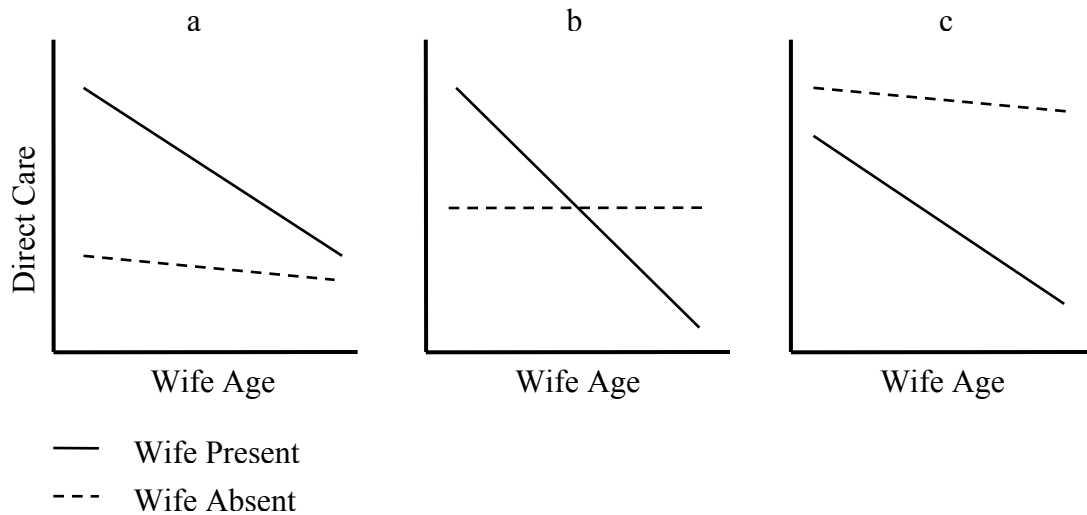
The care that men provide to their children during the wife's absence, however, may also be communicated to her by others, particularly by her kin who also have a vested interest in the welfare of the couple's children. Not only can in-laws inform the wife of the husband's behavior during her absence, they can also have an effect on the probability of her desertion. Of the 17 female mediated divorces recorded (out 167 sampled marriages), parent disapproval of the husband was listed as the cause of one of them. Additionally, the infrequent care that the in-laws provide relative to the mother, father and older siblings, means that they will have less of a diluting effect on male care

through the addition of a caretaker. Based on this logic, men should bias their care to when either the mother or in-laws are present to observe the care.

Mating Effort Hypothesis 2: Men should provide care in relation to reproductive value of wife

The reproductive values of women vary inversely with their age. In addition to this, there exists a strong positive correlation between the ages of husbands and wives ($r=0.838$, $p<.001$, $n=80$ for 30 year female cohort). This means that the reproductive value of the wife of the average man will decrease as he ages. There are many reasons why men may vary the frequency of direct paternal care throughout their lifetimes, even if only their time while in camp is considered. Returns to alternative activities may vary as skill-levels, physical abilities and other needs change through time; actual time in the presence of children may vary; the number of additional allo-caretakers may increase with sibship size, etc. Therefore, the effect of the wife's reproductive value on overall levels of direct care is difficult to isolate. If, however, the reproductive value of the wife mediates a man's desire to impress her, then the wife's reproductive value should have the greatest effect on a man's parental behavior when the wife is present to observe the care. In this way, the amount of care provided in her presence can be explored, while the amount of care in her absence is used as a benchmark for overall care, essentially controlling for all of the extraneous factors. Because age is so strongly correlated with women's reproductive value, it can be used as its proxy. This produces the prediction that there will be a negative interaction effect between the wife's presence and the age of the wife on the probability of a man providing direct care.

Figure 3.1 Possible negative interactions between wife's age and wife's presence on frequency of direct paternal care: a) predicted direction both for wife presence and age; b) no effect of wife presence and predicted direction for wife age; and c) opposite direction for wife presence and predicted direction for wife age.



This prediction could hold even if the effect of wife presence has no overall effect or even one in the opposite direction that that hypothesized by Mating Effort Hypothesis 1. The only requirement is that the effect of the wife's age on the frequency of direct paternal care is greater during times that the wife is present to observe the care. Figure 3.1 displays three possible scenarios: a) predicted direction both for wife presence and age; b) no effect of wife presence and predicted direction for wife age; and c) opposite direction for wife presence and predicted direction for wife age. In all three, the slope of the *Wife Present* line is more sharply negative, indicating an interaction effect.

Alternative Predictions

Finally, it is important to note that direct care may be used by men as a means of impressing women *other* than their wives, meaning that men should provide more care when potential mates are around to see them. There is some evidence that women prefer men that are willing to invest in children (La Cerra 1994), although the fact that these men are already married may nullify this effect (Uller and Johansson 2003). There may be little reason for women to value a man's willingness to invest in children as a quality in short-term mates, and it may therefore do little in increasing a man's prospects of finding extra-marital partners. Because Tsimane men can marry polygynously, however, this still may prove an effective strategy for securing additional wives.

METHODS

Time Allocation

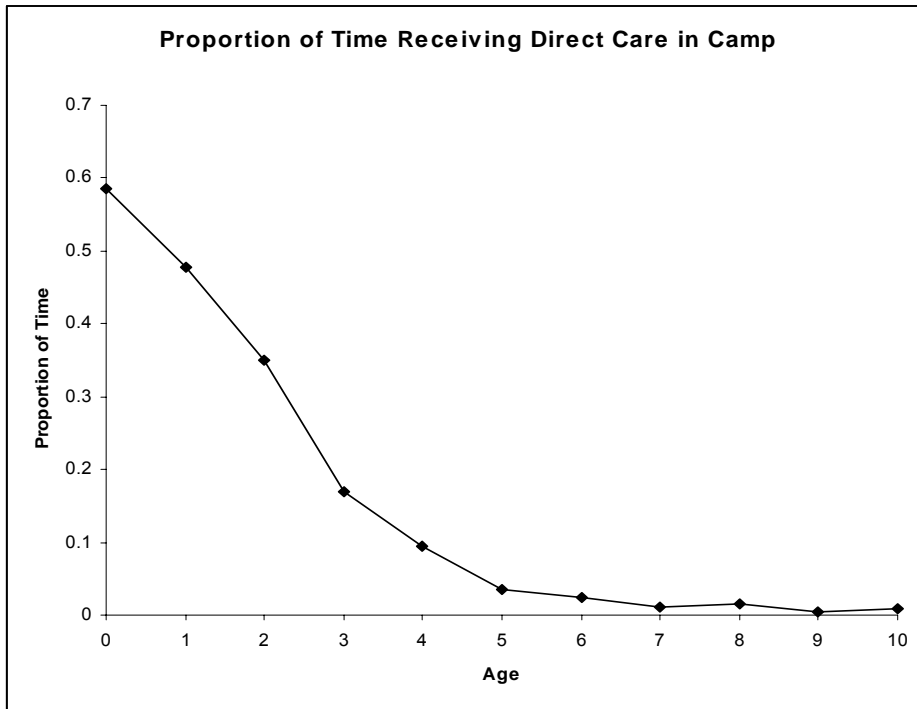
Time allocation observations were collected among four core communities (out of a total of 17 communities in which our team worked), utilizing 3-hour house-hold time blocks (*sensu* Gurven and Kaplan n.d.). Houses were primarily separated into clusters based on proximity (which closely matched kinship). These clusters, averaging approximately 19 persons and just over 3 households per cluster, were sampled randomly without replacement at 7:00 a.m., 10:00 a.m., 1:00 p.m., and 4:00 p.m. in 3-hour time blocks, covering all hours from 7:00 a.m. to 7:00 p.m. During these time blocks, instantaneous scans were taken every half hour, in which the activity, location, and social group of all individuals within the cluster (as well as visitors) were recorded, resulting in six time points per person per time block. This resulted in a sample of 426 individuals

with an average of 88 time points per person, totaling 37,328 person scans. The activity was described as best as possible including objects and interactants. Locations were standardized, allowing for houses, kitchens, yards and fields for each family, and a set of community-specific locales.

The behavioral data were subsequently entered into Excel spreadsheets by creating codes for common behaviors and direct/indirect objects. Up to two behavioral codes could be entered in order to record simultaneous activities. A person is considered to be engaged in any particular behavior if either one of the two activities contains a corresponding code. This means that the sum of proportions of time that a person spends in various activities can be greater than one (e.g. if a person spends all of his or her time talking while holding a baby, that person is engaged in social conversation 100% of the time as well as parental care 100% of the time). Direct care is defined as being engaged in holding, comforting, dressing, fanning, feeding, grooming, or playing with a child. The accuracy of observation was also recorded, including “directly observed”, “reported by third party and verified”, “previously verified and assumed to be continued”, “reported by individual upon departure or arrival”, and “reported by third party and not verified”.

For the purpose of the predictions concerning the effect of others’ presence on men’s care, all records were filtered to leave only those in which a father was directly observed in his cluster in the same location as one or more of his children that were age 3 or younger. This age was chosen because it was the last year that children received considerable direct care (Figure 3.2). Father and child were considered to be in the same location if their location codes were exact matches. Others were considered present (within observation range) if they were in any part of the same family’s homestead (e.g. a

Figure 3.2 Proportion of time spent receiving direct parental care by age.



wife would be considered present with a father and child if she were in the house and the father and child were in the yard).

Demography

Every adult over age 25 in all of the communities (~680 individuals) was interviewed regarding their own reproductive history, and those of their siblings and parents by Michael Gurven. Gurven employed a combination of the methodologies used by researchers with the Ache (Hill and Hurtado 1996), the !Kung (Howell 1979), and the Hadza (Blurton Jones, Hawkes, and O'Connell 2002), to assign all individuals in the sample a year of birth and death, if deceased.

Missionaries have recorded the dates of many births among the Tsimane in the last 50 last years (and many of the deaths occurring in the same period as well). Those known dates of birth and death were used in aging the remainder of the population. For individuals born prior to record keeping, four methods were employed. Approximate age at death and cause of death were elicited for all deceased individuals in the reproductive histories. For children, age at death was estimated using developmental stages (just born, sitting, crawling, walking, talking, carried on the hip, able to run, fished, hunted, etc.), comparisons to known living children, and season of birth and death. For each pair of consecutive siblings, an attempt was made to estimate the birth interval. For pairs in which the older sibling was alive when the younger one was born, the elder's age at birth was estimated, using the above methods for assigning age at death. For pairs in which the older sibling died before the birth, the time interval between death and birth was estimated using information on the ages of other living children in the family and seasonality. Since this procedure yields redundant reproductive histories (e.g. if more than one sibling is interviewed), data was checked for consistency and inconsistencies will be resolved. On the basis of those data, all living and deceased Tsimane in the sample were assigned estimated ages.

The second method was to rank all individuals, both living and deceased, in the sample of reproductive histories by relative age, beginning first with 5-year estimated age classes for relative age rankings. Multiple informants were used for each age class and inconsistencies were investigated and resolved. In addition, significant age-related relationships were investigated, such as 'hip-child', hunting mentor, and playgroup

companions to augment the relative age lists. This procedure yielded ages that can be compared to standard life tables (Howell 1979).

Third, ages for as many people as possible were estimated using historical information and known historical events. For example, a Catholic missionary, Father Marcelino, began working with the Tsimane in 1950, and Father Martin in 1958. Both missionaries are widely known among most Tsimane in the Maniqui region. Another missionary was murdered, and many Tsimane scattered to other regions downstream and in the interior forest back in the late 1920s. The first road was created in the interior forest in 1970 and then refurbished again in 1985. Gurven investigated which people were born (and which were not born) and approximate ages of other individuals, such as younger siblings, or smallest child, with respect to these events.

A final method incorporated a sample of 70 photos of individuals with known ages. For older individuals, there were 50 photos of men and women from ages 50 through 75. These photos were used as a means of aging dead individuals at the time of their death, and for aging themselves or others during the time of death. This method worked in conjunction with comparisons of dead individuals to known individuals in the community and surrounding region. These four methods provided independent estimates of age. When all four estimates yielded a date of birth within a 3-year range, the average was used unless one or two estimates were judged to be superior to the other(s). When larger discrepancies were found, closer inspection often yielded an error that can be corrected. Since a change in one individual's age produced changes in other individuals' ages (in families with reproductive histories and in similar aged individuals in the relative

age lists), adjustments should have lead progressively to greater consistency across the four methods.

Data Analysis

All analyses are performed in SAS 8.02. For the analyses reported in this chapter, each observation is considered a data-point unless otherwise noted. Although this technique is often avoided to prevent spurious inflations of effect sizes, it is the only way to test for factors that vary between observations of individuals, such as wife presence or number of children present. In order to control for the effect of each individual, the Generalized Estimating Equations (GEE) method is employed in the GENMOD procedure of SAS to elucidate the impacts of the hypothesized variables on the probability of providing direct care (Liang and Zegler 1986). The GEE method is essentially a generalized linear model that accounts for the within-subject correlations between dependent variables. This method is robust across many types of distributions of dependent variables and is commonly used to deal with correlated binary data (Ballinger 2004). The method often presents comparable results to those of random coefficient models, except that the parameter estimates relate to population level effects (i.e. pooled within- and between-subject effects) as opposed to just within-subject effects. Furthermore, GEE results have been argued to be more valid than those of random coefficient models when dealing with multiple predictor variables and a single dichotomous response variable (Twisk 2004). For all GEE analyses presented in this chapter, the model assumes an exchangeable correlation structure among within-

Table 3.1 Descriptive statistics for time-allocation dataset.

Individuals n=42				
	Mean	SD	Min	Max
Age	31.667	7.573	22	58
Number of children ≤ 3	1.429	0.542	1	3

Observational Scans				
All scans n=3779, Child and mother present n=591, Child present/Mother Absent n=67				
	Mean	SD	Min	Max
Total scans per individual	88.442	34.336	24	144
Child and mother present	14.071	1.595	1	31
Child present/Mother absent	1.595	1.712	0	7

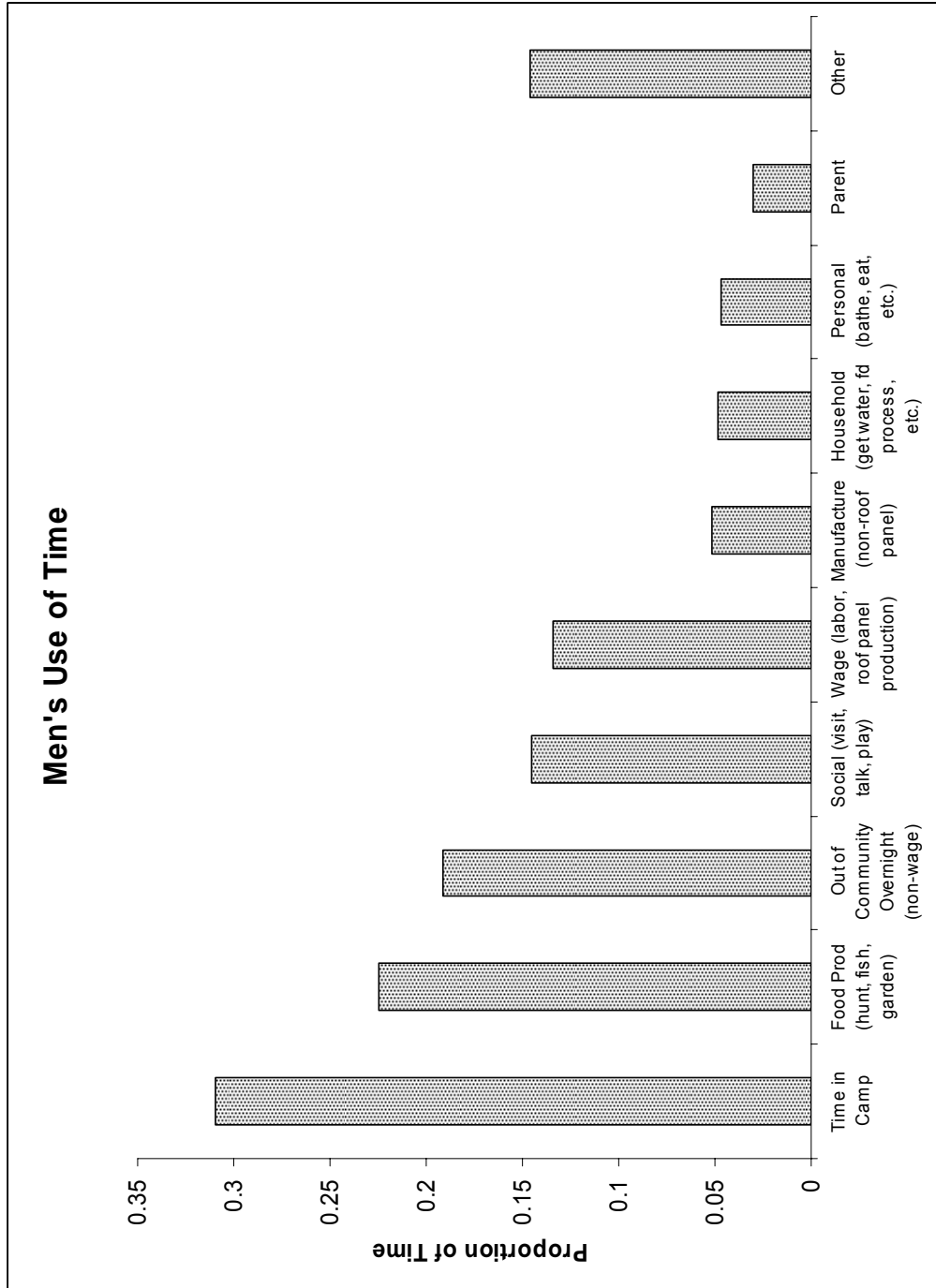
individual responses (care or no care) and the parameter estimates are presented as logit estimates.

RESULTS

Descriptives

Table 3.1 displays the general characteristics of the time-allocation dataset. All men who were ever observed in the same location as a biological child were included, totaling 42 individuals. The average age of these men was 31.7, and they had a mean of 1.4 children under the age of 4. A total of 3779 person scans were recorded among these men over a 10 month period. Figure 3.3 shows the break down of how men are using their time. It is important to note that some activities, such as parenting and personal activities, were only recorded when they were directly observed, most often when the individuals were in camp (31.0% of men's time). This is due to the fact that these activities are often temporally brief in bout length and rarely the main activity that it is

Figure 3.3 Proportion of time men spend in various activities..



reported by others when asked what the individual is doing. This makes it impossible, for instance, to know if an individual is providing childcare or eating a piece of fruit unless they are actually observed doing so. For this reason, the dataset was limited for the purposes of this chapter (unless otherwise noted) to observations that were directly observed in camp.

Of the entire dataset, men were directly observed in the presence of children 17.4% of the time or 658 scans; 10.2% of these, or 67 scans were in the wife's absence. These men were engaged in direct parental care an average of 8.6% of their time in camp. Their wives, on the other hand, were engaged in direct parental care 39.4% of their time. With the removal of one outlier (a 51-year old, polygynously married man who had fathered 22 children and spent much time in parental care), Figure 3.4 shows that there is a slight decline in the frequency of direct care with age, although the effect is not significant ($B=-0.027$, $p=0.135$). This trend is somewhat peculiar, but may be an artifact of older men having more older children that can also take care of their younger siblings.

In addition to the overall disparity in the frequency of direct care provided by men and women, they also differ in the type of care they do provide. The most notable difference is that men are of course unable to nurse their children, an activity that accounts for 17% of all parental care interactions for mothers. Men are significantly more likely to play with the children when interacting with them and less likely to groom them (Figure 3.5). Men tend to focus more on older children compared to women, which again is unsurprising as they are unable to nurse. For all children 12 and under, the average age of the recipient of men's care was 2.22 and 1.54 for women ($N=1006$, $t=-3.81$, $p<.001$). Men also bias their care more towards boys than do their impartial wives.

Figure 3.4 Proportion of time fathers' time spent in direct parental care while in camp by age.

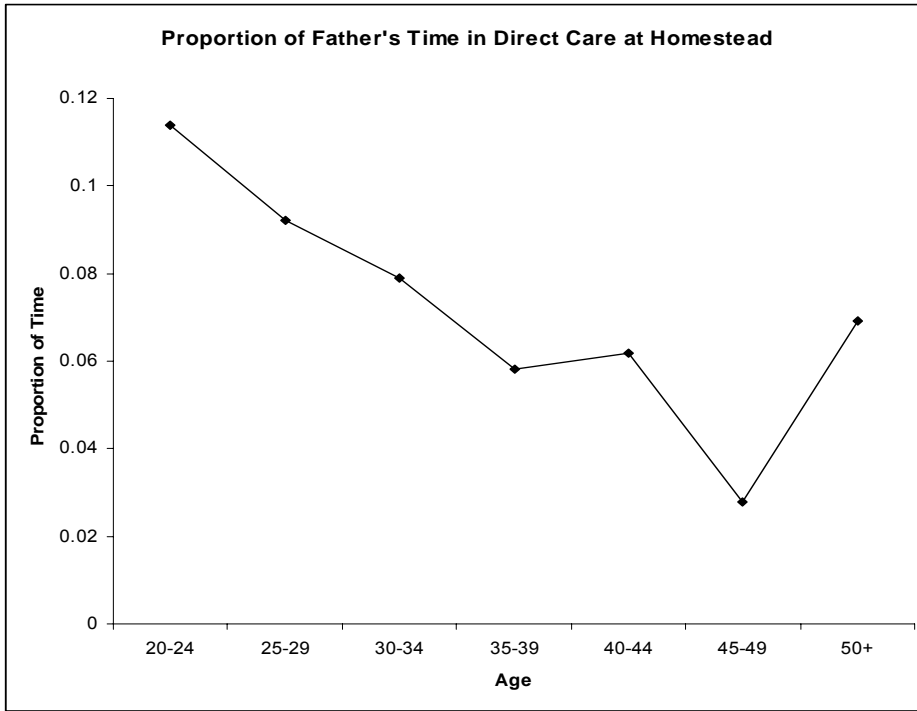
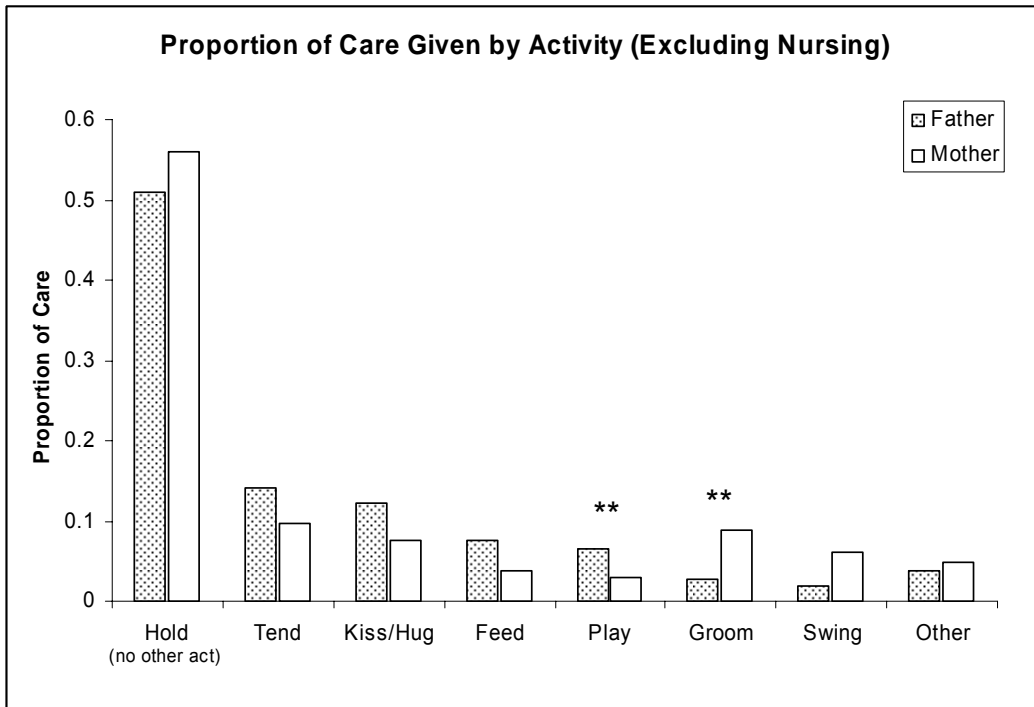


Table 3.2 Generalized estimating equations analysis of the effect of age on the probability of being observed in direct paternal care while in camp.

