PARTIBLE PATERNITY AND HUMAN REPRODUCTIVE BEHAVIOR

A Dissertation

presented to

the Faculty of the Graduate School

at the University of Missouri-Columbia

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

---

by

RYAN M. ELLSWORTH

DECEMBER 2014

The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

PARTIBLE PATERNITY AND HUMAN REPRODUCTIVE BEHAVIOR

presented by Ryan Ellsworth, a candidate for the degree of doctor of philosophy, and hereby certify that, in their opinion, it is worthy of acceptance.

Professor Robert Walker

Professor Craig Palmer

Professor Mark Flinn

Professor David Geary

ACKNOWLEDGEMENTS

First and foremost thanks to my advisor, Robert Walker, and my former advisor, Craig Palmer, as well as Mark Flinn and David Geary. Special recognition to my collaborators and co-authors, Rob Walker, Drew Bailey, Kim Hill, Magdalena Hurtado, and Mary Shenk. Many thanks to Lada Micheas of the Social Science Statistics Center for invaluable assistance with the statistical analyses in chapter 3. I thank Dennis, Anne, Jill, Alyssa, Tilly, and Erin for encouragement and support throughout my graduate career, and for enduring me the last several years.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

Tables

Figures

Chapter 1: Introduction

An egg is released from the ovary and enters the fallopian tube, a route that leads to an encounter with a horde of sperm cells, one of which will succeed in penetrating the barrier and achieving fusion with the egg where eventually the genetic material of the haploid sperm will join that of the egg's. The cascade of events that follow the restoration of diploidy in the zygote produces an individual who is a combination of genes from one mother and one father.

Or such is our modern scientifically informed view of sex and reproduction in organisms such as humans. But relatively recent technological advancements such as the microscope, and the maturation of cell biology, were necessary precedents to this insight (see Mayr 1997 for a brief history), and thus the invisible nature of how babies are made has led to cross-cultural diversity in how this event is explained. For example, Malinowski (1929) relates that for Trobriand Islanders, conception required neither a father, nor even sexual intercourse. Indeed, fathers were not considered to make any material contribution to offspring.

Studies of emic notions of the process of conception which do include a material role for fathers in producing children have identified in numerous cultures the idea that semen plays a formative role in fetal development, as well as the view that repeated acts of intercourse are necessary for *in utero* development and growth (See Gray and Garcia 2013: 217-221 for examples). Many of these outlooks conceptualize semen mixing with menstrual blood or other female substances—from which the fetus takes shape. While such claims seem to allow for the possibility that more than one man could contribute to the production of a single offspring (after all, repeated acts of intercourse, and the accumulation of semen do not necessarily need to involve only one male's labor), the possibility and stated assertion that multiple men *can* and *do* share in the making of offspring appears to be limited to parts of South America (although Beckerman and Valentine [2002: 6] allude to a report on the Lusi of Papua New Guinea where the authors mention that Lusi informants "generally agree that it is *possible* for a person to have more than one father" [emphasis added]). It is there where these claims are institutionalized in the practice of partible paternity.

Partible paternity refers to the concept that children can have more than one genitor. In contrast to the realities of the reproductive process, according to this view conception is a cumulative process that can involve seminal inputs from multiple men in the production of single offspring (Beckerman and Valentine 2002). Such an outlook on reproduction is accompanied by patterns of polygynandrous mating, and has generated cultural institutions for extramarital relationships, alongside socially monogamous and polygynous pair-bonds, in those societies where the concept is found. As mentioned above, the theory and practice of partible paternity appears exclusive to South America, where it is common among indigenous societies of Amazonia, being nearly ubiquitous in the, Carib, Macro-Jê, Pano, and Tupi language families, indicating a deep antiquity (~5,000 years) (Walker, Flinn and Hill 2010).

As discussed in Chapter 2, partible paternity presents something of a challenge to traditionally held views of male and female sexuality. The classic paradigm of sex differences in reproductive strategy is based on Bateman's (1948) observations that male reproductive success increases with number of mates, while a female's reproductive success is independent of the number of mates with which she copulates; hence, there is a selective advantage to male competition for access to multiple mates that is not apparent for females. Trivers (1972) later elaborated on this view by highlighting the connection between the differential costs of reproduction for males and females, and the resulting sex differences in reproductive strategies. Because females typically bear greater obligate costs of parental care, they are under greater selection pressure than males to be discriminative in their choice of mates. The different costs and benefits of mating to males and females leads to a male emphasis on quantity of mates, and a female emphasis on quality of mates.

The classic paradigm of the ardent male and coy female (Daly and Wilson 1978) is indeed a useful heuristic, and (with important and long-acknowledged exceptions) a generally correct summary of basic differences in reproductive strategies between the sexes. However, the paradigm suffers for its elegance in being somewhat overly simplistic. Numerous authors have called into question the generality of the characterization of female reproductive strategies as "coy." Particularly, theoretical arguments and several empirical studies have demonstrated cases in which females may benefit from being sexually ardent, and mating with multiple males (see references in the introduction to Chapter 3). For example, females may engage in polyandrous mating to increase the genetic diversity of their offspring (Ridley 1993), or to promote sperm competition thereby ensuring competitive sperm in male offspring (Keller and Reeve 1995). Females may mate with several males during a single estrus period, thereby creating paternity uncertainty and reducing the risk of infanticide to their offspring (Hrdy 1981). Relatedly, females may distribute possibility of paternity among several males to garner some degree of investment from each (Davies 1986). Females in pair-bonding species may engage in extra-pair copulation to secure extra-pair investment, or to secure superior genes for offspring while maintaining access to resources and paternal investment from pair-bonded mates (Thornhill and Gangestad 2008). Each of the above examples gives a picture of female reproductive strategies that are not as coy as conceived by the classic paradigm (although it is doubtful that any biologist ever seriously thought that the paradigm represented hard and fast empirical reality).

Human social structure is unique among primates, consisting of (mostly) monogamous pair-bonds embedded within multi-male/multi-female communities, or what Chapais (2013) refers to as "multifamily groups." These multifamily groups are themselves embedded in larger nexus of between-group alliances. Pair-bonding facilitated the evolution of intensive, but facultative, paternal investment (Geary 2000; 2010). While levels and types of male parental care vary cross –culturally, paternal investment has been shown in a number of studies to have important impacts on offspring on a number of outcome variables, including mortality, well-being, and social status (see summary in Geary 2010: 146-156; Konner 2010). However, the multi-male/multi-female social groups in which these pair-bonds are embedded present costs and benefits to men of providing parental care versus seeking additional mates, and to women of manipulating paternity certainty and forming sexual relationships outside of the context of pair-bonds. Indeed, concealed estrus and extended sexuality have been argued to function in both fostering pair-bonding and maintaining paternal investment, as well as allowing women to manipulate paternity and facultatively garner investment from multiple males (Alexander and Noonan 1979; Symons 1979; see review in Thornhill and Gangestad 2008).

Partible paternity presents us with an opportunity to investigate the complexity of female strategies and the adaptive logic of polyandrous mating in humans and the trade-offs between mating and parenting. Important questions about partible paternity that need investigation include: How were co-fathers chosen? Why did women often take multiple fathers for their children? What benefits did co-fathers provide to women and their offspring? Did men benefit from sharing fatherhood? These are the kinds of questions that must be addressed in order to understand this institution from a sociobiological perspective that sees human behavior as ultimately grounded in, and the product of, the process of differential reproduction and fitness maximization (Alexander 1979; Barash 1977; Irons 1979; Davies, Krebs, and West 2012). In the chapters that follow, an attempt is made to shed some light on partible paternity from such a perspective, examining the social dynamics, demography, and reproductive consequences of sharable fatherhood. I do not attempt to comprehensively review the subject, but to contribute to the existing literature in hopes that enough important knowledge might accumulate in the near future to allow such a review.

Particular focus in chapters 2 and 3 is on partible paternity in one society- the Ache of Paraguay, a traditional tropical forest foraging people who have been the subjects of steady ethnographic study for the past several decades. More details about the Ache are described in the following chapter. Chapter 2 presents the results of a study that tests some of the hypothesized benefits to men and women of the practice of partible paternity. This is done through analysis of the relatedness and residence patterns of Ache co-fathers. Results indicate that Ache women selected co-fathers for their offspring in ways that increased the availability of investment from secondary fathers, and that men used the partible paternity concept to increase their mating success and establish alliances with kin and other co-resident men.

Chapter 3 more directly addresses the question of reproductive benefits associated with shared fatherhood through an expanded analysis of child survival among the Ache, which builds on previous work by Kim Hill and Magdalena Hurtado (1996). Results of the analyses in Chapter 3 demonstrate a significant survival advantage for children with secondary fathers. Presentation of these findings are followed by an examination of the socioecological factors associated with polyandrous mating and the benefits of multiple fathers.

Chapter 4 includes, but goes beyond, partible paternity to an analysis of reproductive behavior in broad cross-cultural scope. Focus is on two key aspects of human mating systems: reproductive skew and pair-bond stability, and a novel methodology is introduced for measuring these two dimensions simultaneously. The method involves calculating the fraction of full and half siblings. This methodology is applied to genealogical data from a large sample of traditional societies across the world in effort to understand the ecological factors associated with variation in polygynous mating and conjugal stability across populations.

Chapter 2: Relatedness, Co-residence, and Co-fatherhood Among Ache Foragers[*]

Introduction

Anthropologists have long taken an interest in cross-cultural variability of human sexual and reproductive behavior (Betzig, Borgerhoff Mulder, and Turke 1988; Ford and Beach 1952; Low 2000; Marshall and Suggs 1971; Symons 1979). One of the most challenging issues of late concerns the concept and practice of partible paternity, which refers to the institutionalized claim that a child can have more than one genitor (Beckerman and Valentine 2002; Walker, Flinn, and Hill 2010). The concept is found in most indigenous cultures of lowland South America, being nearly ubiquitous across several large language families (Arawá, Carib, Pano, Tupi, and Macro-Je), and possibly as much as three times as common as the concept of singular paternity (Walker et al. 2010). At last count in our sample 61 lowland societies are known to have partible paternity and only 24 with singular paternity.

Partible paternity presents a challenge because it is seemingly at odds with paradigmatic views on human sexuality derived from evolutionary biological theory (Daly and Wilson 1983; Symons 1979). In comparative perspective, paternal investment in humans is more intensive and arguably more important to offspring success than in any other primate (Geary 2000; Bribiescas, Ellison, and Gray 2012). However, within our species, levels of investment vary according to a number of factors, including paternity certainty (Geary 2010). To this end, men place a premium on sexual fidelity of long-term

---

[*] This chapter is adapted from Ellsworth et al. (2014) Relatedness, Co-residence, and Shared Fatherhood Among Ache Foragers of Paraguay. *Current Anthropology* 55: 647-653.

mates and employ a variety of mechanisms to ensure their investment is directed at genetic descendants (Wilson and Daly 1992). Shared paternity implies polyandrous mating and thus is puzzling in light of the aforementioned traits of human males. Recent research has demonstrated that polyandrous arrangements are more common cross-culturally than previously thought (Starkweather and Hames 2012). Thus, serious consideration must be given to the once suspect notion that women can benefit from multiple mating and polyandrous relationships (Hrdy 2000), and that human reproductive strategies are more complex than traditionally conceived by sociobiologists.

Partible paternity must be viewed within the larger context of the dynamic interplay of men's and women's reproductive pursuits. From an evolutionary perspective a crucial question concerns potential fitness benefits to men and women from the concept and practice of divisible fatherhood. Although the concept is widespread among indigenous South American populations, there is variation in its practice. Some societies have traditional prescriptions as to which males may share paternity. For example, the virilocal, patrilineal Curripaco exclude the role of secondary fatherhood except when paternity is shared between brothers (Valentine 2002: 191). Similar restrictions on co-fatherhood are reported for the virilocally-biased Yanomami (Ales 2002: 71, 80). On the other hand, loose regulation of co-fatherhood and extramarital sex is found in societies without strong unilineal descent and virilocality/patrilocality, such as the Canela (Crocker 2002) and Barí (Beckerman et al. 2002). It appears that the Ache did not have explicitly formulated rules or preferences concerning shared paternity. This diversity suggests that no one hypothesis may be universally satisfying. Rather, the behavior surrounding this concept in any given culture will reflect unique histories of inter- and intrasexual reproductive competition, and thus who benefits from its practice, and how, might differ across populations.

The present study presents demographic data from censuses of forest-dwelling (pre-contact) Ache hunter-gatherers of Paraguay that contribute toward an understanding of the reproductive consequences of partible paternity, and how male and female strategies play out within the sociocultural milieu of sharable fatherhood for this particular population. Analysis is focused particularly on 1) patterns of primary and secondary co-fatherhood among men; 2) genealogical relationships between co-fathers; and 3) the relation between band co-residence and co-fatherhood.

Hypothesized Benefits of Partible Paternity

Investigation of patterns of paternity, kinship, and residence permits preliminary testing of some hypothesized benefits of partible paternity to Ache men and women (see Table 2.1). Specifically, with regard to women, it is hypothesized that benefits may derive from garnering investment from multiple males (*multiple investors hypothesis*) (Beckerman et al. 2002; Hrdy 2000; Walker et al. 2010). If so, it is predicted that women should choose co-fathers in ways that maximize the likelihood and amount of long-term investment in themselves and their offspring, and minimize potential costs associated with conflict between co-fathers. Another hypothesized benefit to females is genetic diversification of offspring (*gene shopping hypothesis*) (Walker et al. 2010). In populations with a high level of genetic homogeneity (Ache have one of the lowest levels of genetic heterozygosity in the world, Wang et al. 2007; Lewis 2010), partible paternity may grant women greater leverage in choosing different fathers for successive children.

If women indeed benefit from genetic diversity of offspring, co-fathers should be less likely to be close relatives. A third hypothesis states that women benefit through the short-term exchange of sex for resources (*sex for resources hypothesis*) (Shapiro 2009), resulting in all men who had sex with a woman prior to pregnancy considered as possible fathers. This hypothesis predicts that long-term social ties between women, their children, and co-fathers will not figure as important features of partible paternity systems and that men should give mating presents to women and not the other way around.

