



Are We Monogamous? A Review of the Evolution of Pair-Bonding in Humans and Its Contemporary Variation Cross-Culturally

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Despite a long history of study, consensus on a human-typical mating system remains elusive. While a simple classification would be useful for cross-species comparisons, monogamous, polyandrous, and polygynous marriage systems exist across contemporary human societies. Moreover, sexual relationships occur outside of or in tandem with marriage, resulting in most societies exhibiting multiple kinds of marriage and mating relationships. Further complicating a straightforward classification of mating system are the multiple possible interpretations of biological traits typical of humans used to indicate ancestral mating patterns. While challenging to characterize, our review of the literature offers several key insights. 1) Although polygyny is socially sanctioned in most societies, monogamy is the dominant marriage-type within any one group cross-culturally. 2) Sex outside of marriage occurs across societies, yet human extra pair paternity rates are relatively low when compared to those of socially monogamous birds and mammals. 3) Though the timing of the evolution of certain anatomical characteristics is open to debate, human levels of sexual dimorphism and relative testis size point to a diverging history of sexual selection from our great ape relatives. Thus, we conclude that while there are many ethnographic examples of variation across human societies in terms of marriage patterns, extramarital affairs, the stability of relationships, and the ways in which fathers invest, the pair-bond is a ubiquitous feature of human mating relationships. This may be expressed through polygyny and/or polyandry but is most commonly observed in the form of serial monogamy.

Keywords: monogamy, mating system, sexual selection, anthropology, evolution

INTRODUCTION

How best to characterize the human mating system is a subject of intense and polarized debate. On the one hand, sex differences in reproductive investment, and resultant differing potential reproductive rates, are argued to favor elevated mating effort behavior in males (i.e., a short-term, multiple mate seeking orientation; Symons, 1979) and polygyny. However, on the other hand, an evolved sexual division of labor, with offspring dependence on paternal care, is argued to generate overlapping interests in long-term, monogamous relationships for both men and women (Washburn and Lancaster, 1968; Lancaster and Lancaster, 1987; Kaplan et al., 2000). Given the

varied sources of support for both approaches, disagreement exists on how best to describe mating patterns in humans. Particularly challenging is to generate an agreed upon definition of a species-typical strategy often used in comparative studies. This review is focused on an attempt to offer resolution regarding the current debate. After reviewing the literature on marriage and mating systems in humans, we present a cross-cultural examination as well as comparative and evolutionary evidence for and against particular lines of inquiry.

WHAT IS THE HUMAN MATING SYSTEM?

Confusion and debate describing a human-typical mating pattern are warranted given the diversity of strategies both across and within cultures. For example, data from the Standard Cross-Cultural Sample (Murdock and White, 1969), a representative global sample of primarily pre-industrial societies, indicates that polygynous marriage (one male, multiple females) is sanctioned in nearly 85% of societies (Figure 1). This figure is often used to support claims of the mating effort intensive nature of males given that most societies allow men to have multiple wives. However, upon closer inspection, within a small-scale polygynous society, the majority of marriages are monogamous (Murdock and White, 1969; Flinn and Low, 1986; Binford, 2001). For example, among the Savanna Pumé (South American hunter-gatherers) while polygyny occurs (20% of women and 11% of men are polygynously married at some point during their lives), most marriages are monogamous, consistent with other foraging groups (Marlowe and Berbesque, 2012; Kramer et al., 2017).

