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Choosy But Not Chaste: Multiple Mating in Human Females

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When Charles Darwin set out to relate his theory of evolution by natural selection to humans he discovered that a complementary explanation was needed to properly understand the great variation seen in human behavior. The resulting work, *The Descent of Man and Selection in Relation to Sex*, laid out the defining principles and evidence of sexual selection.¹ In brief, this work is best known for illuminating the typically male strategy of intrasexual competition and the typically female response of intersexual choice. While these sexual stereotypes were first laid out by Darwin, they grew in importance when, years later, A. J. Bateman, in a careful study of *Drosophila* mating strategies, noted that multiple mating appeared to provide great benefit to male reproductive success, but to have no such effect on females.² As a result, female choice soon became synonymous with being coy, and only males were thought to gain from promiscuous behavior. However, the last thirty years of research have served to question much of the traditional wisdom about sex differences proposed by Darwin and Bateman, illuminating the many ways that women (and females more generally) can and do engage in multiple mating.

It wasn't until the late 1970s that the stereotype of the "coy female" began to be challenged. Leading the charge was Sarah Hrdy, who came to question the logic of female coyness during her study of infanticide among the Hanuman langurs. She observed females mating with extra-group males, even though they had plenty of mating options within their own groups.^{3–5} Her explanation, that this could result in paternity confusion that would protect infants from future infanticidal attacks, was one of the earliest hypotheses about a female reproductive strategy that would

favor multiple mating. Since then, the evidence of extra-pair and sequential mating by females in various species has accumulated rapidly, and a suite of explanations has arisen to explain these deviations from traditional sexual selection theory.^{6–10}

With regard to humans, this debate has been slow to develop. Stereotypical assumptions about male and female mating behavior continue to dominate the empirical literature, despite repeated claims that there is variation in both male and female mating behavior.^{11–13} In addition, the role of female choice in women's mating strategies has been questioned because of the often extreme control over women's sexuality by family members and through broader social norms.¹⁴ Nevertheless, we now know that women have both physiological and behavioral mechanisms designed to facilitate multiple mating, even in the face of constraints.

While much of the work on humans continues to emphasize sex differences in mating behavior, we are slowly real-

izing that the ranges in behavior expressed within each sex are far more important than previously thought.^{8,15} The resulting paradigm shift in both the theory and the empirical work on sexual selection is not contradictory to Darwin's original thesis; rather, it allows us to have a broader and more complete understanding of sexual behavior. Hrdy¹⁶ succinctly summed this up when she wrote, "As with many other animals, primate females (including women) can benefit reproductively from polyandrous matings. Understanding this takes us beyond narrow research programs intent on demonstrating 'universal' differences between the sexes, and allows us to study females as flexible and opportunistic individuals who confront recurring reproductive dilemmas and tradeoffs within a world of shifting options." In this review, I will focus on this diversity in women's mating strategies, with particular emphasis on when and why they might gain from engaging in multiple mating. I will examine both the behavioral facets of multiple mating and some known physiological correlates. Throughout, I will use a life-history approach to understand how multiple mating occurs and varies across the life course.

THEORY AND EVIDENCE FOR MULTIPLE MATING IN WOMEN

Conventional interpretations of sexual selection theory predict a reliable sex difference in reproductive variance, with the sex who invests less parental care (typically males) almost always exhibiting greater variation than the sex who provides

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more care (typically females).^{17,18} This theory also contends that the correlation between mating success and reproductive success (RS) is stronger for males than females. This means that males who can gain access to multiple mates will rise in the reproductive hierarchy, while those who fare poorly in intrasexual competition are chosen less often by females and have lower RS. Females, on the other hand, because they supposedly gain little from additional matings, are predicted to have much more stable RS after the first mating. In the years since Bateman's study was first published, there have been several challenges to both the methodology and the theoretical soundness of his work.^{19,20} Recently, the first replication of the study, modernized with DNA data, failed to reproduce his findings even in the *Drosophila* he studied.²¹ Similarly, behavioral data across sexually reproducing species have repeatedly revealed instances of multiple mating enhancing female RS.²²

Despite the length and breadth of this critical literature, Bateman's principle has been instrumental in the development of hypotheses related to sexual behavior in humans. Women are predicted to show lower levels of promiscuous desires and behavior than are males and generally to favor long-term over short-term mating strategies.^{12,13} Similarly, Trivers' parental investment theory¹⁷ predicts that women will concentrate more of their efforts on parenting than mating, reducing time allocated to the search for extra-pair or sequential partners. These predictions appear to be well supported. Women have been shown to desire fewer sexual partners than men do,¹² are more likely to prefer a long-term over a short-term partnership,²³ and are less likely to seek short-term encounters.²⁴ Further, in almost every human society women perform the vast majority of direct child-care and men invest comparatively little.²⁵ Given the consistency in these studies, it is in some ways unsurprising that sex differences have garnered so much attention in both the literature and the public portrayal of evolutionary studies of mating behavior. In recent years, however, empirical work that extends

beyond the Western samples typical of early mate choice studies, as well as theoretical models that challenge some of the basic logic of Bateman's model, have moved the sexual selection debate forward. In particular, they show that female multiple mating is in fact critical to understanding the links between sexual selection and common sex-role behaviors.