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-1.521	0.610	-2.49	0.013
Age	-0.027	0.018	-1.50	0.135

Figure 3.5 Proportion of direct care by mothers and fathers by type of care (n=106 for men, n=953 for women).



*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001; (chi-square)

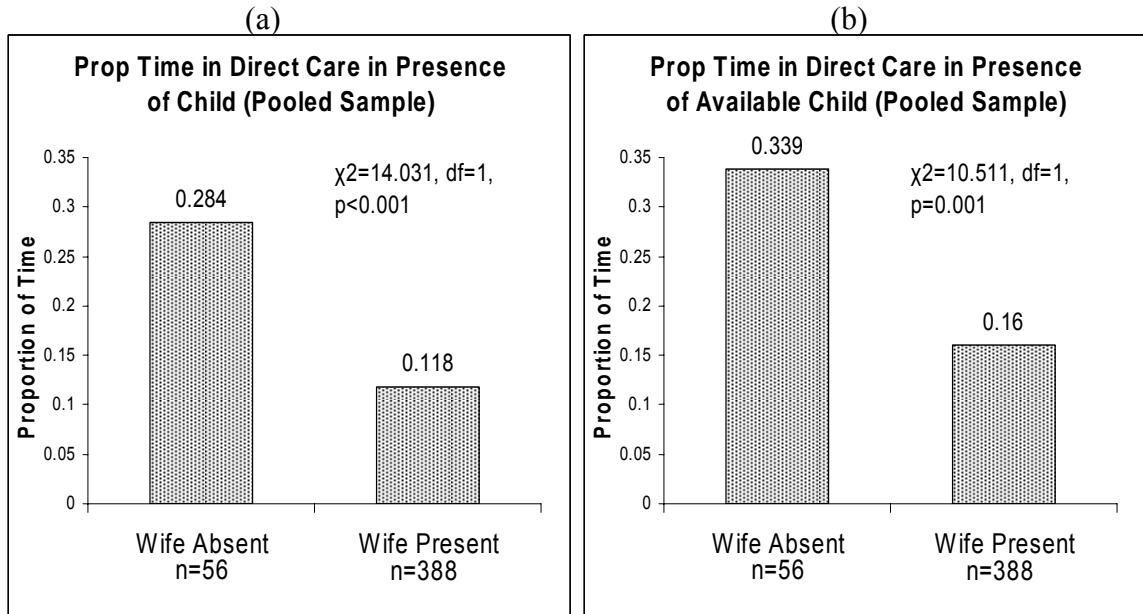
Sons (12 and under) were the recipients of men’s care 67.0% of the time, while only 52.5% of the time for women’s care ($\chi^2=7.45$, $p=0.006$). This effect is surprisingly evident by the child’s second year of life.

Effect of an Audience on Male Direct Care

Wife Presence

Figure 3.6a shows the frequency of direct paternal care by wife presence using the pooled sample of observations. The effect supports the first Paternal Provisioning Hypothesis and refutes the first Mating Effort Hypothesis—men spend significantly *more*

Figure 3.6 Proportion of time in direct paternal care by mother presence out of all observations in which child is simply present (a), and when a child is present and not being cared for by others (b).



time when the wife is absent, when the care is needed more but when the wife is unable to observe the care (Wife absent 0.284, Wife present 0.118, $\chi^2=14.031, df=1, p<0.001$).

Many of the scans with the wife present, however, included only one child who was being cared for by the mother. The mother may be caring for the child precisely because the father never took the initiative to provide the care, but it is equally plausible that the wife is reluctant to give up the child, since she is the only one able to nurse, and may be more adept at providing other care, leaving the father with no option at all. To account for this, the scans in which all of the children in the same location as the father were being cared for by others were removed, leaving only those in which either the father is providing care or a child is *available* for care. This value can be considered the proportion of time that the father cares for the child out of all of the time he has the

option to do so. This is the most liberal analysis with regards to the Mating Effort hypotheses, particularly since mothers are expected to greatly reduce the amount of time the child is available for care, thereby increasing the proportion of this time that men provide direct care. Despite this, as well as the reduction in sample size to 388 scans with wife present and 56 with wife absent, the effect remains significant, if only slightly less pronounced (Wife present 0.160, Wife absent 0.339, $\chi^2=10.571$, $df=1$, $p=0.001$) (Figure 3.6b). All analyses below use this dataset of times during which children are *available* for care.

In order to explore the possible effects of extraneous variables and control for variation in overall levels of paternal care between individuals, the generalized estimating equations method is used with the personal identification number as a repeated subject. The man's age, number of children available age three and under, and average age of children available age three and under were included in the preliminary model as controls. Only the average age of children available proved marginally significant and the other two variables were omitted. The results are displayed in Table 3.3. The average age of the available children remains marginally significant with younger children being more likely to receive care. Wife presence continues to be significantly in the direction predicted by the first Paternal Provisioning Hypothesis ($B=-0.904$, $p=0.005$) with men being significantly more likely to provide care to children when their spouses are absent, even after controlling for the care that others provide.

Table 3.3 Generalized estimating equations analysis of the effect of wife presence on the probability of providing direct care when a child is available for care (n=40 individuals, 444 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-0.158	0.438	-0.36	0.719
Wife Present***	-0.908	0.324	-2.80	0.005
Average Age of Children Available	-0.312	0.165	-1.89	0.056

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Figure 3.7 Proportion of times receiving direct care in which specific relative is the caregiver for children three and under.

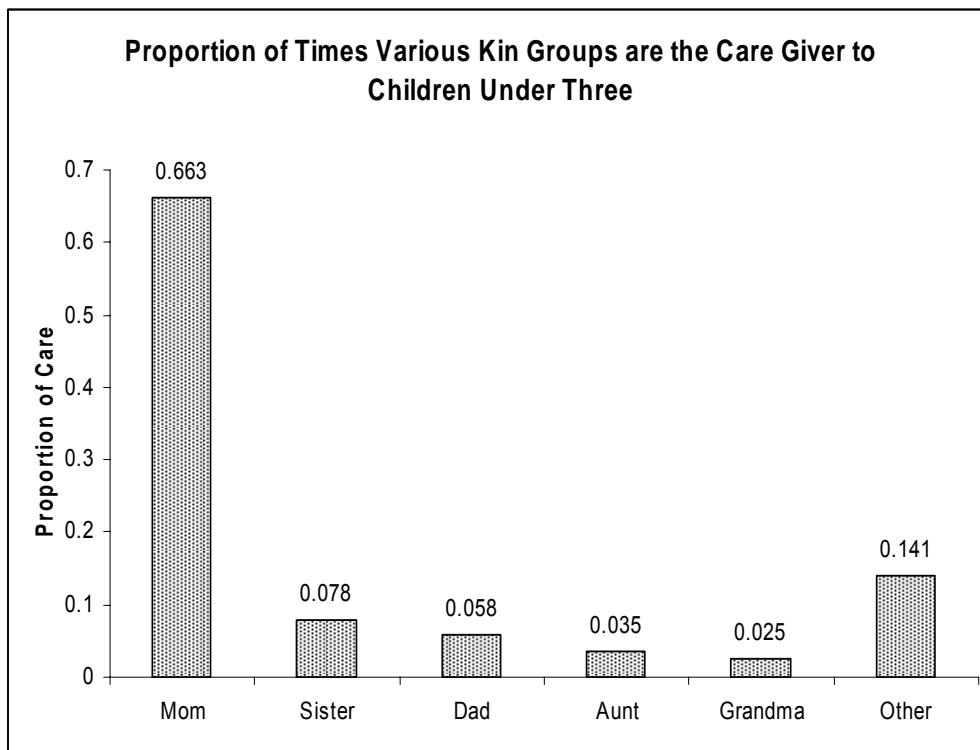


Table 3.4 Generalized estimating equations analysis of the effect of caretaker presence (defined as the wife or older daughter) on the probability of men providing direct care when a child is available for care (n=40 individuals, 444 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-0.014	0.466	-0.03	0.976
Caretaker Present***	-1.013	0.340	-2.98	0.003
Average Age of Children Available	-0.327	0.161	-2.03	0.042

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Table 3.5 Generalized estimating equations analysis of the effect of caretakers other than the wife (older daughters) on the probability of men providing direct care when a child is available for care (n=40 individuals, 444 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-1.016	0.318	-0.26	0.796
Older Daughter Present	-0.367	0.641	-0.57	0.567
Wife Present***	-0.905	0.322	-2.81	0.005
Average Age of Children Available	-0.300	0.165	-1.82	0.069

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

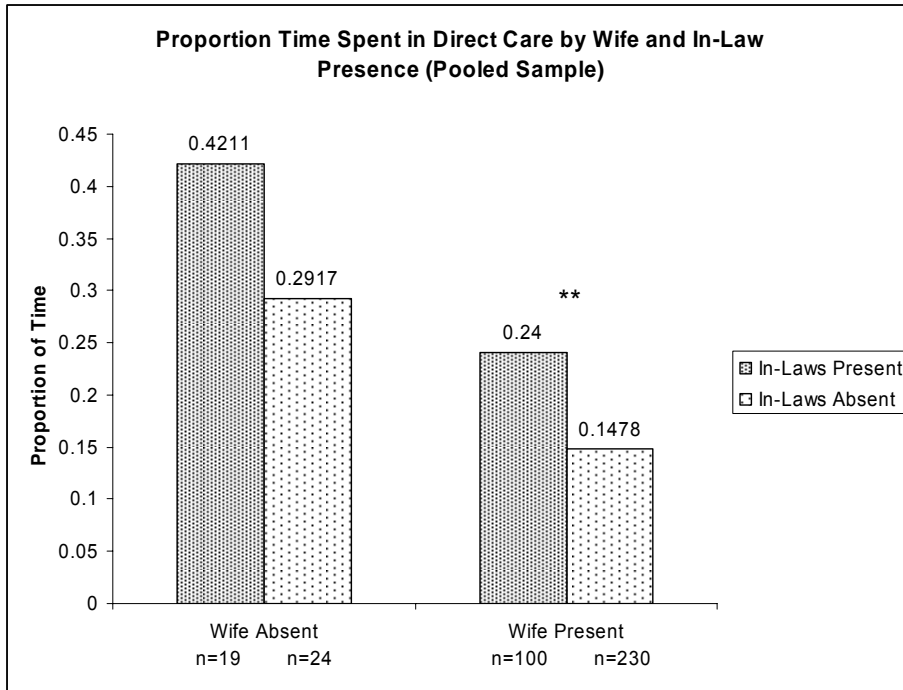
Other Caretakers

In addition to the wife's presence reducing the need for care, so too should the presence of other caretakers. Figure 3.7 shows the most common providers of care to children. Because sisters are the only group (other than mothers) that are more frequently care providers than fathers, caretaker presence is defined by either the mother or a sister over 8 years of age (when girls begin spending significant amounts of time in childcare) being present with the father and child. This variable results in a slightly more significant parameter estimate than wife presence alone indicating that the effect of older sister presence is in the predicted direction (Table 3.4). After controlling for wife presence however, the addition of other caretakers is in the predicted direction, but non-significant (Table 3.5), indicating that the wife's presence is driving the majority of the effect.

In-Laws

In addition to the wife's opinion, a man may also be interested in impressing his in-laws, including the parents and siblings of his wife. Since most men spend at least the first few years of their marriage living with their wives' families, in-laws can prove frequent companions. Despite this cultural trend, age was not found to be a significant predictor of the probability of having an in-law present while being present with a child (Univariate GEE wife absence on in-law presence, $B=-0.036$, $p=0.257$). Figure 3.8 shows the pooled proportions of time spent in direct childcare by wife and in-law presence and Figure 3.9 displays the effect of number of in-laws present on the frequency of male direct care. Men are significantly biasing their care to when their in-laws are present ($B=0.157$, $p=0.010$) (Table 3.6).

Figure 3.8 Proportion of time with child in direct paternal care by in-law and wife presence.



*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001; (chi-square)

Figure 3.9 Proportion of time with child in direct paternal care with child present by number of in-laws present.

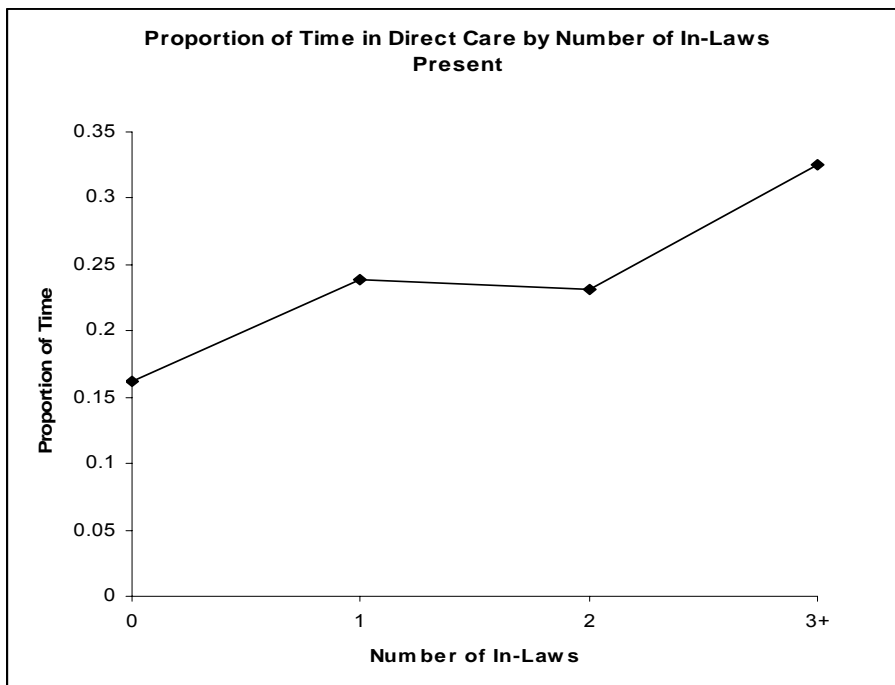


Table 3.6 Generalized estimating equations analysis of the effect of in-law presence on the probability of men providing direct care when a child is available for care (n=40 individuals, 374 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-0.863	0.332	-2.60	0.010
Number In-Laws Present**	0.157	0.067	2.36	0.018
Wife Present	-0.833	0.426	1.96	0.051
Average Age of Children Available**	-0.471	0.210	-2.25	0.025

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Table 3.7 Generalized estimating equations analysis of the effect of the total number of people present on the probability of men providing direct care when a child is available for care (n=40 individuals, 372 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept****	-1.190	0.280	-4.25	<0.001
Total Present****	0.071	0.020	3.58	<0.001
Wife Present	0.747	0.384	1.94	0.052
Average Age of Children Available***	-0.524	0.205	-2.56	0.010

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Table 3.8 Generalized estimating equations analysis of the effect of the presence of different types of people on the probability of men providing direct care when a child is available for care (n=40 individuals, 372 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-0.659	0.469	-1.41	0.160
Number In-Laws Present*	0.121	0.066	1.83	0.068
Number Offspring Present	-0.087	0.119	-0.73	0.467
Wife Present	-0.687	0.396	-1.73	0.083
Others Present**	0.078	0.032	2.46	0.014
Average Age of Children Available**	-0.474	0.217	-2.18	0.029

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Table 3.9 Generalized estimating equations analysis of the effect of the presence of different types of people on the probability of women providing direct care when a child is available for care (n=39 individuals, 1232 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	1.203	0.275	4.38	<0.001
Number In-Laws Present****	0.252	0.065	3.87	<0.001
Number Offspring Present	-0.072	0.038	-1.91	0.057
Husband Present	-0.093	0.129	-0.72	0.469
Others Present**	0.028	0.014	2.01	0.045
Average Age of Children Available****	-0.625	0.111	-5.61	<0.001

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

This effect, however, may be an artifact of the general trend for men to provide more direct care in larger groups. The total number of individuals present is even more significantly associated with the probability that men will provide care when in the presence of children (Table 3.7). The composition of the groups is broken down in Table 3.8. The number of members of the nuclear family (wife and offspring) have negative impacts on frequency of care. The number of in-laws present does have a marginally positive effect, but the presence of others (man’s non-nuclear kin and unrelated individuals) actually have the most significant effect (note that all nuclear family members have a negative effect as they represent potential caretakers). From personal observation, the higher frequency of direct paternal care in large groups is most likely a result of increased group numbers being associated with casual social gatherings, during which time adults are unencumbered with other tasks and available for care. Indeed, women’s direct care shows a similar pattern with respect to group sizes (Table 3.9).

Table 3.10 Generalized estimating equations analysis of the effect of unrelated, reproductive aged women on the probability of men providing direct care when a child is available for care (n=40 individuals, 346 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-1.067	0.411	-2.60	0.009
Number of Unrelated Women	0.176	0.123	1.44	0.151
Average Age of Children Available**	-0.457	0.227	-0.012	0.044

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Unrelated Women

Despite the overall trend for more frequent direct care in larger groups, the presence of unrelated, reproductive-aged women (ages 15 to 45) was not significantly associated with the frequency of men’s direct parental care, although it was in the predicted direction (Table 3.10). This result needs to be qualified by the fact that this sample included women that were married and those which were in-laws, as it was extremely rare for single, unrelated (including non-in-law) reproductive women to be present with a father and child. This may not totally negate the meaningfulness of such an analysis as it is not all that uncommon for women to leave their husbands for other men, and in-laws represent the best pool of potential second spouses as nearly all polygynous marriages among the Tsimane consist of sisters.

Effect of Wife’s Age

If men are truly biasing care with the goal of maintaining access to the fertility of the wife, then the effect of the wife’s presence may be mediated by her reproductive

Figure 3.10 Proportion of time with child in direct paternal care by wife age and presence.

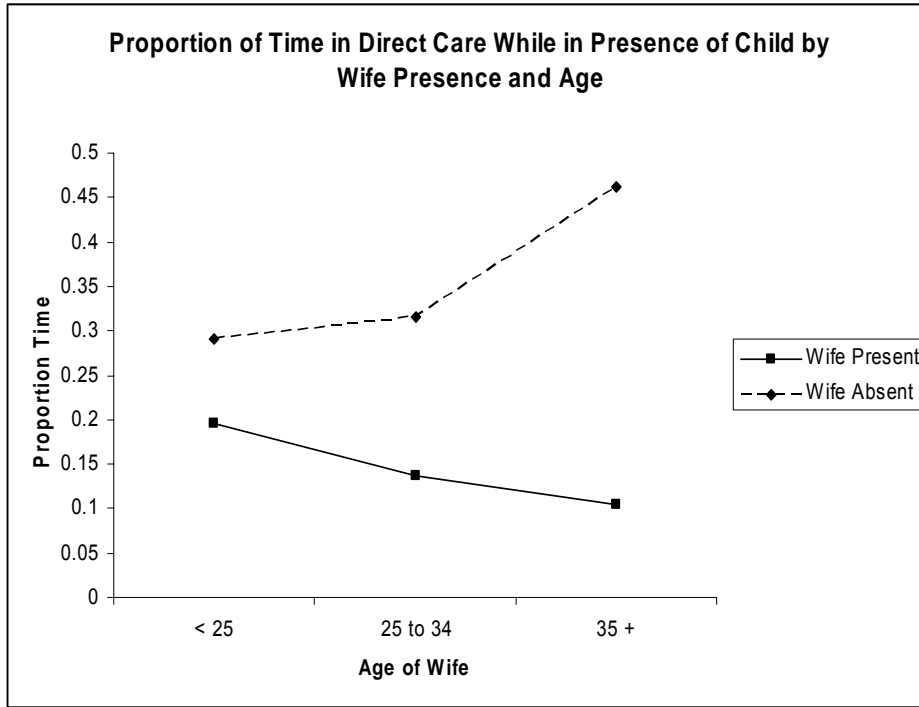


Table 3.11 Generalized estimating equations analysis of effect of wife age, wife presence, and the interaction between the two on the probability of the man providing direct care

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-1.215	1.132	-1.07	0.283
Wife Present	0.588	1.134	0.52	0.604
Wife Age	0.038	0.041	0.93	0.350
Wife Present x Wife Age	-0.055	0.041	-1.32	0.186
Average Age of Children Available	-0.323	0.171	-1.89	0.059

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

value. This can hold true even though the first Mating Effort Hypothesis was not supported (see above). Figure 3.10 shows the proportion of time a man spends in direct care while in the presence of a child by wife presence and age. The interaction between wife's age and presence appears to be in the predicted direction, with men being more likely to provide direct care in the absence of older wives, but *less* likely to do so in their presence. Despite the apparent size of the effect, the proportions at older ages are based on only a few observations, and the effect does not reach significance (Table 3.10), failing to support the second Mating Effort Hypothesis.

Cooperation and Complementarity

The data suggest that although fathers are not frequently employed as baby-sitters, when they do provide care, women are slightly more productive. If a husband's supervision of children allows women to pursue other tasks, then women should be more likely to be away from their children when the father is with the child. To test for this effect, the sample was limited to only data scans in which either the mother or father was directly observed. This eliminates the instances in which entire families were reported together outside of camp and given the same location code, despite it being impossible to know for sure if they were all in the same exact location. If one parent is observed without a child and the other is reported with it, then it is most likely that the child is truly with that other parent. Contrary to the prediction, mothers are actually *more* likely to leave their child when the father is not with the child (Figure 3.11 and Table 3.12). This means that fathers are rarely chosen as babysitters and that most of the time they spend with their children is when they are with both their children *and* wives. Indeed, 93.0% of

Figure 3.11 Proportion of time that mothers spend with children ages three and under by whether or not fathers are with children (n=41 individuals, 892 scans).