Although most marriages are monogamous at any one point in time, over the life course individuals may reenter the marriage market more than once. Among hunter-gatherers, industrializing societies, and many contemporary Western populations, remarriage is common after spousal death and/or divorce, resulting in serial monogamy where both men and women have multiple partners over their reproductive careers (Fisher, 1989; Hill and Hurtado, 1996; Borgerhoff Mulder, 2009; Jokela et al., 2010). Nonetheless, while individuals may have more than one partner across their life, sexual fidelity within a marriage is generally expected. Marriage is common to all human societies and publicly acknowledges who has sexual access to whom, with divorce often resulting from extramarital relationships (Irons, 1983; Marlowe, 2003; Kramer and Greaves, 2011). However, typical of the range of behavioral variation expressed by humans, many exceptions exist, and sex is found outside of marriage both cross-culturally and among individuals in any one society (Box 1: Sex outside of the pairbond across human societies). Yet, while engaging in sex outside of marriage likely occurs to some extent in all societies, because men and women typically live in long-term pairbonds within the same residential unit, they have been described as practicing social monogamy (Reichard, 2003; Strassmann, 2003). While human patterns are distinct from genetic monogamy, defined as two individuals who only reproduce with one another, levels of extra pair paternity are relatively low compared to other socially monogamous species. Estimates of non-paternity rates range

from 0-11% across societies (Simmons et al., 2004; Anderson, 2006; with median values falling between 1.7–3.3%) while among birds these rates regularly exceed 20% (Griffith et al., 2002).

In sum, a simple classification of a human-typical mating system is challenging given the variety of pairing strategies observed. Monogamous, polyandrous, polygynous, and short-term mating patterns are found across contemporary human societies, with most societies exhibiting multiple kinds of marriages and mating relationships (Marlowe, 2000; Fortunato, 2015). What can be most simply distilled from this is that humans form long-term pairbonds. However, while polygynous and polyandrous marriages are found in many societies, ethnographic evidence indicates that most individuals within a society live in monogamous marriages that are generally, but not always, sexually exclusive. It is important also to emphasize that these unions are commonly serially monogamous, and that regardless of divorce rates, this likely would have been the case in the past due to high rates of spousal mortality under premodern mortality schedules (Gurven and Kaplan, 2007).

ANCESTRAL MATING SYSTEM IN HUMANS

Although cross-cultural information may illuminate contemporary variation in mating patterns, it tells us less about their antiquity. To seek additional support to characterize the human mating system, we turn to indicators of ancestral mating patterns. Sexual selection is a widely recognized force influencing behavioral and physical traits across animal taxa (Andersson, 1994). Differences between males and females within and across species can offer insight into both historical and contemporary selection pressures. Mating systems are amazingly diverse across mammals generally, and primates in particular (Dixson, 1997; Kappeler and van Schaik, 2002). Given human placement in the primate order, here we approach human mating from a comparative perspective to better understand behavioral and physical traits that either are shared or distinguish us from our closest living relatives. We target three commonly examined traits in reference to predicting primate breeding systems: sexual dimorphism, testis size, and concealed ovulation (Dixson, 2009). We review each of these and discuss whether the evidence supports a human monogamous past that may serve to explain the mating system's current prevalence.

Sexual Dimorphism

Sexual dimorphism exists within a species when, in addition to differences between the sexual organs themselves, males and females differ in size or appearance (Andersson, 1994). Across primates, minimal levels of sexual dimorphism in body weight and canine size are generally associated with monogamy and low rates of male antagonistic competition (e.g., gibbons; Harcourt, 1981). Size differences are expected to be most pronounced within single-male/multi-female polygynous species where male competition can be intense, and stakes high, because winners have much to gain. For example, among mountain gorillas (*Gorilla beringei beringei*) dominant males monopolize sexual