Men may benefit from increased mating access to more women and, by extension, greater chances at siring offspring with multiple females (*mate competition hypothesis*) (Walker et al. 2010). The Ache recognize two types of fatherhood: primary fathers are often the husband of a child's mother. Secondary fathers are other men who had sexual relationship with a child's mother prior to pregnancy and birth (Hill and Hurtado 1996). If particularly desirable men benefitted from partible paternity through higher potential fertility it is predicted that men who are more often primary fathers should also be frequent secondary fathers. Another hypothesized benefit to men is the establishment and strengthening of alliances between individuals who were co-fathers of the same children (kin bonding or *male alliance hypothesis*) (Walker et al. 2010). This hypothesis predicts that co-fathers would have affiliative types of relationships such as being close relatives and/or residents of the same band.

Study Population

The Ache are Tupi-Guaraní-speaking foragers who traditionally inhabited the tropical forests of Eastern Paraguay (Hill and Hurtado 1996), making first *peaceful* contact with outsiders in the early 1970s, before which they were nomadic hunter-gatherers moving camp every few days. Band size among forest dwellers was flexible and ranged from three to more than 100 individuals at any given time (Hill and Hurtado 1999) with a mean experienced band size of about 20 adults, with—from adult ego's point of view—consanguineal kin (both close and distant) constituting 20%, and unrelated individuals ~25%, with spouse and affines comprising the remainder (Hill et al. 2011). Pre-contact Ache marriages were extremely flexible and based on courtship with minimal influence from parents or other adults. There were no prescribed marriage partners, and incest restrictions extended only to parents, siblings, cross- and parallel first cousins, and godparents (Hill and Hurtado 1996: 227). Polygynous and polyandrous marriages were permitted but infrequent. Informants report that forest-living Ache women exercised considerable autonomy in their choice of mates and in the persistence or dissolution of marital bonds. The Ache showed the highest rate of divorce of any foraging group for which data exist, with women having an average of 10 spouses by age 30 (Hill and Hurtado 1996: 231); although in later years of life marriages tended to have a higher probability of enduring.

According to the Ache, any man that has engaged in sexual intercourse with a woman several months prior to discovering her pregnancy, and up to the day of birth, may contribute to the paternity of that woman's offspring. Paternity was not necessarily limited to one individual, and most Ache claimed more than one man as a father (Hill and Hurtado 1996: 273). The Ache recognized two types of paternity. *Primary fathers* (the "one who put the child in") were usually husbands or men who were involved in long-term mating relationships with a women, and had the most frequent sexual intercourse with her prior to discovery of her pregnancy. *Secondary fathers* included other men who had sex with a woman prior to and during her pregnancy (the “ones who mixed it”). Interestingly, the Ache seemed to recognize that the timing of copulation with a woman in relation to discovery of pregnancy bears on the probability of being the primary father of her offspring (Hill and Hurtado 1996: 274). Secondary fatherhood was most often achieved when men are younger, while older men tended more often to be primary fathers (Hill and Hurtado 1996: 288). As part of the institution of partible paternity, secondary fathers were sometimes expected to undergo dietary and activity restrictions associated with *couvade*, a public statement of their status as new “fathers”.

Assignment of paternity to men was the province of females, and claims of primary paternity were liable to change with a woman’s situation (e.g., when potential fathers died, or were no longer in residence) (Hill and Hurtado 1996: 442). Analyses of childhood mortality have shown that children with a primary father and one secondary father had the highest survivorship, suggesting that having two fathers was optimal for child survival (see Hill and Hurtado 1996: 444, and 465, figure 13.4). The finding that one secondary father is associated with higher survivorship has also been reported by the only other study to examine this effect by Beckerman and colleagues (2002) for the Barí of Venezuela. While for the Barí, Beckerman et al. argued that improved survivorship was due primarily to improved fetal nutrition resulting from provisioning by secondary fathers, the mechanism for the Ache remains uncertain (although protection from infanticide upon the death or desertion of the primary father may be important, see Hill and Hurtado 1996).

Methods

Calculating Primary and Secondary Fatherhood

Previously collected census data for precontact Ache (Hill and Hurtado 1996) were used in calculating primary and secondary fatherhood, which yielded a sample of 237 men. Only men aged 18 or older who were primary fathers or secondary fathers of at least one child were included in the analysis. Of these men, 110 were reported as primary father of at least one child, 20 were reported as secondary father of at least one child, and 107 were reported as primary and secondary father of at least two children. For deceased individuals, "age" was defined as age at death. For living individuals, "age" was defined as their current age. Of the 284 children in our sample, 106 had one father, 120 had two fathers, and 58 had more than two fathers.

To determine the relationship between primary and secondary fatherhood in terms of number of children, the number of children each man was a secondary father of, was entered into a Poisson regression model controlling for age and age squared. The dependent variable was the number of children of whom a man was the primary father.

Calculating Co-residence

To calculate co-residence, censuses are available for 58 pre-contact Ache bands from interviews (Hill et al. 2011). Census data spanned the time frame 1958 – 1970, yielding a total of 157 adult men sampled over this period. Each co-residing dyadic pair of adults was considered a single data point; if the same pair co-resided in more than one band they were counted multiple times with the matrix entry for each dyad representing the proportion of censuses in which both individuals were found to be co-residing together.

Calculating Genetic Relatedness of Co-fathers

Complete genealogical and marital histories for adults in the Ache population covering the 20th century were to calculate relatedness (Hill and Hurtado 1996). The relatedness matrix for the entire Northern Ache population was used to calculate relatedness for the 157 men who appeared in the pre-contact camp censuses. The relatedness values among all Ache men was estimated using Descent software (Hagen 2005). In this calculation, only consanguineal relationships were considered. The estimate takes reported primary fatherhood at face value and assumes that individuals with no known genealogical links have a genetic coefficient of relatedness of zero.

Co-fatherhood, Genetic Relatedness, and Co-Residence

To calculate relationships between co-fatherhood, genetic relatedness, and co-residence, three square similarity matrices were calculated for the 157 men who occurred in the residence censuses. A co-fatherhood matrix, in which all co-father pairs were coded as 1, and all other pairs were coded as 0, was calculated. A genetic relatedness matrix was calculated based on the full genealogy. The values of co-residence were bound between 0 (two men never occurred together in the censuses) and 1 (two men always co-resided in each census).

For analyses, multiple regression on distance matrices (MRM using the Ecodist package in R, [Goslee and Urban 2007]) was used. For regression coefficients, MRM uses permutation tests of significance, and for the following analyses, 10,000 permutations per model were used. First, single predictor models were used to assess the relationships between all three matrices. Next, co-residence was regressed on co-fatherhood and relatedness. Finally, co-fatherhood was regressed on co-residence and relatedness.

Results

Primary and Secondary Co-fatherhood

The results of the Poisson regression model showed that the effect of number of children secondarily fathered on number of children primarily fathered was significant and positive (regression weight = .094; $z = 5.24$, $p < .0001$). Men who had more secondary fatherhood also had more primary fatherhood. A man with 0, 1, 2, 3, 4, or 5 secondary children is predicted to have 2.92, 3.21, 3.53, 3.88, 4.27, or 4.69 primary children, respectively.

Genetic Relatedness of Co-fathers

The distributions of genetic relatedness for co-father pairs and random pairs of men appears in Figure 2. The average genetic relatedness for co-father pairs in this sample was .0388 (SD = .096), compared to .0234 (SD = .073) for pairs of men who were not co-fathers, a significant difference ($t[12244] = -3.13$, $p = .002$). Co-fathers are statistically less likely than chance to be unrelated, although 70% of co-father pairs are still unrelated. Co-fathers are over twice as likely to be cousins or half brothers than expected by chance, and 4% of all co-father pairs are full brothers (Figure 2.1).

Co-fatherhood, Genetic Relatedness and Co-Residence

Results of the single predictor models showed that the relatedness matrix significantly predicted co-residence (B = .25; *p* = .0001). Relatedness also predicted co-fatherhood for this subset of the sample (B = .03; *p* = .003). Finally, co-residence predicted co-fatherhood (B = .03; *p* = .004).

When co-residence was regressed on both co-fatherhood and relatedness, the effect of relatedness remained highly significant (B = .24; *p* = .0001), and the effect of co-fatherhood also remained statistically significant (B = .02; *p* = .02). Together, co-fatherhood and relatedness were associated with 6.1% of the variance in the co-residence similarity matrix. Regression of co-fatherhood on co-residence and relatedness showed that the effects of co-residence (B = .02; *p* = .03) and relatedness (B = .02; *p* = .02) both remained statistically significant, indicating that both variables contribute unique variance to co-fatherhood status (Figure 2.2).

Discussion

The results of the analyses show that men with more secondary fatherhood also had more primary fatherhood. Data on relatedness reveal that co-fathers were more closely related, on average, than were men who were not co-fathers. Co-fathers were also more likely to reside together than men who were not co-fathers. These results offer insight into male and female reproductive strategies related to partible paternity, and permit testing of the aforementioned hypothesized benefits to men and women within Ache society.

Female Strategies and Ache Partible Paternity

The findings reported above concerning relationships among co-fathers, co-residence, and kinship suggest some benefits to females of the practice of partible paternity among the Ache. As already mentioned, it appears that the Ache did not have explicitly formulated rules or prescriptions concerning shared paternity. It is possible that the absence of emphasis on unilineal descent groups, as well as considerable residential flexibility among the Ache account for the lack of formal rules or restrictions on choice of fathers. In any case, fluidity of band composition, absence of regulated co-fatherhood, as well as female control of paternity assignment described above, gave Ache women considerable latitude in selecting mates and co-fathers for their offspring. The finding that primary fathers also tended to be secondary fathers is consistent with women's autonomy in mate choice. Thus, women are expected to have made strategic decisions regarding co-paternity in ways that maximized potential benefits to themselves and their offspring.

The fact that co-fathers were more closely related, on average, than men who were not co-fathers suggests that women selected men who were more likely to invest in their offspring—nepotistically, if not paternally. Aside from the issue of biological paternity, there are theoretical (Alexander 1979, 1987; Hamilton 1964) and empirical (see, e.g., contributions in Chagnon and Irons 1979) grounds for expecting individuals to invest more in kin than non-kin. Sufficiently low paternity certainty of an unrelated co-father may lead to lower levels of investment than would be the case if a co-father were a relative of the biological genitor. By selecting as co-fathers men who are close kin, women would have been increasing the investment in themselves and their offspring;

and, by granting some degree of paternity probability, may have increased levels of investment beyond that from nepotism alone. Also, choosing co-fathers who are closely related may have increased the probability of cooperative relationships, and decreased the probability of conflict between men who share paternal stakes in the same offspring. While relatedness between co-fathers is consistent with the *multiple investors* hypothesis, we cannot rule out the *gene shopping hypothesis* for co-fathers of women's children who were not close relatives of one another.

The fact that co-fathers were more likely to reside together suggests that women selected men who were more able to invest in her and her offspring. Proximity to a woman and her offspring increased the opportunity for direct investment by co-fathers. One important type of relationship among the Ache is referred to as the "*bykuare*" (ones who provided the essence of the child), who supplied a pregnant mother with meat that then inspired the child's name (Hill and Hurtado 1996: 67, 442). These men were described as being especially concerned with a co-child's welfare. Thus, women were likely to have received direct nutritional provisioning from some secondary fathers.

The results concerning patterns of residence and relatedness of co-fathers are most consistent with the predictions of the *multiple investors hypothesis* that women strategically chose individuals as co-fathers in ways that increased the probability and amount of investment in their offspring. Indeed, as reported above, having a secondary father was associated with increased offspring survivorship. Enlisting multiple potential investors can be viewed as an insurance or bet-hedging strategy. High adult male mortality due, in part, to warfare created a female-biased adult sex ratio among the Ache (Hurtado and Hill 1992). Male scarcity, combined with high rates of divorce leads paternal investment to be scarce and unreliable; not only because men themselves are scarce, but also because in contexts of female-biased adult sex ratio men increase mating effort at the expense of parental effort (Barber 2003a; Guttentag and Secord 1983; Harts and Kokko 2013; Kokko and Jennions 2008; Pedersen 1991;Schacht, Rauch, and Borgerhoff Mulder 2014). This suggests the possibility that, by obtaining co-fathers for offspring, women were in essence hedging their bets on male investment should a primary father die or desert while offspring are still dependent.

Public recognition of co-fatherhood through participation in *couvade* rituals, investment in the welfare of women and their children by secondary fathers, and increased offspring survivorship associated with having co-fathers, are all evidence against the *sex for resources hypothesis* (Shapiro 2009). While potential co-fathers did sometimes exchange resources for sexual access, it appears that among the Ache, benefits to women went beyond short-term exchanges to include long-term affiliation among co-fathers, women, and their children.

Male Strategies and Ache Partible Paternity

The findings concerning attributed fatherhood in the current sample are consistent with the prediction of the *mate competition* hypothesis that men with more secondary fatherhood would also have more primary fatherhood. Results suggest that men named as secondary fathers may be valuable or desirable mates; these men had more putative paternity of offspring of more women than men who were not named as co-fathers. However, the exact reason for their higher mating success is unclear. Possibilities include phenotypic indicators of ‘good genes,’ (e.g., sexual attractiveness), high levels of investment or willingness to invest in a female and her offspring, success in male-male competition (social status), or social selection (skilled hunters or men valuable as coalition members allowed/permitted greater sexual access to women). In any case, it appears that some men capitalized on the culturally legitimated extramarital sex attending partible paternity through greater potential reproductive success.

We know that Ache men sometimes mentioned that they wanted to club some men who had sex with their wives and that some co-fathers were despised. However, the results of analyses presented here lead to the conclusion that co-father relations were more often likely to be affiliative given their higher levels of relatedness and higher probability of co-residence. These findings are consistent with the *male alliance hypothesis*. The sharing of mates and fatherhood may have reduced male-male mating competition, thus reducing the corrosive effects of mate competition on social cohesion and male coalitions so important to success in intergroup conflict. Warfare was a major cause of mortality for pre-contact Ache. Among adult males, external warfare accounted for 36% of all deaths (Hill and Hurtado 1996: 163). Shared paternity between close kinsmen could have created or intensified alliances and cooperative relationships.

