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RESEARCH ARTICLE

Elucidating evolutionary principles with the traditional Mosuo: Adaptive benefits and origins of matriliny and "walking marriages"

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ABSTRACT

The Mosuo, arguably the last surviving matrilineal society in China, offers interesting insights into kinship practices that support reproduction. In particular, the modes of courtship and reproduction of the traditional Mosuo revolve around a practice known as walking marriages, which involves no contract or obligations, where the men do not use social status or resources to court women, women do not expect commitment from men, and multiple sexual relationships are permitted for both sexes and seldom incite conflict. Children borne from walking marriages are cared for not so much by fathers but rather their mothers' brothers, and wealth and property are controlled by women and passed on to daughters rather than to sons. By analyzing how familial and mating practices interact with evolved preferences and ecological affordances, we highlight the ways that traditional Mosuo practices facilitate reproductive success despite differing vastly from those familiar to modern, industrialized societies. We suggest that cases that appear like evolutionary exceptions, such as the traditional Mosuo, can bring into question the mating practices and preferences we take for granted as relatively universal and prompt a nuanced understanding of how environments, culture, and evolution mutually constrain and shape one another.

KEYWORDS

mating, kinship, family, culture, matriliny, Mosuo

There is a population of 40,000 people whose culture has long practiced a form of non-contractual marriage that permits having multiple sexual partners; women control the resources, which they hand down through daughters; women do not expect resources from their romantic partners; and people do not have certainty regarding who fathered their children. These interesting practices belong to a group called the traditional Mosuo (Fig. 1), whose mating practices seem puzzling at first glance and present an important challenge to normative assumptions about mating and reproduction.

In this paper, we examine several of these practices and demonstrate how, despite running contrary to views of courtship, marriage, and parenting that are normative to WEIRD (Western, educated, industrialized, rich, democratic) societies, the traditional Mosuo indeed conform to an evolutionary logic that underlies adaptive mating systems. In addition, we illustrate how these unique practices allow the traditional Mosuo to avoid a variety of problems inherent to pair-bonded relationships. By drawing insights from the traditional Mosuo, we contribute an important demonstration of the utility of unorthodox populations as a powerful means of validating evolutionary principles.

ULTIMATE REASONS FOR CULTURAL DIFFERENCES IN KINSHIP AND MARRIAGE SYSTEMS

The foundations of human kinship and marriage systems have been hotly debated (e.g., McKinnon, 2005; Salmon & Shackelford, 2007; Shapiro, 2008). Traditional explanations in the

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social sciences often adopt a socialization lens to explain the emergence and structure of mating rituals and arrangements. This approach stresses the influence of social roles and cultural transmission of norms and practices (Cavalli-Sforza & Feldman, 1981; Eagly, Wood, & Diekman, 2000), such as societal expectations of men and women during courtship (Braboy Jackson, Kleiner, Geist, & Cebulko, 2011; Lamont, 2014) and marriage traditions, customs, and rituals (Baxter & Braithwaite, 2002; Chowdhary, 2016).

While useful as an account of the proximate factors that influence society and people, sociocultural explanations are silent on why particular norms, practices, and rituals exist or how they come about (Buss & Kenrick, 1998; Kenrick & Li, 2000). By contrast, evolutionary perspectives understand human social and organizational systems in terms of adaptive function, or how they facilitate not only the survival but also the reproductive success of people living in them (Aberle, 1961; Daly & Wilson, 2000; Fortunato & Archetti, 2010; Tooby & Cosmides, 1992). More specifically, for an ecology to be sustained, its conditions must be reproductively viable for inhabitants. Hence, societal norms and practices will exist to the extent that they support the production of viable offspring.[1] Many cultures around the world share similar mating arrangements because such arrangements are generally conducive to the reproductive needs and strategies of individuals belonging to those cultures. For instance, because of asymmetries in the costs of mate choice for men and women (Symons, 1979; Trivers, 1972), courtship as a mate assessment and selection process tends to involve the male (and, in many cultures, his family) wooing the female (and her family) through displays and offers of resources (Buss, 1988). As male offspring are high risk yet high benefit from the perspective of parents, wealth is most effective when transmitted through male lineage especially under conditions of polygyny (Hartung, 1976), leading to a male-inheritance bias across many cultures. The evolutionary perspective therefore anticipates certain commonalities across cultures and serves as a useful framework to understand kinship and marriage systems.