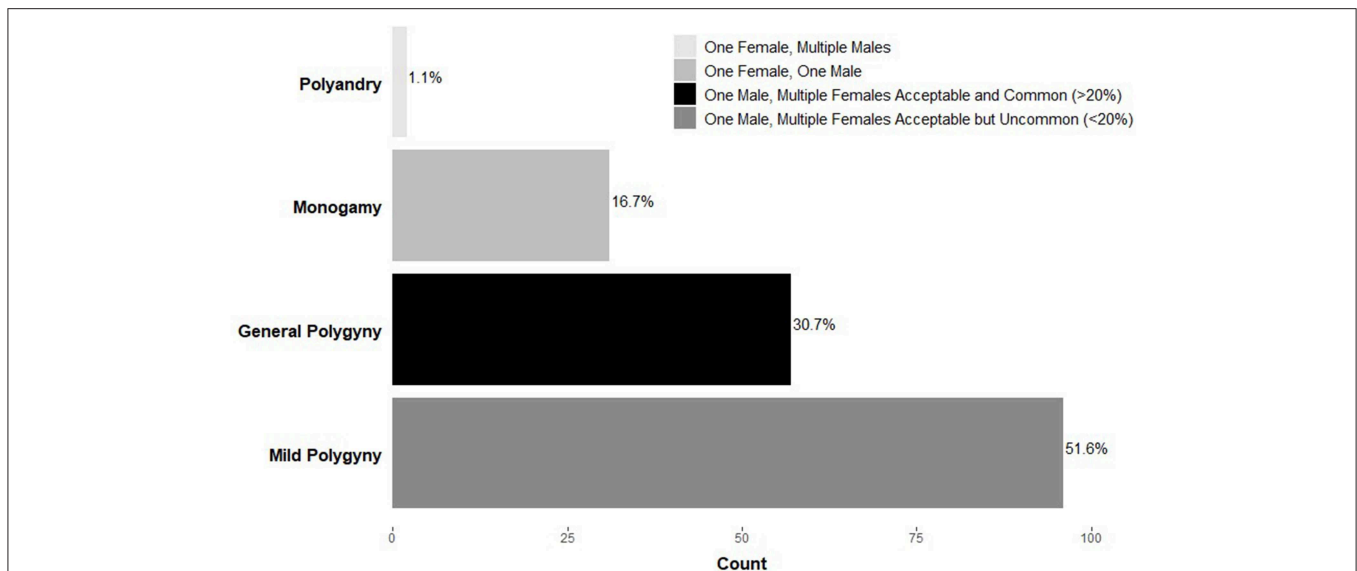


FIGURE 1 | Frequency of marriage systems across societies ($n = 186$) in the Standard Cross-Cultural Sample (Murdock and White, 1969). Adapted from Marlowe (2000).

BOX 1 | Sex outside of the pairbond across human societies.

While humans form long-term pair bonds that are recognized as marriages in all societies, sexual relations also occur outside of marriage. In some societies and incidences these relations are clandestine and considered transgressions with punishments that range in severity. But in other cases, uncommitted sexual liaisons are socially permissible, and generally fall under two well-documented ethnographic contexts. The first occurs prior to first marriage when adolescent girls are in a life stage when they have a low probability of conceiving and are given freedom to explore different premarital relationships (Mead, 1928; Irons, 1983; Parker, 1985; Gregor, 1987). For example, among the Makushi of Guyana, recently sexual mature individuals receive parental support to engage in pre-marital sex (Schacht, 2013). The stated purpose of this mating behavior is to allow for mutual mate choice and the identification of a possible long-term mate. However, once married, copulation outside of the pair-bond is expected to cease. A second socially sanctioned form of sex outside marriage occurs in the context of either partible paternity or wife sharing during prescribed situations. For example, among some lowland South American groups, women regularly have several sexual partners in addition to their husband (Beckerman and Valentine, 2002; Walker et al., 2010). This practice is common where the contribution of multiple men is thought to be required for fetal development. While women do not formalize additional relationships through marriage (i.e., polyandry is not institutionalized), these men are expected to provide protection for and investment in children as they develop – a long-term commitment (Beckerman et al., 1998). In other societies, wife sharing may occur during publicly acknowledged situations. A well-described example comes from many different ethnographic sources of the Inuit, where monogamous couples engage in “wife-swapping” (Boas, 1907; Rubel, 1961; Hennigh, 1970; although husband-swapping may be more accurate). This exchange was reportedly agreed upon by all parties, and often, though not always, resulted in long-term social (and sexual) relationships. Other extrapair relationships are more clandestine, likely because of penalties that may follow (e.g., violence in response to sexual jealousy). Nonetheless, there are many examples of men offering food and other resources in exchange for extramarital sex (Holmberg, 1969; Gregor, 1987; Hill and Hurtado, 1996; Pollock, 2002).