Conclusion

The current study focused on examining some important aspects of partible paternity among pre-contact Ache. Findings provide support for certain hypotheses regarding benefits to both women and men, and evidence against some others. In particular, the results support the *multiple investors* hypothesis of female benefits. Co-fathers appear to have been chosen in ways that increased the likelihood and opportunity for male investment. That co-fathers were more likely to be close relatives to one another is inconsistent with, but does not rule out, the hypothesis that some women benefitted from securing diverse genes for offspring. Results are also inconsistent with the hypothesis of transient benefits to women of exchanging short-term sexual access for resources from men. For males, our findings are consistent with the *male alliance* hypothesis. Fatherhood shared between related and co-resident men suggests that relations among co-fathers were often amicable, rather than antagonistic. Results also support the *mate competition* hypothesis. Patterns of primary and secondary fatherhood suggest that some men use partible paternity to their advantage in increasing potential reproductive success through multiple mates.

In closing, an important point needs to be made about partible paternity, given its recent connection with certain misleading ideas about human sexuality that have gained some public appeal. Contrary to the arguments of some authors (e.g., Ryan and Jetha 2010), the existence of partible paternity in some societies does not prove that humans are naturally promiscuous any more so than the existence of monogamy in some societies proves that humans are naturally monogamous. Human mating dynamics are not well captured with simplifying terms such as “monogamy” and “promiscuity.” Oversimplified views on the nature of human sexuality are perhaps ideologically satisfying, but empirically deficient. Phenomena such as partible paternity call for the development of increasingly sophisticated theory that takes into account the flexible, ecologically-contingent nature of human reproductive strategies.

Hypothesis	*Benefits of partible paternity*	*Predictions*	*Evidence*	*Supported?*
Female strategy				
Multiple Investors	Investment in offspring from multiple men	Females choose co-fathers of offspring in ways that maximize likelihood and amount of investment; Most children will have secondary fathers	Higher survival of offspring with secondary father; Co-fathers more likely to be co-resident and/or kin; Most children have secondary fathers.	YES
Gene Shopping	Genetic diversity of offspring through polyandrous mating	Co-fathers will be unrelated or distantly related.	Co-fathers are more closely related, on average, than men who are not co-fathers.	NO
Sex for Resources	Gifts from males in exchange for short-term sexual access.	Absence of long-term social bonds between co-fathers, women, and offspring.	Participation in couvade rituals signals public recognition of co-fatherhood. Secondary fathers maintain social ties to co-fathered children and mothers.	NO
Male strategy				
Mate Competition	Greater potential fertility through increased sexual access.	Men who have more secondary fatherhood will also have more primary fatherhood.	Secondary fathers have co-children with more women than do men who are not secondary fathers; Men with more secondary fatherhood also have more primary fatherhood.	YES
Male Alliance	Alliances between men who are co-fathers of the same children	Co-fathers will be close kin; Co-fathers will be residents of same band.	Co-fathers are more closely related, on average than men who are not co-fathers. Co-fathers are more likely to be co-resident.	YES

Table 2.1. Hypothesized benefits of partible paternity tested in the current study.

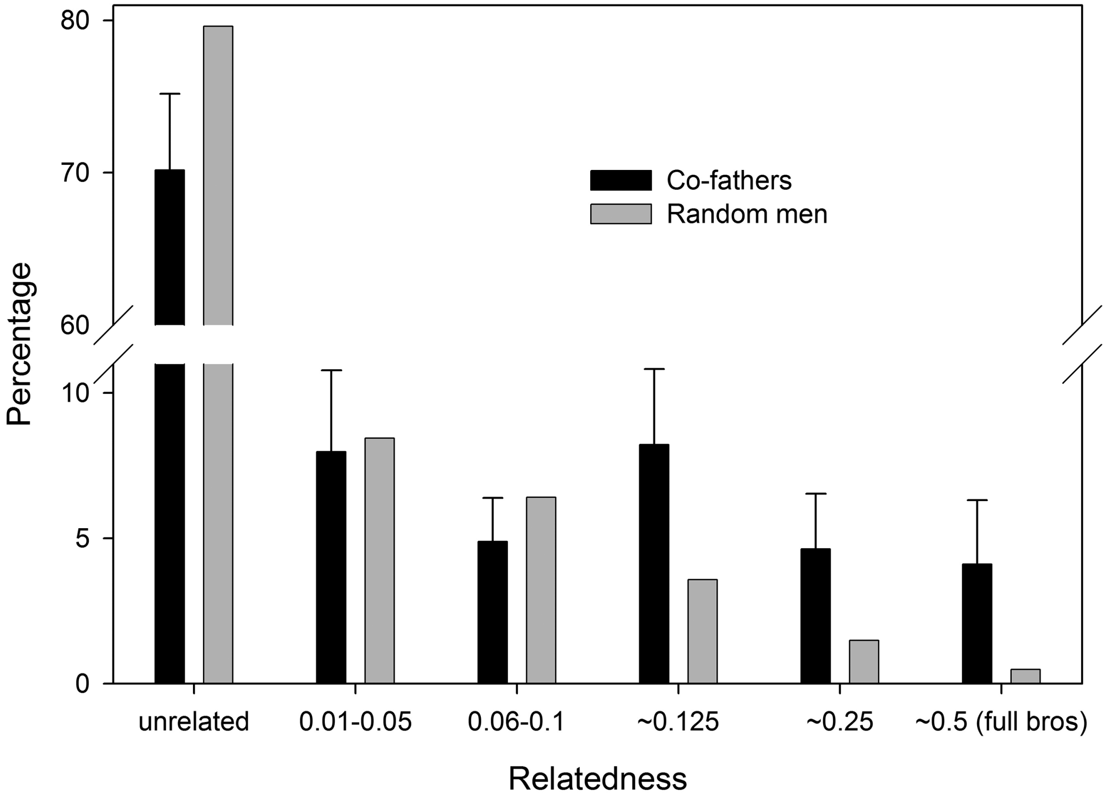

Figure 2.1. Comparison of observed relatedness between co-father pairs against baseline relatedness of random pairs of men alive at the same time. Error bars represent bootstrapped 95% confidence intervals.

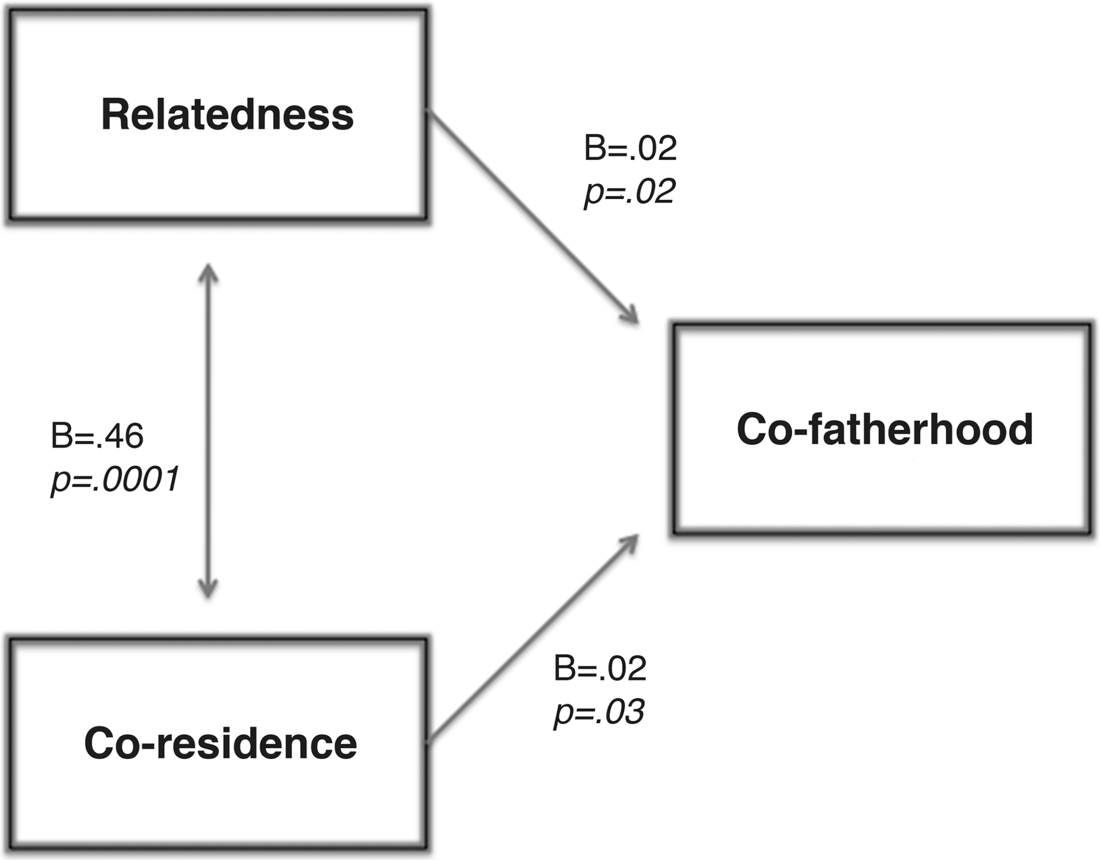

Figure 2.2. Partial correlations among relatedness, co-residence, and co-fatherhood among Ache men.

Chapter 3: Co-fatherhood and Child Survival among Ache Foragers.

Introduction

While polygyny has long been understood as a male reproductive strategy under a broad range of circumstances (e.g., Bateman 1948; Clutton-Brock and Parker 1992; Darwin 1871; Symons 1979; Trivers 1972), the reproductive benefits of polyandry remains a topic of theoretical and empirical debate (e.g., Arnqvist and Nilsson 2000; Hoogland 1998; Hosken and Stockley 2003; Houston, Gasson, and McNamara 1997; Hrdy 1979, 1981; Jennions and Petrie 2000; Keller and Reeve 1995; Scelza 2013; Simmons 2005; Wolff and Macdonald 2004; Zeh and Zeh 2001). In considering the adaptive significance of polyandry in humans, it is important to make a distinction between polyandrous marriage or pair-bonding, and polyandrous mating, as these two possibly quite different behaviors may have different causes and consequences for the fitness of men and women. Here, we are concerned with polyandrous mating in the human female, and the socioecological factors associated with fitness-enhancing consequences of polyandrous mating in partible paternity societies, and specifically among Ache foragers of Paraguay. One of the objectives of this chapter is to further our scientific understanding of conditions or contexts in which females may benefit reproductively from multiple mating.

Partible paternity refers to the idea that children can have more than one genitor; that is, that more than one man may contribute to the production of a single offspring (Beckerman et al. 1998; Beckerman and Valentine 2002). The concept is unique to cultures of lowland South America, where it is found among a majority of indigenous populations and is more common than the biologically correct view of singular paternity (Walker, Flinn, and Hill 2010). Attending the ideology of partible paternity are various forms of institutionalized extramarital sex on the part of men and women, and the mating patterns in these societies can be described, in part, as simultaneous polygynandry. The widespread existence of this traditional behavior among Amazonian cultures raises the question of possible benefits to men and women of divisible fatherhood. One possible benefit to women of the institutionalized extramarital mating attending the concept is investment from multiple men named as co-fathers of a child (the *multiple investors hypothesis* [Walker et al. 2010; Ellsworth, Bailey, Hill, Hurtado, and Walker 2014]).

Where relevant information is available, some amount of investment in a woman and putative co-offspring has been noted for several societies (e.g., Alès, 2002; Beckerman and Lizarralde, 2013; Beckerman and Valentine, 2002; Crocker, 2002; Hill and Hurtado, 1996; Kensinger, 2002; Pollock 2002; Walker et al. 2010). For example, among the Barí horticulturalists in the Maracaibo Basin, secondary fathers provisioned women and co-children with fish and game (Beckerman and Lizarralde, 2013). Similarly, among the Ache of Paraguay, men named as co-fathers supplied meat to the mother of their co-children (Hill and Hurtado 1996: 442). Ache secondary fathers became especially important sources of investment upon the absence of children's primary fathers (Hill and Hurtado 1996: 442-444). For Cashinahua horticulturalists of Peru, acknowledgement of co-paternity by a man "places him under obligation for future economic support for the child and its mother, although not to the same extent as if he were married to the mother" (Kensinger 2002: 21). Among the Yanomami of Venezuela "co-fathers are known, and supposed to supply food to the mother and offspring when husbands or social fathers are absent" (Alès 2002: 68).

Extra-pair investment would be especially beneficial to female reproductive success in contexts of low levels of paternal investment. In milieus of low and unreliable levels of paternal investment, the cultivation of sexual relationships with extramarital partners and subsequent recruitment of multiple investors (men named as co-fathers) may be a more successful strategy than reliance on the investment prospects of a single man. A key question regarding the multiple investors hypothesis is whether co-fathers and their investment have real beneficial consequences on the fitness of mothers and their offspring, and if so, what form or forms these benefits take.

Beckerman et al. (1998) investigated the fitness benefits of partible paternity among the Barí, finding support for the multiple investors hypothesis in terms of child survival. Survivorship to age 15 was higher among children with two fathers, compared to children with a single father. Beckerman et al. attributed the greater survivorship of children with multiple fathers to the extra provisioning of game and fish provided by secondary fathers to pregnant mothers and offspring (see also Beckerman et al. 2002). That investment of co-fathers is responsible for the effect of higher rates of offspring survival among the Barí is reinforced by further findings that siblings of children who had multiple fathers, but who themselves had a single father, did not show increased chances of survival enjoyed by their siblings (Beckerman et al. 2002; Beckerman and Lizarralde 2013).