Multiple Mating and Female Choice in Contemporary Models

Over the last forty years, the stereotypes of the caring female and the

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competitive male, derived from early interpretations of sexual selection theory, have faced a series of strong critiques. In his original work introducing parental investment theory, Trivers, drawing on Bateman, argued that the reason females tend to care more than males is because of their greater preconceptive investment, via ansioamy.¹⁷ This logic was quickly countered when Dawkins and Carlisle²⁶ explained that this argu-

ment committed the 'Concorde fallacy,' which states that the level of future investment should be based on costs incurred in the past. Others then attempted to show that past costs did indeed affect future investment either because losing an existing offspring has greater costs to females than males or because the benefits of continuing investment in current offspring versus switching to produce new offspring are relatively greater for females. Both of these arguments have since been refuted.²⁷

Another set of theories about sexual selection focuses on the adult sex ratio (ASR). When the ASR is balanced, males, on average, cannot reproduce faster than females because every individual has only one mother and one father, a phenomenon called the Fisher condition.^{27,28} Despite this a common assumption in many papers about mate choice and sexual selection was that males had faster reproductive rates than females, inevitably leading them to favor multiple mating over parental care.⁶ Besides, sex differences in reproductive rate alone are not sufficient to favor sex differences in parental investment strategies. There must be variation in reproductive success among males. If the males who provide care father fewer offspring than those who desert, then genes that favor deserting over caring will increase in the population, even though the average reproductive success of males and females will still be the same.²⁹ One way that this variation can arise is through female multiple mating. Deserting males "steal" paternity from caring males either through extra-pair copulations or sequential partnerships with females. Once there is this kind of variation in male success, it will pay for males to desert rather than to care, leading to the standard sex difference in parental investment.^{6,30} Therefore, female multiple mating can set the stage for sex differences in parental care.

A second explanation for why females typically invest more than males arose in the late 1990s, and was also linked to multiple mating. It was argued that because females

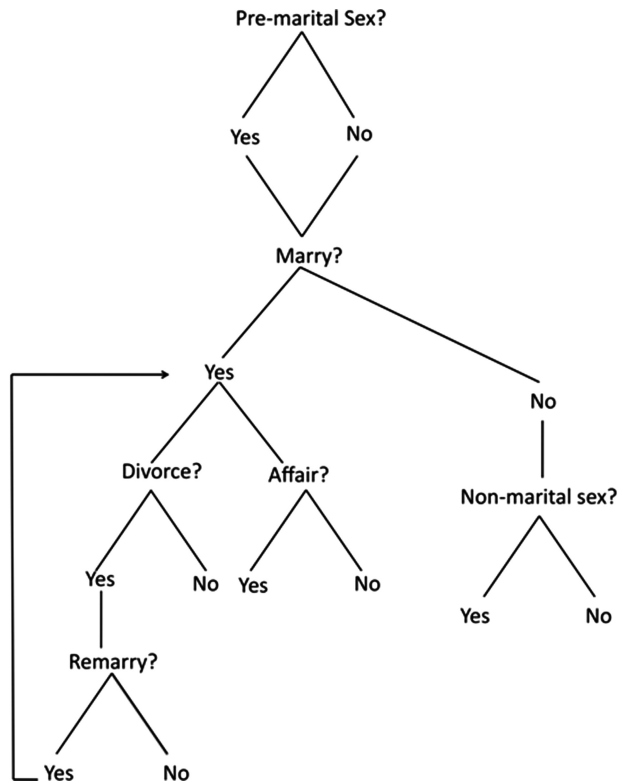


Figure 1. Decision tree showing the choices women may face during their reproductive careers. The sum of these decisions correlates with the total number of mating partners a woman will have during her lifetime.

are more certain of their relatedness to their offspring than males are, females experience reduced costs of parental investment and care more.^{27,30} This is because, on average, the benefits of investment must be devalued by the rate of non-paternity. Once again, to get to a state of considerable paternity uncertainty, a female strategy of multiple mating must be common.

The relationship between female choice and multiple mating is further complicated by the influence of external social factors, which are particularly complex and multifaceted in humans. For example, the extent of paternal care is often tempered by the support of others, mainly female kin (see Mace, this issue). Therefore, in societies in which women are less reliant on men, multiple mating is predicted to be more common.¹⁶ This is because where male care becomes substitutable with investment by others, such as grandmothers and siblings, the benefits to male desertion rise.