access to a group of females and perform up to 70% of all copulations (Stoinski et al., 2009). Unsurprisingly, gorillas exhibit high levels of reproductive skew and males are nearly twice the size of females (Leigh and Shea, 1995). However, for species that live in multi-male/multi-female groups, such as chimpanzees, body size dimorphism tends to be intermediary between monogamous and polygynous species (Dixson, 2009). Given these patterns, what evidence of sexual dimorphism do we see in our hominin line (i.e., the phylogenetic group consisting of all modern humans, extinct human species, and our immediate ancestors) and what inferences can be drawn of ancestral mating systems?

Determining size dimorphism from the fossil record is fraught with debate due to interpretations that vary across researchers (Lockwood et al., 2007; Gordon et al., 2008; Reno et al., 2010; Plavcan, 2012). However, the general consensus is that

dimorphism was greater in our past and has diminished over time. This is often interpreted to suggest that male mating competition decreased in intensity over the course of hominin evolution in conjunction with a rise in monogamy. When this transition occurred, however, is debated. Some researchers speculate that dimorphism was fairly modest around 4 million years ago among *australopithecines* and place monogamy and male provisioning deep in the hominin line (Lovejoy, 1981; Reno et al., 2003, 2010). Others contend that *australopithecines* were highly dimorphic; therefore, monogamy had yet to become established (Lockwood et al., 1996, 2007; Gordon et al., 2008). Nonetheless, because of the fragmentary nature of fossil remains, difficulties in assigning sex, and the number of different species and subspecies, the fossil record may be an unreliable indicator of mating behavior in extinct species (Plavcan, 2000, 2012; Churchill et al., 2012). For example, male competition may be

expressed in many ways besides physical aggression (e.g., sperm competition, social status, and wealth), and so size dimorphism may underestimate male competition (Puts, 2010; Marlowe and Berbesque, 2012).

Regardless of the timing of the reduction in sexual dimorphism, humans today express only slight differences in body size by sex compared to closely-related promiscuous and polygynous species. For example, human body size dimorphism by weight averages about 1.15 (i.e., males are 15% heavier), with chimpanzees at 1.3 and orangutans and gorillas near 2 or more (Willner, 1989; Plavcan and van Schaik, 1992; Dixson, 2009). Humans fit more neatly in the range of variation typical of monogamous gibbons (e.g., *Hylobates lar*) who exhibit very little difference in body size by sex (1.07; Willner, 1989; **Box 2**: Which living ape is the best model for the breeding system of our last common ancestor?).

Testis Size

Testis size is another commonly used metric of mating system as it indicates, generally, female multiple mating, such that large testis relative to body size is positively correlated with the frequency of females mating with multiple males simultaneously (Harcourt et al., 1981; Kenagy and Trombulak, 1986; Møller, 1988; Parker, 2016). Adjusting for body size, human testes are smaller than would be predicted, and, when compared to our closest living relatives, are considerably smaller than those of chimpanzees (Harcourt et al., 1981; **Figure 2**). Together this provides evidence of relatively low rates of sex outside of a pairbond. However, human testes are somewhat larger than those of other monogamous primates, leading some to argue that this hints at a measure of extrapair copulation not expected in a monogamous species. Yet studies employing genetic methods find that rates of non-paternity are low among humans (~2%) when compared to those of socially monogamous birds (~20%) and mammals (~5%; Anderson, 2006; **Box 1**), casting doubt on claims of relatively high rates of extrapair engagement in human males compared to males in other monogamous species.

While testis size is a predictor of the extent to which females multiply mate, it is often mistakenly used as an indicator of monogamy. Testis size cannot discriminate between monogamy and polygyny because, in both cases, females mate with a single male for each offspring, resulting in relatively low sperm competition (Martin and May, 1981; Dixson, 2009). Thus, testis to body size complicates a simple story of ancestral mating derived from sexual dimorphism alone because human values are encompassed within the range of variation found among gorillas and orangutans—great ape species with polygynous mating systems. Therefore, we can only say that human values are consistent with pair-bonded polygynous species, but not with species where females mate multiply.