[1]Societal norms and practices can also emerge as byproducts of initially adaptive cultural features or noise (for discussions on how adaptations, byproducts, or noise are classified, see Barclay & van Vugt, 2015; Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Saad, 2012) and persist insofar as they do not incur substantial reproductive costs on individuals. For instance, wedding ceremonies arose from the need to have witnesses because there was no marriage license or written record, and before the 17th century when honeymoons became customary, the new couple was expected in some cultures to consummate their marriage in public (Lacey, 1969). A purported original task of the groomsmen was to guard the groom against rivals who might seize the bride during the procession (Knowlson, 1910). While the original purposes of wedding ceremonies and groomsmen are no longer relevant in modern contexts, they continue to be practiced because they impose low costs on reproduction and are now iconic aspects of modern wedding customs. On the other hand, the norm of throwing large and lavish wedding dinners, which arose from the need for (typically) the groom's family to signal resource provisioning capabilities at the witness of the entire village, has led to marriages becoming unaffordable and people increasingly opting for simpler ceremonies involving only close family and friends (Burke, 2021). These examples demonstrate how expressions of norms and practices, whether as adaptations or otherwise, are ultimately "constrained in accordance with their effects on the human gene pool" (Wilson, 1978, p. 167).

Utility of "unusual" cultures for the validation of evolutionary principles

Although the evolutionary perspective predicts common features across cultures, it is not deterministic. Instead, it stresses that cultural variations are evoked from ecological differences (Tooby & Cosmides, 1992), reflecting facultative mechanisms that vary adaptively according to the affordances of the environment (Jonason & Schmitt, 2017; Sng, Neuberg, Varnum, & Kenrick, 2018). For example, an evolutionary perspective predicts that a culture would be polygynous to the extent that its females experience greater reproductive success by mating with already mated males rather than with unmated ones (Fitzpatrick & Servedio, 2018; Kaplan & Lancaster, 2003; von Rueden & Jaeggi, 2016). Such cultural variations are insightful as they shed light on human plasticity in the development of social structures that lead to reproduction (Kaplan, 1996). In addition, the existence of varied mating preferences and behaviors is consistent with sexual strategies theory (Buss & Schmitt, 1993), which posits that humans have evolved a complex repertoire of mating strategies to maximize reproductive outcomes across a diverse range of circumstances.

Support for evolutionary principles can also be bolstered by studying cultures with kinship and marriage systems that deviate dramatically from those typically expected from mainstream perspectives on mating (cf., Jonason, 2017). For example, in the case of the Australian Tiwi, young men often married much older women (Hart & Pillig, 1960)—a pattern of behavior that appears to contradict the evolutionary prediction that because fertility declines with age and status increases with age, pairings between older women and younger men should be rare compared to younger women and older men. However, upon closer scrutiny, it was found that traditional Tiwi men married widowed women to gain alliances with their male relatives, who would then betroth their daughters to them (Kenrick, Becker, Butner, Li, & Maner, 2003). Hence, traditional Tiwi men married older women not because of a reversal of evolved attraction preferences, but as a way to gain the younger wives they found most desirable. Such cases that look like evolutionary exceptions on the surface but are actually not upon closer inspection can serve as highly compelling evidence for evolutionary principles.

Unmasking evolutionary design with the matrilineal Mosuo

Matrilineal societies represent another example of a substantially distinct culture from which powerful insights can be gleaned. Matrilineal society, also called matriliny, refers to a socially ordered community that adheres to a kinship system in which ancestral descent is traced through maternal instead of paternal lines (the latter being termed patrilineage or patriliny). In the current paper, we focus on one particular matrilineal society—the traditional Mosuo—as an interesting case study of alternative reproductive arrangements and