Considerable ethnographic evidence is now available to support this assertion. One reliable measure of female kin support is the pattern of postmarital residence. Several studies have shown convincing associations between uxurilocality (living with the wife's kin) and multiple mating. For example, in a phylogenetic analysis of

Amazonian societies, there is a strong association between the presence of partible paternity beliefs and uxurilocal residence.³¹ Similarly, several notable cases of female promiscuity co-occur with strong female kin ties. The Mosuo, who practice *sese*, or "walking marriage," are matrilineal^{32,33}; the Himba, who have one of the highest known rates of extra-pair paternity,³⁴ have patterns of frequent visitation that enable women to maintain strong ties with and support from their kin even though they have patrilocality post-marital residences.³⁵ Within the U.S., in sub-populations in which reliability on male resources is low

as a consequence of high incarceration rates and unemployment, female kin provide critical instrumental and emotional support, and patterns of serial monogamy are common.^{36,37} These patterns illustrate the importance of viewing multiple mating within the context of cooperative breeding, given that both the role of non-parental caretakers and the level of support they provide are likely to affect the need for and desire of men to participate in parenting, which in turn can affect the mating strategies of both sexes.²⁵

A LIFE-HISTORY PERSPECTIVE ON MULTIPLE MATING

Now that the theoretical significance of multiple mating has been firmly established, it will be important to understand how women deploy this strategy. Here, a life-history perspective is used to identify the ways in which women engage in multiple mating at different times in their lives. For example, the same woman may spend part of her life in a strictly monogamous marriage and at other times engage in multiple mating. Therefore, instead of viewing multiple mating as a binary state, it can be seen as a series of choices that women make as they move through their reproductive life spans.

One difficulty in determining the extent of multiple mating in humans is establishing what exactly is included in the term. Multiple mating is typically measured in one of two ways. From a longitudinal perspective, it can be defined as occurring when a person has sequential mates over some period of time. This is typically measured as the number of sexual partners, which, among humans, may or may not coincide with the number of marital partners. Another way of measuring multiple mating is to look at the number of partners an individual is involved with simultaneously. This would include measures of infidelity, as well as formal and informal polyandry. When considered together, these two factors make up the total number of sexual partners an individual has across his or her life span (Fig. 1).

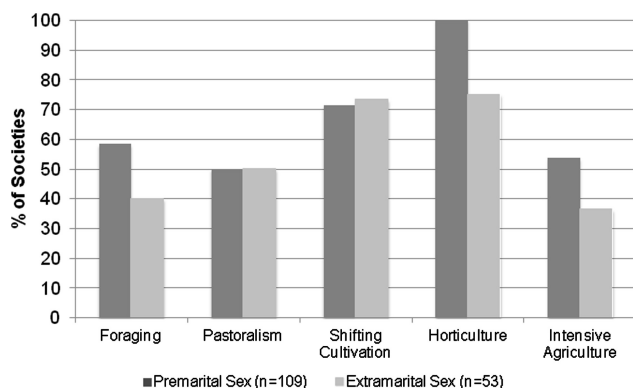


Figure 2. Female sexual behavior across cultures. Shown is the percent of societies, by mode of subsistence, reporting high levels of premarital and extramarital sex. Codes for premarital and extramarital sex are constructed using variables v167 and v171 from the SCCS.⁶¹ A society is coded as having a high level of premarital or extramarital sex by women if it was listed as either “universal” or “moderate.” Codes for mode of production are drawn from v858.¹⁰⁰ Mounted hunters were grouped here with pastoralists.

These measures can be linked to four key decisions that women face about allocating their reproduction: whether to begin reproduction before marriage; whether or not to marry; how many times to marry; and whether to remain monogamous with their marital partner(s). Not all of these decisions are in the hands of women alone. Families often influence the timing and number of marriage partners a woman has, while societal norms place restrictions on premarital sex divorce and infidelity in some societies. Further, infidelity can create physical and material costs that act as deterrents. These extrinsic influences will be considered here within the context of each life-history decision, providing evidence of the extent and importance of each factor within the suite of multiple mating behaviors.

Premarital Reproduction

Premarital sex is relatively common in many small-scale societies (Fig. 2). Among those societies in the standard cross-cultural sample (SCCS) for which data is available, 61.7% have social norms that either permit or only mildly disapprove of premarital sex by females, and almost half (49.1%) report that female premarital sex is a near-universal behavior.³² Across modes of production, it is most common among horticulturalists and least

common among agriculturalists and pastoralists (Fig. 2). This is likely due to a suite of factors linked to mode of subsistence, including the level of female autonomy, patterns of residence and descent, and the presence and direction of material transfers. In horticultural and incipient agricultural societies, in which women contribute more to subsistence, greater sexual freedom is granted to women, including allowances for premarital sex.³⁸ Other cross-cultural studies have shown that a greater value is placed on virginity when men can use the impregnation of an unmarried woman to secure a marriage that betters his social or economic position, a possibility that arises most often in societies with dowries.³⁹ Biology matters as well. Premarital sex has been shown to be more likely to be restricted when the period of maidenhood (the years between menarche and marriage) is long, and the possibility of a premarital pregnancy is higher.⁴⁰