In this chapter, the multiple investors hypothesis is tested further by examining the effect of co-fathers on offspring survival among Ache foragers. Previous analyses by

Hill and Hurtado have demonstrated higher survivorship to age 10 of Ache children with one primary and one secondary father compared to children with a single father (Hill and Hurtado 1996: 444). Thus, as found among the Barí, co-fatherhood is associated with increased survival prospects for Ache children. Here, I extend the examination of co-father effects on child survival to age 15, using statistical methods that allow a finer-grained analysis of patterns of mortality and explore several variables that might affect the previously reported survival advantage associated with secondary fathers. Variables of interest include sex of children, mother's identity, and birth cohort. Inclusion of these variables permits investigation of whether there are sex differences in co-father effects; the effects of co-fathers in the pre-contact forest period and after establishment of contact with outsiders; and how the effects of particular mothers might affect the importance of co-fathers on child survival. Findings confirm a survival advantage to children with secondary fathers and suggest additional considerations on the social dynamics of partible paternity among the Ache.

Methods

The present sample consists of 319 individuals born between 1916 and 1989 for which number of fathers is known. In order to examine effects of co-fathers on child survival, individuals in the sample were categorized into three groups according to number of co-fathers: group 0 representing those children who had only a primary father (n = 120); group 1 those children having a primary father and one secondary father (n = 132); and group 2 those children having a primary father and two or more secondary fathers (n = 67). Logistic regression for discreet survival analysis to age 15 was performed to test for differences in survival between the three groups of individuals. This model had survival outcomes for each year of age clustered under individual ID, with autoregressive residual covariance matrix that provided the best model fit over unstructured and compound symmetry residual covariance matrices. To test for effects of mothers, a second model clustered observations under individual ID as well as mother's ID, with autoregressive residual covariance matrix that provided the best model fit. IMB SPSS 22 Generalized Estimating Equation module was used to analyze the models. Fixed effects of co-father group, pre- and post 1963 birth date, and sex were then added to the model to determine if there are significant differences in log odds of surviving between groups, and if such differences are affected by birth date and sex.

Results

Results of the logistic regression show a significant difference in probability of survival to age 15 between group 0 and group 1. That is, children who had one co-father were significantly more likely to survive to 15, as well as show a higher probability of survival at each year of age, than children without a co-father (see Figure 3.1). However, there was no significant difference between groups 0 and 2, nor between groups 1 and 2 (see Tables 3.1 and 3.2). As illustrated in Figure 3.2, the largest difference between children with a co-father and children without a co-father is probability of surviving the first year of life (predicted mean log odds of survival before age 1 for group 0= .86, 95% CI [.78, .91]; group 1 = .93, 95% CI [.87, .96]). Adding mothers' identity to the regression model did not alter the survival differences between the three groups. There was no significant effect of adding pre-or post 1963 birth date as a variable. Although mortality increased overall in the sample for those individuals born after 1963 compared to those born prior to this year, significant differences in survival by group membership were similar in magnitude for both pre- and post-contact cohorts. Adding sex of individuals' as a variable also did not affect survival differences between group 0 and group 1; significant survival advantages were similar for both males and females in group 1 compared to their peers in group 0.

Discussion

The results of the present study replicate and extend those previously reported by Hill and Hurtado (1996) and Beckerman and colleagues (Beckerman et al. 1998; 2002). Children with one secondary father have a significantly higher probability of survival to age 15 compared to children without secondary fathers. Although male children have a distinct survival advantage over female children in the Ache population generally (see, e.g., Hill and Hurtado 1996: 186), results of the present study demonstrate that children of both sexes with a secondary father enjoy increased survival prospects over their peers without co-fathers. 86 percent of males in group 1 survived to age 15, versus 63 percent in group 0, and 66 percent in group 2; 77 percent of females in group 1 survived to age 15, versus 66 percent in group 0, and 77 percent in group 2.

That accounting for mothers' identity did not alter the significant differences in survival between children in groups 0 and 1 provides further support to the prediction that it is secondary fathers *per se*, that lead to the observed differences in mortality (i.e., possession of co-fathers has an effect on survival independent of any effects of particular mothers on their children's survival prospects). This strengthens the case for the importance of co-fathers among the Ache. That the largest difference in survival between those with a co-father and those without is in the first year of life suggests that, as proposed by Hill and Hurtado (1996), prevention of infanticide upon desertion or death of a primary father may have been an important effect of secondary fathers. Supplemental provisioning of pregnant and nursing mothers by secondary fathers may also play a role in decreasing infant mortality.

The observed advantage in survival for children with one secondary father exists for both those born prior to 1963 as well as those born after this date. This finding indicates that co-fathers continued to play an important role after the establishment of extensive contact with outside influences. Although the institution has now largely disappeared with acculturation, it is uncertain to what degree co-fatherhood remains an important tradition with effects on children born after the period, which the current data encompasses.

The findings of this study confirm that there are significant benefits associated with having secondary fathers for offspring, and shed additional light on the findings reported in chapter 2, that women chose co-fathers for their children who were closely related and who tended to reside together in the same camps— apparently as a strategy that maximized their access to co-father investment. Such findings suggest that reliance on investment from one man was a risky endeavor for Ache women and children. High divorce rates (Hurtado and Hill 1992) and adult male mortality among the Ache (Hill and Hurtado 1996) creates conditions in which the prospects for paternal investment are relatively unreliable, making the recruitment of secondary fathers for offspring an attractive option for women. Among forest living Ache, death of a father and divorce increased child mortality rates about threefold (Hill and Hurtado 1996: 424). Secondary fathers may represent a kind of insurance policy should investment from a husband cease to be forthcoming as a result of death or divorce. Again, this is the essence of the multiple investors hypothesis of benefits to females of partible paternity as a form of hedging one's bets on the support of men.

Support for a bet-hedging strategy in contexts of low or unreliable levels of male investment comes from studies of women's reproductive behavior in impoverished social environments where men and their potential investment are wanting (e.g., Byrd-Craven, Geary, Vigil, and Hoard 2007). In such environments, women tend to have greater numbers of sex partners and reproduce with greater numbers of men. When investment prospects are impoverished, women may gain more resources for themselves and their children through several sexual relationships over monogamous pair-bonding (Borgerhoff Mulder 2009; Cashdan 1993; Hrdy 2000; Lancaster 1989; Lancaster and Kaplan 1992). Indeed, among the Barí horticulturalists of Colombia and Venezuela, unmarried women recruited greater numbers of secondary fathers for their children than married women (Beckerman and Lizarralde 2013) suggestive of a strategy aimed at maximizing male investment by women without a long-term mate.

When levels of paternal investment are sufficiently low, it may be less costly for women to engage in polyandrous mating as a strategy to garner investment from multiple men. Polyandrous mating in partible paternity societies, in this view, might be a response to low paternal investment prospects. Indeed, polyandrous mating may act to reduce levels of paternal investment by encouraging males to devote more resources to mating over parental effort in response to mating opportunities with extramarital partners, thus reinforcing the benefits of spreading investment potential among multiple men. These circumstances create a self-perpetuating pattern in which a strategy of monogamous mating is less advantageous than multiple mating for both sexes.

If the discussion so far seems overly female-centric, we might acknowledge that what is good for women and their offspring is also good for the genitors of those offspring. Thus, if secondary fathers are a boon to children, then they are a boon to the reproductive success of whoever fathered that child (be they the secondary fathers themselves, or the primary fathers who reap the auxiliary aid). The flip side of the multiple investors hypothesis for women is in fact a bet-hedging hypothesis for men. If the benefits of sacrificing sexual monopoly outweigh the costs of high likelihood of offspring death upon a male's departure, then men too can benefit from polyandrous mating, even in the form of extramarital sex by a pair-bonded partner.

More research is needed on the impact of multiple fathers on child survival and wellbeing in additional societies to reveal the general applicability of the multiple investors hypothesis, especially in those partible paternity societies where expectations and obligations of investment on the part of secondary fathers have been noted. Further study of the socioecological factors that increase the likelihood, and benefits, of multiple mating by males as well as females is an important avenue of future investigation if we wish to have a more complete picture of the contextual influences and adaptive plasticity of human sexual and parenting behavior. Factors associated with increased female sexual autonomy are probably particularly important, and as asserted here include pair-bond instability and relatively unreliable male investment; other candidate factors are alloparental support networks, uxorilocal residence, greater female contribution to labor and subsistence, and absence of significant forms or amounts of male-controlled heritable wealth. These are urgent tasks as cultural traditions, including shared fatherhood, are rapidly being disrupted and lost in the face of increasing contact with the modern world.

	Number of Co-fathers		
	0	1	2 or more
Survive to 15	77	109	48
Less than 15	43	23	19
Total	120	132	67
Percent survive	64%	83%	72%

Table 3.1. Total numbers of individuals in each co-father category who survived to age 15 or died before this age. Percentages in bottom row are the percentages of individuals in each category who survived to age 15. Chi square = 11.0195, p < .01

Group	Comparison	Mean Difference	Std. Error	df	Sig.
0 No co-father	1 Co-father	-0.02	0.006	1	0.006
	2 Co-fathers	-0.01	0.007	1	0.394
1	0	0.02	0.006	1	0.006
	2	0.01	0.006	1	0.148
2	0	0.01	0.007	1	0.394
	1	-0.01	0.006	1	0.148

Table 3.2. Pairwise comparisons of estimated marginal means of survival to age 15 of the three groups of children.

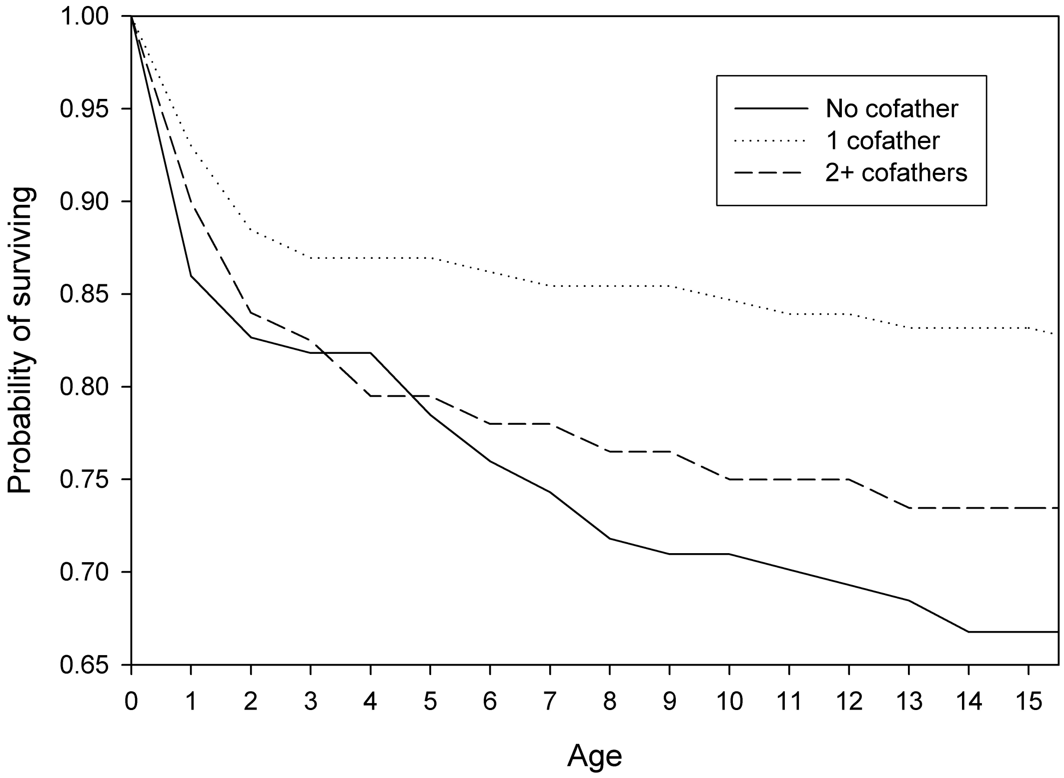

Figure 3.1. Figure illustrating probability of survival from birth to 15 years of age for each co-father category. (No co-fathers = group 0; 1 co-father = group 1; 2+ co-fathers = group 2).

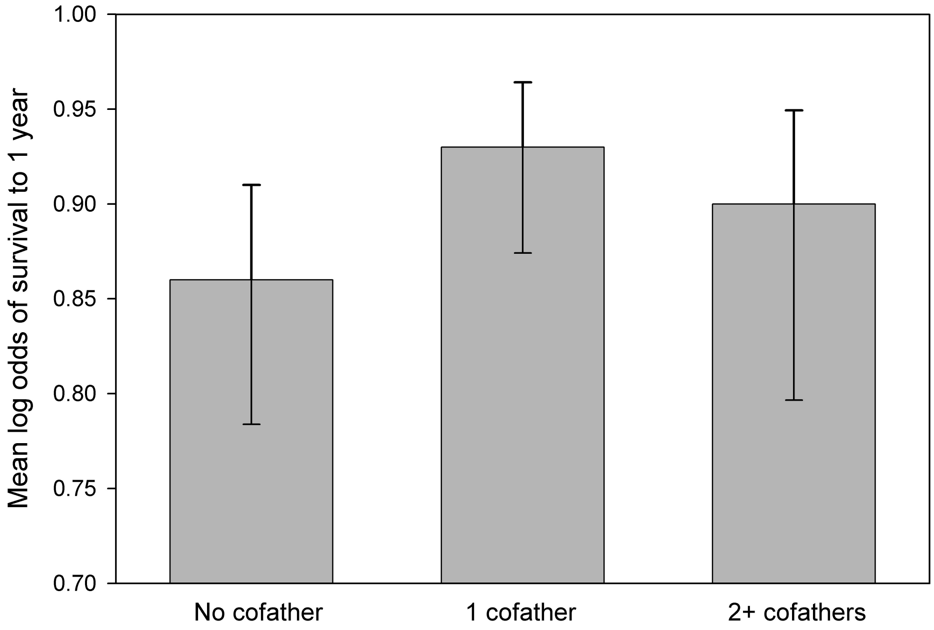

Figure 3.2. Mean log odds of survival to one year for individuals in each co-father category. Mean values are shown by top of each bar, whiskers represent 95% confidence intervals. (No cofather = group 0; 1 cofather = group 1; 2+ cofathers = group 2).