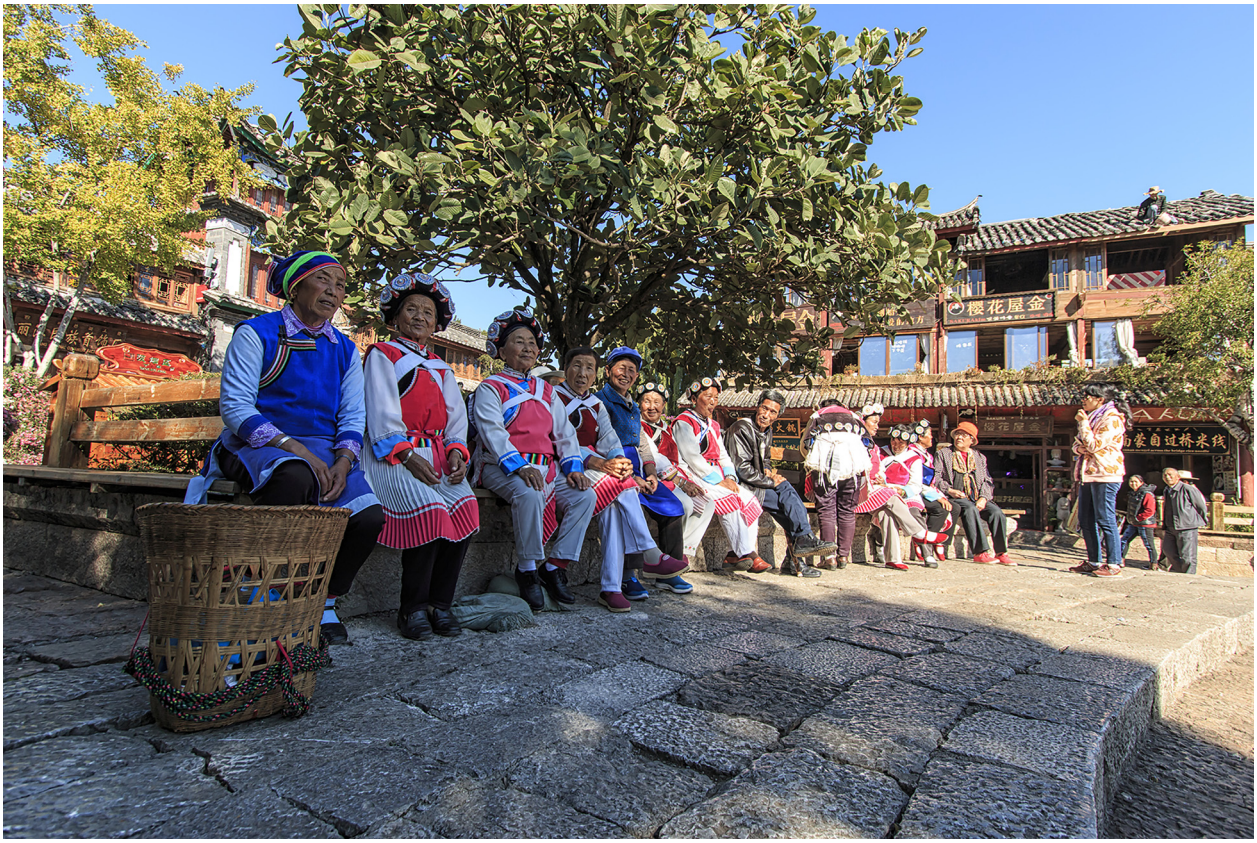

Fig. 1. The traditional Mosuo
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elucidate the evolutionary motives they facilitate. More specifically, we suggest that traditional Mosuo practices work because they enable the Mosuo to overcome adaptive problems typically faced by individuals in pair-bonded relationships that are, by WEIRD cultural standards, supposedly more conventional. Through an analysis of the mating and familial practices of the traditional Mosuo, we postulate several adaptive benefits of Mosuo mating and familial practices, consider the origins that may have set these adaptations in motion, and suggest areas for further research.

ETHNOGRAPHIC BACKGROUND OF THE TRADITIONAL MOSUO

Although rare, matrilineal societies can be found around the world, including Africa (e.g., the Akans), India (e.g., the Nair), and Australasia (e.g., the Vanatinai). The traditional Mosuo represent the last matrilineal society in China and are among the few left in the world that are still somewhat thriving. They consist of a population of roughly 40,000 minority Chinese living in the Himalayan Mountains on the border of Sichuan and Yunnan provinces. How long they have practiced their way of life is disputed, with experts believing the culture to be somewhere between a few hundred to over 2,000 years old (Dawson, 2018; Liu, 2004; Lu et al., 2012; Wen et al., 2004). While the Mosuo have both matrilineal and patrilineal subpopulations due to intermingling with other cultures and the influence of modernization, the current entry focuses specifically on the matrilineal Mosuo residing near Yongning and Lugu Lake, both of which are situated in Yunnan Province (see Figs 2 and 3).