Concealed Ovulation

Human females lack obvious visible signals of ovulation, particularly in comparison to the conspicuous sexual swellings of, for example, chimpanzees and baboons (Strassmann, 1981; Dixson, 1983; Sillén-Tullberg and Møller, 1993; Rooker and Gavrillets, 2018). As a result, human ovulation is argued

to be concealed, with several functional arguments put forward to explain this phenomenon. Commonly claimed is that concealed ovulation and constant sexual receptivity of human females facilitates social monogamy (Morris, 1967; Campbell, 1974; Lovejoy, 1981) by limiting information available to males regarding fertility, thereby promoting monogamy through mate guarding and/or paternal care (Alexander and Noonan, 1979). Specifically, given that humans live in multi male/multi female groups, concealed ovulation is argued to minimize male-male competition and allow for stable, monogamous unions (Marlowe and Berbesque, 2012). However, more recently this association has been rethought as it is increasingly apparent from comparative study that concealed ovulation is not only characteristic of humans and other monogamous primates, but species from other mating systems as well. Many polygynous primates do not have overt signs of ovulation (Sillén-Tullberg and Møller, 1993). While human ovulatory cycles are indeed particularly concealed, what appears to be more remarkable are cycles that are particularly conspicuous. For example, chimpanzee females' estrus swellings are unambiguous and concentrate attention from multiple males during a short window of fertility (Hrdy, 1988; Smuts and Smuts, 1993; Gowaty, 1997; Nunn, 1999).

The traits discussed above, when interpreted singly, allow for different perspectives on ancestral mating in humans. For example, while men are larger on average than women, weight and canine dimorphism are slight compared to that of polygynous gorillas and more comparable to monogamous gibbons (Plavcan, 2012). This relative lack of dimorphism suggests diverging histories of sexual selection among the great apes regarding male reliance on contest competition for reproductive success (Dixson, 2009; Marlowe and Berbesque, 2012). Yet, while size dimorphism suggests a more monogamous past, relative testis size implies the extent to which females mate with multiple partners is higher than would be predicted for a monogamous primate. Human testes to body size values are lower than chimpanzees, higher than that of other monogamous primates, but not significantly different from gorillas. And, while concealed ovulation was once thought to be a human adaptation to promote monogamy, it is common among anthropoid primates, highlighting that what is notable are more conspicuous displays of fertility (e.g., sexual swellings) rather than their absence.

What becomes clear when the traits above are viewed collectively is that humans fall within the range of variation typical of pairbonded species. The lack of exaggerated sexual dimorphism or testis size seems to rule out a history of elevated reproductive skew typical of *highly* promiscuous or polygynous mating systems. Instead, biological indicators suggest a mating system where both sexes form a long-term pairbond with a single partner (Møller, 2003). And while polygyny was likely present in the human past, as it is across contemporary human societies, the weight of evidence seems to support social monogamy. This does not preclude males and females from taking multiple partners through serial monogamy, or by occasionally engaging in uncommitted sexual relationships (as indicated by testis to

BOX 2 | Which living ape is the best model for the breeding system of our last common ancestor?

Which ape mating system best serves as the baseline from which directionality in the fossil record should be interpreted? Chimpanzees have long been used as the behavioral model assumed to best resemble our last common ancestor. However, this has more recently given way to debate about whether past hominins (our bipedal ancestors) lived in multimale/multifemale groups like chimps (Hrdy, 2009; van Schaik and Burkart, 2010; Gavrillets, 2012) or were instead organized in polygynous, gorilla-like harems (Dixon, 2009; Chapais, 2011; Grueter et al., 2012) or had a hamadryas baboon-like structure with multiple single-male groups living together within a larger population. While this debate is ongoing, most researchers agree that ancient hominins were a group living animal, and that these groups were organized in nested multi-level societies (e.g., biological families, extended families, bands, tribes, etc.) with multiple breeding females, who commonly lived within socially recognized long-term pairbonds (Chapais, 2008; Grueter et al., 2012). Thus, whether pairbonds developed in the context of a polygynous or polygynandrous breeding system remain ambiguous. What we can say with certainty is that if our last common ancestor were “gorilla like,” we have become less dimorphic and less polygynous. And if it were more “chimpanzee like,” we have reduced body-size dimorphism only slightly, but have become much less promiscuous.



