Chapter 4
The Unusual Women of Mpimbwe: Why Sex Differences in Humans are not Universal

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Abstract Parental investment theory provides a strong basis for generalizations about how male and female mating strategies might vary, and has generated a large number of successful predictions regarding gender differences in human reproductive strategies. There are, however, many situations in which traditional sex roles are not observed, and behavioral ecologists are beginning to determine how and why this might be. In this chapter, I explore the implications of generalizations about universal sex differences for our understanding of gender differences in sexual and reproductive strategies of humans. First, I examine recent work within behavioral ecology on the status of parental investment as a determinant of sex differences in reproductive strategies. Second, I summarize analyses of reproductive strategies in a rural forager-horticultural population in western Tanzania where variance in women's reproductive success is not significantly different from that of men and where women use serial matings rather more effectively than do men to outcompete their competitors, to show that key sex differences predicated on the mammalian pattern of parental investment are not necessarily observed. Third, I broaden this discussion of an obvious ethnographic exception to examine the relationship between human pair bonds and parental investment, to show again that sex differences in parental investment provide only a partial story. The implications of these observations for claims of universal sex differences and the gap between studies of human and nonhuman reproductive strategies are discussed in the conclusion.

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4.1 Introduction

Much of the legitimacy of applying evolutionary approaches to the study of human behavior has been predicated on the existence of universal sex differences. In our species, men are on average taller (Alexander et al. 1979) and stronger than women, and die earlier and from different causes than women (Teriokhin et al. 2004). Additionally, they are generally thought to show higher variance in reproductive success than women (Barrett et al. 2002). These apparently universal sex-varying traits can be attributed to the common mammalian pattern of reproduction, in which gestation and lactation fall exclusively to women, paternity certainty is never assured, and even small amounts of paternal care are provided facultatively (Trivers 1972). As such, male fitness has, for a long time, been seen as limited by competition over access to females, and female fitness limited by access to resources that can often be acquired through males (Emlen and Oring 1977; Wrangham 1980).

Starting in the 1980s, predictions derived from parental investment theory sparked an evolutionary literature addressing human reproductive and mating strategies (reviewed in Cronk et al. 2000; Low 2000; Dunbar and Barrett 2007). Several findings emerge that suggest (or at least are interpreted as) human universals. For example, rich ethnographic and comparative studies demonstrate the prevalence of competition among men over women (Irons 1979; Betzig 1986; Chagnon 1988; Daly and Wilson 1988; Hawkes 1991), although mating competition is mediated through diverse avenues such as political office, murder, wealth accumulation, or the provision of public goods. Similar kinds of work explore how women (or their parents on their behalf) choose and compete for desirable mates (Dickemann 1979; Buss 1989; Gangestad and Simpson 2000), again through a variety of means, including cognitive preferences, dowry payments, and olfactory cues. Sex differences in mating preferences are also evident, with men tending to favor health and fecundity in their mates whereas women look for ambition and resources, as evidenced both by reported preferences (e.g., Buss 1989; Cashdan 1993) and actual behavior (e.g., Borgerhoff Mulder 1989, 1990). The exquisite sensitivity of mechanisms underlying such preferences to ecological and social circumstances (reviewed in Gangestad 2007) have helped to bring the study of human behavior into mainstream evolutionary theory, as well as to promote popular awareness of humans as yet another uniquely evolved species (e.g., Ridley 1994).

With the success of this work, there nevertheless emerged a dangerous tendency to generalize from specific observations to universal sex differences. Such generalizations are problematic for several reasons (e.g., Smith et al. 2001). First, recognizing the importance of culturally transmitted norms Boyd and Silk (2005, using Buss's 1989 data) demonstrate how cultural factors explain a great deal more of the cross-cultural variation in mate choice preferences than does gender. Second, objecting to the stereotypic portrayal of women as at the mercy of their biology and the antics of men, Hrdy (1986), Smuts (1992) and Gowaty (1997) provide cogent qualitative and quantitative support for the view that women can and do operate with agency and employ a wide array of strategies to subvert and counter the strategies of men. Third, anthropologists and others emphasize the importance of the social and ecological environment in generating variability not fixity in sex roles according to principles well established in behavioral and cultural evolutionary theory (e.g., Laland and Brown 2002).

In recent years, studies of sex differences have become more nuanced. In part, this reflects a growing awareness among psychologists and feminist scholars that gender differences have often been inflated, even derived from poor science (Shibley-Hyde 2005). Evolutionary social scientists too are using ethnographic data to emphasize the flexibility in gender roles, and the overlap in gender differences (e.g., Bliege Bird and Bird 2008). In fact, it is now indeed time to ask "are men and women really all that different?" (Borgerhoff Mulder 2004; Brown et al. 2009), and to reevaluate the extent to which sex differences in human reproductive strategies are contingent on sex differences in postzygotic investment.

In this chapter, I scrutinize the notion of universal sex differences in the reproductive strategies of men and women. My goal is cautionary. I do not argue that parental investment theory is wrong, but rather that other factors need to be taken into consideration, factors that may be of particular importance in humans. To demonstrate this point, I present empirical data on a horticultural-hunter-fisher population in Tanzania (Pimbwe) where the variation in fitness among women equals the variance in fitness of men and, quite contrary to the normative pattern, women benefit more from multiple marriages than do men. Finally, I consider how anthropologists think about the relationship between pair bonding and parental care. I finish by considering what my conclusions mean for the gap between human and nonhuman studies, the theme of this volume.