Until recently, the majority of Mosuo were subsistence agriculturalists, growing crops such as buckwheat, corn, wheat, potatoes, and garden vegetables primarily for consumption while engaging in animal husbandry as a sideline.

Fig. 2. The Mosuo reside at the border of Sichuan and Yunnan provinces
Source: Adapted from Joshua Project/Global Mapping International (https://joshuaproject.net/people_groups/18610/CH).

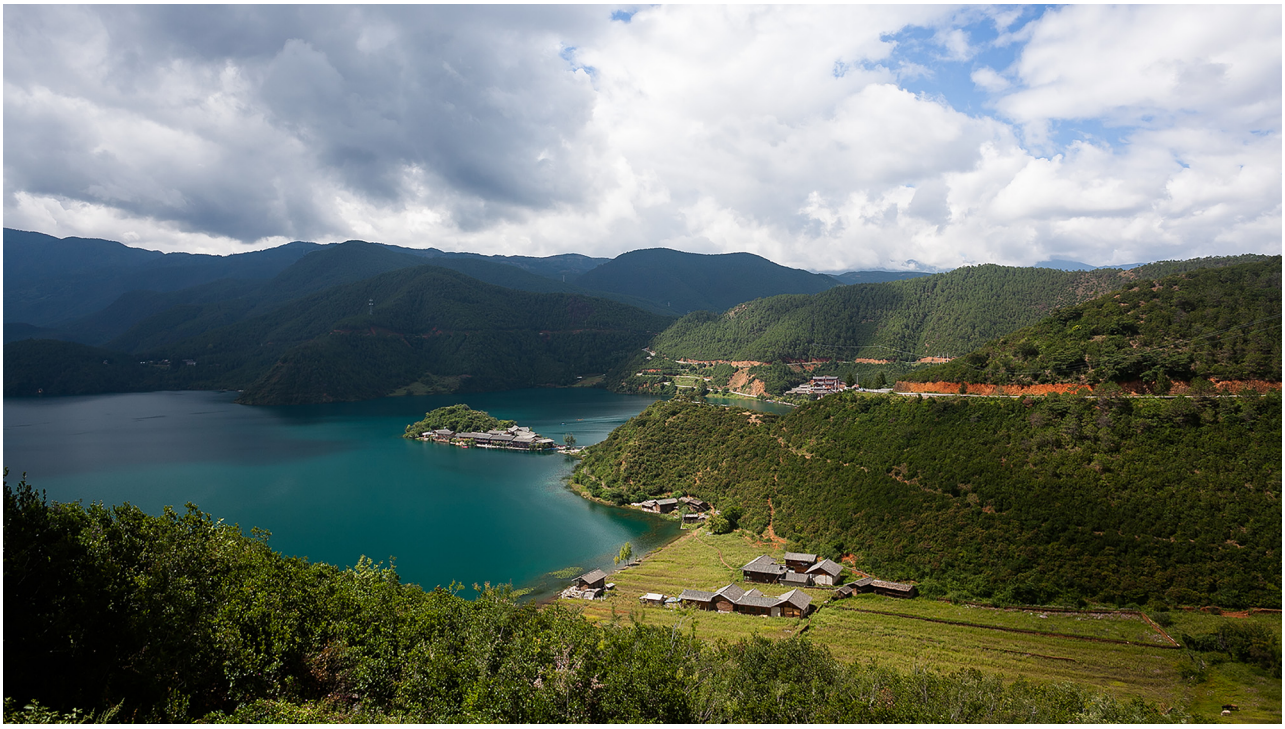

Fig. 3. Lugu Lake

Note: Located in the northwest of the Yunnan plateau at an elevation of 2,685 meters, Lugu Lake is the highest lake in Yunnan Province, with the middle of the lake forming the border between the Ninglang County of Yunnan Province and the Yanyuan County of Sichuan Province. The lake's shores are inhabited by several minority ethnic groups (e.g., the Mosuo, Norzu, Yi, Pumi, Tibetan), among which the Mosuo are most numerous.