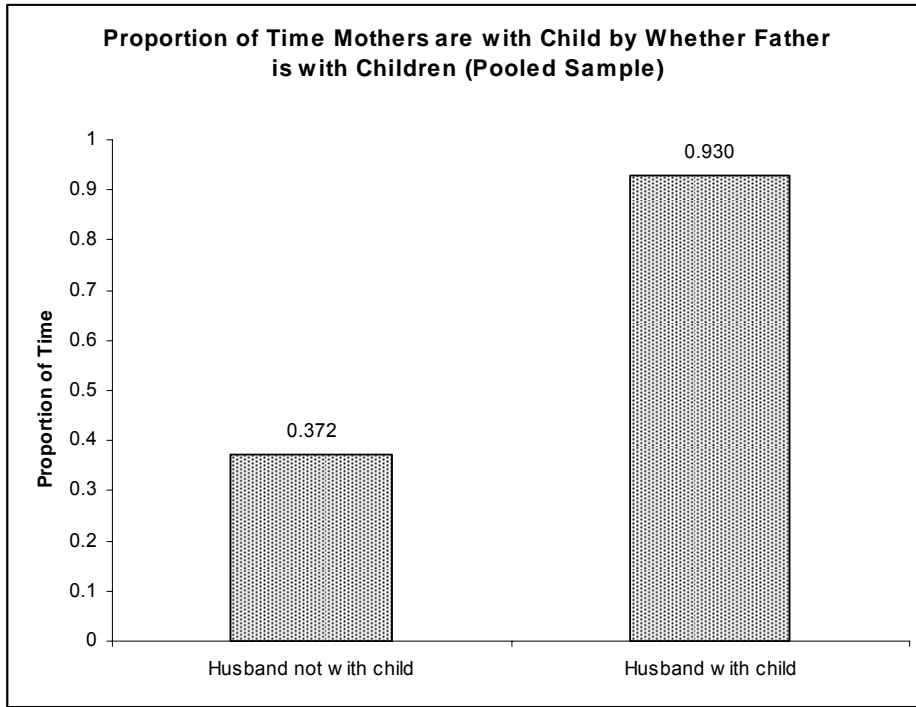
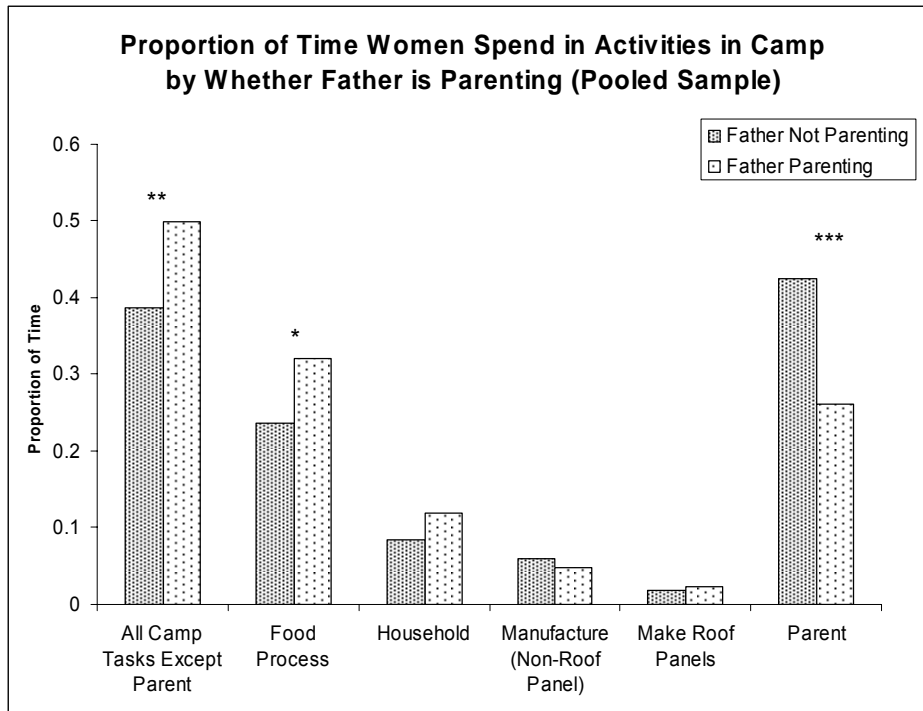


Table 3.12 Generalized estimating equations analysis of probability that wife will be with child age three and under by whether or not father is present with child (n=41 individuals, 892 scans).

Variable	Parameter Estimate	Std. Error	Z	p
Intercept	-0.400	0.238	-1.68	0.093
Husband With Child****	2.988	0.315	9.50	<0.001

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Figure 3.12 Proportion of time mother spends in camp activities with child and father in camp by whether or not father is providing direct care (n=40 individuals, 930 scans).



*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001; (chi-square)

Table 3.13 Univariate generalized estimating equations analysis of probability that mother is engaged in specific work activities while in camp with child and father by whether or not father is providing direct care. Parameter estimates relate to the effect of father parenting for task listed. (n=40 individuals, 930 scans) (Intercepts have been omitted).

Task	Parameter Estimate	Std. Error	Z	p
All Camp Tasks Except Parenting*	0.466	0.248	1.88	0.060
Food Process	0.488	0.321	1.52	0.128
Household (Clean, Wash Clothes, etc.)	0.376	0.418	0.90	0.369
Manufacture (Non-Roof Panel)	-0.169	0.435	-0.39	0.698
Manufacture Roof Panels	-0.105	0.501	-0.21	0.835
Parenting**	-0.955	0.400	-2.39	0.017

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

the time that a man spends with his children is in the company of his wife. Of the times that mothers are away from their children, fathers are with the children only 18.9% of the time. There were no significant effects, however, of men's care on the probability of the mother engaging in any particular task.

When both husbands and wives are in camp as well as at least one child, men's direct care appears to allow women to be slightly more productive (Figure 3.12). Mothers are significantly less likely to be providing care to other children when the father is providing care, and marginally more likely to be engaged in some other productive task (Table 3.13).

DISCUSSION

The overall examination of the effects of the presence of different individuals on men's care appears to support the Paternal Provisioning Model. Tsimane fathers were found to be more likely to provide direct care to a child when the mother is absent, even after controlling for the care that is provided by others, indicating that child need weighs more heavily on a father's decision to provide care than does the ability to display. Testing the effect of the presence of *any* potential caretaker, including both wives and older daughters, increased the significance of the test, although the effect of the presence of older daughters in addition to the wife was not significant by itself. Although the presence of the wife and additional caretakers was used to operationalize the need of children for this analysis, other proxies should also prove predictive, such as the health status of the child, the child's age (which is proven to be a significant predictor when including children up to the age of 5), and the danger that any situation presents. The

wife's age appears to make men slightly more likely to provide care in the presence of the wife relative to her absence, but this effect proved non-significant. Finally, the presence of in-laws was significantly associated with a higher probability that men would provide care, although this was argued to be an artifact of both fathers *and* mothers providing more care when in large social gatherings.

Contrary to the second Paternal Provisioning Hypothesis, women were actually more likely to leave their children when their husbands were also away from them, indicating that fathers are not often chosen to be the substitute caretaker in the mother's absence. This does not necessarily imply that fathers are *never* chosen as baby-sitters, only that other individuals are employed more frequently. Male care does appear to offer women slightly more opportunity to engage in alternative tasks while in camp, although the effect was only marginally significant. It was shown that men's care is selectively directed towards boys and to older children and that their care is more likely to involve play. Perhaps fathers specialize more in areas such as skill development and knowledge, particularly for sons, while leaving the majority of the caring and nurturing to their more adept wives.

Although the first mating effort hypothesis was not supported, this does not necessarily mean that the goal of impressing the wife has no impact on men's decisions to provide direct care. It is possible that if men were solely interested in increasing the fitness of their children, they would offer drastically lower levels or no direct parental care at all when the wife is present to provide the care, and that the desire to impress the wife actually augments their involvement to the observed levels. Unfortunately, it is difficult to separate the opposing effects of the wife's presence on male care, as she

potentially represents an additional caretaker as well as the target for the husband's displays. This is perhaps why Hector, Seyfarth and Raliagh (1989) chose an experimental design when conducting similar research with vervets. They found that when subordinate male vervets were placed in an area with an infant, they behaved much more civilly towards the infant if they could see that the mother was observing through a transparent barrier. The barrier prevented the mother from providing care, but allowed her to observe the male's behavior.

Although the goal of the research presented here is to explore whether Tsimane men bias the delivery of care towards *biological* children to when it better functions as a display, the study of step-children could also prove valuable. Since males do not receive any direct fitness benefits from increasing step-offspring quality, step-fathers are expected to more strongly bias any care to when it can function to reduce the probability of the wife's desertion. Such a test could more precisely determine whether men truly utilize the providing of direct care as a strategy to win and maintain relationships. Flinn (1988b) found that stepfathers of a Caribbean village engaged in a higher proportion of agonistic interactions with their stepchildren when the mother was absent, but not so with biological children. Unfortunately, the stability of the marriages among the Tsimane and the practice of leaving children of previous unions with grandparents resulted in a sample of only 4 stepchildren within the core villages.

Future work could avoid the ambiguities listed above by utilizing well controlled, ethical experimental designs that are able to control the mother's observation. For instance, our anthropological studies have often involved interviews, economic games and the like. Often times, individuals must participate one-by-one in separate, closed-off

areas in order to ensure privacy. When mothers are called in, others are often left to tend to their young children. Such events could easily be modified to test for the effects of a woman's observation by altering whether or not the woman can see her husband and children. An alternative to experimental designs could be the investigation of other forms of investment for which the presence of the wife does not dilute the effectiveness of the investment. For instance, the proportion of money men spend on items for children compared to those for themselves could be explored between trips to the market with or without their wives.

Despite the difficulties listed above, this research showed that a child's need is a stronger determinant of whether a Tsimane father will offer care than is the impact the care can have on the wife's impression of him. Other studies have shown that men invest more in biological children of current mates over biological children of previous mates presumably because of the additional mating benefits outlined in the mating effort pathway (Anderson, Kaplan, and Lancaster 1999). Although such benefits may drive these fathers to provide more care overall, it appears that these benefits are not great enough to significantly alter the way in which men deliver that care.

CHAPTER 4: TIMING OF MEN'S EXTRA-MARITAL AFFAIRS

INTRODUCTION

A corollary exercise to the study of men's parental decisions is one of men's extra-marital behavior. Paternal care and mating effort were traditionally portrayed as mutually exclusive investments for men, but this dichotomy has been extensively criticized in the last two decades. This is largely due to the observation that paternal care in many animals as well as in humans is often succeeded by the offering or the continuation of sexual access by the female, resulting in a pathway through which paternal care can increase not only the quality of offspring, but the quantity of future fertility to which a male has access (Anderson, Kaplan, and Lancaster 1999, Rohwer, Herron, and Daly 1999, Smuts and Gubernick 1992, van Schaik and Paul 1996). Similarly, men's individual social positioning, while winning them prestige, resources, and sexual access, may also result in greater social capital that can be inherited by their children or indirectly benefit them (Hewlett 1992c). Some forms of parental care and mating effort, however, are unambiguously exclusive. A widower who invests heavily in his motherless children must incur some impairment in his ability to attract a new wife. Similarly, the act of surreptitiously pursuing extra-pair sexual relationships can offer nothing to a man's family but disinvestment of time and resources. The understanding of this fact by the Tsimane is implicit in their belief that a father's philandering can directly lead to his children's sickness and death. Based on a large demographic sample, the father's philandering was explicitly mentioned as the primary cause of death for at least 12 of 305 children who died in their first year of life. Because extra-marital behavior is

so sharply at odds with paternal investment, this chapter explores the utility of applying the paternal care hypotheses (in reverse direction) to the study of men's extra-marital behavior within and across marriages.

The underlying sentiment of the Tsimane women's belief, that men's affairs can be harmful to their families, appears to be universally understood. Although women of many cultures are ostensibly accepting of men's unfaithful behavior, Jankowiak, Nell and Buckmaster (2002) found that women's attempts to curtail husbands' extra-marital liaisons were cross-culturally quite similar. In another study, infidelity was found to be the most commonly cited factor as a potential cause of divorce for both men and women in the Standard Cross Cultural Sample (Betzig 1989). In Western populations, extra-marital sex has frequently been found to be the strongest predictor of divorce (Amato and Previti 2003, Fan and Lui 2004, South and Lloyd 1995), and although women are less likely to seek divorce following their partner's indiscretion, infidelity is the strongest predictor within each sex (Amato and Rogers 1997). Not only does infidelity frequently lead to divorce, but the offended partner often suffers through psychological pain, shame, anguish, depression and other injurious affective states (Abraham Spring and Spring 1996, Cano and O'Leary 2000, Gordon, Baucom, and Snyder 2004).

Despite its numerous consequences, extra-marital sex remains quite common. Previous studies involving the U.S. population have presented estimates ranging from 20% to 60% of men and 10% to 50% of women reporting at least one occurrence of extra-marital sex in their lifetimes (see Buss and Shackelford 1997, Wiederman 1997 for references). Many factors are associated with one's propensity to engage in extra-marital sexual activity. The most commonly reported factor, as illustrated by the previous

statistic, is gender. Studies consistently find that men commit adultery more frequently than women (e.g., Atkins, Jacobson, and Baucom 2001, Leigh, Temple, and Trocki 1993, Wiederman 1997). Age is occasionally found to be significantly negatively associated with the incidence of extra-marital sex for women and not for men (Wiederman 1997), for men and not for women (Edwards and Booth 1976), or for neither men nor women (Choi, Catania, and Dolcini 1994). The effect of age, if real, appears to be weakly negative. Similarly, there is some evidence that the duration of marriage is also a significant predictor, with individuals engaging in extra-marital pursuits more frequently as they spend more time in a marriage (Fair 1978), although more robust analyses have called this contention into question (Li and Racine 2004). Many other factors have also been associated with higher incidence of extra-marital sexual behavior, such as personality traits like narcissism, psychoticism, low conscientiousness and low religiosity (Atkins, Jacobson, and Baucom 2001, Buss and Shackelford 1997), and contextual factors such as marital satisfaction (Thompson 1983) and opportunity (Atkins, Jacobson, and Baucom 2001, Gangestad and Thornhill 1997, Greeley 1994).

Unfortunately, most survey studies only report the results of exploratory investigations and lack a cohesive, explanatory theoretical framework. The few evolutionary studies on infidelity have focused on factors expected to alter the returns to pursuing extra-marital relationships. For instance, evolutionists hypothesize that one of the primary benefits that extra-pair relationships offer to females is the acquisition of higher quality genes for their children (Fisher 1958, Gangestad and Simpson 2000). Because infidelity poses so many risks for women, they are expected to bias their extra-pair sex to when it is most probable that it will result in conception. Indeed, two

independent studies found that women were more likely to have sex with their extra-pair partners during high-fertility periods of their menstrual cycle, although they were no more likely during this time to engage in in-pair sex (Bellis and Baker 1990, Gangestad, Thornhill, and Garver 2002). For men, the benefits of extra-pair relationships are mostly accrued through greater access to fertility and an increase in the number of offspring sired. Therefore, factors that influence a man's ability to win extra-marital fertility should increase the frequency of extra-marital sex. Gangestad and Thornhill (1997), for instance, found that more symmetrical men had more frequently cheated on their partners, seemingly because their attractiveness facilitated finding extra-pair partners. Buss and Shackelford (1997) similarly predicted that individuals that had higher mate value than their spouses would be more likely to have an affair than their same sex counterparts, although they failed to find any significant effect. The lack of significance may have been due to the fact that mate values were determined by the ratings of two interviewers, and that the study only tested self-reported probabilities of future infidelity.

These studies, however, did not consider familial characteristics that mediate the costs of investing in extra-marital affairs, mainly those associated with the dependency load of the family and the amount of fertility the man risks losing if discovered. According to the paternal provisioning pathway, any factor that increases the cost of diverting resources away from the family should, all else being equal, decrease the probability of extra-pair sex. Stated another way, any factor that increases the returns to investing in one's family (again, all else being equal) should decrease the probability of investing in other pursuits. A father who is faced with an ill child in need of medicine is

less likely to spend his last dollar in the pursuit of an extra-pair liaison precisely because that dollar can do so much good if invested in his child.

A second cost of extra-marital activity is the threat of wife desertion, a very real possibility as argued above. Not only can divorce lead to lower fitness outcomes for the children already sired within the union (see Chapter 5), but also results in a total loss of access to the wife's remaining fertility. All else being equal, men should therefore be more likely to pursue extra-marital relationships when they are less likely to be discovered, when the wife is less likely to desert, and when they have less future fertility to lose. Again, the Paternal Provisioning Model and the Mating Effort Model produce predictions that are in opposing directions, since, as it is argued below, the remaining fertility of the wife and the probability that she will desert vary inversely with the need of the family.

HYPOTHESES AND PREDICTIONS

Paternal Provisioning Hypothesis 1: Men should provide care in relation to the need of children

As argued above and in Chapter 1, the benefits conferred through the paternal provisioning pathway are heavily dependent on the need of a man's progeny. A proxy of this need is the number of dependents co-residing with the man (Hames 1992). Like many resources, parental investment provides diminishing returns to its recipients. This means that after the first unit of investment, men with multiple dependent children will receive greater returns from parental investment than parents of singletons, as they have multiple utility curves to climb. Investing in extra-marital affairs diverts resources from

the family and into selfish pursuits. All else being equal, men with more children, and hence needier families, should be less likely to engage in extra-marital affairs.

Mating Effort Hypothesis 2: Men should provide care in relation to the reproductive value of the wife

The mating effort pathway suggests that the goal of maintaining access to a wife's fertility drives men's familial behavior. Pursuing extra-marital relationships can increase the probability of marriage dissolution and loss of access to that fertility through two pathways. Firstly, the effects of disinvestment in the family can increase a woman's dissatisfaction with her husband and lead to divorce. Secondly, and perhaps most importantly, the discovery of such an affair can lead directly to her desertion due to the harmful effects listed previously, exacted by an evolved psychology designed to be sensitive to such blatant signs of disinvestment. The fitness costs imposed by the loss of fertility are directly related to the wife's reproductive value, which varies inversely with a woman's age. A man who is deserted by a post-menopausal wife suffers no loss of fertility. Additionally, a woman with many dependents and low reproductive value may be more reluctant to desert a philandering husband because of lower prospects of remarriage. Husbands of older wives may therefore not only experience reduced costs of divorce but reduced risk as well. This leads to the prediction that men should be more likely to have extra-marital affairs when they have older wives. Because the number of dependent children increases with the wife's age (until it stabilizes in early thirties), this prediction is qualitatively in the opposite direction with that produced from the paternal provisioning pathway.

METHODS

The Interview

Retrospective longitudinal interviews were conducted to assess men's investment in seeking extra-marital sexual partners throughout the course of individuals' marriages. Men that had been divorced or widowed were asked questions concerning their current or latest marriage in order to avoid small sample sizes due to truncated first marriages and to increase the variation in age at marriage. It is important to note that the Tsimane do not have strong taboos concerning conversations about sexual behavior, and freely make humorous remarks in large groups and even around children. Actual instances with particular individuals are less openly discussed, although joking about the subject and discussions concerning the objects of individuals' desires are rampant, particularly within male-male groups.

The interview (Appendix 4.1) primarily aimed to determine the years of marriage in which the individual had an affair, the number of women with whom he had affairs, and the length of each affair. This was done by first asking with how many women the individual had had affairs, and then elucidating the timing and duration of each relationship. Because the Tsimane are often unaware of their age or of particular dates, I determined this by asking which of their children had been born when the affair occurred. At the end of the interview, interviewees were given four fishhooks and ten meters of fishing line.

Reporter bias is of considerable concern when dealing with self-reports of sensitive issues. As stated before, Tsimane men do not seem very reticent to discuss

reproductive matters, although they do have an interest in ensuring that particular individuals do not know of their behaviors. I informed all of the men within the two communities, on an individual-by-individual basis, that I would be conducting such interviews and that their participation was completely voluntary. No translators were used during the interviews to increase the participants comfort levels and increase the likelihood that they would provide accurate responses. I assured each participant that I would not discuss the details of his particular interview with others, and that only his personal identification number, and not his name, would be recorded on the data sheet. Additionally, the names of women with whom the participants had had relationships was never discussed. After having developed a rapport with the members of two communities for nearly a year, I found the men to be willing to discuss these matters and had all but one of the 39 men present volunteer for the interview. Two men were excluded due to polygynous marriages (to avoid ambiguity concerning the pursuit of additional wives versus extra-marital affairs), and two were excluded since their previous wives were unavailable for demographic interviews. These exclusions resulted in a total sample of 34 men.

Demography

Refer to Chapter 3 for a description of the demography methods. This dataset was used to determine ages, years of marriages, and the number of dependent children for each year of marriage.

Data Analysis

From the interviews, I extrapolated a dataset consisting of data-points for each year of each individual's marriage, creating 508 risk years. I used the Generalized Estimating Equations (GEE) method in the GENMOD procedure of SAS to test for effects of the hypothesized variables (see Chapter 2 for a review of the GEE method). For all GEE analyses presented in this chapter, the model assumes an auto-regressive correlation structure since affairs can last longer than a year and may therefore be clumped in time. Personal identification numbers were used as repeated subjects, and all parameter estimates presented are logit estimates.

Within each marriage, the husband's age, the wife's age, and the number of years of marriage covary perfectly. Any true effect of any one of these variables will result in all of them being significant in separate univariate analyses; in multivariate analyses, such colinearity would lead to unclear and questionable results. Therefore, for the multivariate model, I included year of marriage (how many years since the couple was married) for each year to determine the effect of these three variables (or simply time) within the marriage. I then added husband's age at marriage and wife's age at marriage to determine the cross-individual effects of these two variables. In this way, I can distinguish between the separate effects of the three variables. If the man's age is producing the true effect, both years in marriage and man's age at marriage need to be significant, and likewise for wife's age. If the effect is driven by years in marriage, than only this variable should be significant. I also calculated the number of dependent children for each year of marriage. Dependent children were defined as those age 10 and under, as this was found to be the age around which children begin spending substantial

Table 4.1 Descriptive statistics for dataset (n=34 men, 508 risk years).

Variable	Mean	Std. Dev.	Min	Max
Number of Dependents	2.079	1.579	0	7
Years of Marriage	14.942	11.203	1	49
Husband Age at Marriage	20.645	4.294	16	37
Wife age at Marriage	17.400	2.711	12	26

amounts of time in food production activities. To test the validity of this demarcation, all analyses presented were also performed by defining dependents as children under the age of 5 and under the age of 1—no results changed direction or significance.