4.2 Parental Investment Theory and Beyond

Models predicated on the differential postzygotic investment of males and females (Trivers 1972) have dominated the study of sexual and reproductive strategies in most mammals, and provided a theoretical context for the classic finding that males benefit more from multiple matings than do females. Key to this discussion has been the regression of reproductive success on mating success, known as "Bateman's gradient (Bateman 1948). Whichever sex has the steepest gradient is the sex that experiences the stronger sexual selection pressure on traits that enhance mating success (Andersson and Iwasa 1996).

In mammals, gestation and lactation fall exclusively to females, paternity certainty is never assured, and paternal care is provided facultatively. Therefore male fitness is seen as limited by competition over mates, and female fitness by access to resources that can in some but not all cases, be acquired through males (Emlen and Oring 1977; Wrangham 1980). Thus, the reproductive strategies of each sex, in particular decisions over mating effort and parenting effort, are analyzed as a product of sex differences in parental investment. Trivers' model (in an expanded form that deals more explicitly with the operational sex ratio and potential reproductive rates, Clutton-Brock and Vincent 1991) can in fact predict much of the variation in sexual selection across taxa and has important implications for sex roles. As noted earlier, its successes in predicting human sex differences in reproductive strategies brought prominence to the new discipline of evolutionary social science (Borgerhoff Mulder et al. 1997).

In the intervening years, theoretical and empirical work in behavioral ecology has taken a richer and more dynamic approach to sex roles (reviewed in Borgerhoff Mulder 2009a). First, there has been a rethinking of the internal logic and consistency of Trivers', and specifically Maynard Smith's (1977) model (Queller 1997; Houston and McNamara 2005; Kokko et al. 2006). These revisions do not change the basic prediction that the caring sex is more likely to be choosier and the object of more competition, but fundamentally alters the evolutionary sequence. In the conventional sequence, differences in prezygotic investment determine potential reproductive rates which then shape payoffs to postzygotic care. In the revised sequence, prezygotic investment generates the conditions for sexual selection as numerically abundant male gametes compete for access to rare female gametes. This lowers the confidence of males in paternity and, given male-male competition for access to females (and/or female choice), creates an elite subset of males that are more eligible to mate (Kokko and Jennions 2003). This revised logic gives more salience to sex differences in competition over mates and less to sex differences in parental care.

Second, and independent of these revisions, both theoretical and empirical work shows that anisogamy does not always produce classic sex roles (Gowaty 2004) and that competition and choice are not mutually exclusive (Kokko et al. 2006), as indeed long recognized in empirical studies of nonhuman primates (Hrdy 1986). In other words, choosiness is not simply a function of operational sex ratios, with the limiting sex enjoying the luxury of choice; it is also dependent on variance in quality among potential mates (Owens and Thompson 1994; Johnstone et al. 1996), the costs of reproduction (Kokko and Monaghan 2001; Maness and Anderson 2007), and extrinsic survival rates (Gowaty and Hubbell 2005).

Third, there is evidence that there are some species in which females are the principal caregivers, but compete more frequently and more intensively with each other than do males. In meerkats (*Suricata suricatta*, Clutton-Brock et al. 2006) and many other cooperatively breeding vertebrates (Holekamp et al. 1996; Hauber and Lacey 2005), females gain greater reproductive benefits from dominance than do males (e.g., Engh et al. 2002, for spotted hyenas, *Crocuta crocuta*), and accordingly are more competitive with one another, thereby demonstrating that sex differences in parental investment are not the only mechanism capable of generating sex differences in reproductive competition. Finally in some species, notably cooperative breeders with single breeding pairs, sex differences in fitness variances are unrelated to differences in mate number, thus providing evidence that counters Bateman's gradient (the idea that males benefit more from multiple mates than do females, Hauber and Lacey 2005). Higher female than male variance in fitness is also observed in sex role-reversed species such as dusky pipefish, Syngnathus floridae (Jones et al. 2000) and wattled jacanas (*Jacana jacana*) (Emlen and

Wrege 2004). Recognition of these additional selective considerations generates a much richer picture of how competition and choice can figure in the strategy of each sex and how these may vary over the life time and across populations.

In short, contemporary perspectives within behavioral ecology provide a broader framework within which to study the great diversity of sex differences in nature than that afforded by the simple parental investment model that guided seminal work in the evolutionary social sciences until the late 1990s.

4.3 The Unusual Women of Mpimbwe

The Pimbwe live in the Rukwa Valley of present day western Tanzania. Impacts from German, Belgian, and British colonial escapades in this central African region were indirect (Tambila 1981), but colonial wildlife policies had more severe impacts, effectively displacing Pimbwe from parts of their traditional chiefdom (Borgerhoff Mulder et al. 2007). In the socialist era (mid 1970s), Pimbwe families were settled in government villages, but many have now returned to ancestral lands that lie outside areas protected for wildlife. Modern Pimbwe rely primarily on a mix of subsistence and cash crops, supplemented by foraged resources and poultry keeping. Small enterprise activities, such as trading, traditional medicine, hunting, fishing, honey production, carpentry, and beer brewing supplement farm income for men and women. Livelihoods are unpredictable because of highly seasonal rainfall that creates critical periods of food shortage and labor demand (Wandel and Holmboe-Ottesen 1992; Hadley et al. 2007), poor infrastructure that makes cash cropping risky, and very poor health services. Between 40 and 50% of households in the district fall below the basic needs poverty line (United Republic of Tanzania 2005), and development initiatives are seriously jeopardized by prevalent beliefs in witchcraft. These and following general observations are based on intermittent fieldwork between July 1995 and February 2008, as well as previous studies in the area.