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Starting in the 1980s and increasingly through the 1990s, some of the Mosuo inhabiting the areas near Lugu Lake have carved a living through profits from tourism (Mattison, 2011; Walsh, 2005). While family-owned hotels and tourist shops have led to significant income variation among households, families residing further from the lake maintain agriculture as their major mode of subsistence, and individuals in many of these families also have salaried employments ranging from wage laborers to television anchors (Mattison, 2011).

The traditional Mosuo generally live in multigenerational families within the same house. Children take their mother's family name, and family property and resources are controlled by female heads of households (a position held by the oldest woman in a family) and are passed on to their daughters and their daughters' children (Shih, 2010) (Fig. 4). Although Mosuo men do act as temporary co-stewards of resources, whatever rights they have to resources (nominal or real) will eventually be transferred to their sisters' children. Mosuo men are expected to prioritize and dedicate labor to their natal households rather than to their romantic partners' households (Cai, 2001). As we will discuss in more detail later, Mosuo men and women romantically consort in the woman's home, after which it is common for the men to return to their own residences to continue investing in their natal households, providing caregiving primarily to their sisters' children. As lineage affiliation among the traditional Mosuo is matrilineal, offspring come under their mother's lineage and typically reside with her throughout their lives. The most important inherited resource shared by a household until recently was land, but money and other durable goods have increasingly become more important, especially in areas where tourism is prevalent (Mattison, 2011).

While some scholars have asserted that traditional Mosuo culture has, despite socioeconomic, political, and modernizing pressures, "remained very much afloat and intact" (Renda & Kanenawa, 2021, p. 79), other reports highlight an increasing desire among Mosuo youths to leave their villages for cities, pursue modern careers, have monogamous relationships, and start nuclear families (An End to Matriarchy, 2017). Thus, it is important to stress at this juncture that our focus is on behaviors associated specifically with the traditional Mosuo, from which our analysis of matrilineal and other unconventional practices proceeds.

REPRODUCTIVE PRACTICES OF THE TRADITIONAL MOSUO

The traditional Mosuo practice a system of romantic pairing known as *tisese*, or "walking marriage" (Cai, 2001; Mattison, 2011; Shih, 2010). When females come of age (~13 years), they can start to take male lovers from within their