Cross-cultural data on the number of premarital births has rarely been recorded, especially for small-scale, natural fertility populations. This is why the previously mentioned studies discuss norms for premarital sex rather than the frequency of premarital births. More often, demographic data includes illegitimacy rates, which include not only premarital births, but also those that occur among women who never marry and

those who give birth between marriages. Births that occur out-of-wedlock are notably and expectedly lower than those for premarital sex, since not all sex leads to a pregnancy, although in some places such as the Caribbean out-of-wedlock births can still reach 50%.⁴¹ More generally, they range from virtually nonexistent in countries like Japan (1.4%), Sri Lanka (1.4%), and Cyprus (1.6%), to the majority in El Salvador (73.2%), Panama (79.9%), and Iceland (65.2%).⁴²

Placing premarital sex and reproduction within the larger life-history framework is important if we are to understand how these behaviors coincide with other multiple mating strategies. There is some evidence showing systematic correlations at the societal level between the extent of premarital and extramarital sex women engage in.⁴³ However, other studies have not found consistent trends in the level of sexual permissiveness within societies, indicating that premarital reproduction does not necessarily lead to a multiple mating strategy later in life.⁴⁴ One pertinent study examined the permissiveness of sexual norms across the life span, from sex play and immodesty in childhood to virginity restrictions in adolescence to extramarital sex in adults. Levels of permissiveness at one stage are not consistently correlated with permissiveness at other stages.⁴⁵

Women may have one or several premarital partners and then go on to marry and remain monogamous for the rest of their lives. Such early promiscuity is sanctioned in several of the most well-studied foraging societies. Among the Ache, it has been reported that most young women had sex with at least one man before reaching menarche, and most had 2–4 sexual partners by that time.⁴⁶ Young Hadza women also typically have several suitors before settling into marriage⁴⁷ and sex play is common for young !Kung women.⁴⁸ However, while these temporary relationships before marriage may be common among foragers, the likelihood that they will result in pregnancy is probably quite small

due to the early age at marriage and adolescent periods of sub-fecundity.

In developed nations, there is more evidence that premarital reproduction is part of a longer-term pattern of multiple mating. Premarital births are associated with lower levels of relationship stability, decreased likelihood of ever marrying, and higher rates of eventual divorce.⁴⁹ A conditional reproductive strategy to invest in short-term mating when prospects for relationship and investment stability are poor may be in play in these contexts. Evidence of this comes from studies of the association between premarital reproduction and the population sex ratio. Where the sex ratio is female-biased, indicating a scarcity of men, women have higher rates of teen pregnancy and illegitimate births.^{50,51} In another study, spanning 85 countries, the number of illegitimate births correlated with both the level of male unemployment and a female-biased sex ratio.⁵² In this situation, women may be attempting to make the best of a bad situation and capitalizing on their youth to improve their reproductive prospects.

While the links between unstable future investment prospects and premarital reproduction are fairly strong in some developed countries, alternative explanations are equally viable in smaller-scale societies, where premarital reproduction is also common. Here, premarital reproduction may be part of a multiple mating strategy for high-quality women who, being more generally desired, have greater fitness and a greater number of partners both within and outside of marriage.

There are also other advantages to women having a premarital partner. First, all else being equal, women who begin reproducing earlier should have higher fertility due to their longer reproductive life spans. Therefore, if marriage is delayed, an out-of-wedlock birth provides a way to begin reproducing earlier. Premarital births may also increase female choice in societies with arranged marriage because it may force parents to accept a daughter's mate choice because of a pregnancy or allow her to have at least one child by a partner of her choice before set-

ting into marriage with a partner of her parents' choosing. Among the Ju/'Hoansi, young women sometimes elope with their lovers in the hopes of escaping a parentally arranged union.⁵³ Premarital reproduction also may allow women to better assess the quality of a potential spouse before making a long-term commitment. This has been shown in the form of "trial marriages" in the Andes, where a couple live together and sometimes have children before entering into legal marriage.⁵⁴ This is a risky strategy because if trial marriages fail, a young woman may wind up unmarried with a child and no partner support. However, these risks may be buffered early if women are still living at home and can rely on kin support that would not be available if she began reproduction in her marital home. For all these reasons, a multiple mating strategy that begins with a premarital partner can aid in female choice and possibly improve her overall fitness.