The traditional marriage pattern, reported as clan controlled, monogamous, and accompanied by bridewealth (Willis 1966), must have been seriously challenged by the high rates of labor outmigration in the colonial period (Tambila 1981). Marriage is now effectively characterized by cohabitation, initiated with a facultative transfer of bridewealth and a celebration (Fig. 4.1). Polygyny appears never to have been common. Nowadays, marriage can be defined as sharing in the production and consumption of food and shelter, with the expectation of exclusive sexual relations. Divorce is permitted and, like marriage, can be defined by the physical movement of one or both partners out of the house, requiring no legal or formal procedures. Divorces occur often when one spouse starts an extramarital relationship, with both sexes tending to claim responsibility for abandoning the relationship. At divorce, children under the age of 8 are supposed to stay with the mother (or the mother's kin), whereas older children should stay with their father. In practice, the fate of children is quite variable. Sometimes fathers "kidnap" very young children from

Fig. 4.1 A longterm monogamously married husband and wife sitting outside their house in Mirumba

their mothers, sometimes mothers leave a recently weaned child with a divorced husband; older children may live with a range of maternal or paternal kin.

Given these residence patterns, parental care is highly facultative. Wives typically take primary responsibility for the direct care of their own small children, with some assistance from older children and/or other kin, including their own mothers or husband's mothers. Regarding indirect care, the bulk of farming is done by husbands and wives, but there is considerable variability within marriages as to how the fruits of joint farm labor are allocated among family subsistence needs, joint family benefits (like health and education), individual cash purchases, or capital for individual economic enterprises (such as using maize for beer brewing). These allocations prompt frequent spousal arguments, and one spouse may even place locks on the family granary to exclude "inappropriate" use of resources by the other spouse. There are no significant heritable resources in this population; men and women get access to land and houses opportunistically from maternal or paternal relatives (or from unrelated individuals) who happen to have unused land or living sites available in the village. Commonly they clear land and build houses anew, such that there is very little to inherit in the way of bequests.

Basic demographic data were collected in all households of a single village in seven different study periods between 1995 and 2006 (for details see Borgerhoff Mulder 2009a) and analyses include only individuals who are assumed to have neared completion of their reproduction (>44 years), yielding 138 men with a mean age of 60.3 years (range 45.3–92.7) and 154 women with a mean age of 59.2 years (range 45.0–86.8) dropping younger men (<55 years), produced statistically equivalent results. Variables used in the analyses presented here are age, sex, number of livebirths, reproductive success (measured as the number of offspring surviving to

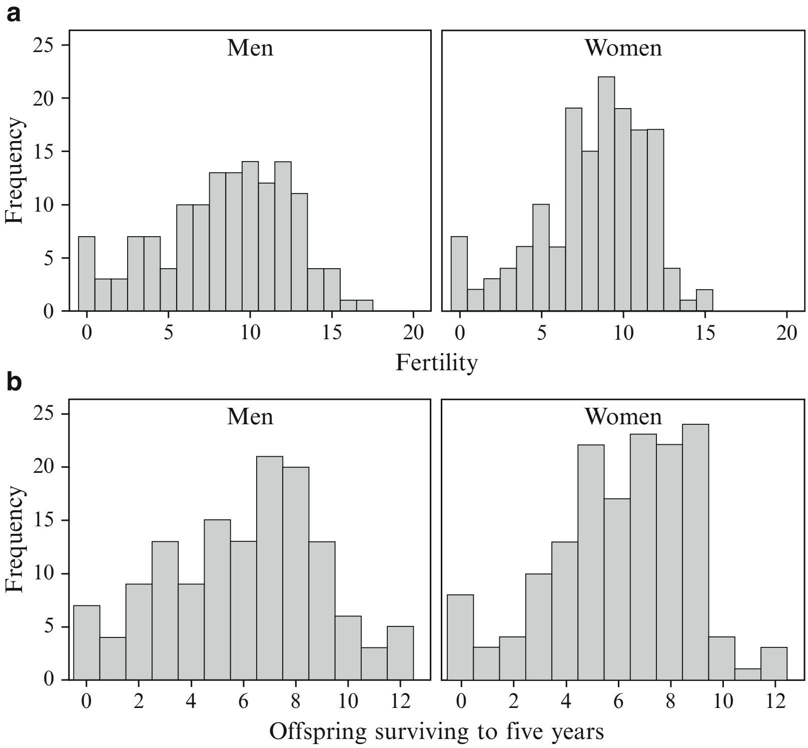

Fig. 4.2 Variance in (**a**) fertility and (**b**) reproductive success for Pimbwe men and women

5 years of age, beyond which mortality is low), and number of spouses over the lifetime, categorized as 1, 2, 3, or more.