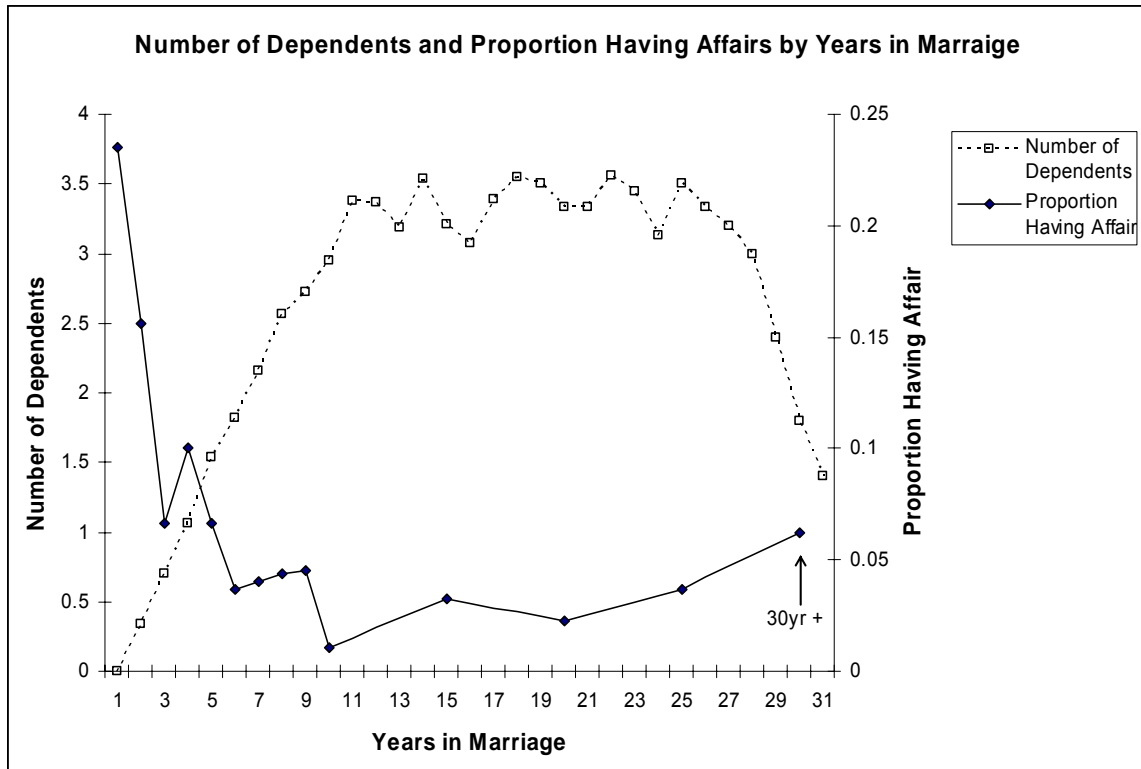
RESULTS

Descriptives

Table 4.1 displays the descriptive statistics for the variables included in the model. As a marriage progresses, the number of dependents grows until there are as many children reaching 11 years of age as there are new children being born. This equilibrium is typically reached in the second decade of marriage between 3 and 4 dependents, lasting until the wife reaches menopause, usually around 25 years into the marriage (Figure 4.1).

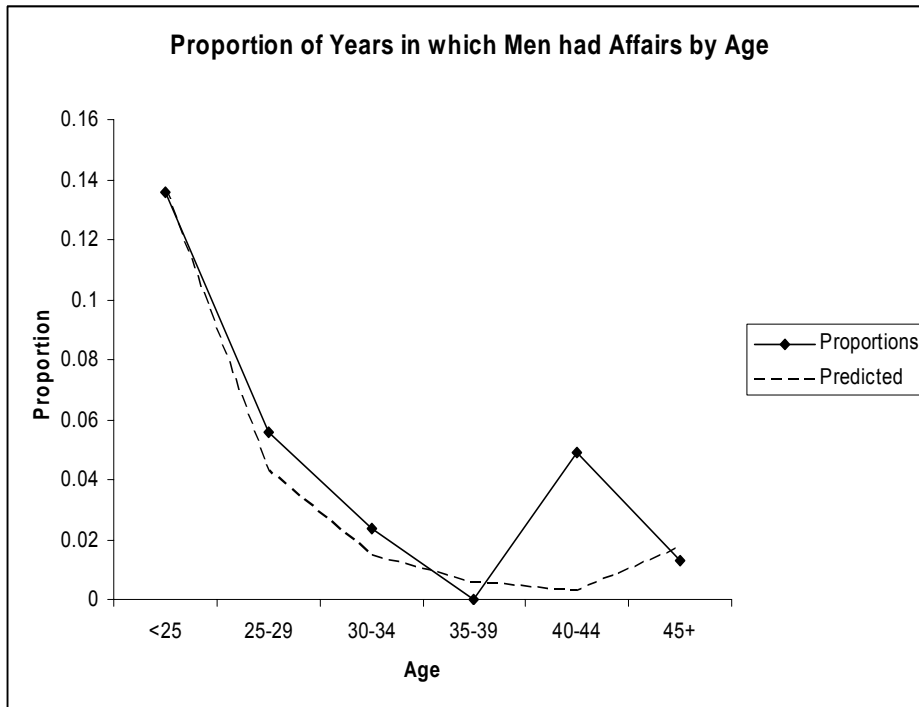
The 34 men provided 508 risk years of marriage, with an average of 14.9 years. Age at first marriage ranged from 16 to 26 years with a mean of 20.6. Five of the men sampled gave responses relating to second marriages, which occurred at ages ranging from 24 to 38 and a mean of 32.2. Three of the cases resulted from the first wife's death and the other two from the desertion of the first wife. In order to test the reliability of

Figure 4.1 Number of dependents and proportion of men having an affair by year of marriage.



informants' responses, two logistic regressions were performed. The first analysis was conducted to test whether men were more or less likely to report an affair in the first year of marriage (the highest-risk year of having an affair) as a function of how long ago they were married when the interview was conducted. Using the calendar year of marriage as the dependent variable, there is no significant effect of years since marriage on the probability of reporting an affair in the first year ($B=0.286$, $p=0.593$). This also indicates an absence of a cohort effect. The second analysis tested whether the number of years since the year in question had an effect on a man's reporting of affairs (if perhaps men

Figure 4.2 Proportion of men having an affair per year by age. (Predicted curve is logit estimate for age plus age squared).



were better able to remember more recent affairs or more reluctant to discuss them).

Again, a logistic regression shows no significant effect ($B=-0.006$, $p=0.764$).

Of the 31 men that had been married for more than five years, 9 of them, or 29%, reported at least one affair in those first five years of marriage. Affairs appear to be heavily concentrated in the early twenties, during the first years of first marriages (Figures 4.1 and 4.2). Men in this age bracket are over twice as likely as men of other ages to have had an affair in any given year, and were the only ones who reported to have had affairs with multiple women in a single year. After this period, there is a precipitous drop of extra-marital activity, followed by a slight but significantly positive quadratic effect in the later years. This later increase, however, is driven by only a few older men (Table 4.2).

Table 4.2 Generalized estimating equations analysis of the effect of the man's age (and his age squared) on the probability that a he will have an affair in any given year.

Variable	Estimate	Std. Error	Z	p
Intercept	4.248	2.155	1.97	.049
Age**	-0.376	0.138	-2.72	0.007
Age ² **	0.004	0.002	2.16	0.031

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Effects of Predictor Variables on Extra-marital Behavior

Table 4.3 and 4.4 present the results of the univariate GEE analyses of the effects of the two predictor variables. In Figure 4.3, it is clear that the number of dependents is negatively associated with the probability of a man having an affair in a given year. The years of highest risk for men's extra-marital behavior are during the first years of first marriages, in a man's early twenties when he has no or very few children. This is also the time during which a man's wife is at her youngest age, leading to a significantly negative association between frequency of affairs and wife's age, opposite of that predicted by the mating effort pathway. The square of wife's age is also significant when added to the univariate model, similar to the pattern seen with the man's age, although the slope of the predicted curve is not positive until the wife is age 40.

Because previous evidence suggests that a man's age and the number of years within a marriage may have an effect on one's probability to have affairs, these variables were included in the full multivariate model. Table 4.5 presents the results of a GEE analysis of this full model, which includes the log of years in marriage, man's age at marriage, wife's age at marriage (see Data Analysis section above for a justification of

Table 4.3 Generalized estimating equations analysis of the effect of the number of dependents on the probability that a man will have an affair in any given year.

Variable	Estimate	Std. Error	Z	p
Intercept	-1.909	0.365	-5.24	<0.001
Number of Dependents***	-0.476	0.175	-2.71	0.007

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Table 4.4 Generalized estimating equations analysis of the effect of the wife's age on the probability that a man will have an affair in any given year.

Variable	Estimate	Std. Error	Z	p
Intercept	-0.522	0.990	-0.53	0.597
Wife's Age**	-0.085	0.038	-2.26	0.024

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

Figure 4.3 Proportion of years in which men had affairs by number of dependents.

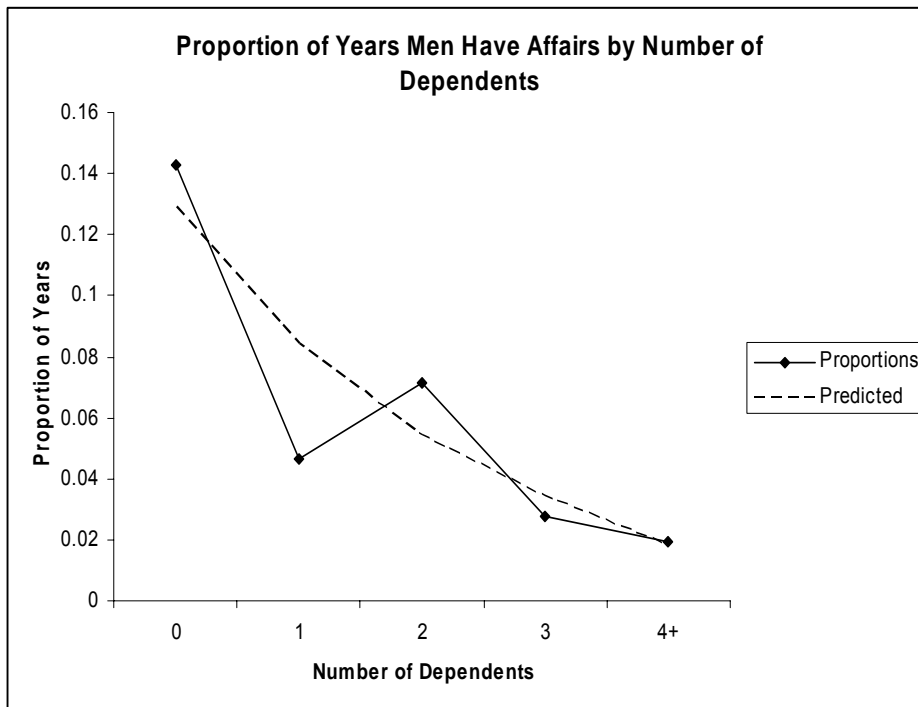


Table 4.5 Generalized estimating equations analysis of full model.

Variable	Estimate	Std. Error	Z	p
Intercept	1.173	1.686	0.70	0.487
Number of Dependents	-0.076	0.276	-0.28	0.782
Wife's Age at Marriage	0.047	0.062	0.76	0.445
Man's Age at Marriage**	-0.159	0.075	-2.11	0.035
Log Years in Marriage**	-0.797	0.397	-2.01	0.045

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

the use of man and wife's age at marriage). The log of years in marriage was used due to greater fit to the data and is testament to the sharpness of the decline of frequency of extra-marital affairs within the first few years of marriages. Although both hypothesized predictors, number of dependents and wife's age at marriage, are in the predicted directions, neither is significant. After controlling for age at marriage and years in marriage, men that have more dependent offspring or younger wives are not significantly less likely to engage in extra-marital sex. The probability of doing so is significantly associated with the man's age at marriage and the log of the number of years within marriage. This means that across marriages, those men that marry earlier have more affairs than those who marry later and that within marriages, men have more affairs in the first few years. This result can be interpreted in two ways: the two variables can truly be having additive effects (men that marry younger and men in earlier years of marriage have more affairs), or the effect can be driven solely by the man's age, since it is simply the sum of the man's age at marriage and the number of years within marriage. A direct test including years in marriage and age may be dubious because of the strong colinearity between the two variables (within subject $r=1$, across all $r=0.875$). When we test the reciprocal, however, using age at marriage and man's age (instead of years in marriage),

only man's age is significant. In this example, the number of years in marriage is simply man's age minus age at marriage. The lack of significance of age at marriage implies that the duration of marriage really has no effect, and that age is truly driving the association. This returns us to the original model that includes age and its square as the best fit model.

This last assertion, that age drives the effect, must be tempered with the fact that the removal of the five individuals for whom the data correspond to their second marriages (and thus those with the highest ages at marriage) results in only the log of years in marriage being significant and age at marriage being non-significant. These men did not engage in any extra-marital behavior in their second marriages. Since three of these men were widowers, self selection is less likely to be a confounder and their inclusion in the sample more appropriate.

As a final test, only the first five years of marriage are examined with a categorical variable indicating whether the couple has produced a child. This is to determine if the presence or absence of dependents, as opposed to their number, has an effect on the probability that a man will have an affair. The analysis shows that the categorical variable does have a stronger effect, but that it still fails to reach significance (Table 4.6). Additionally, the age of the bride has no effect on the probability that the man will engage in extra-marital activity even during the first five years of marriage. Indeed the direction of the parameter estimate is opposite that predicted by the second Mating Effort Hypothesis.

Table 4.6 Generalized estimating equations analysis of the effect of having at least one dependent has on the probability that a man will an affair in the first four years of marriage.

Variable	Estimate	Std. Error	Z	p
Intercept	3.093	2.278	1.36	0.175
Dependent	-1.036	0.751	-1.38	0.168
Wife's Age at Marriage	-0.081	0.105	-0.77	0.440
Man's Age at Marriage	-0.142	0.117	-1.26	0.207
Log Years in Marriage	-0.286	0.523	-0.55	0.585

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

DISCUSSION

Univariate models show that the frequency of affairs varies inversely with the number of dependents within the family, supporting the prediction of the paternal provisioning pathway. The parameter estimate of the wife's age was actually significantly negative, in the reverse direction of that predicted by the mating effort pathway. After controlling for age and number of years in marriage, however, the data show no support for an effect of the family's need or the wife's reproductive value on the probability of a man having an affair. What we do see is a life history trend in which men invest most heavily in extra-marital affairs in their twenties; in midlife, the frequency of adultery drastically decreases and it finally experiences a slight upturn in the later years (although a larger sample size is needed for this period to verify the effect).

Behavioral studies are often complicated by confounding variables and self selection, resulting in multiple alternative explanations of observed trends. Prior to evaluating the proposed hypotheses, alternative explanations are considered below.

The first few months or even years of a marriage may function as a period of evaluation for both partners, and thus represent the time of greatest risk of divorce

(Blurton Jones et al. 2000). Not only do spouses judge the personality and behavior of their partners during these first few years, but also their fecundity. Infertility is found as a common cause of divorce the world over (Betzig 1989). Despite these assertions, these men are having elevated rates of affairs until the fifth year of marriage, when the average household has 1.5 dependent children. By this time, it's hard to imagine that these men are simply pursuing additional relationships in order to maximize their future options in case their marriage should end. Furthermore, no married couple in this dataset failed to produce a child.

Perhaps young men's returns to extra-marital pursuits are greater. Although women place greater importance on attractiveness for short-term relationships (Buss and Schmitt 1993), there's little evidence that women find youth attractive (Buss 1989, Jones 1995). Younger men could enjoy a competitive advantage in the intra-sexual or male-male aspect of short-term mating competition (as opposed to female choice). Younger men may be more willing to take risks to find short-term mates, whether these risks entail distant journeys or angry fathers, and indeed they may be more successful at winning direct contests. These advantages, however, could not be conferred through greater physical ability and health, as Tsimane men's strength profiles do not peak until the late twenties (Gurven n.d.), during which the frequency of affairs is dramatically decreasing. Additionally, these men have had more time to build up the small amount of equity that Tsimane individuals can attain, providing them with greater ability to give gifts, a trait that is also valued by women in short-term mates (Buss and Schmitt 1993).

The unpredictability of early marriages and differing return rates to extra-marital pursuits appear to be poor explanations for the observed pattern of affair behavior.

Men's concern with the amount of fertility they risk losing also fails to explain the pattern. Among this Tsimane sample, the pattern seems to indicate that men are essentially oblivious to the potential fertility that they are risking by pursuing extra-marital relations. Men are engaging in a behavior that unambiguously angers their wives at a time when the wives have the most to offer the men and the least to lose from leaving them. Although divorce is relatively uncommon amongst the Tsimane, of those couples that do divorce, roughly two thirds do so within the first five years (21 of 32 divorces recorded in demography of four villages). The brazenness of men's exploits during this period and the seeming carelessness with which they risk their marriage is underscored by the fact that most men during this time are living with their wives' families.

If men were simply optimizing their extra-marital behavior along with the probability of maintaining their current union, they would wait until they had many children, essentially forcing the woman to choose between staying with the philandering biological father of her children or face the prospects of finding a step-father or convincing her parents to take over raising the larger brood. In other words, as her cost of desertion increases, men should increase their boldness in step if they were solely concerned with maintaining the union. Indeed, Fan and Lui (2004) found that the presence of dependent children served as a buffer for divorce upon the discovery of infidelity among a Hong Kong population (although the sex of the offender was not controlled for). Yet, with the Tsimane, a corresponding increase in extra-marital behavior is not observed.

The number of dependents was a significant univariate predictor, but this effect seemed to have been driven by the man's age. This is perhaps indicative of a general life

history pattern characterized by a strategic shift from a mating effort intensive strategy towards one of greater pair-bond and parental involvement as the ability to win a wife and the opportunity to invest in children increase. We see the lowest frequency of extra-marital affairs during the thirties, while the number of dependents under the age of 10 is holding at a stable maximum between three and four in a typical marriage. There even appears to be a slight return to higher extra-marital investment just as the number of dependents begins decreasing after the wife's menopause. This life history shift is also supported by a study conducted by Wood and Hill (2000) among the Ache of Paraguay. They presented men with two pictures depicting foraging parties, each group containing the same number of available women. The only difference between the two groups was that one indicated that the men were poorer hunters by displaying fewer killed animals at their feet than the other picture. Men were then asked to choose which group they would go with on an extended foraging trek. Despite a small sample size, the strength of the effect drove the significance of the study. The men that had dependent young nearly universally chose the group with better hunters, while the bachelors chose the group of poor hunters in which their own skills would be best displayed to the available women. Similarly, younger Ache men were more likely to be named as secondary fathers, a distinction that indicates possible but not probable paternity and one that may be an artifact of greater investment in short-term sexual relationships (Hill and Hurtado 1996). As Ache men age, they attain long-term relationships and become more likely to be named as primary fathers within these pair-bonds.

Throughout the world, men appear to go through this transition. Young and sexually loose Maasai warriors mature into elders and are then allowed to marry. College

is considered a time of sexual experimentation in western culture, but when a man trades in his sports car for a minivan, he makes an unmistakable investment in his family at the expense of his ability to display his short-term mate value. Indeed, the pattern is reminiscent of the surreptitious mating tactics used by young males of many species (e.g., Gross and Charnov 1980, Le Boeuf 1974). These males must rely on alternative strategies until they reach a level of maturity and competitiveness to openly lay claim to a female's fertility. The extended learning curve of men's foraging strategies (Gurven n.d., Kaplan et al. 2000, Walker and Hill 2002) and the universal female preference for older men for long-term mates (Buss 1989) may indicate that young men are simply not competitive enough to win a wife and are therefore relegated to a short-term strategy. Only when they are able to secure a wife and have children in whom they can invest do they appear to give up their philanderer's lifestyle.

CHAPTER 5: EFFECT OF FATHER ABSENCE ON CHILD WELL-BEING

INTRODUCTION

The study of the effect of father absence on family dynamics and child well-being has a long history in the fields of psychology, sociology and family studies (e.g., Russell 1957, Shaw and McKay 1932, Sutherland 1930). These studies tend to focus on the harmful effects of father absence on the psychological, cognitive and behavioral development of children in Western populations (see Adams, Milner, and Schrepf 1984, Lamb 1997 for reviews). More recently, evolutionary-minded anthropologists have begun to explore the “father effect” as well, often within traditional populations, focusing more on easily measured fitness outcomes such as survivorship (Blurton Jones et al. 2000, Hurtado and Hill 1992), growth (Sear, Allal, and Mace n.d.), and reproduction (Flinn 1988b, Quinlan 2001, Waynforth 2002).

All of these studies assume that by studying the differences between children raised with and without fathers, one could elucidate, by simple means of subtraction, the value of the father’s presence (Lamb 1997). Indeed, researchers have used cross-cultural variation in the father effect as a predictor of levels of divorce and female-headed households, arguing that men would be less willing to stay in a marriage and women less willing to maintain a husband if a father’s investments were unimportant (Hurtado and Hill 1992, Lancaster 1989). This chapter will explore the merit of this interpretation of the father effect and review the existing literature on the subject. Finally I will test for a father effect in the survivorship, morbidity, growth, and reproduction of offspring among

the Tsimane and explore how the existing evidence and data reported here relate to the proposed models concerning men's parental care.

THE FATHER EFFECT—WHAT DOES IT MEASURE?

The common assumption that the effect of father presence accurately assesses the value of men's care needs to be qualified by two main points. The first is that children of complete and broken homes are not randomly distributed, meaning that parents self-select their children into these groups along both genetic and behavioral parameters. Secondly, the impact of a father's absence on the behavior and well-being of individuals other than the children, and the effect of this change on the success of children, is often ignored, obscuring the true effect a father's care.

Self Selection

Divorce, single-parenthood and father mortality are often all included in studies of father absence, although they pose different problems with respect to self-selection. Death is less frequently the cause of broken homes in Western populations, but constitutes a significant proportion of the cases of fatherless children in studies of traditional populations (Blurton Jones et al. 2000). Father mortality is most likely less self-selected than divorce, although genetic predispositions to diseases can lead to both increased mortality in fathers and children, leading to a spurious inflation of the father effect. Similarly, behavioral traits associated with higher mortality risks, such as aggressiveness or risk-taking, may also be associated with lower levels of paternal investment while the father is alive.

The causes of divorce and single parenthood are numerous and often complex, leading to the potential for external factors to both influence the probability of father absence and the success of children. Regardless of whether the impacts of these factors on child well-being are imposed before or after the father's disappearance, the result is an apparent and potentially spurious effect of father absence. For instance, the lack of male investment and involvement has been found to be a commonly reported reason for women to seek divorce (Betzig 1989, Kitson 1992). If such father behavior is associated with less fit children within marriages as well as a higher probability of divorce, then a difference between the success of children with and without fathers will be found regardless of any subsequent impacts endured after the dissolution of the marriage. Similarly, if certain female characteristics are associated with both husband desertion and the success of children, the same self-selection problems present themselves. There may also be social or economic factors that influence child outcomes and probability of divorce or single parenthood, such as income level, mating opportunities, or levels of violence (Lancaster 1989). Finally, if there is any heritable predisposition to reproductive strategies, the behavioral patterns in children raised in single-parent homes may be driven in part by these genetic predispositions that they share with their father and mother in stead of or in addition to the influence of the father's absence (Comings et al. 2002, Moffitt et al. 1992, Rowe 2000).