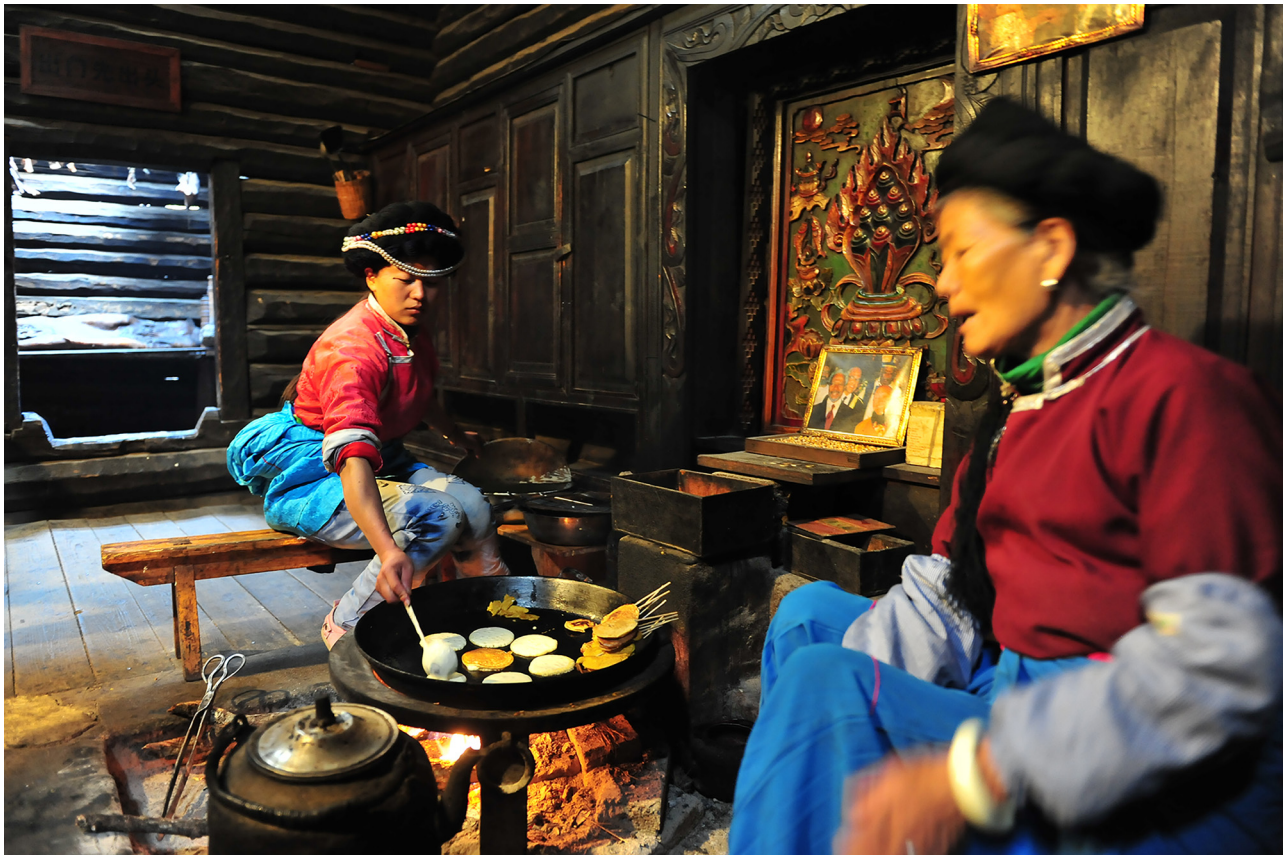

Fig. 4. The traditional Mosuo live in multigenerational families headed by the most senior woman.
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community, having as many or as few as they desire over their lifetime. Male companions spend their days helping in their own homes or carrying out jobs such as fishing, farming, or construction and visit the women's homes mostly at night, and often secretly at first (Shih, 2010). The only prerequisite to a relationship is a mutual agreement between the man and the woman to grant sexual access to one another, whether for one night or for an extended period of time. Thus, couples typically retain separate residences throughout the course of their unions.

According to ethnographers of the traditional Mosuo, walking marriages involve no formal contract between lovers (and thus even the term "marriage" is somewhat of a misnomer), economic cooperation to raise children is not expected from sexual unions, paternity is not only unassured but also generally unimportant, and multiple concurrent unions are possible[2] and rarely incite jealousy (Cai, 2001; Ember, Gonzalez, & McCloskey, 2021; Shih, 2010; Yan & Song, 1983). Moreover, men engaging in *tisese* have little obligation to participate in their partners' households. Although it is possible for cordial affinities to form between a visiting male and the female's family (Shih, 2010), men generally refrain from becoming too involved as they may be seen as interfering in their partners' households or neglecting their own family (Cai, 2001; Mattison, 2011). As such, where father figures are concerned, the children that result from walking marriages are raised less by their biological fathers and more by the brothers of the mother. One Mosuo man said, "I am closer to my nieces than to my daughter, because I must always consider their upbringing and their education," while also adding that the most important man in his childhood years was not his father but his maternal uncle (cited in Married to the Mob, 1995). As the provisioning of resources and nurturance of offspring are mainly provided by the mother's kin in alloparenting and cooperative breeding arrangements, investments from biological fathers are rendered non-essential. Nevertheless, Mosuo men may sometimes opt to care for putative children, with evidence showing that paternal investment can have a positive impact on child outcomes (Mattison, Scelza, & Blumenfield, 2014). As such investments are largely voluntary, there are neither circumstances where a child can be considered illegitimate nor stigma attached to not knowing who a child's father is (Shih, 2010).

[2]Because traditional Mosuo norms do not impose constraints on the number of romantic relationships that people can have, Mosuo individuals are free to change partners as often as they wish and may sometimes have more than one partner at a time (Zhu, 2012). Despite this possibility (which has led to misconceptions of their culture as promiscuous or polyamorous), Mosuo individuals tend toward serial monogamy, particularly when children are sired from a walking marriage in order to focus on caring for them (Yang & Mathieu, 2003).