Among men and women who had completed their reproductive careers, only 3 (2.2%) men and 2 (1.3%) women had never married, indicating that marriage is virtually universal in this population. The mean values of fertility (men 8.41; women 8.17) and reproductive success (men 5.99; women 6.14) are not statistically different from each other, which suggests that there is no distortional sex bias to the sample. While men show greater variance in fertility (16.16) than women (11.34, Levene's test for equality of variances $F = 5.87$, $p = 0.016$, Fig. 4.2a), there is no significant difference in the variances in completed reproductive success (men 9.00; women 7.27, Levene's test $F = 2.15$, ns, Fig. 4.2b).

When fertility (Fig. 4.3a) and the numbers of offspring reaching 5 years of age (Fig. 4.3b) are shown in relation to number of spouses (1, 2 and 3 or more), an unexpected pattern emerges. Men fail to benefit in terms of fitness from multiple marriages, but women who marry three or more times produce more surviving children than do other women. Fertility and completed reproductive success are regressed on age, sex, and the number of spouses in a number of different models (Table 4.1a, b). Generally, across models, the number of spouses is negatively

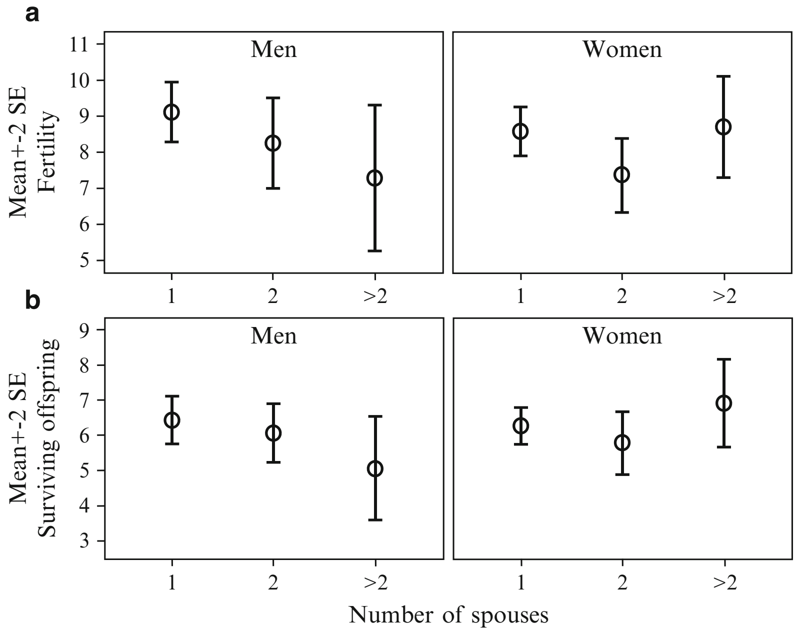

Fig. 4.3 The associations between number of spouses and (**a**) fertility and (**b**) reproductive success for Pimbwe men and women. The mean is shown with a *circle*, and the standard error (*2) with a *bar*. For statistics see Table 4.1

Table 4.1 Regression models for how sex, age, and number of spouses affect fertility and number of surviving offspring (showing beta, standard error, and significance). (a) fertility, (b) number of surviving offspring

(a)	Model 1	Model 2	Model 3	Model 4
Sex	−0.244 (0.433)	−0.172 (0.425)	−0.285 (0.415)	−1.862 (0.985)+
Age		0.067 (0.020)***	0.061 (0.020)**	0.067 (0.020)***
No. of Spouses			−0.516 (0.284)+	−2.045 (0.912)*
Sex* No. of spouses				1.015 (0.575)+
(b)	Model 1	Model 2	Model 3	Model 4
Sex	−0.144 (0.333)	−0.174 (0.332)	−0.117 (0.328)	−1.281 (0.776)
Age		0.028 (0.015)+	0.022 (0.015)	0.028 (0.015)+
No. of spouses			−0.223 (0.224)	−1.578 (0.718)*
Sex*#Spouses				0.899 (0.453)*

***$p<0.001$, **$p<0.01$, *$p<0.05$, + $0.05<p<0.10$

associated with fertility and the number of surviving offspring, and there are interaction effects between spouse number and sex, which reflect the pattern shown in Fig. 4.3, namely that men suffer reproductively from multiple marriages in a way that women do not. The models also show that age is positively associated with fertility and less consistently with reproductive success, suggesting (in this postreproductive sample) that levels of fertility were slightly higher in cohorts that finished reproduction in the 1980s than in the 2000s, which is to be expected in a community where some individuals are beginning to choose smaller family sizes.

In this population, sex differences in fitness variances are not pronounced. While men do show greater variance in the number of live births, reproductive success is equally variable across the sexes, suggesting that men with very high fertility raise few of these “extra” children. A sex difference, or lack thereof, in variance does not, however, shed much light on the operation of sexual selection (Sutherland 1985; Hubbell and Johnson 1987). Much more illuminating is the relationship between breeding success and physiological or behavioral phenotypes (Clutton-Brock 1988). Thus, the finding that men and women benefit differently from multiple marriages is interesting. While the data are very variable (large standard errors), women appear to gain more from multiple mating than do men; furthermore, the same statistically significant effect is observed as a control variable in a different sample of younger women (Borgerhoff Mulder 2009b). Note, however, that it would be analytically more revealing to look at the probability of bearing (and successfully raising) a child as a function of the marital status of the parents – the present analysis shows only that reproductive performance is correlated with the number of spouses married over the lifetime. Note also that these findings take no allowance of the marital status of the spouse. It is tempting to think that women who have married many men should be married to men who have had many wives, but this is not necessarily the case.