Chapter 4: Comparative Study of Reproductive Skew and Pair-Bond Stability Using Genealogies from 80 Small-Scale Human Societies

Introduction

There is considerable complexity and variation in marriage practices and family structure across human cultures (Fox 1967; Murdock and White 1969; Flinn and Low 1986). Human mating systems integrate strategies common in other organisms, such as control of resources to attract mates, direct competition for control of mates, and advertisement of phenotypic indicators of heritable qualities (Emlen and Oring 1977; Dixson 1998; Shuster and Wade 2003;Thornhill and Alcock 1983; Thornhill and Gangestad 2008). Unlike other species, reproductive decisions in humans are often not simply autonomous choices made by individuals but are culturally regulated and controlled by parents and other kin (Apostolou 2007; Apostolou 2010). Uniquely, humans often depend on support networks of kin-based alliances and coalitions to negotiate and exchange mating and marriage opportunities that often extend across multiple communities (Lévi-Strauss 1949; Fox 1967; Chagnon 1982; Chapais 2008). Morphological physiological, and behavioral evidence suggests that our recent evolutionary history has been characterized by predominantly (serial) monogamous pair-bonding with facultative polygynous and, to a lesser but not insignificant degree, polyandrous mateships on both long and short terms (Dixson 2009; Geary 2010; Low 2000; Starkweather and Hames 2010; Symons 1979). Cross-culturally, a majority of societies permit polygamous marriages, although most conjugal unions in all human populations are monogamous (Murdock 1967; Marlowe 2000), and most sexual behavior and reproduction occurs, with important exceptions, within the context of long-term pair-bonds with biparental care of offspring (Gray and Garcia 2013; Symons 1979).

There are two primary dimensions of variation in human mating systems that deviate from stable monogamy and beg for socioecological explanations. The first is male reproductive skew ranging from mostly monogamous (low skew) to strongly polygynous (high skew) mating patterns (Betzig 2012; Low 1988). The second dimension is pair-bond stability ranging from low to high rates of conjugal dissolution and serial mateships (Betzig 1989; Barber 2003b). While these two dimensions have received considerable attention, progress has been hampered by studying each in isolation and by measurement difficulty. Pair-bond stability has proven particularly recalcitrant. Ethnographers generally describe divorce and divorce rates with incomparable descriptors such as “rare”, “not difficult”, “easy”, and “common.” Rarely do ethnographies report actual frequencies or rates of divorce (see, e.g., Pearson and Hendrix 1979: 378).

In this chapter, a methodology is advanced that allows for both reproductive skew and pair-bond stability to be analyzed simultaneously using information on the prevalence of different sibling types gleaned from genealogies. Full sib sets originate from stable monogamous pair bonds. Paternal sibs primarily stem from male reproductive skew through polygynous mating or serial monogamous mating when men remarry younger wives or are simply more likely to remarry or obtain new mates than widowed or divorced women. Maternal sibs indicate the dissolution of pair bonds due to divorce or male death. While unstable pair bonds also generate paternal sibs, the overall effect is likely to be small in comparison to that generated by male reproductive skew because male reproduction is not as time limited as that of females given the interbirth interval necessary for pregnancy and lactation, as well as menopause (Marlowe and Berbesque [2012] estimate forager female physiological reproductive span to be 34 years, and that of males to be 71 years). Pair-bond instability is also likely to potentiate reproductive skew since some men will be more able to find new partners than other men. Hence, the simple calculation of the fraction of sib dyads of different types allows for quantification of human reproductive variation into dimensions of stable monogamy (represented by full sibs), male reproductive skew (paternal sibs), and pair-bond instability (maternal sibs).

Polygyny and Reproductive Skew

Measuring male reproductive skew in humans, although hampered by paternity uncertainty, is commonly reported with various measures of polygynous marriages (Low 1988). Here, focus is on previous research specifically addressing the factors associated with variation in polygynous marriage across cultures. This allows predictions to be tested against genealogical data to assess the congruency between more traditional measures of polygyny described below and the current method of measuring reproductive skew via patterns of siblinghood.

One early attempt at systematic investigation of variation in polygyny cross-culturally was that of White and Burton (1988), who found that two significant predictors, as measured by percentage of women married polygynously, were climate zone and female contribution to subsistence. Polygyny is more prevalent in tropical and temperate zones where women contribute more to the diet. Low (1990) examined the relationship between pathogen stress and marriage patterns and reported a higher incidence of polygyny, as measured by several different metrics, in those societies inhabiting regions of high pathogen stress. More recently, Marlowe (2000), also found polygyny as measured by percentage of polygynously married women to be highest among horticulturalists, where men contribute the least to subsistence. The negative relationship between degree of polygynous marriage and male contribution to subsistence holds within each mode of subsistence (Marlowe 2000; Marlowe 2003). A study by Marlowe (2003) of 36 hunter-gatherer societies confirmed previous findings that degree of polygyny, as measured by percentage of polygynously married women, is positively correlated with pathogen stress (which is higher at lower latitudes) and negatively correlated with male contribution to subsistence. These factors are all interrelated in that pathogen stress tends to be higher at lower latitudes, male contribution to subsistence is greater at higher latitudes, and polygynous marriage is more prevalent among societies at lower latitudes.

A crucial issue from the standpoint of understanding human reproductive patterns is the extent to which marriage systems reflect the actual mating system, as revealed by reproductive outcomes. If measures of polygyny using data on marriage are accurate depictions of reproductive reality, then given the observed relationships between pathogen stress and climate, and male contribution to subsistence and latitude (Kelly 1995), reproductive skew should be highest among societies inhabiting lower latitudes. That is, it is predicted that paternal sib fractions will be greater at lower latitudes.

Pair-bond Instability

While marriage patterns have been analyzed in depth by numerous anthropological researchers, systematic investigations of quantitative measures of pair-bond instability and divorce have been given much less attention (but see e.g., Blurton Jones et al. 2000; Quinlan and Quinlan 2007; and discussion below). Here, predictions must necessarily be more speculative. Given the association between mode of subsistence and male contribution to diet, as well as between subsistence mode and amassable, defendable, and heritable resources, the following three predictions are derived: 1) Pair-bond instability will be greater where male contribution to subsistence is lower. Thus, according to Marlowe's findings on male contribution to subsistence by subsistence mode, horticulturalists should exhibit the highest fraction of maternal sibs, and agropastoralists the lowest; 2) Given the greater dependence on male contribution to subsistence at higher latitudes (Kelly 1995), pair-bond instability will be lower at higher latitudes, irrespective of subsistence mode; 3) Pair-bond instability will be greater in the absence of amassable, heritable resources. Where women are not dependent on male controlled resources for offspring success, they may be less constrained to dissolve a pair-bond. Foragers and horticulturalists should exhibit the highest, and agropastoralists the lowest fraction of maternal sibs.

Partible Paternity

Recent documentation of partible paternity in lowland Amazonia has added an interesting twist to traditional perspectives on human mating and marriage. Partible paternity refers to the concept that children can have more than one genitor and is common among many indigenous societies of lowland South America (Beckerman et al., 1998; Beckerman and Valentine 2002; Walker, Flinn, and Hill 2010). Partible paternity implies polygynandrous extramarital mating that may destabilize marital unions leading to more maternal sibs given a combination of sexual jealousy and reduction or splitting of paternal investment. Hypothesized benefits of partible paternity include gene shopping by females, the procurement of investment from multiple men, and mate competition by males (see Walker et al. 2010). In this context, high quality men may obtain greater numbers of sexual partners and sire more offspring. To the extent that genealogical data reflect actual paternity, it is predicted that partible paternity societies will have higher fractions of paternal sibs than singular paternity societies. Because of the extra-pair sexual relationships entailed in the practice of partible paternity, it is also predicted that pair-bond instability will be greater among partible paternity societies compared to singular paternity societies; partible paternity societies will have higher fractions of maternal sibs than singular paternity societies.

Methods

Genealogies and marriage records for this study are mostly online at the KinSources website (http://kinsources.net). Additional genealogies were added for 5 hunter-gatherers societies from Hill and colleagues (2011) and 18 Amazonian horticultural societies from Walker and colleagues (2013). The small-scale societies used here are categorized as hunter-gatherers (*n* = 38), horticulturalists (*n* = 33), agriculturalists (*n* = 6), and pastoralists (*n* = 3). Because the latter 2 categories are small, they are lumped together for statistical purposes as agropastoralists. The total sample includes 80 societies that yield 165,379 sib dyads. An Amazonian subset of 26 societies with known paternity beliefs (Walker et al. 2010) is used to compare singular versus partible paternity societies.

Genealogies range in depth from 3 to 16 generations but variation in genealogical depth does not affect results because only information for both of ego's parents is needed to count sib types. Individuals with missing data for mother or father or both are excluded. Relationships between fathers and offspring were taken at face value as reported by informants. For partible paternity societies, the primary father (generally mother's husband) is assumed to be the biological father.

Results

Sibling types

The percent of sibs in the overall sample (Supplementary Information) shows that most sib dyads are full (63%, range 25-100% across societies) while fewer are paternal (29%, range 0-65%) or maternal (8%, range 0-31%). A ternary plot (Figure 4.2) shows that many societies have sib fractions that cluster towards stable monogamy (more full sibs). Most variation occurs along the paternal sib axis and is roughly twice that of variation in maternal sib axis likely due primarily to differences in maximum reproductive rates between males and females. Despite the fact that pair-bond instability generates both paternal and maternal sibs, there is no correlation between the two (Table 4.1), probably because male reproductive skew swamps the variation in maternal sibs. Variation in levels of maternal sibs exists across the entire spectrum of paternal sibs. This suggests that male reproductive skew and pair-bond stability are independent sources of cross-cultural variation in human mating patterns. Moreover, *the different modes of* *subsistence do not co-vary with fractions of sib types.* Horticulturalists and agropastoralists have only slightly higher counts of paternal sibs than foragers in the sample (0.24 versus 0.18 on average), but the relationship is only a statistical trend (t = 1.92, p = 0.06, n = 80). In other words, these results show a very weak relationship between subsistence mode and male reproductive skew, nor is there a significant relationship between subsistence mode and pair-bond stability.

Variation in paternal sibs correlates with more polygynous marriages measured as number of wives per married man from marriage records (Figure 4.3). And while there is no systematic co-variation between subsistence mode and reproductive skew, the relationship between polygynous marriages and variation in paternal sibs is similar for societies within each category of subsistence mode. The correlation between paternal sibs and polygynous marriage is expected yet important in that it indicates congruency between marriage and mating patterns, and provides validity to using measures of polygynous marriage as an indicator of male reproductive skew in our sample. However, as argued below, paternal sib counts may actually be a better measure of male reproductive skew than polygynous marriage for a number of reasons (see Discussion).

Latitudinal Gradients

Higher latitude societies have significantly fewer paternal sibs, as predicted given previous studies (e.g. Low 1990; Marlowe 2000) of latitudinal gradients of polygynous marriage (Table 3.1). Partly confirming our predictions, full sibs are also more common at high latitudes, indicative of a greater degree of monogamous mating. Multiple regressions of sib fractions as a function of latitude and subsistence consistently show that latitudinal gradients are strong for full and paternal sibs with little evidence for differences across subsistence or for interaction effects between latitude and subsistence. There is also no observed difference in maternal sib fractions by subsistence mode or latitude in our sample of societies. This means that the effect of latitude on sib fractions is not due to variation in subsistence modes associated with latitude, but may be explained by latitudinal variation in male contribution to subsistence.

Partible Paternity

Sib fractions in lowland South American societies vary systematically with paternity concept. Societies with partible paternity have lower full sib fractions overall (0.54, 95% bootstrapped confidence interval 0.47-0.62) than do singular paternity counterparts (0.72, 95% bootstrapped confidence interval 0.63-0.80, Figure 4.4). Paternal sib fractions are higher in partible paternity societies, while maternal sib fractions do not differ significantly by paternity concept (Table 4.1). As predicted, partible paternity appears to correlate with more male reproductive skew. However, inconsistent with our other prediction, partible paternity does not appear to be associated with greater pair-bond instability. The primary difference between partible and singular paternity societies in our sample, then, is a greater degree of monogamous mating by males in singular paternity cultures.

Discussion

The findings of the present study show that the majority of human reproduction occurs within pair-bonds that are stable and monogamous, given that 63% of all sib dyads in the sample are full sibs. Variation away from pair-bond stability and monogamous mating trends primarily towards more male reproductive skew arising from polygynous mating and resulting in higher fractions of paternal half sibs.

Results demonstrate a latitudinal gradient on sib fractions, such that full sib fractions increased, and paternal sib fractions decreased at higher latitudes. Societies at lower latitudes are characterized by more polygynous mating consistent with a combination of both greater female contribution to subsistence and female gene shopping in environments of high pathogen load (e.g., Low 1990; Marlowe 2003). As reported above, this latitude gradient is not mediated by subsistence mode; that is, degree of reproductive skew is not explained by mode of subsistence *per se* in our sample of societies. This finding is in contrast to previous research demonstrating a higher incidence of polygynous marriage among horticulturalists compared to other subsistence types (e.g., Marlowe 2000), and a more general relationship between subsistence and marriage patterns (e.g., White and Burton 1988). Therefore, instead of, or in addition to, broad comparisons between subsistence mode, it may prove more fruitful to focus on particular socioecological contexts, that perhaps occur independently of subsistence, that lead to differences in male reproductive skew. The current results show no effect of subsistence type on full or half sib fractions. To the extent that subsistence plays a role in variation in male reproductive skew, it may be related to the relative contribution to subsistence of men and women. For example, the societies in the current sample for which data exist show that among foragers in North America, male contribution to subsistence increases with latitude (Kelly 1995: 263).