FIGURE 2 | A chimpanzee brain in comparison to a single testis. Photo credit: Martin N. Muller.

body size values). However, while extra-pair paternity (EPP) varies across socially monogamous animals, human rates of non-paternity are comparatively low.

CAUSES AND CONSEQUENCES OF MONOGAMY

The human life history pattern (i.e., short birth intervals, relatively high child survival, and a long period of juvenile dependence) means that mothers are often in the position of supporting multiple dependents of various ages simultaneously. Because infants, juveniles, and adolescents each require different kinds of time and energy investments, mothers are posed with an allocation problem throughout much of their reproductive career: how to care for infants and small children without compromising time spent in activities that provide food and other resources for older children (Lancaster, 1991; Hurtado et al., 1992; Hrdy, 1999; Kaplan et al., 2000; Kramer, 2005b, 2010; Kramer and Veile, 2018). How mothers resolve this trade-off to support a rapid reproductive pace has long been theoretically tied

to monogamy and the cooperation of fathers, siblings, and others to help mothers raise dependents.

Cooperative Breeding

Humans are typically described as cooperative breeders (although see Bogin et al., 2014), which in addition to male parental investment, is a key defining aspect of human sociality, cognition, and demographic success (Hrdy, 2005, 2009; Kramer, 2010; van Schaik and Burkart, 2010; Kramer and Greaves, 2011). Several recent phylogenetic analyses provide compelling evidence that cooperative breeding in bird, insect, and mammalian taxa was preceded by an ancestry of monogamy (Hughes et al., 2008; Cornwallis et al., 2010; Lukas and Clutton-Brock, 2012). The logic is that in a non-monogamous mating system, a sexually mature individual is likely to be more closely related to his or her own offspring ($r = 0.5$) than to siblings who may have a different parent (r between siblings = 0.25). Consequently, after sexual maturity, individual fitness is generally maximized by investing in one's own offspring rather than helping to raise siblings. In a monogamous mating system, however, the value for a sexually mature sibling to stay

in his/her natal group and help full siblings is equal to that of rearing one's own offspring ($r = 0.5$ for both) (Boomsma, 2007, 2009; Lukas and Clutton-Brock, 2012, 2013). Because kin-based benefits are diluted under female multiple mating, monogamy is hypothesized to be a critical step to raise relatedness within groups and sibships and thus to favor the evolution of kin-biased cooperative breeding (Boomsma, 2007, 2009; Hughes et al., 2008; Lukas and Clutton-Brock, 2012).

To add a bit of complexity, while monogamy may motivate the evolution of cooperative breeding and explain why reproductive-aged individuals help, non-reproductive individuals are able to realize kin-based benefits regardless of mating system. In many human societies, juvenile siblings and older females constitute much of the childrearing work force, contributing not only to childcare but also to resource provisioning (Flinn, 1988; Ivey, 2000; Lee and Kramer, 2002; Lahdenpera et al., 2004; Kramer, 2005b; Leonetti et al., 2005; Hrdy, 2009; Kramer and Veile, 2018). This help is empirically associated with improved maternal fertility and offspring outcomes (Turke, 1988; Blurton Jones et al., 1994; Hawkes et al., 1995a; Bliege Bird and Bird, 2002; Ivey et al., 2005; Kramer, 2005a, 2010). Among cooperative breeding mammals and eusocial insects, juveniles and subadults make important contributions to rearing and ensuring the survival of other's offspring (Clutton-Brock, 2002, 2009; Russell, 2004; Gilchrist and Russell, 2007; Boomsma, 2013). And, while grandmothing is rare in other species (McAuliffe and Whitehead, 2005), it is well-documented in humans (Hawkes et al., 1998). As a general point, while monogamy may facilitate the cooperation of sexually mature siblings, cooperation between a mother and juvenile, and a grandmother and her daughter can be favored irrespective of breeding system because of high coefficients of relatedness and low opportunity costs (reviewed in Kramer and Russell, 2014, 2015).