Possible reasons why men and women make multiple serial marriages are discussed in more detail elsewhere (Borgerhoff Mulder 2009a). Ethnographic observations suggest that lazy and heavy-drinking men are often divorced and end up marrying postreproductive women. In some cases, these men have dependent children and clearly remarry to find help from a new wife in raising their kids. For these men, multiple marriages therefore, rather counter-intuitively, reflect parenting effort rather than mating effort, although why anyone would want to marry them remains a puzzle.

There are a host of hypotheses to account for multiple mating in females (e.g., Jennions and Petrie 2000; Setchell and Kappeler 2003), entailing both direct and indirect benefits. Women may gain direct benefits by mating with and marrying multiple men if their husbands help them to obtain the resources needed to support reproduction. Pimbwe women benefit from the farming activities of men, as well as from the products of their hunting, fishing, honey production, and other enterprises, but all of these are highly unpredictable, in part because of poor farming conditions and in part because of the current illegality of entering protected areas where fish and meat are plentiful (Borgerhoff Mulder et al. 2007). Given the potentially high inter- and intraindividual variability in male provisioning, it is quite possible that women switch mates to maximize economic income, the “musical chairs” hypothesis reviewed by Choudhury (1995). A similar argument has been made for the instability of marriages among the poor in contemporary USA (Kaplan and Lancaster 2003, see also Maness and Anderson 2007 for Nazca boobies, *Sula granti*). Parallels can also be drawn with baboons (*Papio cynocephalus*) where serial if nonexclusive pair bonds produce temporary male protectors for mothers whose success in raising offspring is heavily influenced by their social networks and matrilineally inherited dominance rank (as reviewed by Silk 2007).

As regards indirect (or genetic) benefits, numerous mechanisms have been proposed (including the maximization of male genetic potential, bet hedging, prevention of inbreeding, and confusion of paternity certainty to avoid infanticide). The most plausible in this context is the idea that a woman can afford to forego the benefits of paternal care (and to risk the dangers of a stepfather in house) for mates with high genetic potential. This argument has been made most forcefully for humans by Gangestad and Simpson (2000) and is particularly plausible in environments with high disease loads where demonstration of heritable fitness is very important (Hamilton and Zuk 1982). In support of this explanation is the fact that Mpimbwe is beset by all of the health problems typical of rural tropical Africa (Hadley and Patil 2006; Hadley et al. 2007) and has a minimal health care infrastructure. If Pimbwe women were choosing genetically superior males and keeping them we would expect once-married women to show highest fitness, but they do not show this. In addition, if Pimbwe women were choosing genetically superior males and then losing them to other women, we would expect multiply married men to show elevated fitness, which is not observed.

In sum, the Pimbwe analysis, while provisional, provides clear evidence that a key sex difference predicated on mammalian patterns of parental investment, the Bateman gradient, is not observed. Whether this results from sex differences in the range of quality in potential mates (Owens and Thompson 1994; Johnstone et al. 1996), costs of reproduction (Kokko and Monaghan 2001; Maness and Anderson 2007), extrinsic mortality rates (Gowaty and Hubbell 2005), or other factors is not yet known. However, the cautionary tale here is that just because humans are typical mammals with all the polygynous tendencies predicated on gestation and lactation, conventional sex-differentiated reproductive strategies are not assured!

Therefore, if Pimbwe women enter into marital bonds to reap direct benefits, does this mean that pair bonds are best thought of as a universal adaptation whereby women trade sex for paternal care? The simplicity of this scenario is alluring, but again the reality more complex.

4.4 Pair Bonds in Humans

Claims regarding the universality of human pair bonds are controversial but this is so because they are often confused with statements about origins. The ethnographic record displays a range of grouping patterns, from small two-adult "family" groups to large multimale/multifemale bands (e.g., Pasternak et al. 1997), but *within these formations*, specialized relationships emerge, between (usually) heterosexual individuals, typically glossed as "marriage." Although it is widely recognized that these bonds do not map precisely onto sexual relationships (Fox 1967), male sexual access to females is key to the definition of marriage, even if it is given quite different salience across cultures (Bell 1997). Furthermore, despite the well-known "double standards" in sexuality (Betzig 1989), Jankowiak et al.'s (2002) survey of detailed ethnographic material shows that in all the 66 societies studied, men *and women* actively mate guard, indicating that sexual propriety is a core component to marital unions, even if much violated. Precise definitions of marriage may be elusive, but in all cases, rights and responsibilities are exchanged (Needham 1962), concerning legitimacy of offspring (Gough 1959), property (Leach 1955) and economics (Murdock 1949). In short, marital bonds are about sexual access, and although additional rights and responsibilities are emphasized in different cultural contexts, these bonds are always identifiable. Societies sanctioning total promiscuity as the principle mating system do not exist (Bell 1997; Kunstadter 1963; Rodseth et al. 1991). Note that this is a claim about the universality of pair bonding in the ethnographic record, not about its more contentious evolutionary origins (as discussed in Knight and Power 2005), to which I now turn.