Marriage record data and sibling analysis demonstrate a positive relationship between polygynous marriage and reproductive skew for societies in the present sample, suggesting that marriage patterns do closely correspond to patterns of mating. However, counting paternal sibs has several advantages over counting polygynous marriages. First, variation in male reproductive skew measured by paternal sibs includes polygynous mating outside of marriage either in the form of children born out of wedlock or children born from extra-pair matings (assuming ethnographers at least occasionally ascertained the identities of actual fathers). Second, available marriage records are often snapshots in time, while genealogies extend over multiple generations. Third, although reproductive skew and polygynous marriage were closely correlated in the current sample of societies for which both kinds of data are available (hence supporting the use of marital patterns to extrapolate reproductive skew), it is not obvious that this will be the case in other societies. Fourth, genealogies represent actual reproductive outcomes and not just marriages that may or may not result in offspring. Therefore, information on paternal sibs likely constitutes a more comprehensive index of male reproductive skew than that available from the prevalence of polygynous marriages alone. Additionally, measures of actual reproductive outcomes via patterns of siblinghood across multiple generations gives an additional index of the strength and directions of sexual selection within populations over time that complements other methods of assaying differential reproductive success (see e.g., Brown, Laland, and Borgerhoff Mulder 2009). Alternatively, one could attempt to measure skew by estimating the dispersion of paternity across men. However, this was found to be difficult because later generations in genealogies include many men that have not yet finished their reproduction, a problem that is circumvented by using paternal sib fractions.

Pair-bond instability has been given much less attention than marriage systems, and as mentioned above, has proven difficult to quantify in the ethnographic record, hampering the types of comparative analyses like those done for polygyny. The method of counting maternal sibs shows little systematic variation across subsistence types, latitude, or paternity concept. A study by Apostolou (2010) showed that divorce is reported as common across societies of all subsistence types, and regression analyses indicated that divorce commonness is independent of mode of subsistence. The present findings on maternal sibs appear to corroborate those of Apostolou, but leave unresolved the question of what socioecological variables are related to marital stability.

One variable shown to be reliably associated with divorce and pair-bond stability in humans and nonhuman species is adult sex ratio (Barber 2003b; 2005; Blurton Jones et al. 2000; Guttentag and Secord 1983; Liker, Freckleton, and Szekely 2014; Pedersen 1991). Where adult sex ratios are female-biased, males have greater opportunities to acquire new and multiple mates, and rates of divorce consequently tend to be higher in such contexts. However, adult sex ratio in the present sample of societies shows no systematic relationship with pair-bond stability.

Other factors that have been identified include socioeconomic development and female labor participation (Trent and South 1989). The issue of socioeconomic development in the present study cannot be addressed, as this factor is rather ill-defined for traditional societies. Female labor force participation has been shown, in developed and developing countries to be positively associated with divorce (see refs in Trent and

South 1989). Additionally, anti-promiscuity moral attitudes have recently been found to correlate with women's economic dependence (Price, Pound, and Scott 2014). This, presumably, has something to do with a lessening of female dependence on male provisioning in those ecologies where females contribute more their household economies. As Irons (1983) has argued, in such contexts, females may expend more effort in establishing and maintaining social relationships with other females (co-wives, sisters, cousins) than with husbands, and this trade-off may thus attenuate the conjugal dyad.

In the present sample of traditional small-scale societies, labor force participation would seem to be comparable to female contribution to subsistence, and assuming a latitudinal gradient in male contribution to subsistence (with males contributing relatively more at higher latitudes), pair-bonds appear to be more monogamous where males contribute the majority to subsistence. However, a study by Quinlan and Quinlan (2007) of divorce in societies of the SCCS found a curvilinear relationship between contribution to subsistence and pair-bond stability, with increases in pair-bond instability associated with increasing disproportion in contribution to subsistence by one sex or the other. In the present sample, there is no significant systematic difference in pair-bond stability.

In partible paternity societies, the strong pattern of higher fractions of paternal sibs, indicating high male reproductive skew, could arise from mating systems where some males are able to sire disproportionately more children, irrespective of marriage patterns or pair-bond stability. However, partible paternity societies do have a higher level of polygynous marriages on average than singular paternity counterparts (1.37 versus 1.23 wives per married man), as well as more polygynous mating as indexed by fractions of paternal sibs. Institutionalized extramarital sexual relationships attending the partible paternity concept could be another source of the higher male reproductive skew in these populations, albeit surprising that ethnographers have been able to document the identity of actual fathers as opposed to social fathers married to the mother. More likely, some males who do not marry polygynously are able to remarry quicker and with younger wives in serial monogamy that contributes to more male reproductive skew. Such a pattern must hold for only some men because average rates of pair-bond dissolution, as indicated by maternal sib fractions, do not vary between partible and singular paternity societies.

High rates of male death in tribal warfare (Beckerman and Valentine 2008; Walker and Bailey 2013) in the more traditional and unacculturated partible paternity societies may make male investment relatively unreliable and risky from women's perspective. Unreliable paternal investment and higher degrees of polygynous mating and marriage result in an interrelated suite of traits emerging in partible paternity systems that includes more male mating effort, low levels of paternal investment, and high male reproductive skew. Within such a milieu, women may benefit from spreading investment potential among multiple men, in effect securing insurance on male investment in self and offspring upon cessation of investment from a primary mate as a result of divorce or otherwise. Female mating strategies in these contexts are expected to be tuned to choosing males both within and outside of marriage in ways that optimize access to limited and unreliable paternal investment.

Conclusion

Anthropologists have long struggled with the question of how best to document the comparatively rich diversity of human reproductive strategies around the world. The ethnographic record is often qualitative in nature, but statistics and hypothesis testing benefit from quantitative estimates of cultural variation. A common solution to this problem is for anthropologists to lump societies into discrete categories (e.g., rare versus common polygyny or divorce). Sib counts from genealogies provide an alternative solution to investigate cross-cultural mating and marriage practices by quantifying reproductive variation on a continuous scale. The endeavor appears valuable in that it further confirms previous results (e.g., latitudinal gradients in polygyny) and opens new horizons for comparative ethnological analyses.

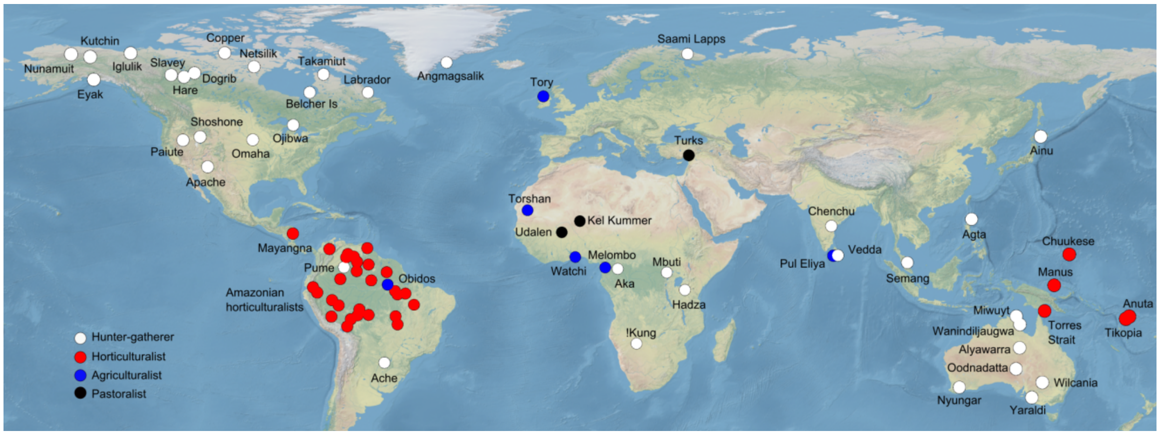

Figure 4.1. Map of societies used in this study with designations for subsistence type.

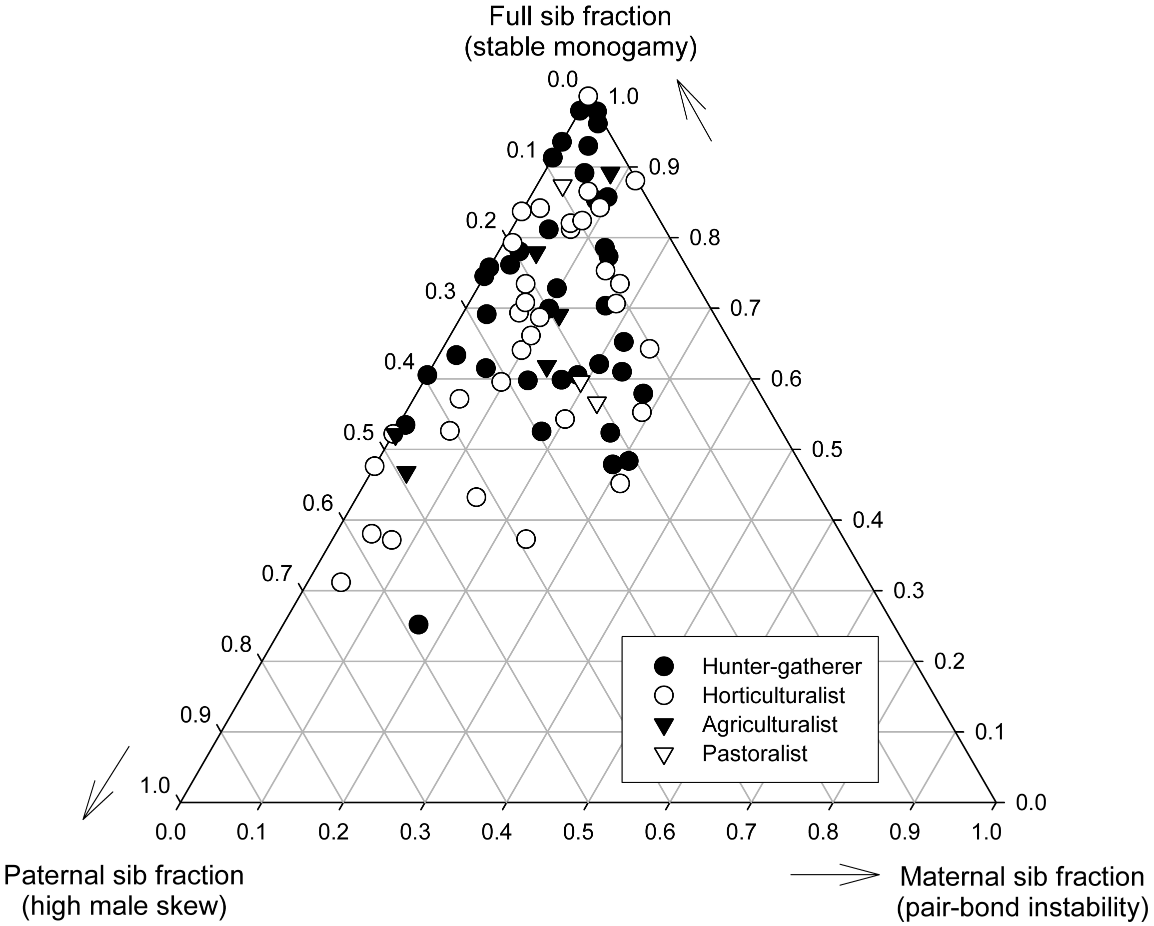

Figure 4.2. Ternary plot of the proportion of different sib types. Maternal sib fraction is on the x-axis, full sib fraction is on the y-axis, and paternal sib fraction is on the z-axis. Societies are designated by subsistence category. Many societies cluster towards stable monogamy (more full sibs) with variation extending mostly in the z-axis (more paternal sibs and male reproductive skew) and less variation in the y-axis (more maternal sibs and pair-bond instability).

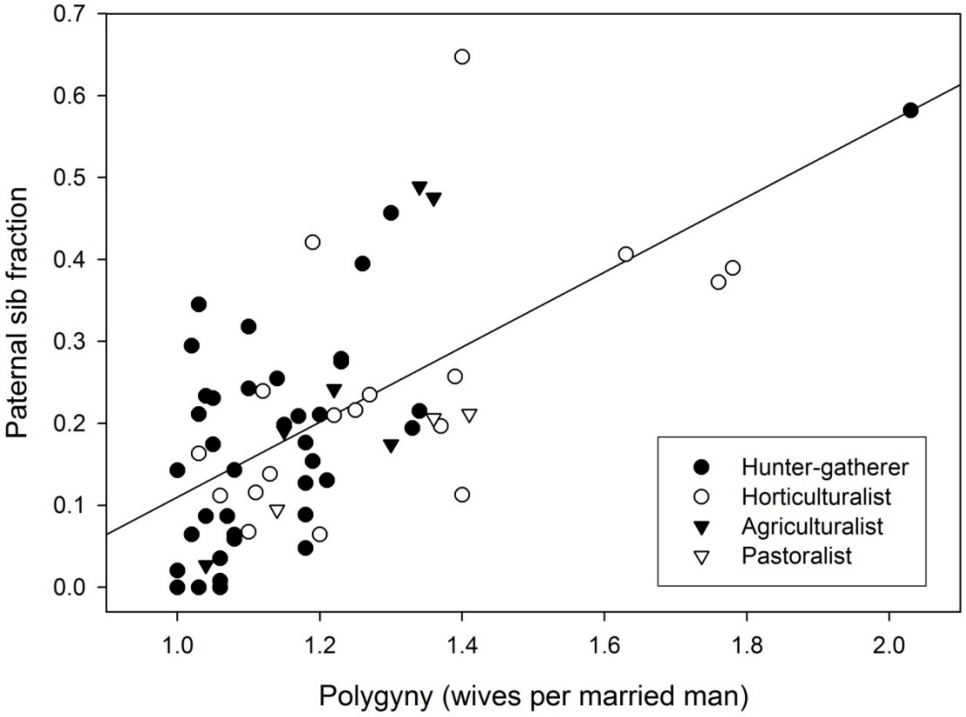

Figure 4.3. Positive relationship between paternal sib fractions and polygynous marriages.