Given these problems, the optimal study that would be most free of any self selection bias would be one of children whose fathers had died of accidents (although predisposition to risk-taking behavior might also have a heritable component). Such studies, however, would be plagued by small sample sizes due to the rarity of such

events. In the Tsimane sample used here, nearly three quarters (72 of 98) of the cases of father absence were due to the death of the father. Because infectious disease is the most common cause of mortality for all ages, the results presented here must be reviewed in light of the potential for heritability of susceptibility to various infectious diseases (Cooke and Hill 2001).

Effect of Father Absence on Others' Behavior

Because father absence presents a loss of provisioning and care, other family members may compensate by increasing their own levels of investment. This would in effect diminish the apparent value of men's care. Although children's outcomes may be constant across families with and without fathers, the true cost of father absence may be incurred by alternative caretakers, such as mothers, stepfathers or grandparents who must increase investment in order to offset the loss (Blurton Jones et al. 2000). The validity of the interpretation of the father effect, therefore, depends on the question being asked. If one wants a measure of men's absolute contribution within a marriage, then the father effect may be a gross underestimate; if, however, one is attempting to measure the cost of divorce to males in terms of the decrease in offspring quality, or the value to offspring of being raised by both biological parents over alternative situations, then the father-effect would be more appropriate.

It should also be noted that the effect of father absence on the behavior of others can occasionally occur in the opposite direction. Mothers and kin of children who do not have fathers may actually *reduce* care because of a low expectation of the children's success. For instance, among the Ache of Paraguay, children without fathers were 3.9

times as likely to be the victim of homicide in each year of life (Hill and Hurtado 1996). Although this increased risk may be due to the lack of the father's protection, it may also be driven by directed infanticide perpetrated by kin who do not want to take on the excessive burden of raising a fatherless child. Again, this requires a more precise interpretation of the father effect, for although such a tendency is indicative of a cultural understanding of a strong father effect, it nevertheless inflates the true value of a man's contribution to the family.

Despite problems of self-selection, the investigation of the effects of father absence on the well-being of children can prove a useful exercise if the effect is interpreted correctly. That is, the effect measures the increase in offspring fitness that is conferred by being raised in a household with both biological parents over that of being raised in a family with a different composition of caretakers. Finally, the effect can also be interpreted as an accurate measure of the cost to the absent father in terms of the decrease in the fitness of his offspring.

OVERVIEW OF REPORTED EFFECTS

Previous studies of the father effect can be divided into two large categories of studies. The first pertains to the studies that have focused on psychological, cognitive and behavioral measures, usually involving Western populations. This literature is indeed vast, but an attempt to summarize it will be provided below. The second category includes those studies involving more salient measures of fitness outcomes, such as survivorship, growth and fertility that have typically involved traditional populations.

Effects of Father Absence on Psychological, Cognitive and Behavioral Measures

Early studies of the father effect grew out of the investigation of the development of sex-roles, an area in which fathers were considered to play an integral role, particularly for boys (Lamb 1997). Thus, many early studies focused on the effect of father absence on the healthy development of sex-role identity in children, although the results were often mixed (Beatty 1995, Biller 1969, Covell and Turnbull 1982, Santrock 1970). The study of the father effect then diversified as researchers focused on various measures of offspring success. Many investigated the effect of father absence on the mental health of children, finding it to be associated with a range of conditions, including schizophrenia (Heacock and Seale 1968), sleep disturbances (Herzog 1980), low self-concepts (Parish and Taylor 1979), and many others (Franz et al. 1999, Lavigne et al. 1996). Despite these findings, however, other studies reported no effect of father presence on the probability of mental disorder (Langer 1963) or specifically of later depression (Munro 1966). Furthermore, in societies in which men are unable to provide adequate resources to their families, children of broken homes may actually show better psychological adjustment than those of intact homes, apparently because there are no adult men in these homes to drain the family's resources (Brown 1973, Lancaster 1989).

Many studies also focused on the effect of fathers on the cognitive performances of children, most often finding some deficiency in father-absent children (Bernstein 1976, Chapman 1977, Kardas and Langenmayr 1999, Sutherland 1930), although some found no effect (Collins 1969). Similarly, a number of studies found that father absence is negatively associated with academic achievement in children (Anderson 1999, Heacock and Seale 1968, Lancaster and Kaplan 2000, Mulkey, Crain, and Harrington 1992).

Some evidence even suggested that father absence was associated with boys having greater verbal skills than math skills, a reversal of the traditional pattern and possibly a mixture of the effects of father absence on sex-role identity and cognitive abilities (Nelson and Maccoby 1966), although again, there were studies that failed to find such effects (Moffit 1981).

Finally, a large body of work has focused on the delinquent behavior of children and its association with father absence (see Wells and Rankin 1985, Wells and Rankin 1991). Although some evidence is mixed, most studies point to an increase in juvenile delinquency in children of broken homes, particularly for less serious offenses (Rebellon 2002, Wells and Rankin 1991).

Despite the numerous studies that fail to find effects, the fact that no (or extremely few) studies found effects in opposite directions implies that these effects are indeed real, if perhaps small. Overall, this literature suggests that within Western populations, fatherless children tend to be less well adjusted to their sex-specific roles, more prone to mental problems, exhibit lower cognitive performance and are more likely to engage in delinquent behavior.

Effects of Father Absence on Measures of Fitness and Reproductive Strategies

More recently, researchers working from an evolutionary theoretical framework have begun to study the effect of father absence on measurable fitness outcomes, often within traditional populations. These studies can be broken into two large camps: those investigating the deleterious fitness impacts of father absence on children, and those exploring its effect on children's future reproductive strategies.

Fitness Impacts of Father Absence

Many studies of the father effect were not necessarily designed to investigate the impact of father absence, but that of step-father presence. These studies typically compare the outcomes of children living with biological versus step-fathers and do not consider other family arrangements (e.g., Daly and Wilson 1985, Flinn 1988b). This will inflate the apparent father effect when the presence of step-fathers have negative impacts on offspring success relative to other arrangements (e.g., Sear et al. 2002, Tooley et al. 2005), and it will diminish the effect when step-fathers buffer the harmful effects of paternal absence (e.g., Chapman 1977). Whether or not studies compared children of intact homes to only those including step-fathers will therefore be noted below.

Perhaps the most salient measure of fitness is survivorship—those children who do not survive cannot reproduce. The negative impact of father absence on child survivorship has been well documented in Western populations (Bennett 1990, Gaudino, Jenkins, and Rochat 1999, Golding, Henriques, and Thomas 1986, Scholer, Mitchel Jr., and Ray 1997). Under certain circumstances, such as when men are unable to adequately contribute household income, father absence can actually be positively associated with child survivorship. This was found among men of the Dominican Republic, for whom employment opportunities are scarce (Brown 1973). Across traditional populations, the magnitude of the father effect on child mortality varies greatly. The highest effect thus far reported was found among the Ache foragers of Paraguay, for whom the presence of a father confers a 62% proportional increase in the likelihood of offspring survival to adulthood (Hurtado and Hill 1992). Among the !Kung and Hiwi foragers of Botswana

and Venezuela respectively, the effect is smaller, but apparent (Hurtado and Hill 1992, Pennington and Harpending 1988), while there is no apparent effect found among the Hadza foragers of Tanzania (Blurton Jones et al. 2000), or among a rural Gambian horticultural population (Sear et al. 2002).

Few studies have fully investigated the potential causes of these survivorship effects, such as increased morbidity or violence or decreased nutritional intake. Hurtado and Hill (1992) found that, among the Ache, deaths caused by sickness experienced the greatest proportional increase out of all causes of death for father-absent children. Yanomamö children of divorced or junior mothers were more likely to be found with ectoparasite infection (Hagen et al. 2001), although no other significant differences were found in morbidity levels (Hames, Oliver, and Chagnon n.d.). Death from violence was significantly elevated in fatherless children among the Ache as well (Hurtado and Hill 1992), although this may be due to infanticidal practices that target fatherless children (see above). Additionally, there is a large body of evidence indicating that living with a step-father greatly increases the probability of infanticide in Western populations (Daly and Wilson 1985). Fatherless children may even suffer higher rates of accidents due to reduced supervision. Tooley et al. (2005) found that children living without their fathers in an Australian sample experienced higher mortality rates due to accidental injury. They also found that step-fathers actually *increase* the risk of accidental death beyond that experienced by children living with only their mothers.

Weights and heights of children co-residing with step-fathers within a Caribbean community were lower than those living with both biological parents (Flinn, Leone, and Quinlan 1999). No differences were found in such measures, however, between children

with and without fathers among the Yanomamö (Hames, Oliver, and Chagnon n.d.) or a rural Gambian population (Sear, Mace, and McGregor 2000). Heights of British children were found to be negatively affected by parental divorce for a 1958 sample (Li, Manor, and Power 2004), but not so for a 1991 sample (Li and Power 2004). Interestingly, Flinn et al. (1999) found that children living with step-fathers had lower levels of fluctuating asymmetry than did children living with both biological parents. Low levels of fluctuating asymmetry have long been argued to be a signal of developmental stability—indicating superior genetic fitness, resistance to disease, and nutritional intake—making the result quite peculiar (Gangestad and Thornhill 2003, Van Valen 1962, Zakharav 1981).

In the only study to look at reproductive success, Flinn (1988b) found that both sons and daughters that had lived with step-fathers had fewer children living to their first year than did children that only lived with both biological parents.

Effect of Father Absence on Reproductive Strategies—The Psycho-Social Stress Model

Draper and Harpending (1982) and Belsky, Steinberg and Draper (1991) formulated a novel hypothesis to account some of the behavioral differences recorded between children of intact and broken homes. They argued that humans had evolved to use the family formation strategies of parents as a proxy for the importance of pair-bond stability and bi-parental care in the environment and population into which they were born and to alter their reproductive development and future strategies accordingly. Unstable parental pair-bonds would be indicative of an environment in which investment in children's competitiveness is less important, favoring an accelerated development and

short-term sexual strategy. Belsky, Steinberg and Draper (1991) then looked to attachment theory to provide a proximate mechanism, arguing that the effect could be caused by the fact that fatherless children grow up to be less securely attached due to the psychosocial stress involved with being raised in a single-parent family and that the effects of this insecure attachment (e.g. difficulty in establishing long-term relationships) predispose the children to the appropriate reproductive strategy.

Based on this logic, children of broken homes should be sexually precocious and more likely to raise children in single-parent homes as well. There is a large body of evidence suggesting that in relation to children of intact homes, daughters of broken homes reach menarche earlier (Hoier 2003, Maestripieri et al. 2004, Moffitt et al. 1992, Quinlan 2003, Romans et al. 2003), have their first sexual experience earlier (Ellis et al. 2003, Hoier 2003, Quinlan 2003), and both sons and daughters of broken homes have less stable marriages as adults (Lancaster and Kaplan 2000, Quinlan 2003, Quinlan and Flinn 2003). All of these studies, however, focused on Western populations in which food stress is rarely a limiting factor to the onset of reproductive functioning. In traditional populations, the negative impacts of father absence on nutritional levels of children may actually delay maturation and consequently offset the acceleration of reproductive development that it also entails. Indeed, father absence was not associated with first age of reproduction for women of a rural Caribbean community (Quinlan 2001) or Ache men of Paraguay (Waynforth 2002), and significantly *positively* associated with age of first reproduction for Mayan men of Belize and Ache women (Waynforth 2002).

Finally, it is important to note that some researchers have raised the issue of self-selection in this body of research, noting that any effect may be driven by heritable

predispositions to reproductive strategies (Comings et al. 2002, Moffitt et al. 1992, Rowe 2000). Specifically, some researchers have attributed the association to an androgen-receptor gene which was found to be linked with sexual compulsivity and a higher number of lifetime sex partners in men and precocious sexual development in women (Comings et al. 2002), although these effects were not repeated in a subsequent study (Jorm et al. 2004).

Summary of Literature

It is quite evident that studies of Western populations dominate the investigation of the effects of father absence. Within these populations, we see a consistent negative effect of father absence on child survivorship. Additionally, there is fairly strong evidence that father absence influences the psychological, cognitive and behavioral development of children. Evidence concerning traditional populations is more scarce and variable. Within these populations, the most common measure that is utilized to evaluate the effect of father absence is child survivorship, with the results showing no consistent effect. Few go beyond to investigate possible proximate mechanisms that lead to mortality differences (see Hames, Oliver, and Chagnon n.d., Sear, Mace, and McGregor 2000 for exceptions). A small number of studies did investigate the effect of father absence on child growth and morbidity levels, again reporting mixed effects. Finally, no study has specifically investigated the *true* cost of family abandonment for men of any population, which is the reduction in the summed reproductive values of the progeny the men leave behind. This can only be deduced by an evaluation of the effect of father absence on child survivorship *and* reproduction. Only one study investigated

reproductive successes of children, but this was specifically a comparison between children that lived with a biological father versus children that lived with a stepfather. This research will attempt to partly fill this void in the literature by providing a comprehensive analysis of the effect of father absence on multiple measures of offspring fitness within a single population.

HYPOTHESES AND PREDICTIONS

The various hypotheses concerning paternal care and provisioning produce differing predictions with respect to the true value of the father's presence. As argued in Chapter 1, the Paternal Provisioning Model posits that men invest directly in their children in order to increase their fitness (as well as increase wife's fertility), and therefore predicts the greatest effect of father presence on offspring success. Because husbands and wives experience high levels of complementarity, their combined efforts are expected to result in greater overall levels of investment even if wives increase their own investment to compensate for the loss of a husband.

The Mating Effort Model, on the other hand, produces more ambiguous predictions with respect to the value of a father's presence. Despite the fact that the goal of men's care may be to impress their wives, their care may nevertheless produce appreciable increases in offspring fitness. The model does, however, predict that there should be no differences between children living with a biological father and children living with a step-father. The Tsimane dataset does not allow for this prediction to be tested, but it is discussed below in relation to the existing literature.

Table 5.1 Predicted effects of father absence by theoretical model.

Variable	Predicted Direction for Father-Absent Children		
	Paternal Provisioning	Tolerated Theft	Psychosocial Stress
Survivorship	<i>Negative</i>	<i>N/A</i>	<i>N/A</i>
Morbidity	<i>Positive</i>	<i>No Difference</i>	<i>N/A</i>
Height for Age	<i>Negative</i>	<i>No Difference</i>	<i>N/A</i>
Weight for Age	<i>Negative</i>	<i>No Difference</i>	<i>N/A</i>
Completed Fertility for Age	<i>Negative</i>	<i>N/A</i>	<i>N/A</i>
Age of First Reproduction	<i>N/A</i>	<i>N/A</i>	<i>Negative</i>

The Tolerated Theft Model proposes that men do not direct the distribution of the resources that they target and they are therefore unable to invest in their families (Hawkes, O'Connell, and Blurton Jones 2001b, Hawkes, Rogers, and Charnov 1995). Under this model, the amount of resources available to the children should be independent of the father's presence, and his presence should therefore have no impact on such measures as growth or morbidity (his presence may still confer protection or social benefits).

Finally, the Psycho Social Stress Model suggests that children base their developmental trajectories on the reproductive strategies of their parents, and that children of fatherless homes should therefore begin reproducing earlier than children of intact homes. Although the testing of this model does not directly relate to the theoretical goals of this research, the ease with which the test is conducted and the lack of such data from traditional populations makes the exercise worth-while. A synopsis of all the predicted effects is presented in Table 5.1.

METHODS

Demography, Definition of Fatherless Homes

Refer to Chapter 3 for a synopsis of the demography methods. From this dataset, the entire reproductive histories of all individuals of the four core communities and their parents were used to determine years of birth, death, divorce and residence. Children that were stillborn were not included in this sample. Individuals were excluded if the mother died before the age of 15 unless the individual had died before the mother. Individuals were also excluded if any of the following variables were unknown: year of mother's death, year of father's death, or marital status of parents. Attempts were made to acquire all missing information, particularly for individuals who had lost their father since this sample was smaller. Father absence was defined by a father's death or a divorce in which the father did not continue to raise the children. On the occasion that custody was not explicitly mentioned in the demography data, fathers were assumed to be absent if they resided in a separate community. Cases in which father custody could not be determined were excluded.

Although it was assumed that children stayed with their mothers upon the loss of the father, it is important to note that widowed or divorced mothers sometimes leave their children with their parents upon remarriage. Unfortunately, the demographic data were not detailed enough to always know who was caring for the children once the father was gone. Therefore, all father-absent children were included unless their mothers had actually died. Although this may inflate the effect of father absence, it still provides an accurate measure of the cost of desertion to the man as well as the benefit of being raised by both biological parents over alternative situations. The fact that the caretakers were

not always known also precluded any tests of the effect step-parental presence on the fitness outcomes of children.

Survivorship

Using the demography dataset, survival analysis was performed to determine the effects of father absence on children's survivorship (see Data Analysis section below). The effect of father absence on levels of adult mortality could not be determined due to a bias inherent in the data collection methods. Individuals provided information on only their own reproductive histories, those of parents and those of siblings. Since inclusion into this sample required demographic information of parents, older individuals who had already died were not available to provide this information. Therefore, this sample was biased at later ages towards individuals that had actually survived and were available to provide information concerning their parents.

Morbidity

Data for morbidity cover two years of data collection. For the first year, three Bolivian physicians visited the core communities at relatively regular intervals and conducted surveys of everyone that was in the village. During the second year, two of the physicians continued to sample each community twice. During their visits, they asked if any individuals had medical complaints. The physicians would then analyze any patient with a complaint, diagnose the problem and provide proper treatment. All complaints and diagnoses were recorded; individuals that did not report any complaints were marked as healthy and those not present in the community were marked as absent.

Height and Weight

Anthropometric data was collected at the beginning of the first year of data collection by myself, Michael Gurven, three other graduate students, and three translators. Heights for individuals old enough to stand were collected using a stadiometer, while infant length was measured with a measuring tape. Weight was measured with a Tanita BF series digital scale. Infant weight was determined by subtracting the mother's weight from her weight while holding the baby.

Cumulative Fertility and Age of First Reproduction

Cumulative fertility (number of births by age and number of living children by age) and the age of first live birth was calculated from the demography dataset.

Data Analysis

For analyses of discrete one-time events, including death (survivorship) and first reproduction, survival analysis (often referred to as event history analysis) is employed. Survival analysis tests the effects of independent variables on the probability of an event happening through time and is particularly useful when using censored data. A subject may be censored if he or she leaves the sample before the study is complete or the event does not take place by the termination of the study. The PHREG procedure in SAS was used to perform regression models based on the Cox proportional hazards model. This model allows for time-dependent predictor variables, such as father presence/absence.

For the morbidity data, a generalized estimating equations model is applied (refer to Chapter 3 for description) in order to test the effect of father absence on the probability of being diagnosed with a medical condition for individuals 10 years of age or younger. Personal identification number is included as a repeated subject and the analysis is run using a binary distribution, logit link and exchangeable correlation structure. Age and sex are included in the model as controls.

For anthropometric measures, the samples are divided into adult periods and childhood periods based on a qualitative assessment of the timing of the cessation of growth. Height appears to level off around the age of 15 where as weight continues to increase until the age of 20. The GLM procedure is utilized in SAS to perform multiple regression analyses on the data for male and female children and adults.

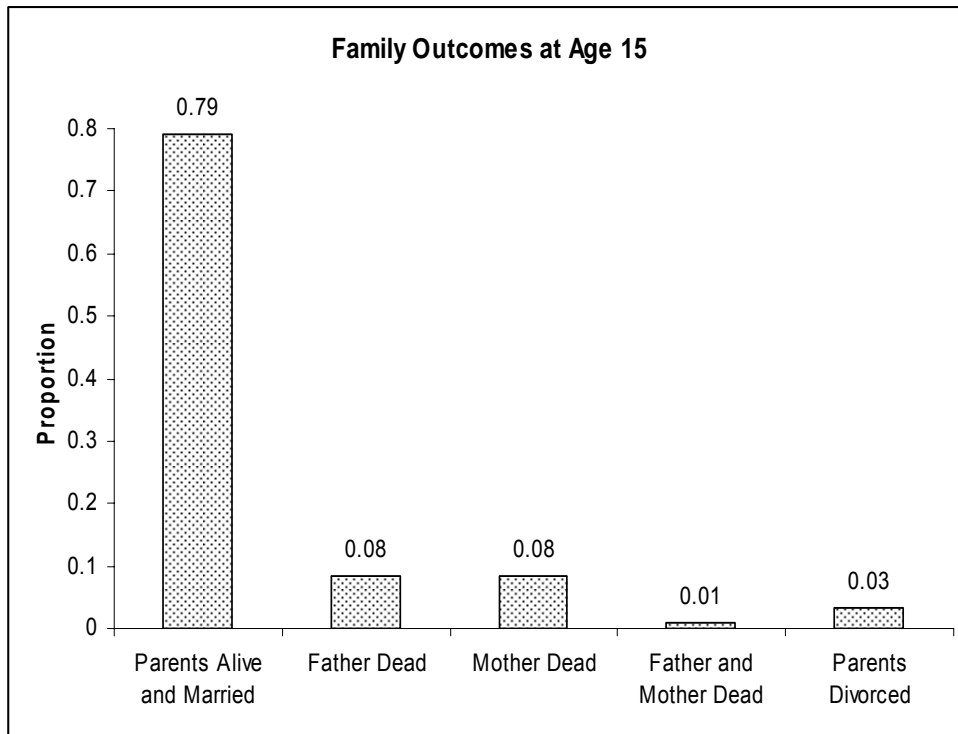
Because cumulative fertility is a count variable measuring total number of births (or living children), Poisson regression is employed in the GENMOD procedure in SAS (Frank and Heuveline 2005, Waynforth 1999b).

RESULTS

Descriptives

766 births were recorded with 146 deaths prior to the age of 15. 100 individuals had experienced the death of a father before the age of 15 and 27 had lost their father due to parental divorce before this age. Figure 5.1 displays the proportion of individuals in each family outcome at the age of 15. Because individuals with absent fathers may have been over sampled in the full dataset (see Methods section), this figure only pertains to individuals age 15 and older that were living in the core communities at time of data

Figure 5.1 Proportion of children in each family outcome at age 15 (n=120).



collection. Very few individuals (4 of 120) were children of divorced parents, which is testament to the remarkable stability of Tsimane marriages. From the reproductive histories of two of the core communities, 36 divorces were recorded. Of these, the latest divorce occurred after 17 years of marriage. As a conservative measure, we can assume that marriages that last at least 20 years are no longer at risk for divorce. 76 marriages were recorded that had taken place prior to 1983 (20 years prior to the data collection), of these, 15 or 19.7% ended in divorce. Nine of these marriages had produced children, although the average number of surviving children at the time of divorce was only 0.92, accounting for the small number of children of divorced parents at 15 years of age.