Marriage, Divorce, and Remarriage

Marriage is often thought of as one of the true human universals. In fact, there are almost no societies where marriage is unheard of and, in the vast majority of societies, the choice never to marry is quite atypical. In a study of women aged 40–44 in 57 countries spanning Europe, the Middle East, and parts of Asia and other English-speaking nations, on average 8% of women were never married.⁵⁵ In most cases, the choice of to never marry, especially if it is linked to lifelong celibacy, is an undesirable outcome. However, in a few cultures, marriage is rare and disassociated from reproduction. In China, the Mosuo practice *sese*, or 'walking marriage,' which means that women reside with their kin; their sexual partner(s) visit them at night, but do not traditionally provide economic or social support to the woman's offspring; and women are permitted to have multiple lovers.^{32,33}

Multiple marriages, which are one way to increase a woman's number

of lifetime partners, are affected by both a woman's ability to procure a divorce, and the norms and prospects for remarriage. The frequency of such sequential mating varies substantially across human populations.⁵⁶ In, general, men typically have more options to increase their number of lifetime marriage partners than women do. This is a consequence of both the higher incidence of polygyny than polyandry and men's greater freedom to divorce and remarry. However, women frequently can and do have multiple spouses during their lifetimes (Fig. 3). Divorce and remarriage for women are most widely accepted among horticulturalists, but even among intensive agriculturalists, where these behaviors are most likely to be restricted, more than half allow women to divorce and remarry as easily as men.

Many of the divorces that occur among hunter-gatherers take place within the first five years of marriage.⁵⁷ Often, the arrangements of these early marriages are fraught with conflict between parent and child. Parental coercion can constrain female choice, particularly in the case of first marriages and when brides are young.¹⁴ Among the Ju/'Hoansi bushmen, more than 60% of brides reported that they were mildly or strongly reluctant about their first marriage, but parental interests often win out in the end. Only 26% of first marriages ended in divorce in the first 5 years.⁵³

Parental constraints notwithstanding, Ju/'Hoansi women exhibited several of the ways that women typically use divorce to exert partner choice. In early marriages, women actively seek divorce when they are dissatisfied; Ju/'Hoansi wives initiated 90% of the divorces in first marriages. After a divorce, women appear to have considerably more authority in choosing, or at least approving, their next spouse. The finding that remarriage is associated with increased autonomy is typical of many small-scale societies and may be an important factor in the negotiation of conflicting interests between parents and children in the arrangement of marriages. For

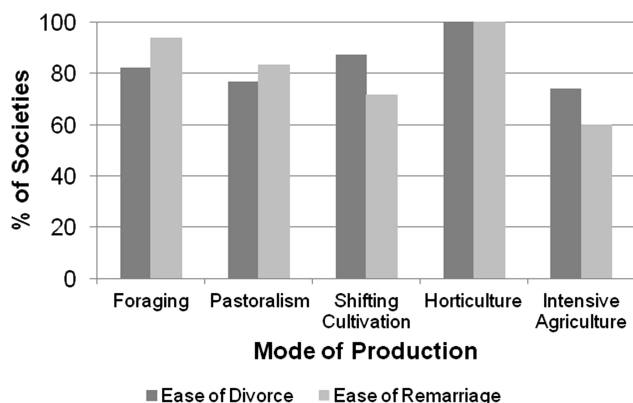


Figure 3. Ease of divorce and remarriage for women across cultures. Shown is the percent of societies in the SCCS reporting an equal or enhanced ability of women to divorce or remarry. Ease of divorce was coded using the SCCS variable v610.¹⁰¹ Percentages reflect societies coded as either 'divorce equally possible, no indication of bias' or 'divorce is possible for both, but more difficult for male, or in theory only available to female.' Ease of remarriage was coded using SCCS variable v611. Percentages reflect societies coded as 'equally possible for both men and women.'

example, among the Himba, only 9% of women's first marriages were love matches, as opposed to 62% of second marriages. Therefore, divorce may be an important way for women to exert choice through mate switching.

Staying Faithful

Women can also increase their number of mates through either formal or informal simultaneous partnerships. Formal polyandrous marriage systems are quite rare in human societies. Of the few that do exist, most are restricted to two geographic areas, the Himalayas and the South Pacific.⁵⁸ However, there are also societies in which married women have sexual partnerships with multiple men and each of these men has some economic responsibility for the children they have sired. If these societies are included, an additional 53 societies can be added to the list of polyandrous societies.⁵⁹ Most of these cases of non-classical polyandry occur in egalitarian hunter-gatherer and horticultural societies, particularly ones that experience unbalanced sex ratios favoring males.

In several societies in the Arctic, sub-Saharan Africa, aboriginal Australia, and native North America tra-

ditionally permitted formalized wife lending or spouse exchange exists.^{60,61} The benefits to men from these exchanges have been well documented as a reinforcement of male alliances, but there may have been benefits to females as well, especially in cases in which women had some choice in whether they engaged in such relationships.