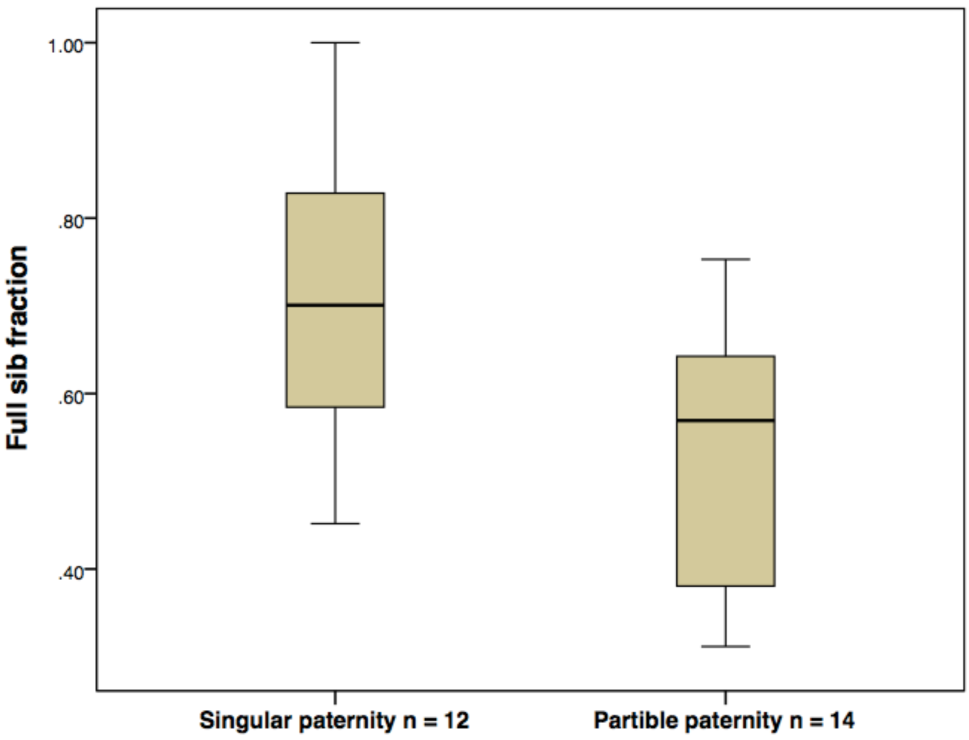

Figure 4.4. Boxplot of full sib fraction for singular paternity versus partible paternity societies. Boxes represent mid-50% of sample, lines in middle of boxes are the medians, whiskers contain 95% of the sample.

	n	Maternal sib fraction	Paternal sib fraction	Full sib fraction	Absolute latitude	Polygyny
Paternal sib fraction	80	-0.044				
Full sib fraction	80	-0.467**	-0.863**			
Absolute latitude	80	-0.167	-0.325**	0.372**		
Polygyny	65	0.162	0.633**	-0.602**	-0.380**	
Partible paternity	26	0.168	0.466*	-0.529**	0.142	0.282

Table 4.1. Correlation matrix for the relevant variables in this study. Statistical significance is marked as follows: * $p < 0.05$ and ** $p < 0.01$.

Chapter 5: Conclusion

Human sexuality and reproductive strategies are extremely complex. Part of this complexity lays in the co-evolution of human sexuality with the human psyche over the last several million years in which increasingly rapid and autocatalytic intraspecific runaway selection operated in a milieu of within-group cooperation and between-group competition (Alexander 1990; 1989; 1979; Alexander and Noonan 1979). The vast array of socioecological diversity across human populations also adds much to this complexity, and has no doubt favored high levels of contingency and plasticity in human mating and parenting behavior. The previous chapters represent an attempt to shed analytical light on this complexity and elucidate the adaptive logic and ecological correlates of variation in human reproductive strategies.

Chapters 2 and 3 were concerned with male and female strategies related to partible paternity among Ache foragers of Paraguay. Hypotheses on the benefits to men and women of the institution of sharable fatherhood were tested in chapter 2, and it was found that Ache women chose co-fathers for their offspring in ways suggestive of increasing investment in themselves and their offspring; co-fathers were more likely to be relatives, and to be more often co-residents of the same bands. It was also found that men appear to capitalize on women's relative autonomy in mate choice among the Ache. Men who were more often primary fathers were also more often secondary fathers; that is, these men had greater sexual access to multiple mates. Patterns of relatedness and co-residence among co-fathers indicates that men who shared in the fatherhood of the same children were allies, and these alliances may have facilitated investment in women and children, and promoted greater cooperation between co-fathers.

Chapter 3 examined more directly the hypothesis that multiple paternity has reproductive benefits through analysis of co-fatherhood and child survival among the Ache. Children with a secondary father were significantly more likely to survive to age 15 than children with only a single father. This survival advantage suggests that women (and men) had a vested interest in recruiting additional sources of investment in offspring in the context of high rates of divorce and adult male mortality, which characterized Ache social life. It appears that kin other than mothers and fathers had little effect on child mortality among the Ache (Hill and Hurtado 1996: 424). This makes secondary fathers the primary source of alloparental investment for Ache children, and thus polygynandrous mating was certainly adaptive behavior, beneficial to mothers, children, and biological genitors alike.

Chapter 4 diverted from focus on partible paternity to a broader scope of patterns of reproductive behavior cross-culturally. In that chapter, a methodology was advanced for simultaneously measuring two key dimensions of variation in human mating systems: male reproductive skew and pair-bond stability. This method involves calculation of fractions of different types of siblings, which are easily culled from genealogical data. This method was applied to a large sample of small-scale traditional societies around the world. The main findings were that polygynous mating shows a close correlation with levels of polygynous marriage; reproductive skew shows no systematic variation with mode of subsistence, but does show a latitudinal gradient, with higher levels of reproductive skew at lower latitudes. This latitudinal gradient in polygynous reproduction is consistent with hypothesized relationships between polygyny and pathogen prevalence, as well as male contribution to subsistence. According to Low (1990), when pathogens constitute a prominent hostile force of nature, variance in male reproductive success is more pronounced as a result of female choice for parasite and disease resistance. Marlowe (2000) attributes higher levels of polygyny to lower levels of male contribution to subsistence at lower latitudes, implicating less female dependence on male provisioning and more male competition for multiple mates in these contexts. More work is needed to separate out these two hypotheses for the sample used in chapter 4. To return briefly to partible paternity, South American societies that practice partible paternity are characterized by higher levels of polygynous marriage and reproductive skew than are singular paternity counterparts. Polygyny indexs male mating effort, which trades off against parental effort. Thus, this finding lends further credence to the argument that partible paternity is a response to low and unreliable paternal investment prospects. Surprisingly, there were no systematic correlates found for pair-bond stability, suggesting this is still a problematic issue in behavioral ecology that merits further study.

Much remains to be discovered about the contingencies and range of variation in human social and reproductive dynamics. The exploration and description of human nature is greatly served by investigation of the sociocultural and ecological variation that still exists, but is continuously and increasingly threatened by the homogenizing forces of Western encroachment and globalization. There are strong arguments to be made for a pan-human psychology (e.g., Tooby and Cosmides 1992), but an important goal is understanding its variable expression in response to variable environments that present variable problems that require variable solutions. Reproductive behavior and mating systems are deserving of a central place in the sociobiological study of humans because they have important effects on demography, life history, and directions of natural and sexual selection. Reproductive strategies also affect more pragmatic human concerns at a societal level such as competitive and sexual violence, resource inequality, and health. In the pursuit of self-knowledge for scholarly or practical purposes, it is probably a good rule to keep in mind that all functions of life are subservient to reproduction (Tooby and Cosmides 1992; Williams 1966). Our cognition, emotion, and behavior are guided by adaptations that gave our ancestors an edge in terms of descendant-leaving success over their competitors (Palmer and Steadman 1997). For 4 billion years, differential genetic proliferation has been the name of the game, and, however sophisticated our species version of the game is, we are part of that world “populated by organisms striving to no end but rather playing ridiculous sexual games, a world in which the brain is an extension of the gonads” (Ghiselin 1973: 968).

Bibliography

Ales, C. 2002. A story of unspontaneous generation: Yanomami male co-procreation and the theory of substances. In *Cultures of multiple fathers: the theory and practice of partible paternity in lowland South America.* S. Beckerman, and P. Valentine, eds. Pp. 62-85. Gainesville, FL: University Press of Florida.

Alexander, R. D. 1979. *Darwinism and human affairs.* Seattle, WA: University of Washington Press.

Alexander, R. D. 1987. *The biology of moral systems.* New York: Aldine De Gruyter.

Alexander, R. D. 1989. The evolution of the human psyche. In *The human revolution*. C. Stringer and P. Mellars, eds. Pp. 455-513. Edinburgh: University of Edinburgh Press.

Alexander, R. D. 1990. How did humans evolve? Reflections on the uniquely unique species. *Univ. Mich. Zool. Special Publication* 1: 1-38.

Alexander, R. D., and Noonan, K. M. 1979. Concealment of ovulation, parental care, and human social evolution. In Chagnon, N., and Irons, W. (eds.) *Evolutionary biology and human social behavior* (pp. 436-453). North Scituate, MA: Duxbury Press.

Apostolou, M. 2007. Sexual selection under parental choice: the role of parents in the evolution of human mating. *Evolution and human behavior* 28: 403-409.

Apostolou, M. 2010. Sexual selection under parental choice in agropastoral societies. *Evolution and human behavior* 31: 39-47.

Arnqvist, G., and Nilsson, T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* 60: 145-164.

Barash, D. 1977. *Sociobiology and behavior*. Elsevier.

Barber, N. 2003a. Paternal investment prospects and cross-national differences in single parenthood. *Cross-cultural Research* 37: 163-177.

Barber, N. 2003b. Divorce and reduced economic and emotional interdependence: A cross-national study. *Journal of divorce & remarriage* 39: 113-124.

Bateman, A. J. 1948. Intra-sexual selection in Drosophila. *Heredity* 2: 349–368

Beckerman, S., and Lizarralde, R. 2013. *The ecology of the Barí: Rainforest horticulturalists of South America.* Austin: University of Texas Press.

Beckerman, S., R. Lizarralde, M. Lizarralde, J. Bai, C. Ballew, S. Schroeder, D. Dajani, L. Walkup, M. Hsiung, N. Rawlins, and Palermo, M. 2002. The Barí partible paternity project, phase one. In *Cultures of multiple fathers: the theory and practice of partible paternity in lowland South America.* S. Beckerman and P. Valentine, eds. Pp. 27-41. Gainesville, FL: University Press of Florida.

Beckerman, S., and Valentine, P., eds. 2002. *Cultures of multiple fathers: the theory and practice of partible paternity in lowland South America*. Gainesville, FL: University Press of Florida.

Beckerman, S., and Valentine, P., eds. 2008. *Revenge in the cultures of lowland South America.* Gainesville: University Press of Florida.

Betzig, L. 1989. Causes of conjugal dissolution: A cross-cultural study. *Current Anthropology*: 654-676.

Betzig, L. 2012. Means, variance, and ranges in reproductive success: Comparative evidence. *Evolution and Human Behavior* 33: 309-317.

Betzig, L., Borgerhoff Mulder, M., and Turke, P. 1988. *Human reproductive behaviour: A Darwinian perspective.* Cambridge: Cambridge University Press.

Binford, L. R. 2001. *Constructing frames of reference: An analytical method for archaeological theory building using ethnographic and environmental data sets*. Berkeley: University of California Press.

Blurton Jones, N. G., Marlowe, F., Hawkes, K., and O'Connell, J. F. 2000. Paternal investment and hunter-gatherer divorce rates. In: Cronk, L., Chagnon, N., and Irons, W. (eds.), *Adaptation and human behavior* (pp. 69-90). Chicago: Aldine de Gruyter.

Borgerhoff-Mulder, M. 1990. Kipsigis women's preferences for wealthy men: evidence for female choice in mammals? *Behavioral ecology and sociobiology* 27: 255–264.

Borgerhoff Mulder, M. 2009. Serial monogamy as polygyny or polyandry? Marriage in the Tanzanian Pimbwe. *Human Nature* 20: 130-150.

Bribiescas, R. G., Ellison, P. T., and Gray, P. B. 2012. Male life history, reproductive effort, and the evolution of the genus *Homo*. *Current Anthropology* 53: S424-S435.

Byrd-Craven J., Geary D. C., Vigil J. M., and Hoard, M. K. 2007. One mate or two? Life history traits and reproductive variation in low-income women. *Acta Psychological Sinica* 39: 469-480.

Cashdan, E. 1993. Attracting mates: effects of paternal investment on mate attraction strategies. *Ethology and Sociobiology* 14: 1-24.

Chagnon, N. A. 1982. Sociodemographic attributes of nepotism in tribal populations: Man the rule breaker. In King's College Sociobiology Groups (eds.), *Current Problems in Sociobiology.* Cambridge: University of Cambridge Press.

Chagnon, N. A., and Irons, W., eds. 1979. *Evolutionary biology and human social behavior: An anthropological perspective.* North Scituate, MA: Duxbury Press.

Chapais, B. 2008. *Primeval kinship: How pair-bonding gave birth to human society.* Cambridge: Harvard University Press.

Chapais, B. 2013. Monogamy, strongly bonded groups, and the evolution of human social structure. *Evolutionary Anthropology* 22: 52-65.

Clutton-Brock, T. H., and Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology* 67: 437-456.

Crocker, W. H. 2002. Canela "other fathers": partible paternity and its changing practices. In *Cultures of multiple fathers: the theory and practice of partible paternity in lowland South America.* S. Beckerman and P. Valentine, eds. Pp. 86-104. Gainesville, FL: University Press of Florida.

Daly, M., and Wilson, M. 1978. *Sex, evolution, and behavior.* North Scituate, MA: Duxbury Press.

Daly, M., and Wilson, M. 1983. *Sex, evolution, and behavior*, 2nd edition. Belmont, CA: Wadsworth Publishing Company.

Darwin, C. 1871. *The descent of man, and selection in relation to sex.* London: John Murray.

Davies, N. B. 1986. Reproductive success of dunnocks, *Prunella modularis,* in a variable mating system. I. Factors influencing provisioning rate, nestling weight and fledging success. *Journal of Animal Ecology* 55: 123-138.

Davies, N. B., Krebs, J. R., and West, S. A. 2012. *An Introduction to Behavioral Ecology, 4th edition.* Oxford: Wiley-Blackwell.