Several sources of evidence point, at least indirectly, to a long history of pair bonding in our species, for example, relatively limited sperm competition (Birkhead 2000), little sexual dimorphism in size dating back in our lineage to 1.8 mya (McHenry 1996), and a distinctive patterning of testosterone production with pair bond status (e.g., lower levels in undergraduate men in well-established romantic relationships: Gray et al. 2004). Furthermore, a notion of "romantic love" is observed across the vast majority of human cultures (Jankowiak and Fischer 1992), mediated by various neuro-endocrinological systems (e.g., Carter 1998). Much more controversial is the role of male provisioning in the evolution of pair bonded behavior.

Pair bonds evolving from male provisioning were once central to narratives of human origins (Washburn and Lancaster 1968). Bipedal hominins could carry meat (Lovejoy 1981), opening up the possibility for a complementary division of labor in which males provide resources to females encumbered with dependent offspring in return for sexual exclusivity. Modern attempts to unravel the origins of pair bonding attribute very different roles to paternal provisioning. In some formulations, males provision because both parents are assumed to have identical reproductive goals. Thus, Fisher (1989) suggests that divorce rates peak after 4 years, because this is when a typical forager child is safely through the period of dependence, and both parents are free to look for new spouses. Others view the relationship as one in which both cooperation and competition exist. In a carefully argued scenario that links intelligence, longevity, altriciality and diet, as coevolved traits, Kaplan et al. (2000) posit that long lifespan and a cooperative division of labor coevolved as humans moved into a foraging niche where food acquisition (hunting) required great skill and knowledge, and partners could benefit from specialization and exchange (Gurven et al. 2009). In other scenarios, marital bonds are believed to be entirely independent of paternal provisioning. In one version, pair bonds are deemed to have emerged from mate guarding, with males favoring pair bonds to avoid incessant fighting over females (Symons 1979) and females to find refuge from harassment (Blurton Jones et al. 2000) and/or infanticide (Hawkes 2004). A different idea that again relies not on paternal provisioning (rather on *female* provisioning) is that once females discovered how to increase the diversity and density of food value through cooking, they were worth monopolizing (Wrangham et al. 1999). In the latter kinds of scenarios, paternal care is more likely to have evolved after the emergence of pair bonds in our lineage, and not be a necessary condition for the evolution of pair bonding (Chapais 2008).

Phylogenetic analyzes of the relationship between mating systems and paternal care shed light on this origins debate. In mammals, Brotherton and Komers (2003) show that monogamy evolved more often in the absence of paternal care than in its presence, and propose that paternal care most likely arose subsequently (although in birds biparental care may have preceded avian pair bonds, Burley and Johnson 2002). Similar conclusions are being reached for nonhuman primates. Since direct paternal care is present only in some species, it is most likely that monogamy is a preadaptation facilitating the evolution of paternal care rather than a consequence (Palombit 1999; van Schaik and Kappeler 2003). In short, despite the apparent universality of pair bonds in contemporary human populations and cogent models that these evolved to subsidize the high costs of reproduction and encephalization (Kaplan et al. 2000; Gurven and Kaplan 2006), there is little clear comparative evidence that pair bonds evolved in mammals to facilitate paternal provisioning, nor is there much evidence from nonhuman primates to support such a claim. Humans, however, with their exceedingly large brain and unusually long lifespan, may be unique in this respect.

To gain more insight into the nature of the pair bond, anthropologists turn to ethnographic materials, both within and between population analyzes. One question pertinent to this debate is whether men's economic activities are best characterized as mating effort or parental effort. There are cases where men work particularly hard when their mates are lactating (Hadza: Marlowe 2003), allowing the latter to do less work at this energetically demanding time (Hiwi and Ache: Hurtado et al. 1992). These data suggest that men's activities are a form of parenting effort. Similarly, there are cases where men's allocation of effort to food production fits closely with expectations derived from the paternal effort model (Tsimane: Gurven and Kaplan 2006); Although Tsimane men invest in mating effort through extra-marital relations, they do so early in the marriage when there are few, if any, children to care for, rather than later, when paternal contributions are most needed (Winking et al. 2007). In addition, confronted with hypothetical scenarios, Ache and Hadza men show preferences for hunting groups with good hunters that yield high returns for provisioning but low returns for mating effort, rather than groups of poor hunters where provisioning benefits are small and mating benefits large (Wood and Hill 2000; Wood 2006). These patterns support the parental effort hypothesis, as do demographic and economic data that show how brides are hard to find (Borgerhoff Mulder 1990; Cashdan 1993) and quick to leave (Betzig 1989) when men's provisioning resources are not forthcoming, patterns also observed in the modern US when marriage transitions are analyzed in relation to income (Nakosteen and Zimmer 1997; Burgess et al. 2003). However, in other studies, men's economic activities are better characterized as mating effort, as with Hawkes' (1993) analysis of hunting in the Hadza and Smith et al.'s (2003) study of turtle feasts of Mer islanders in the Torres Straits. In both these cases, it is argued that men specialize on risky resources, ones that are better characterized as public goods to be ostentatiously shared (the show off hypothesis: Hawkes 1991) than as reliable streams of paternal provisioning. Despite strong arguments on each side, it seems most likely that men everywhere exhibit elements of both paternal and mating effort in their economic exploits (Anderson et al. 1999a, b; Gurven and Hill 2009), for example in the Marlowe's analyzes of the Hadza (1999).