Multiple mating via extra-pair partnerships that are not socially sanctioned is much more difficult to quantify in most societies because of the sensitive nature of adultery. As with divorce, the general pattern is that extramarital sex is more widely condoned and less severely punished among men than women.⁶⁰ Although 54% of societies coded in the SCCS condone men's engagement in extramarital sex, only 11% condoned women's.⁶¹

A cross-cultural study of non-paternity rates has indicated that the rate of extrapair paternity typically is quite low, between 1 and 10%.⁶² However, the vast majority of samples in this study were from industrialized countries. We have very little empirical data on non-paternity rates in small-scale societies. In fact, cross-cultural data on behavioral and social norms indicate that the rates may be much higher than those in industrialized nations. Female infi-

delity is actually relatively common, occurring at a universal or moderate level in 55% of societies in the SCCS.⁶¹ As with the frequency of premarital sex, extramarital sex is most common among horticulturalists and shifting cultivators; it is least common among agriculturalists (Fig. 2). Also, as with the findings relating to premarital sex, allowances for female extramarital sex can be tied to societal norms about inheritance and other material transfers. Modes of production such as foraging and horticulture, which have few heritable resources, generally allow more sexual freedom for women.⁶³ The presumed reason for this is that when men are uncertain of their paternity they should be wary of passing down resources to children who may not be their biological heirs. For example, one study that combined variables from the SCCS on extramarital sex and wife-sharing found that higher levels of these types of extra-pair matings by women were associated with less inheritance of material wealth through the male line.⁶⁴

Ethnographic evidence on female infidelity in small-scale societies has been reported for the !Kung,^{65,66} Ache,^{46,67} Yanomamo,^{68,69} Tsimane,^{70,71} Bari,⁷² and Tiwi,⁷³ among others. In Western societies, estimates of the rate of female infidelity range between 20% and 50%.⁷⁴ In some societies, female infidelity is actually normatively sanctioned. For example, across parts of lowland South America, beliefs in partible paternity (the idea that more than one man can be the biological father of a child) lead to non-exclusive mating relationships and frequent affairs, for which women are rarely punished, and prudish behavior can even be condemned.^{31,72,75} Similarly, among the Himba of northwestern Namibia, affairs are frequent and, indeed, an expected part of married life.³⁴

Like divorce, infidelity is a way that females can exert choice in their mating partner in the face of social constraints. Having an affair may allow a woman to gain reproductive access to the man of her choosing, despite having succumbed to an

arranged marriage, or to assess the quality of a potential future spouse while continuing to secure investment from her current one. Among the Himba, for example, all of the reported cases of extra-pair paternity resulted from arranged marriages rather than “love matches,” indicating that infidelity in this context is used to increase female choice when women are otherwise constrained.³⁴ However, in many cultures female adultery is severely punished. This is particularly true of agricultural societies.^{60,76} Therefore, while infidelity is one of a suite of behaviors available to women as part of their mating strategy, social and ecological factors make it unlikely to be universally expressed.

THE BENEFITS OF MULTIPLE MATING

Knowing that females in many species do engage in multiple mating, either some or all of the time, it is important to understand what, if any, benefits they gain from this behavior. One possibility is that they do not gain at all, that the divergent strategies of males and females lead to coercion, and females engage in short-term or multiple mating only when they lose in situations of sexual conflict.⁷⁷ Among humans, this could occur in a variety of ways, including rape, forced polyandry due to shortages of women or limited resources, or wife sharing that occurs for male alliance-building. Although these circumstances certainly exist, the data from primates and other species showing that females do derive benefits from multiple mating imply that women can secure similar gains, at least some of the time. The benefits exhibited by females of other species fall mainly into two categories, improved genetic quality of progeny and increased access to support or resources that can be used to sustain self and offspring. There is now increasing evidence that the same benefits apply to women.

Genetic Benefits

In both birds and mammals, female mating with extra-pair males

can improve the genetic quality of offspring.²² There are several types of genetic benefits that can be gained by multiple mating. A female can ‘trade-up’ by mating with a male who is of higher genetic quality than her current mate. This can occur through either extra-pair mating or mate switching. Multiple mating can also allow females to produce offspring with increased heterozygosity, which can increase their chances of survival, as has been shown in the blue tit.⁷⁸ Females may also engage

...the data from primates and other species showing that females do derive benefits from multiple mating imply that women can secure similar gains, at least some of the time.

in bet-hedging, mating with multiple males to produce offspring with greater genetic diversity.⁷⁹

No studies have compared the genetic quality of in-pair and extra-pair young among humans. Indeed, practical and ethical considerations make it unlikely that such studies will be done. Similarly, there are no known studies of bet-hedging as a female mating strategy among humans. Instead, genetic studies have concentrated on proxy measures of quality, such as facial symmetry or MHC compatibility, and on determining whether and when women prefer these traits. For example, undergraduate men with greater facial attractiveness and lower fluctuating asymmetry were rated as more desirable extra-pair partners than were other men.⁸⁰ Women report more extra-pair desires and actual affairs when they have greater MHC similarity with their long-term partner; an indicator of genetic incompatibility.⁸¹

The level of pathogen stress in a given society is associated with mate choice for improved genetic quality in humans. Across societies, those with higher pathogen stress are more likely to have polygynous mating systems than monogamous or polyandrous ones.⁸² In these cases, it is thought that women might be more willing to share a high-quality mate, who has greater resistance to pathogens, than to have a lower-quality mate all to herself. Another way that women might obtain the same benefit is through multiple mating, seeking an extra-pair mate of higher quality for his genetic benefits while paired with a lower-quality long-term mate from whom she derives other advantages, such as help with child care. To find evidence of this, individual-level data on infidelity would need to be matched to proxies for genetic quality, such as facial symmetry. Such studies have yet to be done.