Dixson, A. 1998. *Primate sexuality.* Oxford University Press.

Dixson. A. 2009. *Sexual selection and the origins of human mating systems.* Oxford: Oxford University Press.

Dyson-Hudson, R., and Smith, E. A. 1978. Human territoriality: An ecological reassessment. *American Anthropologist* 80: 21-41.

Ellsworth R. M., Bailey, D. H., Hill, K. R., Hurtado, A. M., and Walker, R. S. 2014. Relatedness, co-residence, and shared fatherhood among Ache foragers of Paraguay. *Current Anthropology* 55: 647-653.

Emlen, S. T., and Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223.

Flinn, M.V., and Low, B. S. 1986. Resource distribution, social competition, and mating patterns in human societies. In: *Ecological aspects of social evolution,* In: D. Rubenstein & R. Wrangham (eds.), pp. 217-243. Princeton, NJ: Princeton University Press.

Ford, C. S., and Beach, F. A. 1952. *Patterns of sexual behavior.* Scranton, PA: Harper & Brothers.

Fox, R. 1967. *Kinship and marriage: An anthropological perspective.* Cambridge: Cambridge University Press.

Geary, D. C. 2000. Evolution and proximate expression of human paternal investment. *Psychological Bulletin* 126: 55-77.

Geary, D. C. 2010. *Male, female: the evolution of human sex differences,* 2nd edition. Washington, DC: American Psychological Association.

Ghiselin, M. T. 1973. Darwin and evolutionary psychology. *Science* 179: 964-968.

Goodale, J. C. 1971. *Tiwi wives.* Seattle: University of Washington Press.

Goslee, S. C., and Urban, D. L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22: 1-19.

Goody, J., and Tambiah, S. J. 1973. *Bridewealth and dowry.* Cambridge: Cambridge University Press.

Gray, P. B, and Garcia, J. R. 2013. *Evolution and human sexual behavior.* Cambridge, MA: Harvard University Press.

Guttentag, M., and Secord, P. 1983. *Too many women?* Beverly Hills, CA: Sage.

Hamilton, W. D. 1964. The genetical evolution of social behaviour, I & II. *Journal of Theoretical Biology* 7: 1-52.

Harts, A., and Kokko, H. 2013. Understanding promiscuity: when is seeking additional mates better than guarding an already found one? *Evolution* 67: 2838-2848.

Hartung, J. 1982. Polygyny and inheritance of wealth. *Current Anthropology* 23: 1-12.

Hill, K., and Hurtado, A. M. 1996. *Ache life history: The demography and ecology of a foraging people*. New York: Aldine De Gruyter.

Hill, K., and Hurtado, A. M. 2009. Cooperative breeding in South American hunter-gatherers. *Proceedings of the Royal Society, B* 276: 3863-3870.

Hill, K., and Kintigh, K. 2009. Can anthropologists distinguish good from poor hunters: Implications for hunting hypotheses, sharing conventions, and cultural transmission. *Current Anthropology* 50: 369-377.

Hill, K. R., Walker, R. S., Bozicevic, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A. M., Marlowe, F., Wiessner, P., and Wood, B.. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331: 1286-1289.

Hoogland, J. 1998. Why do female Gunnison's prairie dogs copulate with more than one male? *Animal Behavior* 55:351–359

Hosken, D. J., and Stockley, P. 2003. Benefits of polyandry: a life history perspective. *Journal of Evolutionary Biology* 33: 173-194.

Houston, A. I., Gasson, C. E., and McNamara, J. M. 1997. Female choice of matings to maximize parental care. *Proceedings of the Royal Society, B* 264: 173-179.

Hrdy, S. B. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1: 13–40.

Hrdy, S. B. 1981. *The woman that never evolved.* Cambridge, MA: Harvard University Press.

Hrdy, S. B. 2000. The optimal number of fathers: Evolution, demography, and history in the shaping of female mate preferences. *Annals of the New York Academy of Sciences* 907: 75-96.

Hurtado, A. M. and Hill, K. 1992. Paternal effect on offspring survivorship among Ache and Hiwi hunter-gatherers: Implications for modeling pair-bond stability. In B. Hewlett, ed. *The father child relationship*. Pp. 31-56. Chicago: Aldine.

Irons, W. 1979. Cultural and reproductive success. In N. Chagnon & W. Irons (eds.) *Evolutionary Biology and human social social behavior: An anthropological perspective.* North Scituate: Duxbury Press.

Irons, W. 1983. Human female reproductive strategies. In Wasserman, S. K. (ed.), *Social behavior of female vertebrates* (pp. 169-213). Academic Press.

Jennions, M. D., and Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Bio Rev Camb Phil Soc* 75: 21-64.

Kaplan, H., and Hill, K. 1985a. Hunting and reproductive success among male Ache foragers: Preliminary results. *Current Anthropology* 26: 131-133.

Kaplan, H., and Hill. K. 1985b. Food sharing among Ache foragers: Tests of explanatory hypotheses. *Current Anthropology* 26: 223-245.

Kaplan, H., and Lancaster, J. B. 2003. An Evolutionary and ecological analysis of human fertility, mating patterns, and parental investment. In: K. W. Wachter and R. A. Bulatao (eds.) *Offspring: Human fertility behavior in biodemographic perspective* (pp. 170-223). Washington: The National Academies Press.

Keller, L., and Reeve, H. K. 1995. Why do females mate multiply with multiple males? The sexually selected sperm hypothesis. *Advances in the Study of Behavior* 24: 291–315.

Kelly, R. L. 1995. *The foraging spectrum.* Washington: Smithsonian Institution Press.

Kokko H., and Jennions, M. D. 2008. Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* 21: 919-948.

Konner, M. 2010. *The evolution of childhood: Relationships, emotion, mind*. Cambridge, MA: Belknap Press.

Lancaster, J. B. 1989. Evolutionary and cross-cultural perspectives on single parenthood. In: Bell, R. W., & Bell, N. J., eds. *Sociobiology and the social sciences.* Texas: Texas Tech University Press. Pp. 63-72.

Lancaster J. B,. and Kaplan, H. 1992. Human mating and family formation strategies: The effects of variability among males in quality and the allocation of mating effort and parental investment. In: Nishida, T., McGrew, W. C., Marler, P., Pickford, M., & de Waal F. B. M., eds. *Topics in primatology.* Tokyo: University of Tokyo Press. Pp. 21-33.

Levi-Strauss, C. 1949. *Les structures élémentaires de la parenté.* Paris: Presses Universitaires de France.

Lewis, C. M. 2010. Hierarchical modeling of genome-wide short tandem repeat (STR) markers infers Native American prehistory. *American Journal of Physical Anthropology* 141: 281-289.

Liker, A., Freckleton, R. P., and Szelkely, T. 2014. Divorce and infidelity are associated with skewed adult sex ratios in birds. *Current Biology* 24: 880-884.

Low, B. S. 1988. Measures of Polygyny in Humans. *Current Anthropology* 29: 189-194.

Low, B. S. 1990. Marriage systems and pathogen stress in human societies. *American Zoologist* 30: 325-339.

Low, B. S. 2000. *Why sex matters: A Darwinian look at human behavior.* Princeton, NJ: Princeton University Press.

Malinowski, B. 1929. *The sexual lives of savages in north-western Melanesia*. London: Routledge.

Marlowe, F. 2000. Paternal investment and the human mating system. *Behavioural Processes* 51: 45-61.

Marlowe, F. 2003. The Mating system of foragers in the standard cross-cultural sample. *Cross- Cultural Research* 37:282-306.

Marlowe, F. 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology* 14: 54-67.

Marlowe, F., and Berbesque, J. C. 2012. The human operational sex ratio: Effects of marriage, concealed ovulation, and menopause on mate competition. *Journal of Human Evolution* 63: 834-842.

Marshall, D. S., and Suggs, R. C. 1971. *Human sexual behavior: Variations in the ethnographic spectrum*. New York: Basic Books.

Mayr, E. 1997. *This is Biology: The science of the living world*. Cambridge, MA: Belknap Press.

Murdock, G. P., and White, D. R. 1969. Standard cross-cultural sample. *Ethnology* 8: 329-369.

Palmer, C. T., and Steadman, L. B. 1997. Human kinship as a descendant-leaving strategy: A solution to an evolutionary puzzle. *Journal of Social and Evolutionary Systems* 20: 39-51.

Pearson, W., and Hendrix, L. 1979. Divorce and the status of women. *Journal of Marriage and the Family* 41: 375-385.

Pedersen, F. A. 1991. Secular trends in human sex ratios: Their influence on individual and family behavior. *Human Nature* 2: 271-291.

Pollock, D. 2002. Partible paternity and multiple maternity among the Kulina. In *Cultures of multiple fathers: The theory and practiceof partible paternity in lowland South America.* S. Beckerman, and P. Valentine, eds. Pp. 62-85. Gainesville, FL: University Press of Florida.

Price, M. E., Pound, N., and Scott, I. M. 2014. Female economic dependence and the morality of promiscuity. *Archives of Sexual Behavior* 43: 1289-1301.

Quinlan, R. J., and Quinlan, M. B. 2007. Evolutionary ecology of human pair-bonds. *Cross-Cultural Research* 41: 149-169.

Ridley, M. 1993. Clutch size and mating frequency in parasitic Hymenoptera. *American Naturalist* 142: 893-910.

Ryan, C., and Jethá, C. 2010. *Sex at dawn.* New York: Harper Perennial.

Scelza, B. A. 2013. Choosy but not chaste: Multiple mating in human females. *Evolutionary Anthropology* 22: 259-269.

Schacht R., Rauch, K. L., and Borgerhoff Mulder, M. 2014. Too many men: The violence problem? *Trends in Ecology and Evolution* 29: 214-222.

Sellen D. W., and Hruschka D. J. 2004. Extracted-food resource-defense polygyny in native western North American societies at contact. *Current Anthropology* 45: 707-714.

Shapiro, W. 2009. *Partible paternity and anthropological theory: The construction of an ethnographic fantasy*. Lanham, MD: University Press of America.

Shuster, S. M., and Wade, M. J. 2003. *Mating systems and strategies*. Princeton, NJ: PrincetonUniversity Press.

Simmons, L. W. 2005. The evolution of polyandry: Sperm competition, sperm selection and offspring viability. *Ann Rev Ecol Evol Syst* 36: 125-146.

Starkweather, K. E., and Hames, R. 2012. A survey of non-classical polyandry. *Human Nature* 23: 149-172.

Symons, D. 1979. *The evolution of human sexuality.* Oxford: Oxford University Press.

Testart, A. 1982. The significance of food storage among hunter-gatherers: Residence patterns, population densities, and social inequalities. *Current Anthropology* 45: 707-714.

Thornhill, R., and Alcock, J. 1983. *The Evolution of Insect Mating Systems.* Cambridge, MA: Harvard University Press.

Thornhill, R., and Gangestad, S. 2008. *The evolutionary biology of human female sexuality.* Oxford: Oxford University Press.

Tooby, J., and Cosmides, L. 1992. The psychological foundations of culture. In Barkow, J. H., Cosmides, L., and Tooby, J. (eds.), *The adapted mind* (pp. 19-136). New York: Oxford University Press.

Trent, K., and South, S. J. 1989. Structural determinants of the divorce rate: A cross societal analysis. *Journal of Marriage and the Family* 51: 391-404.

Trivers, R. L. 1972. Parental investment and sexual selection. In B. Campbell (ed.), *Sexual selection and the descent of man* (pp. 136-179). Aldine, Chicago.

Valentine, P. 2002. Fathers that never exist: Exclusion of the role of shared father among the Curripaco of the northwest Amazon. In *Cultures of multiple fathers: the theory and practice of partible paternity in lowland South America.* S. Beckerman and P. Valentine, eds. Pp. 178-191. Gainesville, FL: University Press of Florida.

Walker R.S., and Bailey, D. H. 2013. Body counts in lowland South American violence. *Evolution and Human Behavior* 34: 29-34.

Walker, R. S., Beckerman, S., Flinn, M. V., Gurven, M., von Rueden, C. R., Kramer, K. L., Greaves, R. D., Córdoba, L., Villar, D., Hagen, E. H., J. Koster, M., Sugiyama, L., Hunter, T. E. and Hill, K. R. 2013. Living with kin in lowland horticultural societies. *Current Anthropology* 54: 96-103.

Walker, R. S., Flinn, M. V., and Hill, K. R. 2010. Evolutionary history of partible paternity in lowland South America. *Proceedings of the National Academy of Sciences USA* 107: 19195-19200.

Walker, R. S., Hill, K. R., Flinn, M. V., and Ellsworth, R. M. 2011. Evolutionary history of hunter-gatherer marriage practices. *Plos One* 6(4): e19066.

Wang, S., Lewis, C. M. Jr, Jakobsson, M., Ramachandran, S., Ray, N., Bedoya, G., Rojas, W., et al. 2007. Genetic variation and population structure in Native Americans. *PLoS Genetics* 3: e185.

White, D. R., and Burton, M. L. 1988. Causes of polygyny: Ecology, economy, kinship, and warfare. *American Anthropologist* 90: 871-887.

Williams, G. C. 1966. *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.

Wilson, M., and Daly, M. 1992. The man who mistook his wife for a chattel. In *The adapted mind.* L. Cosmides, J. Tooby and J. H. Barkow, eds. Pp. 289-322. New York: Oxford University Press.

Wolff, J. O., and Macdonald, D. W. 2004. Promiscuous females protect their offspring. *Trends in Ecology and Evolution* 19: 127-134.

Zeh, J. A., and Zeh, D. W. 2001. Reproductive mode and the genetic benefits of polyandry. *Animal Behavior* 61: 1051-1063.

VITA

Ryan Ellsworth received his MA and PhD in anthropology from the University of Missouri. Current research focuses on the application of evolutionary and life history theory to understanding variation in social dynamics in traditional societies, as well as human uniqueness among primates from a comparative perspective. Regional focus is lowland South America where he has conducted fieldwork in Central Brazil.