Survivorship

Figure 5.2 displays the survival and mortality curves for children with and without fathers. For each risk year, an individual's inclusion into either group is determined by whether the father had left prior to that year. For example, an individual whose father leaves at the age of 5 would be included in the Father Present group until age 5 and then in the Father Absent group thereafter. Clearly, fathers provide a buffer to child mortality, at least for the first decade. Survival analysis affirms this point (Table 5.2). Mortality hazards were evaluated up to the age of ten. Sex and year born were included in the survival model in order to control for any sex or cohort effects. Although these controls are not significant, they enhance the significance of father absence. Father absence doubles the risk of dying in any given year in the first decade of life ($B=0.694$, Hazard=2.002, $p=.026$). Father death produces the greatest increase in risk, while the loss of a father through divorce appears to have little impact on child survivorship. The small sample size of 27 individuals with divorced parents, however, may hinder any meaningful interpretation. After the first decade, the mortality hazards of children with and without fathers are very similar and both very low.

Figure 5.3 displays the causes of mortality under the age of 15 for all children. Disease poses by far the greatest risk to children and is nearly 10 times as frequent as the second most common cause of mortality—accidents. Gastrointestinal diseases are more frequently the cause of disease related deaths among infants, while measles grows in frequency as children age (Figure 5.4). Aside from disease and accident, the other four listed causes of deaths are all nearly equally as rare. Fathers would most likely have no appreciable impact on the probability of infant deaths due to

Figure 5.2 Survival and mortality hazard plots for children with and without fathers.

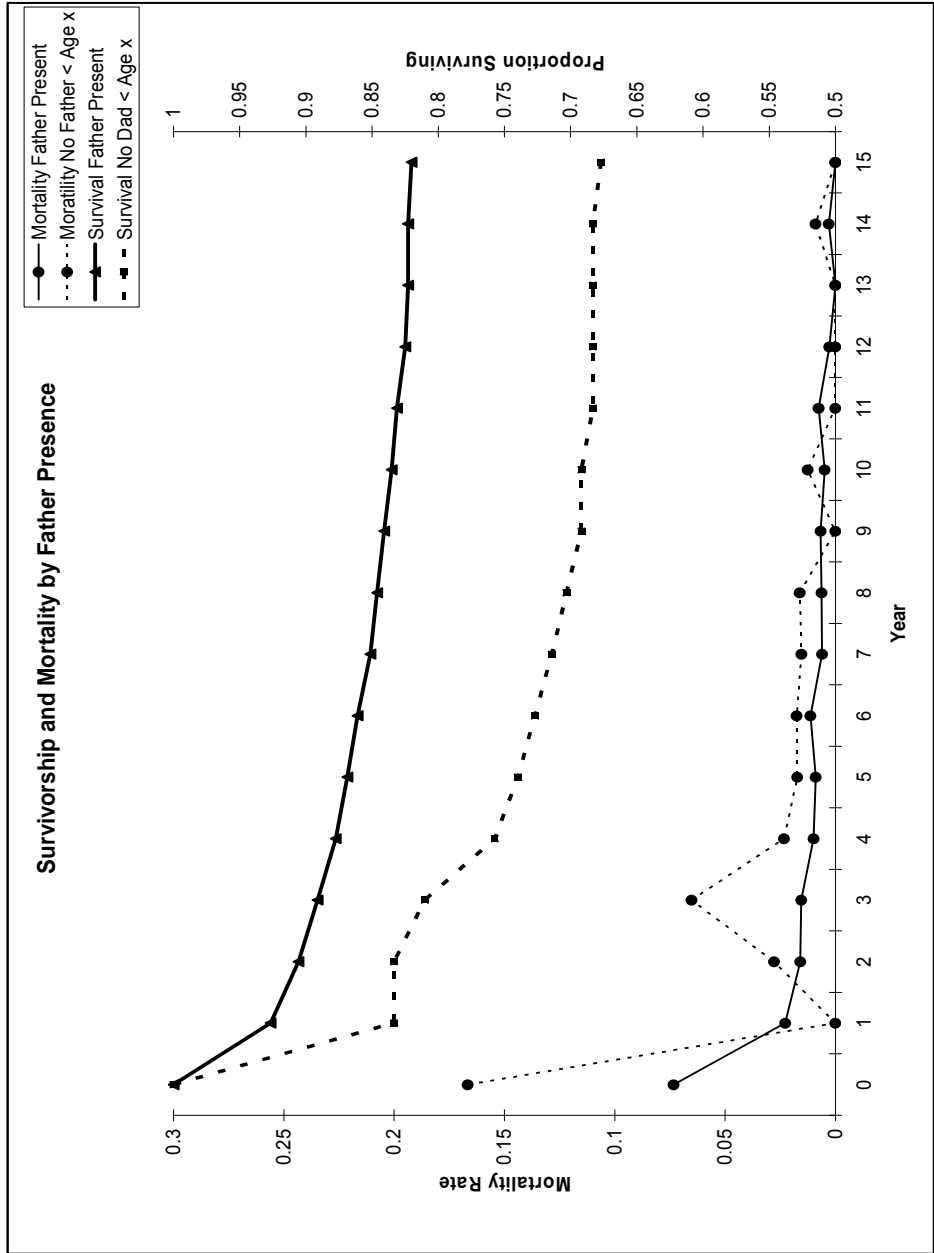


Table 5.2 Survival analyses using Cox proportional hazards model for varying types of father absence up to age 10.

Variable	Parameter Estimate	Std. Error	Hazard Ratio	p
Father Death and Divorce				
Father present n=668, father dead n=72, parents divorced n=26. Model Likelihood Ratio: $\chi^2=5.588$, df=3, p=0.134				
Father Absence**	0.694	0.311	2.002	0.026
Sex (Male=1)	-0.195	0.168	0.823	0.247
Year Born	-0.002	0.004	0.998	0.580
Father Death				
Father present n=668, father dead n=72 Model Likelihood Ratio: $\chi^2=6.905$, df=3, p=0.075				
Father Absence**	0.925	0.358	2.522	0.010
Sex (Male=1)	-0.222	0.170	0.801	0.192
Year Born	-0.001	0.004	0.999	0.787
Parents Divorced, No Father				
Father present n=668, parents divorced n=26 Model Likelihood Ratio: $\chi^2=0.905$, df=3, p=0.824				
Father Absence	0.130	0.589	1.139	0.825
Sex (Male=1)	-0.140	0.173	0.870	0.421
Year Born	-0.002	0.004	0.998	0.624

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

the last three causes (mother's death, premature birth, birth defect), but they may very well buffer children from the risk of dying from the first three (sickness, accidents and infanticide). In this dataset, only 13 deaths prior to the age of 10 were recorded amongst individuals who had lost their fathers. Although this may seem too small to warrant the effects reported above, many deaths were concentrated in the first years, during which the risk set was much smaller since fewer individuals had lost their fathers by this time (this would make the mortality rate higher). Of these 13 deaths, 10 were due to illness and 3 were due to infanticide (two perpetrated by step-fathers and one by maternal kin).

Figure 5.3 Childhood mortality rate by cause of death (n=804 risk individuals for age <1; n=646 for age 1 to 5; n=451 for age 6 to 15). Rates refer to entire age brackets.

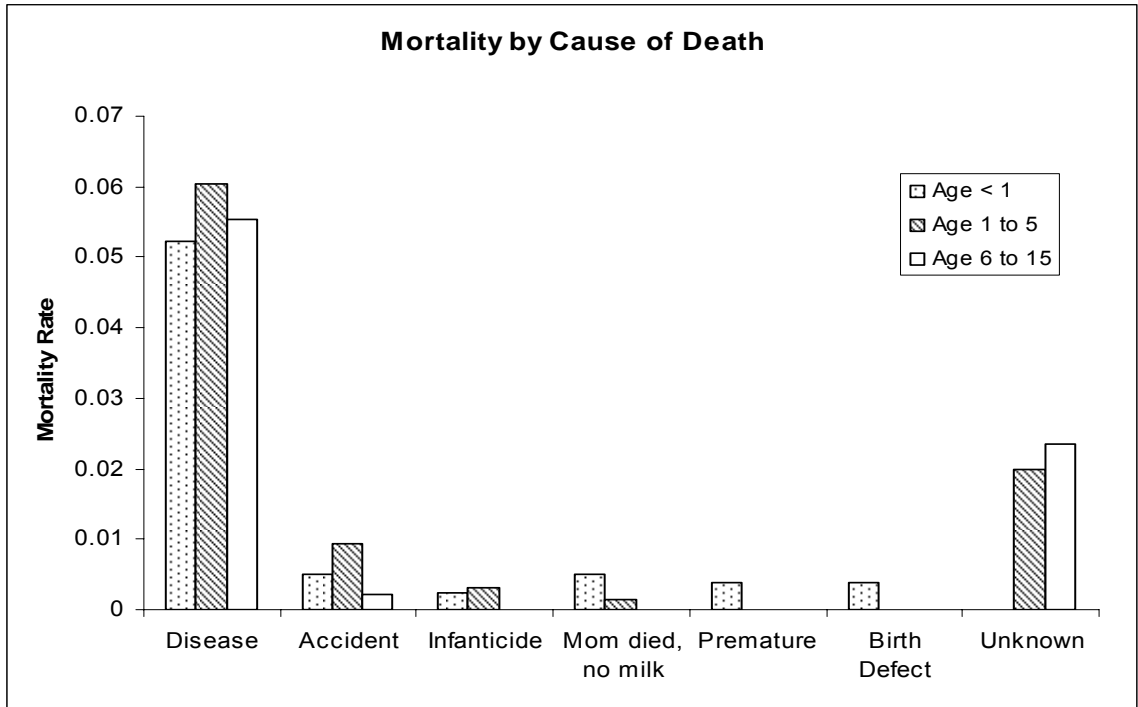


Figure 5.4 Proportion of all disease related deaths caused by different disease groups (n=39 deaths for age <1; n=39 for age 1 to 5; n=21 for age 6 to 15, n=20).

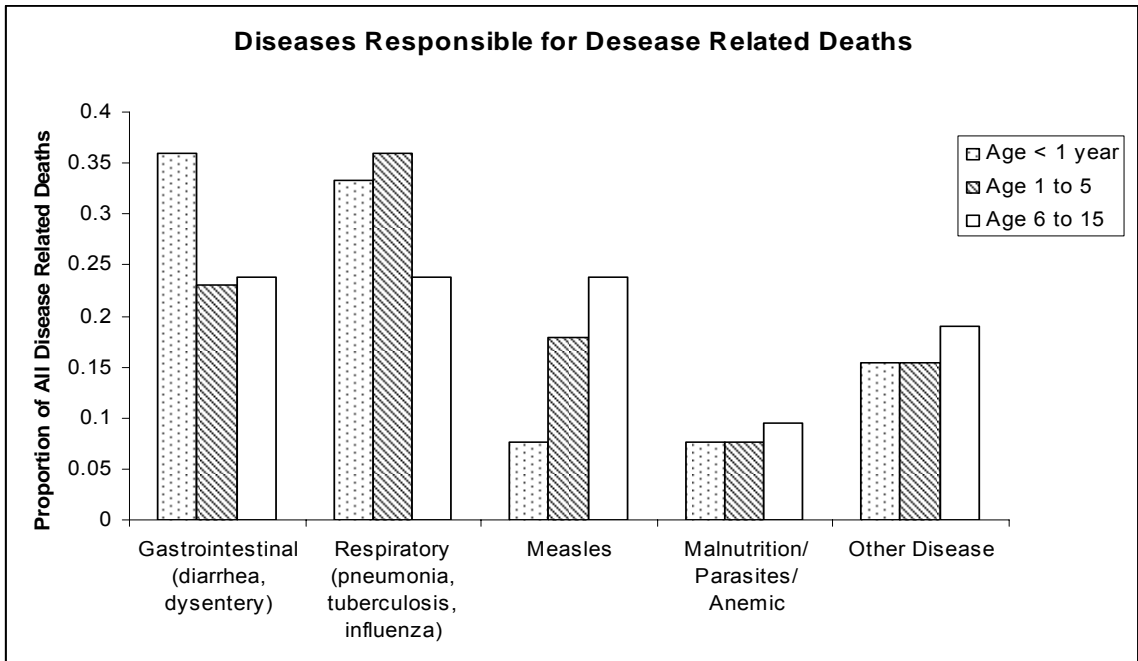


Table 5.3 Survival analyses using Cox proportional hazards model for different causes of death. Individuals dying of other causes were considered censored with no event.

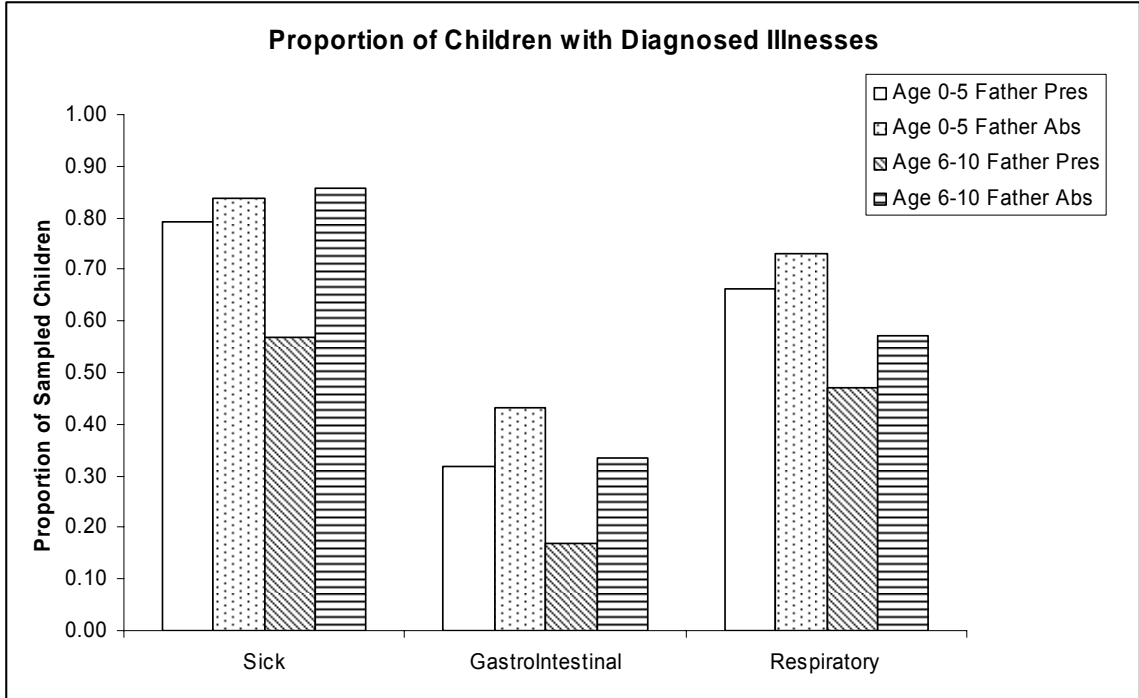
Variable	Parameter Estimate	Std. Error	Hazard Ratio	p
Disease Related Death				
Father present n=639, father dead n=72, parents divorced n=26 Model Likelihood Ratio: $\chi^2=5.114$, df=3, p=0.164				
Father Absence**	0.779	0.362	2.180	0.032
Sex (Male=1)	-0.237	0.209	0.789	0.256
Year Born	-0.002	0.005	0.998	0.662
Accident Related Death				
Father present n=639, father dead n=72, parents divorced n=26 Model Likelihood Ratio: $\chi^2=1.149$, df=3, p=0.765				
Father Absence	-14.159	1555	0 ¹	0.993
Sex (Male=1)	-0.026	0.634	0.98	0.968
Year Born	0.004	0.017	1.004	0.807
Infanticide				
Father present n=639, father dead n=72, parents divorced n=26 Model Likelihood Ratio: $\chi^2=16.148$, df=3, p=0.001				
Father Absence****	4.885	1.369	132.291	<0.001
Sex (Male=1)	0.465	1.060	1.592	0.661
Year Born	-0.022	0.030	0.978	0.464

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

¹ No individuals with absent fathers experienced accidental deaths

Despite the small number of events, father absence is strongly associated with a greater probability of dying from disease (B=0.799, Hazard=2.180, p=0.032) and infanticide (B=4.885, Hazard=132.291, p<0.001) (Table 5.3). The fact that no accidental deaths were recorded for children of father-absent homes leads to a positive parameter but an inability to calculate the hazard ratio. Regardless of this, because only one such death would be expected (8.2% of 14 = 1.1), the test is highly non-significant.

Figure 5.5 Proportion of medical evaluations in which children (10 and under) are diagnosed with any disease, a gastrointestinal disease and a respiratory disease (n=15 individuals, 58 total evaluations for fatherless children; n=135 individuals, 662 total evaluations for children with fathers present).



Morbidity

As shown above, fathers may buffer their children from the risk of dying from disease. In order to assess whether father presence decreases the risk of developing an illness in the first place, medical data collected over a two year period were analyzed. Because this data only pertains to individuals that were children at the time of data collection (unlike the retrospective survivorship data), only 15 children age 10 and under were sampled that were not living with their fathers. These individuals were examined an average of 3.9 times by the medical team. 135 children were sampled that were living with their fathers with an average of 4.9 doctor visits per person. Figure 5.5 displays the

proportions of diagnoses from the pooled samples. In each category and age bracket, fatherless children experience higher rates of illness. Table 5.4 displays the results of the generalized estimating equations analysis testing whether father absence at the time of the examination is predictive of whether or not individuals were diagnosed with an illness. Older children appear to be less likely to be diagnosed with an illness for all three categories. The probability of being diagnosed with an illness and specifically with a gastrointestinal illness is marginally higher if the father is absent (Sick, $p=0.082$; Gastrointestinal, $p=0.088$). The effect of father absence on the probability of being diagnosed with a respiratory illness is in the predicted direction, but non-significant. The direction and significance levels of the tests do not substantially change with the use of a continuous variable instead of the categorical variable for father absence (i.e. number of years of father absence).

Anthropometry

Father absence appears to have no systematic effect on anthropometric measures. Figure 5.6 displays the plots of heights and weights by age for men and women by whether or not the father was present until the end of the tenth year. Regression lines are also plotted that were calculated for the periods of childhood (0 to 15 for height and 0 to 20 for weight) and adulthood. The divisions were made to better assess the effect of father absence on completed height as well as the growth rate and were assigned by qualitatively determining the best fit. The fact that the two lines come very close to

Table 5.4 Generalized estimating equations analysis of probability that a child will be diagnosed with any disease, gastrointestinal disease or respiratory disease by father absence, age and sex. Parameter estimates are logit estimates.

Variable	Parameter Estimate	Std. Error	Z	p
Sick				
Father present n=135 individuals, father absent n=15 individuals				
Intercept	1.643	0.188	8.74	<0.001
Father Absence*	0.467	0.268	1.74	0.082
Age****	-0.022	0.170	-0.13	<0.001
Sex (Male=1)	-0.143	0.021	-6.72	0.896
GastroIntestinal				
Father present n=135 individuals, father absent n=15 individuals				
Intercept	-0.426	0.175	-2.44	0.015
Father Absence*	0.479	0.281	1.71	0.088
Age****	-0.139	0.021	-6.51	<0.001
Sex (Male=1)	0.015	0.160	0.09	0.927
Respiratory				
Father present n=135 individuals, father absent n=15 individuals				
Intercept	1.083	0.176	6.15	<0.001
Father Absence	0.212	0.252	0.84	0.401
Age****	-0.144	0.019	-7.56	<0.001
Sex (Male=1)	-0.048	0.157	-0.31	0.760

*p<0.10 (and in predicted direction), **p<0.05, ***p<0.01, ****p<0.001

connecting for all of the father-present samples (the largest samples) indicates that the age demarcations are relatively accurate. The better fit of this method, however, comes at the expense of reducing the sample sizes for each category.

The detailed results of the multiple regression analyses are displayed in Table 5.5. Included in these models are father absence at the time of measurement (or prior to end of the tenth year of life for individuals older than 10), age and an interaction between these two. No effects are significant in the predicted direction. Indeed, the only effect that is

Figure 5.6 Plots of men and women's height and weight by age and father presence. Regression lines are derived from separate analyses for childhood (ages 0 to 15 for height and 0 to 20 for weight) and adulthood (see Table 5.5 for sample sizes).

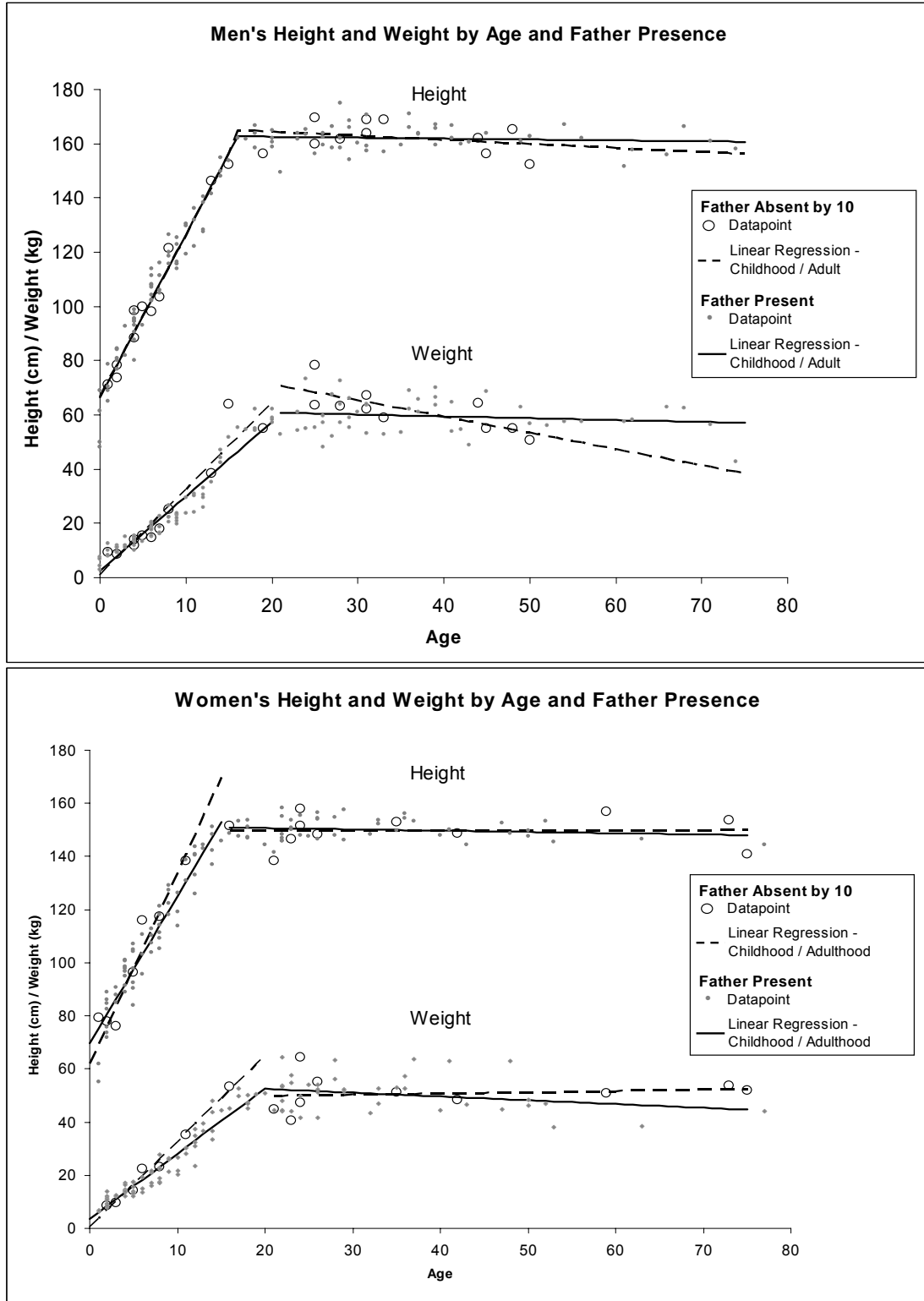


Table 5.5 Multiple regression analysis of men's and women's height and weight by age and father presence. Analyses are done separately for childhood (ages 0 to 15 for height and 0 to 20 for weight) and adulthood.