Material Benefits

The genetic studies discussed here propose that women are looking for different qualities in their long-term and short-term mates, a dual-mating strategy.⁸³ An alternative explanation is that women seek multiple partners to enhance their ability to obtain similar benefits from a larger number of men. In this scenario, women partner with multiple men, each of whom provides some level of support to her and her children. A central critique of this hypothesis is that women do not necessarily fare better by accruing investments from multiple males than they do by gaining all benefits together from the same father.⁸⁴ However, the sum of investment by multiple males can outweigh that of a single father. Also, multiple mating can reduce risks if there is ecological uncertainty or if a woman’s primary partnership dissolves through death or divorce.⁵⁹ These explanations appear to be significant among South American societies with partible paternity, in which women receive food and gifts from multiple partners and, if their primary partner dies, sometimes marry their

extra-marital partners. In such cases, multiple mating can be a form of insurance.³¹ In some cases, this translates directly to fitness, as children with multiple fathers have greater survival prospects.^{46,72}

Infidelity can have similar benefits. Among the Himba, where affairs are common, both men and women report that men provide gifts of food and livestock to children they have fathered outside of marriage, even though women continue to reap support and resources from their long-term marital partners. Additional evidence from small-scale societies shows that higher-status men attract more extra-pair mates.^{46,85} However, it is unclear whether these men are chosen because of their superior genetic quality, because they have more resources to offer, or both.

Does Multiple Mating Improve Reproductive Success?

To clearly show that multiple mating is an adaptive strategy for women, the behavior should be associated with increased reproductive success. There is good evidence of such links in species ranging from insects to birds and mammals.^{22,86}

Among humans, the evidence is more limited, probably at least partly because of the difficulties in obtaining accurate data on paternity in many societies. One exception is the Himba, where both men and women are willing to reveal extra-pair paternity assertions. Here, women who have more children through affairs have significantly higher overall reproductive success.³⁴ The reason for this association is unknown, but the fact that women have significantly higher rates of extra-pair paternity among offspring from arranged marriages versus 'love matches' indicates a role for female choice in their strategy. However, it is not yet known whether these women are using infidelity to enhance their access to material resources or to obtain better genetic matches. A third but not mutually exclusive possibility is that Himba women who engage in more multiple matings are more highly desired than others are because they possess

some advantageous intrinsic quality, a phenotypic correlation that has nothing to do with the quality or resources of the male. This could explain the positive correlation between the number of extra-pair offspring and overall fertility. More detailed studies of the benefits to be gained from multiple mating and the pathways through which those benefits lead to improved fitness are needed, not only among the Himba, but in other populations as well.

Data are somewhat easier to obtain in cases of multiple mating via sequential partnerships. Among the Pimbwe, multiple marriages benefit women more than men.⁸⁷ Among Pimbwe men, there is a negative relationship between the number of spouses and the number of surviving offspring, but women with more than two husbands have greater reproductive success than do women who married only once or twice. Once again, the mechanism linking multiple mating to greater reproductive success is unclear, and more work is to understand how multiple marriages allow women to increase their fitness.

There are also examples of the opposite pattern, which follows Bateman's predictions. Among a historic population of Nordic Sami, lifetime reproductive success increased for men who were married twice, but did not increase for women married twice.⁸⁸ In another study in the contemporary U.S., men increase their number of surviving offspring by having multiple spouses, but women do not.⁸⁹ Similar results were found in contemporary Sweden.⁹⁰ A larger sample of studies from various cultures would help us to understand the range of reproductive variance men and women exhibit under different conditions.

THE PHYSIOLOGICAL CORRELATES OF MULTIPLE MATING

If multiple mating is a critical component of women's mating strategies, we might expect there to be physiological adaptations that enhance women's ability to secure

multiple mates. Work in this area has focused on two aspects of women's reproductive physiology, the presence of concealed ovulation and changes in sexual receptivity and proceptivity across the menstrual cycle.

Human females do not conspicuously advertise their fertility, making it difficult even for women themselves to detect their ovulation. This may appear to be a maladaptive trait because it reduces the efficiency with which women can become pregnant. However, several theories propose benefits arising from concealed ovulation that might overwhelm these detection costs.^{11,91} One prominent theory, first proposed by Sarah Hrdy, is that concealed ovulation can be used to promote multiple mating by confusing paternity, which can either reduce the risk of infanticide³ or promote investment by multiple males.¹⁶ Multiple mating is further aided by the combination of concealed ovulation and continual sexual receptivity. If estrus is not obvious and women have the ability and desire to mate at all times, males may have more difficulty guarding their mates and female extra-pair copulations may become less costly. Continual receptivity may also allow women to maintain more than one mate, a benefit if females benefit from multiple mating for any of the reasons discussed.