Paternal Care

Established claims in the anthropological literature posit that human mothers can support a rapid reproductive pace compared to our other ape relatives because fathers provide investment to both a partner and children (e.g., calories, protection). This argument hinges on an assertion that during human evolution, the increased need for paternal investment (due to big brains and expensive children) generated selective pressure for long-term pair bonds and a sexual division of labor (Washburn and Lancaster, 1968; Lancaster and Lancaster, 1987). However, phylogenetic analyses suggest that paternal care evolves only *after* monogamy becomes established in a population (Brotherton and Komers, 2003). Because male investment likely would have resulted in male absence (e.g., through resource provisioning), caring males would have faced potential fitness costs due to freerider males who are liable to steal paternity (Hawkes et al., 1995b; Gavrillets, 2012). Specifically, males that do not care benefit directly from caring males' investments in offspring that are not theirs. As a consequence, the assumption that paternal care drives monogamy is likely overly simplistic (Mathews, 2003; Fromhage et al., 2005). For example, a recent survey found that over 40% of socially monogamous species exhibit no indication of male care (Lukas and Clutton-Brock, 2013).

While paternal care is rare across animal taxa, it is generally present across human societies. However, if the needs of offspring did not drive the evolution of male care, how did it come to be? Under certain circumstances, monogamy can increase male fitness more than deserting a partner and remating (Grafen and Sibly, 1978; Yamamura and Tsuji, 1993; Fromhage et al., 2005; Schacht and Bell, 2016). Social and ecological factors that reduce male mating opportunities, such as females being dispersed or rare, reduce opportunity costs associated with monogamy and allow for selection to act on male paternal investment. Under these conditions, selection is expected to favor paternal investment if this investment improves offspring survival or quality, particularly when payoffs to desertion are low and paternity certainty is high (Dunbar, 1976; Thornhill, 1976; Perrone and Zaret, 1979; Clutton-Brock, 1991; Westneat and Sherman, 1993). Once biparental care becomes established, specialization of care tasks by males and females may serve to stabilize the pair-bond. The modal pattern cross-culturally is a life history characterized by specialization in child care by females (i.e., direct investment) and resource provisioning by males (i.e., indirect investment; Murdock and Provost, 1973). This specialization can result from and further lead to synergistic fitness benefits tied to offspring success (Leonetti and Chabot-Hanowell, 2011; Barta et al., 2014). These payoffs both constrain the behavioral options available to a parent and decrease sex-biased asymmetries in the costs of performing a parental investment task. Thus, task specialization can serve to strengthen biparental care once it emerges against invasion by other strategies.

Human fathers regularly provide care to dependent offspring well into the second decade of their life, and often care for multiple children at the same time (e.g., Kaplan et al., 2000; Gurven and Hill, 2009; Gray and Anderson, 2010). However, men still regulate the time and energy they allocate between mating and parental effort (Kaplan and Lancaster, 2003; Ross et al., 2016). Human paternal investment, while often substantial in relation to other mammals, is facultative rather than obligatory, and the anthropological record indicates considerable cross-cultural variability in how and how much fathers invest in their children (Marlowe, 2000; Lamb, 2004; Gray and Anderson, 2010; Shwalb et al., 2013). A key variable found associated with male investment is paternity certainty. Often males invest less where extra-pair relationships are more common (Gaulin and Schlegel, 1980).