Cross cultural data can also be used to address, at least indirectly, the question of whether pair bonding is associated with the provision of paternal care or with the defense (or guarding) of mates. Quinlan and Quinlan (2007) find that marital stability (a low divorce rate) is associated with substantial male contributions to subsistence, an absence of alternative caretakers, and late weaning, all indices of the potential value of male assistance. However, marital stability is also associated with high levels of polygyny, a possible proxy for the difficulty men face in finding new mates. The authors therefore conclude that pair bonds likely evolved in response to multiple selection pressures – a need for male care and a strategy for each sex to deal with intense mate competition. In fact, there may even be two different kinds of human pair bonds – one geared to child rearing and one geared toward male reproductive competition (Quinlan 2008).

All in all, studies of contemporary populations do little to resolve whether pair bonds evolved for paternal investment or mate guarding. Why so little progress? First, despite the wealth of empirical studies we have puzzling cases where different data sets from the same population support different models. Second, comparative studies raise multiple problems for interpretation – for example is divorce prevalence really a valid indicator of the importance of pair bonds? A more appropriate variable might be the number of people who actually do marry in the population. Third, contemporary correlates of a trait do not necessarily shed light on its evolutionary origins. While human behavioral ecologists maintain that studies of current behavioral diversity illuminate the flexibility of human nature to different social and ecological triggers (e.g., Smith et al. 2001), extrapolating to evolutionary sequences is much more tenuous. Now that pair bonding is in place, paternal care might be very important in contemporary populations. However, to claim that it was the original selective pressure for pair bonds is an interpretative error, Chapais (2008: 169) dubs the "pitfall of modern family reference" (see also Marlowe 2007). Finally, investigators often talk about men and women as if they had a single sex-specific strategy. In the modern USA, for example, upper strata parents use biparental care to invest in highly profitable education for their children, whereas lower strata women raise children alone and both sexes have serial and simultaneous relationships (Kaplan and Lancaster 2003); multiple strategies characterize many other populations (see, for example, Dickemann 1982). In so far as an individual's optimal mating and reproductive strategy depend on the behavior of both same- and different-sexed conspecifics, multiple strategic spaces emerge. Only recently have theoreticians begun to tackle this, as greater computing power allows model parameters to be generated by individual strategies rather than fixed at *a priori* levels (e.g., Cotar et al. 2008, and for more general discussion see Kokko et al. 2006).

As such, it is perhaps more productive to think about pair bonds in terms of sexual conflict (Borgerhoff Mulder and Rauch in prep). Sexual conflict theory does not inherently avoid the pitfalls of making generalizations about sex differences, but it provides a more dynamic framework for analyzing variable sex roles. For example, it examines the question of how much a wife and husband should work and when they should break their contract, in terms of broader market (supply and demand) conditions. Economists focus on each spouse's bargaining power, the well-being a lady can expect without the cooperation of a gentleman, and *vice versa*; differential bargaining power sets each spouse's "threat point" (Manser and Brown 1980), the resource sharing contractual arrangement at which the lady (or gentleman) would be better leaving than staying. Anything that improves an individual's bargaining power with their spouse, such as relatively larger earnings, gender-biased divorce laws, or greater chances of remarriage, increases that person's share of the marital pot (e.g., Lundberg and Pollak 1996). Accordingly, the benefits of a marriage are not expected to be shared equally, but in accordance with bargaining power. The implications of these considerations for marital stability, marital assortment, and equilibrial states of the marriage market can be explored with game theory, as demonstrated in models of the "better options" hypothesis for divorce in birds (e.g., McNamara et al. 1999) where divorce rates are shown to decrease with individual quality (fewer "better options" assuming a good first pairing), and age (no time to recoup the costs of divorce).

A key factor affecting these conflicts is whether spousal labor is complementary or substitutable (Kaplan and Lancaster 2003). If mum feeds and dad protects the baby, parental roles are complementary, in so far as each activity is valueless without the other. If mum (or dad) uses salary to pay rent and school fees, parental roles are substitutable and marriages become more brittle (and subject to corner solutions). Changes in divorce rates and prevalence cross culturally might be usefully examined from this perspective. Rather intriguingly, Quinlan and Quinlan (2007) find that divorce is least common in populations where both sexes contribute approximately equally to household production, suggesting (albeit indirectly) that marriage is indeed a more stable institution where spouses' work is complementary.