Studies of receptivity and proceptivity across the menstrual cycle show that women desire different traits closer to ovulation. For example, college-aged women in the U.S. dress more provocatively around ovulation^{92,93} and prefer more masculine faces.⁹⁴ These preference changes are moderated by the quality of a woman's current partner. Women whose partners had high levels of fluctuating asymmetry or were otherwise less sexually desirable reported being more attracted to extra-pair men during their fertile periods, but women with desirable partners showed little variation across their cycle.^{95,96} These studies support the hypothesis that women have a dual-mating strategy, the combination of maintaining a long-term partner with whom they can

co-parent and interest in short-term partners from whom they can obtain superior genes for their offspring.^{83,97}

One limitation of the current studies is that subjects are drawn almost exclusively from U.S. student populations, probably because of historical precedents within evolutionary psychology and the methodological difficulties of conducting such studies in the field. However, it will be important in the future to expand this work to natural-fertility populations in which women cycle much less frequently and lactation and conception often overlap, potentially creating different hormone profiles than would occur in U.S. student populations.^{98,99} Another limitation of these studies is that they focus largely on extra-pair mating as a “good-genes” strategy that explains women’s short-term mating. However, multiple mating can occur for other reasons, such as mate switching. The effect of hormonal changes on mate switching remains largely unexplored.

THE FUTURE OF MULTIPLE MATING STUDIES

In the 30 years since Sarah Hrdy first published *The Woman Who Never Evolved*, great strides have been made toward defeating the stereotype of the “coy female.” Among humans and other species, definitive cases of serial and simultaneous polyandry, as well as their myriad benefits, have been highlighted. A growing body of theoretical work has challenged us to reorient our thinking about what should be the expected behavior of each sex. Yet, to a surprising degree, the tendency to equate female choice with chastity persists in the evolutionary literature and more attention is given to the differences between the sexes than to variations within them. The studies described here illustrate the variation in women’s mating strategies and provide insight about the contexts in which multiple mating may be beneficial.

An important next step in the study of multiple mating is to integrate the various pieces of the puzzle that have, until now, been studied

mainly in isolation. Premarital sex is common among the Ju/Huansi. Divorce and remarriage have reproductive benefits for Pimbwe women. The Himba regularly engage in extra-marital sex and bear offspring through affairs. Among the Bari, partible paternity beliefs allow women to accrue benefits from multiple “fathers.” While each of these findings is interesting in its own right, it will be critical in the future to understand the interplay among women’s strategies across the life span. Do women who engage in more premarital sex also have more affairs after they are married? At what time during a woman’s life is multiple mating most valuable?

...to a surprising degree, the tendency to equate female choice with chastity persists in the evolutionary literature and more attention is given to the differences between the sexes than to variations within them.

We should not expect universal answers to these questions. Rather, the socioecological context will be critical to understanding how multiple mating is actually enacted by women around the world. We have good evidence that demographic factors, such as the number of potential mates, affect the frequency of premarital reproduction and polyandrous mating. It is likely that life-history factors that affect women’s choice of marriage partners, such as age, parity, and intrinsic measures of quality, will also affect her likelihood of seeking and attracting multiple mates.

The costs and benefits of multiple mating are also linked to the larger social support networks women have. Where women have more access to and support from their kin,

multiple mating seems to occur more often, as with the uxori-local bias in partible paternity societies in South America and the association between female promiscuity and matrifocal family structures in several parts of the world. These links could occur because women have more options for mate switching because they can rely on kin for support during transitional times or because of some third causal factor, such as generally increased female autonomy, which is associated with more female support and higher divorce or adultery rates. Once again, a life-span perspective could help to move these studies forward. Women’s support networks change significantly as they age. Early on, many women rely heavily on their mothers and other kin, but as they move through their reproductive careers and often change residence, support can be shifted to children and affines. The shift from consanguineal to affinal support could have great effects on the prospects of multiple mating because affines should be less supportive of extra-marital affairs or divorce than a woman’s own kin would be.

This focus on local context should not completely prevent us from looking for certain variables that may be associated with multiple mating behavior across societies. For example, research on changes in women’s preferences for long-term versus short-term mates across the menstrual cycle has produced robust results, but almost all of these studies have been done with college students in developed countries. It will be important to determine whether the same patterns exist across cultures and age groups, particularly in natural fertility populations in which women spend much less time cycling because of more frequent pregnancy and lactation and often conceive under different hormonal conditions due to simultaneous ovulation and lactation.⁹⁸

A final challenge is to determine the mechanisms whereby multiple mating leads to increased reproductive success in women. A multi-method data collection strategy would be ideal for understanding the

interaction of physical, genetic, hormonal, and behavioral factors. This individual-level data will help to move us beyond simple correlations between multiple mating and reproductive success, such as those seen in the Pimbwe and the Himba, to more fully understanding the causes and consequences of variation in women's mating decisions.

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