Thus, while a gender division of labor appears to be a human universal, paternal investment is sensitive to a variety of conditions and seems to be regulated, at least in part, by testosterone. Testosterone is an androgenic steroid hormone that supports many aspects of male mating effort, including the development and maintenance of sexually dimorphic musculature and bone structure as well as courtship and male-male aggression (Archer, 2006; Bribiescas et al., 2012). Accordingly, testosterone levels are argued to reflect a male's allocation to reproductive effort at a particular point in time. Levels of circulating testosterone in males are thus reasoned to reflect the evolved hormonal regulation of investment in mating vs. parenting effort (Wingfield et al., 1990). In

support of this claim, cross-sectional and longitudinal evidence indicates that married men have lower testosterone levels than unmarried men, and that married men with children have the lowest levels. These results suggest that partnered men, and in particular fathers, are hormonally primed to invest more time and energy into parenting rather than mating effort (Gettler et al., 2011; Gray, 2011).

Kin Discrimination

While mammalian mothers are certain of their maternity, fathers may be uncertain of their paternity. Monogamy ensures relatedness between fathers and their purported children, and permits for both the paternity confidence and relatedness necessary to favor investment by fathers. Because cooperation among close relatives increases the fitness benefit gained by cooperators, mechanisms for discriminating between kin and non-kin, and between close and more distant kin, are critical for its evolution (Hatchwell et al., 2001; Griffin and West, 2003; Chapais, 2008, 2009). If fathers and siblings are able to identify one another, relative payoffs to investment vs. desertion increase for fathers, as do the payoffs for cooperative breeding among siblings. For humans, language and the ability to identify a range of relations through kin classificatory systems likely amplified payoffs to kin-biased cooperation by allowing distinctions in relatedness among group members to be recognized (Kramer and Greaves, 2011; Kramer and Russell, 2014). Complex kin systems are highly developed in traditional human societies and permit distinguishing classificatory from biological kin and close kin from distant kin. This allows individuals to selectively identify and cooperate with close kin, and to make decisions about when and how much to help. In the case of fathers, kin discrimination allows for a range of paternal relationships (e.g., biological, social, and/or stepfathers), all of which have societally prescribed roles.

One interesting implication of language-based kin classificatory systems found in all human societies is that, even in the absence of monogamy, they allow children to identify their siblings and father and fathers to identify their children. Because serial monogamy was likely the norm throughout human history due to long breeding careers and high rates of spousal death and divorce, kin terms allow parents and children to identify each other and close relatives despite not cohabiting or living in proximity. Moreover, kinship classificatory systems attenuate the requirement of monogamy for the maintenance of

cooperation between mothers, fathers, and siblings by facilitating payoffs to investing in kin outside of a current household (Kramer and Russell, 2015). Thus, the range of breeding systems that we see across and within human societies may be an outcome of our ability to identify close relatives and preferentially invest in them even in the absence of monogamy.

CONCLUSION

Consensus on a human-typical mating system has remained elusive in the literature. Across human societies today, monogamous, polyandrous, polygynous, and short-term mating patterns are present, with most societies exhibiting multiple types of marriages and mating relationships. Further complicating a straightforward classification of mating system are the multiple possible interpretations of biological traits typical of humans used to indicate ancestral mating patterns. While challenging, our review of the literature offers several key insights. 1) Although polygyny is socially sanctioned in most societies, monogamy is the dominant marriage-type within any one group cross-culturally. 2) Sex outside of marriage occurs across societies, yet human extra pair paternity rates are relatively low when compared to those of socially monogamous birds and mammals. 3) While the timing of the evolution of certain anatomical characteristics is open to debate, human levels of sexual dimorphism and relative testis size point to a diverging history of sexual selection from our great ape relatives.

In sum, we conclude that while there are many ethnographic examples of variation across human societies in terms of mating patterns, the stability of relationships, and the ways in which fathers invest, the residential pair-bond is a ubiquitous feature of human mating relationships. This, at times, is expressed through polygyny and/or polyandry, but is most commonly observed in the form of monogamous marriage that is serial and characterized by low levels of extra-pair paternity and high levels of paternal care.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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