Variable		Child			Adult		
		Parameter Estimate	Std. Error	p	Parameter Estimate	Std. Error	p
Height		Male – n=64 dad; 11 no dad; p<0.001 Female – n=62 dad; 6 no dad; p<0.001			Male – n=54 dad; 11 no dad; p=0.662 Female – n=47 dad; 11 no dad; p=0.792		
Intercept	Male	66.367	1.513	<0.001	163.207	1.702	<0.001
	Female	69.820	1.745	<0.001	151.654	1.672	<0.001
Father Absence	Male	0.104	3.681	0.978	4.209	5.516	0.448
	Female	-7.994	6.269	0.207	-2.145	3.309	0.520
Age	Male	6.020	0.200	<0.001	-0.033	0.045	0.448
	Female	5.533	0.218	<0.001	-0.048	0.049	0.334
Father Absence*Age	Male	-0.040	0.493	0.935	-0.116	0.153	0.451
	Female	1.651	0.942	0.084	0.054	0.083	0.517
Weight		Male – n=73 dad; 11 no dad; p<0.001 Female – n=72 dad; 7 no dad; p<0.001			Male – n=46 dad; 10 no dad; p=.030 Female – n=39 dad; 10 no dad; p=.412		
Intercept	Male	2.360	0.894	0.010	62.219	2.740	<0.001
	Female	3.578	0.761	<0.001	55.320	3.090	<0.001
Father Absence	Male	-1.700	2.456	0.491	21.07	8.567	0.017
	Female	-3.354	2.583	0.198	-6.358	5.754	0.275
Age	Male	2.758	0.093	<0.001	-0.069	0.067	0.307
	Female	2.455	0.078	<0.001	-0.141	0.085	0.105
Father Absence*Age	Male	0.421	0.261	0.111	-0.530	0.228	0.024
	Female	0.777	0.298	0.011	0.188	0.138	0.180

relatively consistent is that father-absent children seem to grow faster. The interaction effect is significantly higher for female weight and marginally so for female height and male weight. Looking at the plots, however, it is clear that these effects are driven by only a few individuals. Finally, the slope of men's weight in adulthood is significantly more negative for men from father-absent families. This effect is puzzling and again driven by only a handful of individuals. If the effect is indeed real, it may indicate

Table 5.6 Poisson regression analyses of men's and women's cumulative fertility by age and father presence.

Variable	Total Number of Births				Number of Surviving Children			
	Param Est	Std. Error	Chi-Square	p	Param Est	Std. Error	Chi-Square	p
Males								
Father present n=147, father absent by 10 n=15								
Intercept	-0.299	0.652	0.21	0.647	-0.613	0.733	0.70	0.403
Years Dad Present	-0.303	0.058	27.23	<0.001	-0.270	0.026	27.21	<0.001
Age	0.133	0.023	33.27	<0.001	0.138	3*10 ⁻⁴	54.78	<0.001
Age ²	-0.002	2*10 ⁻⁴	74.61	<0.001	-0.002	0.064	17.64	<0.001
Age*Yrs Dad Pres	0.007	0.002	22.52	<0.001	0.006	0.002	13.16	<0.001
Females								
Father present n=101, father absent by 10 n=23								
Intercept	-2.760	0.630	19.17	<.0001	-4.380	0.819	28.62	<.0001
Years Dad Present	0.052	0.045	1.32	0.251	0.139	0.057	5.92	0.015
Age	0.190	0.024	62.70	<.0001	0.246	0.031	61.77	<.0001
Age ²	-0.002	2*10 ⁻⁴	56.36	<.0001	-0.002	3*10 ⁻⁴	57.00	<.0001
Age*Yrs Dad Pres	-0.002	0.001	5.24	0.022	-0.005	0.001	13.01	<.0001

accelerated senescence due to overall lower fitness or the effects of an accelerated life-history trajectory.

Cumulative Fertility

Because all individuals that have reproduced are older than ten, the number of years the father was present was used as the measure of father absence. Age and Age² were included in the model to account for the deceleration of cumulative fertility with age. Finally, an interaction term between years of father presence and age was included to allow for differing slopes. The effect of father absence appears complex and differs between the sexes and through time, although this may be an artifact of the small sample sizes. For men's number of births and surviving children, both the number of years of

Figure 5.7 Total number of births and surviving children for age for men. Regression curves are results of Poisson regression with age and age^2 controlled along with interaction variable between age and number of births/surviving children.

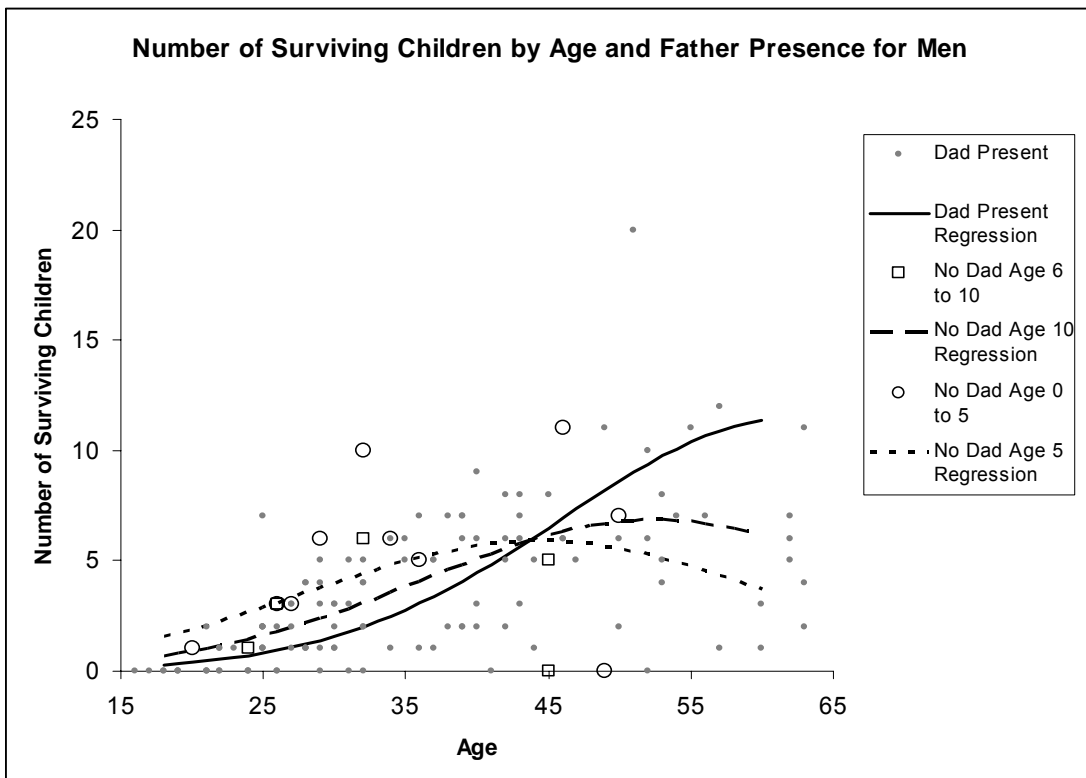
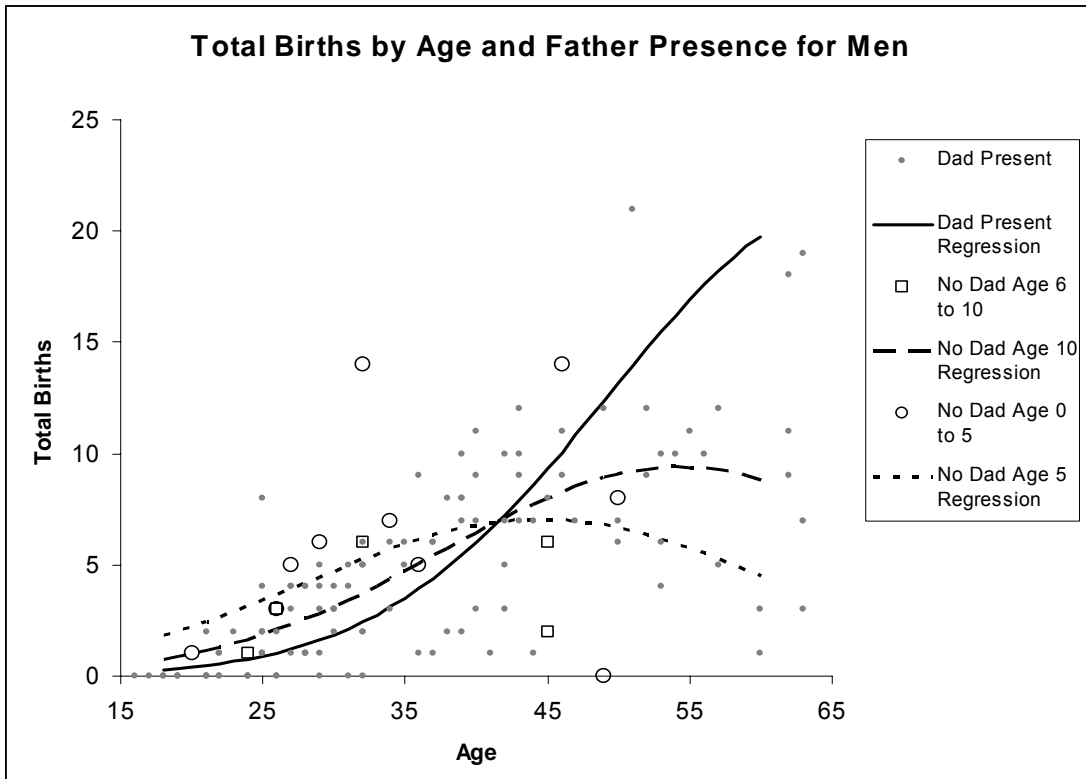
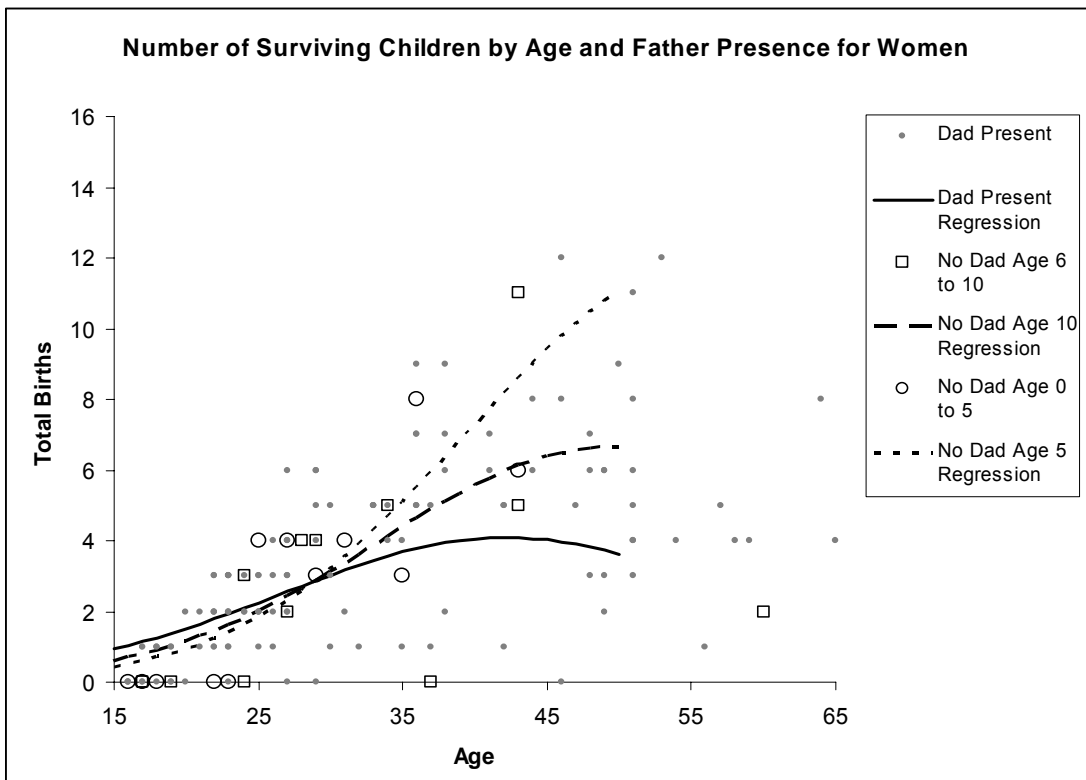
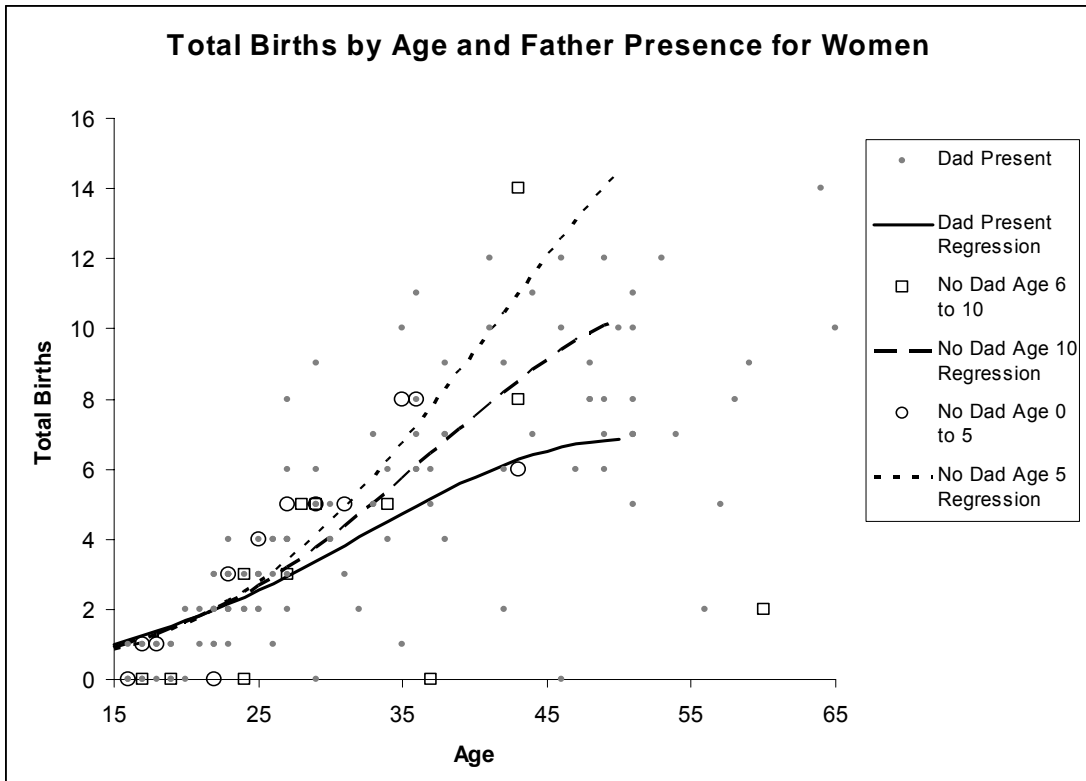


Figure 5.8 Total number of births and surviving children for age for women. Regression curves are results of Poisson regression with age and age^2 controlled along with interaction variable between age and number of births/surviving children.



father presence and its interaction with age are significant but in opposite directions, resulting in the predicted values being higher for father-absent children in the early years of men's reproductive careers and then lower in the latter years (Figure 5.7 and Table 5.6). Father absence actually appears to have a *positive* effect on women's completed fertility for age (Figure 5.8 and Table 5.6). Although the effect of years of father presence is negative, it is dwarfed by the significantly positive interaction effect.

Age of First Reproduction

Father absence is not significantly associated with age of first reproduction for men or for women, although once again, small sample sizes shed doubt on the reality of the results. Figure 5.9 shows the proportion of individuals having reproduced by age for individuals from father-absent and father-present homes and Table 5.7 displays the corresponding survival analysis. Men from fatherless households outpace men from intact homes for the first few years of reproduction, resulting in a median age of first birth that is lower (23.40 for father-present, 21.50 for father absent), but a number of fatherless individuals do not reproduce until very late or fail to do so completely. By age 36 (35 was the highest age of first birth), only 1 out of 42 individuals that were raised with fathers had failed to reproduce, but 2 out of 5 individuals who had lost their fathers had not yet reproduced ($\chi^2=10.850$, $df=1$, $p<0.001$). If we remove the extremely late reproducers that had not father a child by 30, then the years of father present term becomes significantly negative ($B=-0.117$, Hazard Ratio=0.890, $p=0.015$), indicating that for those men who are not somehow inhibited from marrying and reproducing, father absence is associated earlier first reproduction. For the model including all men, the

Table 5.7 Survival analysis of year of first birth by sex and years father present.

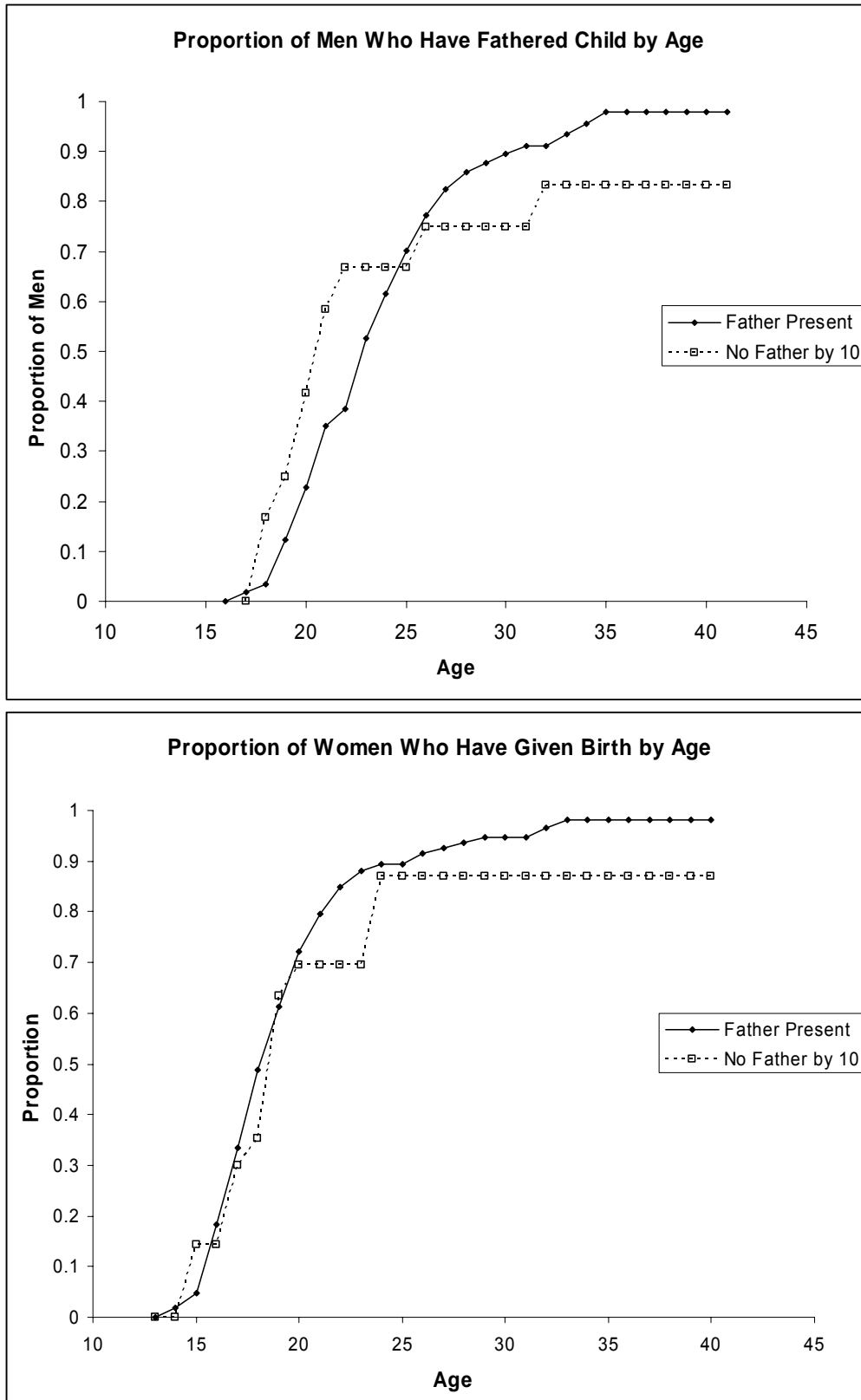
Variable	Parameter Estimate	Std. Error	Hazard Ratio	p
Males				
Father present n=97, father absent by 10 n=12. Model likelihood ratio: $\chi^2=7.340$, df=2, p=0.025				
Years Dad Present	0.011	0.044	1.011	0.801
Year Born	0.020	0.008	1.020	0.011
Females				
Father present n=110, father absent by 10 n=22 Model likelihood ratio: $\chi^2=4.428$, df=2, p=0.109				
Years Dad Present	-0.011	0.047	0.989	0.815
Year Born	0.014	0.007	1.014	0.043

early reproduction by some father-absent individuals is offset by the late reproducers, which leads to no overall effect of growing up with no father on the hazard of first reproduction. For women, the results are non-significant as well, and except for one woman who failed to reproduce, the curves appear very similar. Finally, the significance of the birth-year variable indicates a historical trend for earlier reproduction.