Thinking about the marriage as a complementary division of labor raises the interesting question of when and how the benefits of specialization can be offset by positive assortment of skills (Borgerhoff Mulder 2004). When are the public goods produced by a breadwinner and homemaker eclipsed by two extremely successful breadwinners who might bicker over homemaking? In traditional economies, where most tasks are gender-specialized, the benefits of the sexual division of labor are unlikely to be dwarfed by positive assortment for skills. One might expect, however, that in a modern economy, where most jobs can be done by men or women, positive assortment counterbalances the division of labor (corporate executives intermarry and hire an *au pair*). Positive assortment among mates for various skills is found in many modern economies (e.g., Logan et al. 2008). Indeed a study testing whether US university students show preferences to assort on similar traits (rich men like rich women, and *vice versa*) or on reproductive potential (high earning men prefer beautiful women, and *vice versa*) showed that the first pattern is much stronger than the second (Buston and Emlen 2003); this suggests that the complementary marital relationship is disappearing in some western societies. We see here how far an evolutionary-based discussion of marriage in terms of sexual conflict and bargaining theory has moved us away from the simple constraints of mammalian reproduction.

4.5 Mind the Crack: Concluding Observations

What are the implications of this discussion for universal sex differences and the gap between studies of human and nonhumans? Early evolutionary studies identified predicted sex roles, but failed to consider variation. Nowadays, with more sophisticated theoretical models and richer empirical evidence, we see that the roles of men and women can be highly variable. The Pimbwe study shows how some women, despite common mammalian constraints, can use multiple sequential pair bonds to out-reproduce their monogamous counterparts. Similarly, the broader discussion of the relationship between pair bonds and paternal care reveals limits to the conventional view of marriage as a trade of sex for paternal resources. Men and women have negotiable roles in marriage, for which models from behavioral ecology (beyond conventional parental investment theory) and economics can be brought to bear.

In what sense do we differ from nonhuman primates in this respect? Anthropologists once viewed regularly patterned family behavior (and particularly marriage, e.g., Levi-Strauss 1949) as what divides us from the other primates, contrasting the apparent promiscuity of our apelike cousins to, initially, our nice nineteenth century stable monogamous families, and later the wide range of family types evident in the ethnographic record. However, the gap is nowhere so big as once thought and is better viewed as continuum (e.g., Foley and Lee 1989; Rodseth et al. 1991) or just a crack. This is so in part because over the years so much has been learned about the complexity of nonhuman primate kinship and social behavior. With long-term studies of known individuals, the sophistication of primate kinship behavior is now well appreciated. The narrowing gap also reflects the fact that the human pair bond, with dad provisioning mum in exchange for sex, is now no longer viewed as necessarily the supreme human adaptation that sent us down our distinct evolutionary route. In fact, as I have tried to argue, the contemporary human pair bond is a highly variable trait which, while most likely universal in some form, functions very differently in different social and economic contexts, and has hotly contended evolutionary origins.

Another reason why crack (rather than gap) better characterizes the distinction between sex-differentiated reproductive strategies in human and nonhuman primates is that there are so many parallels between contemporary debates within primatology and human behavioral ecology. I end with a consideration of some of these.

First, nonhuman primates generally exhibit rather low levels of direct paternal care. Males can be important for protection, particularly from infanticide (e.g., Palombit et al. 1997), and males do in some cases provide direct care to their offspring (Buchan et al. 2003), but with a few exceptions (e.g., Goldizen 1987), paternal care is not extensive among primates. Furthermore, as we have seen in humans, there is lengthy debate over whether male activities are designed for improving offspring survival or enhancing access to mates (e.g., Smuts and Gubernick 1992; van Schaik and Paul 1996). In short, as in mammals more generally, male care is not extensive, and where it occurs, its relationship to paternity, and its impact on offspring survival, is debatable (Woodroffe and Vincent 1994). The situation is rather similar in the study of humans, as reviewed in this chapter. The traditional view that paternal care is central to our evolutionary trajectory is now in question, and suggestions that pair bonds originated for mate defense and avoidance of harassment are gaining attention. Humans do, however, look different with respect to the *current function* of pair bonds: the division of labor over the production and consumption of food among spouses is particularly developed in our species, hence the foray into economics for new theoretical tools (and see Noë et al. 2001, for similar applications of economic theory to nonhuman primates).

Secondly, related to low paternal care is the significance of female-bonded kin groups in nonhuman primates. If males are not helping, who is? In many species, amongst them cercopithecine monkeys (Silk 2007), the fertility and reproductive success of females is heavily influenced by social networks and matrilineally derived access to resources. Such social systems are increasingly being used as a model with which to think about human evolutionary origins and the importance of cooperation among kin in subsidizing the costs of childbearing (Hrdy 2005a, b). This marks a radical departure from seeing our origins in the social organization of the male-bonded apes (e.g., Rodseth et al. 1991).

A final parallel trend lies in the prevalence of multiple mating by females. Female primates commonly mate with multiple males to avoid infanticide, and rather rarely mate for resources or good genes; indeed, preferences for dominant individuals dissolve once the male loses dominance, suggesting that protection is more prominent in this preference than genetic quality (Setchell and Kappeler 2003). Interestingly, human behavioral ecologists turned initially to birds for models for mating systems (Flinn and Low 1986; Borgerhoff Mulder 1990) because of the clear importance of paternal investment in many extent societies. This, however, may have distracted us away from very different (and non paternal care-based) arguments for the *origins*, if not the *current function*, of pair bonds in our species.

In sum, there are several parallels between the arguments advanced in this chapter and current debates within primatology that support the claim that we should perhaps be minding a crack rather than a gap.

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