DISCUSSION

Father absence was shown to be associated with a significant decrease in survivorship in the first decade of life, doubling the risk of dying in any given year. Specifically, deaths due to disease and infanticide are more common among fatherless children than among children of intact homes. Compared to other traditional groups, the “father effect” of Tsimane dads is somewhere in the middle, providing children with a 22% proportional increase in the probability of living to adulthood (see Blurton Jones et al. 2000). This is corroborated by the fact that fatherless children are more likely to be

Figure 5.9 Survival analysis of year of first birth by sex and years father present.



diagnosed with a disease when visited by the medical team. Anthropometric measures, however, did not fit this pattern. Father-absent girls actually grow more rapidly, although there is no effect on the growth of boys or on the overall completed size of men and women. The effects of father absence on reproduction were also somewhat convoluted. Tsimane men who grow up without fathers appear to reproduce earlier, yet have lower total fertility and a higher probability of failing to reproduce. Interestingly though, women who have lost their fathers tend to have higher completed fertility for age although they do not start reproducing any earlier. These results and those of previous studies are discussed below in relation to the different models.

The survivorship and morbidity data clearly support the Paternal Provisioning Model. A father's presence buffers children from the risk of death and disease. This means that a) Tsimane men do experience a fitness cost to family desertion in the form of reduced offspring quality, and b) children raised in households with both parents fair better than those raised under alternative arrangements. From the literature, it is clear that this effect is the norm rather than the exception, and although this effect may not be an accurate reflection of the value of men's care, it is at least evidence that such care does make a difference.

The most common cause of childhood death for the entire sample was disease, and fatherless children are more than twice as likely to die from it in any given year. Similarly, children from father-absent homes are marginally more likely to be diagnosed with a disease in medical surveys, again supporting the Paternal Provisioning Model (and refuting the Tolerated Theft Model). Tsimane fathers may be providing some benefit that allows children to allocate more energy to immune function, most likely through

increased provisioning, but possibly through reduced workloads and stress levels as well. Fathers are also instrumental in acquiring medical attention for their children when needed. Men are the main wage earners in families and are therefore responsible for purchasing medicines and paying off medical debts. Additionally, men are typically much more familiar with the nearest town of San Borja, where the only hospital is located, and better able to communicate with medical professionals in Spanish. Consequently, children are nearly always accompanied by their fathers on any trips taken for medical reasons.

Although rarer, the proportional increase in the risk of dying of infanticide experiences an even greater increase (much greater) in fatherless children than does that of dying of disease. Although the data preclude any tests concerning the effect of step-fathers on child well-being, the fact that two of the three infanticides were perpetrated by step-fathers is indicative of some difference in parental behavior. Step-fathers often provide great amounts of support to children they know not to be their own, but the literature abounds with reports of disparities between biological and step-parental care. This fact alone makes it clear that the Mating Effort Model cannot solely explain men's parental behavior, and that investment in biological children must provide fathers significant additional benefits through the increasing of offspring quality (Anderson 1999).

According to the anthropometric data, Tsimane children without fathers do not suffer any stunting or decelerated growth. In only one of three other subsistence populations that have been studied was a significant effect found of father presence on childhood growth (and this was in direct comparison to step-children), strengthening the

argument that the absence of a father's provisioning can often be compensated for by others (Flinn, Leone, and Quinlan 1999, Hames, Oliver, and Chagnon n.d., Sear, Mace, and McGregor 2000). Although these data support the prediction of the Tolerated Theft Model, it is important to note the lack of an effect of father absence could also be due to other caretakers increasing investment to compensate for the loss of a father.

In light of the survivorship and morbidity data, it is peculiar that the children, if anything, actually grow *faster* in father absent homes. This is, however, exactly what would be predicted by the Psychosocial Stress Model. According to this model, individuals raised in fatherless homes would be set on an accelerated life history trajectory, which would favor greater allocation to precocial development at the expense of mortality reduction. Perhaps this leads these individuals to allocate a larger proportion of energy to growth relative to immune function compared to their father-present peers.

Men's cumulative fertility and age of first reproduction also appear to fit the pattern of accelerated development detailed above, although again the effect is not clear. The fact that the fatherless men in this sample were more likely to have never reproduced and that their completed fertility appeared to be lower may indicate that these individuals are making the best of a bad situation. Indeed, a combination of the Psychosocial Stress Model, predicting precocial development, and the Paternal Provisioning Model, predicting lower fitness outcomes, best fits the men's data.

The women's reproductive data, however, indicate that father absence actually has a *positive* effect on the future fertility of Tsimane daughters, although it has no effect on when they actually start reproducing. The effect of father absence on cumulative fertility is quite puzzling and was not predicted by any of the models. Further tests need

to be performed to confirm its validity (the small sample size sheds some doubt), but if true, it may reflect that Tsimane women receive some unknown benefit from being raised without a father (or some cost to being raised with one). The fact that women did not start reproducing early is also intriguing, particularly since much of the support for the Psycho-Social Stress Model stems from research that focuses on the sexual development of women. As argued before, however, these studies have usually involved Western populations in which sexual development would not have been limited by the possible food stress that father absence may have entailed. The three other subsistence populations in which the predictions of the Psychosocial Stress Model have been investigated have also failed to find effects in the predicted direction (Quinlan 2001, Waynforth 2002).

Conclusion

The results of many of the analyses presented in this chapter are limited in clarity due to their small sample sizes, a problem that will hopefully be solved with continued research. Despite this, all three of the models tested in this chapter received some support. Father presence clearly provides a benefit to Tsimane children, although the fact that it does not increase offspring growth sheds some doubt on whether the main benefit is realized through increased provisioning. Additionally, there is some evidence that father absence is associated with precocial development, although this effect was not straightforward.

The study of father absence provides a good starting point in the estimation of the benefits men receive from parental care in terms of increased offspring success, and has

shown that men can impact offspring well-being in various ways. It also provides an accurate measure of the costs men and women must consider when contemplating divorce. Such studies, however, are hindered by the problems detailed at the beginning of this chapter and by the fact that they are relegated to only report the gross effects of the presence or absence of fathers, muddling the impact of the loss of paternal care with those from all of the other ramifications that go along with it—increased stress levels, changes in other caretakers' behaviors, changes in children's own behavior, etc.

If the goal is to investigate the value of paternal care, the resolution could be greatly fine tuned if instead of testing over this categorical distinction of father absence or presence, one were to investigate a continuous measure of actual investment. Some studies have provided tentative support that variation in paternal provisioning across intact families does impact offspring success. For example, Hill and Hurtado (1996) found that the children of better Ache hunters had slightly lower mortality, while Hawkes (1993a) reported greater weight gains in weaned children of better Hadza hunters. Although these studies present a more precise measure of male investment, they failed to report actual resource flows from fathers to children and therefore are complicated by the practices of widespread sharing in each population. Indeed, in a subsequent analysis, Hawkes, O'Connell and Blurton Jones (2001b) argued that the effect found among the Hadza was more likely due to better hunters being married to harder working wives. In order to by-pass all of these doubts and arguments concerning control of distribution and the goal of big-game hunting, the actual number of calories fathers provide to children could be used as an unambiguous measure of paternal investment. This would provide answers to the questions: Is variation in paternal provisioning predictive of child

outcomes? Are fatherless children actually consuming fewer calories? And if not, who is compensating for the lack of paternal provisioning? Researchers focusing on Western populations have also been trying to increase the resolution of their studies by investigating the effects of father “involvement” on offspring outcomes, although there has been some disagreement concerning the proper measurement of such a variable (Lamb 1997). The very difficulty involved with the measuring of such continuous variation in paternal investment may have been the primary reason that researchers began studying the salient distinction of father absence or presence in the first place.

Despite the methodology’s shortcomings, however, the long history of the study of father absence has given us insight into the value of an intact home to children, and hence to fathers and mothers. Among the Tsimane, we found that father presence has the largest impact on a child’s health and survivorship, greatly improving the chance that a child will live to adulthood. Disentangling the many possible pathways through which these effects could have been realized remains to be done.

CHAPTER 6: SUMMARY AND CONCLUSIONS

The goal of this dissertation was to test predictions derived from the prominent evolutionary models of paternal care in humans among the Tsimane of central Bolivia. To review, three models were examined. The Paternal Provisioning Model postulates that men invest in their children because of the direct benefits they receive from enhanced offspring fitness and the increase in wife fertility that it allows. The Mating Effort Model holds that men provide investment as a means of winning and maintaining access to the fertility of the mother of the recipients of that investment, and finally, the Tolerated Theft Model argues that men target resources that they are unable to invest in their children and that they maintain extended reproductive relationships with women because it is a more effective means of obtaining access to fertility than seeking sequential short-term partners.

I specifically chose tests for which the different models produced competing predictions in order determine which model best accounts for men's parental behavior. In addition to these, however, predictions that were unique to each model were also tested. From these tests, the Paternal Provisioning Model received the greatest support. The results indicate that Tsimane men can positively impact the well-being of their children, and the manner in which they deliver care implies that they are more concerned with this goal than enhancing their reputation with their wives. I provide a review of each chapter below, followed by a comprehensive summary of the data.

REVIEW OF RESULTS

Effect of Wife's Presence on Men's Parental Behavior

In Chapter 3, I examined the effect of the presence of others, particularly the wife, on the probability that a man would offer direct paternal care to a child. I showed that the need of the children was a better predictor of whether men offered care than was the ability to impress the wife, as men were significantly more likely to provide care when the wife was *absent*. In addition to this, men with younger wives did not bias their care more heavily to when their wife was present than did men with older wives, indicating that the fertility benefits left to be had within a marriage do not affect men's desire to impress their wives.

Despite strong evidence for the effect of children's need on men's care, the hypothesis that that men cooperate with wives to maximize the productivity of the marriage was only tentatively supported. When men were present with children, and therefore available for supervision, women were found to be significantly more likely to be with the children as well. Men's offering of care while in camp, however, did appear to enhance their wives' ability to engage in alternative productive tasks.

Timing of Men's Extra-Marital Affairs

Chapter 4 explored variation in the timing of men's extra-marital affairs. I argued that the pursuit of extra-marital affairs represents a clear investment away from the family. According to the Paternal Provisioning Model, such behavior should decrease in frequency as the size and consequent need of a man's progeny grows—as family need increases, so too should the returns to investing in his family, and consequently,

investments in pursuits that do not benefit his family should therefore decrease. The Mating Effort Model, however, predicts that men, concerned with the fertility they risk losing, should act most nobly, and refrain from pursuing extra-marital relationships, when they have wives of higher reproductive value. Since the number of children increases through time in a marriage, during which the reproductive value of the wife decreases, the two pathways again produce opposing predictions.

I found that men's affairs tend to be concentrated in the early twenties, during the first few years of marriage. This also happens to be the time during which men have few children and young wives of high reproductive values. Because of this, univariate models showed that the probability of having an affair in any given year was significantly negatively associated with the number of children and with the age of the wife, supporting the Paternal Provisioning Model and refuting the Mating Effort Model. Despite this, after controlling for the age of the man and the number of years in marriage, neither the number of children nor the age of the wife proved significant. I argued that this pattern was indicative of a general life history trend in which males change from a mating-effort intensive strategy to a paternal-investment intensive strategy as they develop the skills and competitiveness required to win a long-term mate and sire children in which they can invest.

Effect of Father Presence on Child Well-being

In Chapter 5, I presented results concerning the effect of father absence on various measures of children's well-being. The Paternal Provisioning Model predicts the greatest negative effect of father absence on offspring success, while the Tolerated Theft Model

predicts that the amount of resources available to the children is independent of the father's presence, and his absence should therefore have no impact on measures most associated with caloric intake, such as growth or morbidity. This chapter also introduced the Psycho-Social Stress Model, which argues that children use the family formation strategies of parents as a proxy for the importance of pair-bond stability and bi-parental care in that particular environment and population, and that they alter reproductive development and future strategies accordingly. Thus, father absence is argued to set children on an accelerated developmental trajectory, leading to precocious sexual maturation and activity and a short-term reproductive strategy.

Fitting with the logic of the Paternal Provisioning Model, I found that fatherless children experience nearly twice the risk of dying in any given year during their first decade of life. They were also found to be significantly (one-tailed) more likely to be diagnosed with a disease during medical surveys. Despite this, tests of differences in anthropometric and reproductive measures failed to clearly support the Paternal Provisioning model. Father absence was significantly associated with *accelerated* growth in height for girls and marginally so for boys' heights and girls' weights. It had no effect, however, on completed sizes for men or women. There was tentative evidence that men from fatherless homes begin reproducing earlier, yet have lower completed fertility. For women, however, father absence was not associated with first age of reproduction but was significantly associated with *higher* cumulative fertility for age.

The lack of any effect of father absence on the growth of children indicates that the caloric intakes of fatherless children must be comparable to those of children with fathers, supporting the Tolerated Theft Model. This fact, however, is difficult to

reconcile with the increased morbidity levels and risk of dying from disease. Finally, the accelerated growth and earlier reproduction of men supports the Psycho-social Stress Model, indicating that fatherless children do mature more rapidly.

Summary

The data, for the most part, support the Paternal Provisioning Model. It was shown that Tsimane men can indeed increase the fitness of their children and, as expected, deliver their care with respect to the need of the children. There was only tentative evidence, however, that men's direct caring of children facilitates female labor. Additionally, the fact that children without fathers grew as well as children with fathers indicates that Tsimane men may not be able to greatly increase the amount of nutrients available to their children above that which others are willing to provide in their absence.

Research elsewhere has suggested that men augment the care they give to biological children they have with current wives because such care reduces the possibility of being deserted by these wives. Despite this, there was no evidence that clearly showed that these mating benefits are great enough to significantly alter the way in which Tsimane men provide this care, particularly when the goal of impressing one's wife competes with increasing offspring fitness.

GENERALIZABILITY

The goal of most evolutionary studies of human behavior is to develop a better understanding of the causes of variation in the behavior of *all* humans. Despite this, most studies are very culturally specific, as costs and benefits to nearly all behaviors are

mediated by cultural institutions, practices and beliefs. There is, however, no other way to explore variation in human behavior than to actually go out and investigate these populations, one-by-one if necessary.

It is important to review the results presented in this work within the context of the Tsimane culture and environment. This is a population in which men's contributions to a family are largely in the form of the labor involved with clearing and maintaining fields, hunting, fishing and earning money. It is also a population in which pair-bonds are extremely stable and fathers have a significant impact on the well-being of their children.

Some of the effects presented in this work may indeed not be found in other populations, or may actually be found in the reverse direction. For example, in populations in which women are fully capable of raising children on their own and paternal care is less important to offspring well-being, the mating-effort benefits of such care may prove greater than those conferred through the direct increasing of offspring fitness. This would result in the exact opposite pattern than that observed among the Tsimane, with men biasing their care to when they have younger wives and when these wives can observe the care. Finding such an effect would by no means diminish the importance or validity of the Paternal Provisioning Model, but would simply imply that men employ facultative parental strategies that are responsive to socio-ecological conditions. The research presented here has shown that men have, at least under certain conditions, a greater concern for the well-being of their children than for impressing their wives; whether or not these priorities reverse direction under different conditions remains to be proven.

FUTURE RESEARCH

In addition to the need for more research to allow for the investigation of cross-cultural variation, many methods traditionally used in the study of men's parental behavior could be improved upon to enhance our understanding of the subject and further fine-tune the conclusions reached in this dissertation. Firstly, as mentioned in Chapter 5, direct measures of levels of paternal care and provisioning across intact and broken families would prove invaluable to the study of the goals of and the benefits to paternal care. Three potential benefits of paternal care were proposed by the three models—increasing offspring fitness, increasing mate fertility and increasing the proportion of mate fertility that the caregiver has access to (the Tolerated Theft Model proposes that there is no paternal provisioning). Knowing absolute levels of paternal investment would allow one to test if variation in these levels is predictive of these three variables, particularly within traditional populations in which fertility and offspring well-being would be more strongly associated with the provisioning that men provide. Many previous studies indicate that levels of paternal investment are associated with all three. Studies of father absence have shown that fathers can greatly impact offspring well-being along various measures (see Chapter 5). Better hunters have also been shown to have children that are more likely to survive and that grow better (Hawkes 1993a, Hill and Hurtado 1996). Marlowe (2001) found that cross-cultural variation in the male contribution to the diet was strongly predictive of population wide fertility rates, suggesting that a father's provisioning has the opportunity to greatly increase wife fertility. Finally, many studies have shown that a failure of men to provide investment is

a common cause for female initiated divorce (Betzig 1989, Goode 1956, Kitson 1992, Levinger 1966).

These studies are limited, however, in that they employ only indirect measures of paternal investment (husband presence/hunting rates, male contribution to diet, ex-wives' reports of investment). This muddles the effect and leads to many doubts, such as whether the distribution of the additional resources that better hunters acquire can be directed to their children, or whether women that claim a lack of investment for divorce really had less productive husbands or simply had greater demands. Future studies could avoid these problems by utilizing direct measures of investment, such as absolute resource flows from fathers (and others) to children. We could then determine if variation in amounts of food that fathers provide their family relates to offspring success, mate fertility, mate retention, or all three. Similarly, this would allow us to determine if father absence is associated with an absolute decrease in nutritional levels of children and who may be boosting support in order to compensate for the loss.

Finally, future tests of men's parental behavior should explore situations that allow for better isolation of the factors predicted to affect such behavior by the different models. The tests conducted in this dissertation specifically focused on situations in which the various models produced competing predictions, meaning that only one could be supported (e.g. men either spend more time in direct care when the wife is either absent or present). This was done by design in order to determine which model best accounted for men's behavior. And although a number of tests in this work provided for unique predictions of each model to also be tested, future research could better isolate

variables to determine, for instance, whether the proposed benefits conferred through the mating effort pathway have *any* effect on the way that men deliver their care.

CONCLUSION

Human males are quite exceptional in the levels of investment they provide to their children, yet variation across and within populations indicate that men are not blindly driven by paternal love. Researchers have proposed numerous models that outline different pathways through which men can receive benefits from paternal care. The ultimate goal of this exercise is to explain why human males enjoy such greater returns to the behavior than other primates, as well as account for its variation within humans. The research presented here explored three of these models. I showed that Tsimane men can positively impact the well-being of their children, and that they appear more concerned with this goal than enhancing their reputation with their wives. Clearly, more work needs to be done to fine tune the conclusions presented here. Future work will hopefully allow for the examination of the effects of men's care on offspring success, mate fertility and mate retention with much greater accuracy, as well as provide a larger cross-cultural sample to examine how these effects vary across populations. With the data presented here, however, we can affirm that men, at least under certain conditions, are most driven to provide care by a sincere desire to improve the well-being of their children.

APPENDIX 4.1
Extra-marital Behavior Interview

I'd like to ask you about your relationships with women, because I want to know why there are certain marriages that last for a long time in which both the man and woman are happy, yet there are others that do not last and in which both partners are unsatisfied. Why do some men have many affairs while others have none? No one will know or hear of your specific answers.

Yo quiero preguntarte sobre tus relaciones con mujeres, porque yo quiero saber por que hay matrimonios que duran por mucho tiempo en que la mujer y el hombre estan contentos, pero hay otros que no duran en que los dos estan triste. Por qué hay algunos hombres que tienen muchas relaciones fuera de su matrimonio, pero hay otros que no los tienen. Nadie va a saber ni escuchar de tus respuestas especificas.

Yu ma'je peyacsi mo'in pen in cacaij na yu ma'je chij jun buty mu'ya vämidye in mu'ya pen majoi j Judyeya vä'm'tyi majoi j. Men bä'vi jäm' in. Judyeya mu'ya yocsi vämidye mu'ya pen are vä'm'tyi tari, ma'je cajoij mo. Jun buty mu'ya son rä jcan vovoi j Judyeya mu'ya yocsi jam ma'je vovoi j. Jam jun chij'in cuisi vorjeyacdye cacaij na jam tyi seve in.

How many women did you court before courting your current wife?

Cuantos mujeres cortejaste antes de casarte con tu esposa?

Juñucsi buty pen chabañe mi jambi'dyem vämi mi?

1a) How long did you court each of these women?

Por cuanto tiempo cortejaste cada de estas mujeres?

Juñucsi buty mayedye are semana chabañe oij in pen in mi?

1b) Were you married to any of these women?

Te casaste con una de estas mujeres?

Vämi ca mi oijtum pen in are jam?

1b.1) Did you leave or did your ex-wife leave?

Saliste tu o salio tu esposa?

Cajoij ca mi are pen mi?

1b.2) How many years were you married before you/she left?

Por cuantos años te habias casado con esta mujer?

Juñucsi ca yomodye/ivaj vämi mi oijtum pen juns i cajo i mi/mo jiquej?

1b.3) Did you have any children with this marriage?

Tuviste hijos con esta mujer?

Mu'ya ca ava mi oijtum pen?

1b.4) How long were you married when you had your first child?

Cuantos años vivias con la familia de tu esposa?

Juñucsi ca yomodye vämi mi juns i ya nays i tasches ava mi?

1b.4a) Where do the children live now?

Donde viven estos hijos ahora?

Jana ca bä'yi oij ava mi quindy e?

1b.5) Why did you/she leave?

Por que saliste/salio?

Jun buty cajoi mi/mo?

1b.6) How many years did you live with your ex-wife's family?

Por cuantos años vivia con la familia de su ex-esposa?

Juñucsi ca yomodye/ivaj bä'yi mi pen'situm chätidye?

1b.7) Did you have any affairs while married to your ex-wife?

Tenias relaciones con otras mujeres cuando estaba consado con tu ex-esposa?

Vovoi ca mi junsi ya vämi mi oijtum pen?

1b.8) How many?

Cuantos?

Juñucsitum buty pen?

1b.9) How long were you married before you had your first affair?

Cuantos años habias estado casado cuando tenias relaciones con otra mujer por la primera vez?

Juñucsi ca yomodye/ivaj vämi mi oijtum pen junsi ya tasche vovoi mi jiquej?

2) How long did you court your current wife before marrying?

Por cuanto tiempo cortejabas tu esposa?

Juñucsi buty mayedye are semana chabañe mi mo pen'dyes mi?

3) How many years did you live with your current wife's family?

Cuantos años vivias con la familia de tu esposa?

Juñucsi ca yomodye/ivaj bä'yi mi pen'situm chätidye?

How long were you married when you had your first child?

Por cuanto tiempo habia estado casado cuando tuviste tu primero hijo?

Juñucsi ca yomodye vämi mi junsi ya nayi tasches ava mi?

Have you ever had any affairs with other women?

Has tenido relaciones con otras mujeres durante tu matrimonio?

Vovoi ca mi yocsitum pen junsi ya vämi mi oijtum pen?

5a) How many?

Cuantos?

Juñucsitum buty pen?

5b) How long were you married before you had your first affair?

Por cuantos años habias estado casado cuando tenias relaciones con otra mujer por la primera vez?

Juñucsi buty yomodye/ivaj vämi mi oijtum pen junsi ya tasche vovoi mi?

6) How many women did you have relations with before marrying your first wife?

Con cuantos mujeres habias tenido relaciones antes de casarte con tu primera esposa?

Juñucsitum buty pen vovoi mi jambidyem vämi mi tasches pen mi?

6a) (If applicable) How many women did you have relations with after your first marriage ended?

(Si se aplica) Con cuantos mujeres tenias/has tenido relaciones despues de tu primero matrimonio?

Juñucsitum buty pen vovoi mi jäquive tas tasches vämidye mi?

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