CHALLENGES TO RELATIONSHIP ORTHODOXY

From an evolutionary perspective, adaptations are features and characteristics that exist to promote the reproductive success of organisms (Williams, 1966). Adaptations also include psychological traits such as mating preferences and strategies, which guide individuals toward acquiring mates who are most likely to bring them the highest chance of reproductive success (Buss & Barnes, 1986; Buss & Schmitt, 1993; Li et al., 2002). Parental investment theory (Trivers, 1972) posits that because reproduction necessarily hinges on women's valuable reproductive resources (e.g., limited eggs, heavy investment in offspring) which decline with age, men may have evolved to value cues to youth and fertility in their partners (Buss, 1989; Kenrick & Keefe, 1992; Symons, 1979). Just as importantly, biologically obligate processes of reproduction (e.g., pregnancy, childbirth, childrearing) are costly to women and render them highly vulnerable. Thus, in contrast to men, who are less biologically constrained and can directly increase their overall reproductive success by increasing the number of partners they inseminate (von Rueden & Jaeggi, 2016), women are the more heavily investing sex and have evolved to be more cautious and selective than men when considering potential mates. Correspondingly, women may have evolved a preference for partners who make committed husbands and good fathers—those who can offer sufficient resources and protection to their partners and offspring (Geary, 2000; Geher, Derieg, & Downey, 2004; Lu, Zhu, & Chang, 2015).

Many cultural practices reflect these evolved sex differences in mating dynamics and strategies. For example, courtship across a wide range of cultures tends to involve males wooing relatively younger females through displays of resources ranging from wedding rings to bride prices (Borgerhoff Mulder, 1988; Kenrick & Gomez-Jacinto, 2014). As resources and status have a stronger positive impact on male than on female reproductive success, many societies practice male rather than female inheritance (Kaplan & Lancaster, 2003). Mirroring the greater parental investment of women than men, data from hunter-gatherer and horticultural societies show higher levels of childrearing involvement from mothers (~43–98%) than from fathers (~9–22%) (Konner, 2005), while in modern societies, mothers are similarly more present and involved (~65–66%) than fathers (~33–44%) (Lamb, Pleck, Charnov, & Levine, 1987; Pleck, 1997). If a husband and wife have children and they separate, some countries have family laws that factor a disadvantage for women in the mating dynamic based on implicit assumptions that men are more likely to be parentally irresponsible or maritally unfaithful. In Singapore, for example, the women's charter gives women the benefit of the doubt and dictates that men should, by default, pay alimony after a divorce if dependent children are present (unless there are significant mitigating factors such as proof of the wife's infidelity).

Fatherhood is also the norm across many human societies as the support afforded by fathers in addition to mothers can increase the survival and reproductive viability of offspring (Geary, 2000). As such, women may have evolved to find men with fatherhood qualities, such as the ability to provide resources and protection and to nurture young, attractive (Buss & Barnes, 1986; Lu et al., 2015). The benefits of having both parents raise children also motivates the desire for long-term pair-bonding in humans. Reflecting these preferences and dynamics, monogamous heterosexual marriages are practiced across a sizeable number of modern cultures around the world (Fortunato & Archetti, 2010; Herlihy, 1995).

A mainstream view of families as comprising children raised by monogamously pair-bonded parents prevails, in large part because much of the Western and industrialized world practices such familial arrangements while driving the discourse that shapes popular notions of acceptable behavior (Blum, 2017; Henrich, Heine, & Norenzayan, 2010). This "mononormative" bias (cf., Emens, 2004) may, however, severely limit our understanding and appreciation of the diverse ways by which reproduction can be achieved. For instance, critiques of parental investment theory have highlighted a broader range of factors beyond parental investment (e.g., offspring needs, the quality and mortality rate of either sex, differences in pre-fertilization and post-fertilization investment) that lead to a variety of mating strategies, many of which deviate significantly from those expected by the theory (Jennions & Kokko, 2010; Kokko & Jennions, 2008; Kokko & Johnstone, 2002). In addition, "the assumption that monogamous marriage is the only relationship structure that provides desirable social and relational outcomes" has been shown to drive moral stigmatization against practices perceived as violating such expectations (e.g., consensual nonmonogamy), despite these practices carrying immense benefits for the people who engage in them (Mogilski et al., 2020, p. 2). Studies of cultures and practices that oppose such mainstream views are, thus, an important means of evaluating our assumptions and promise to be highly illuminating.

The mating approaches of the traditional Mosuo are indeed different and unique in several important ways. Paternal investment is not essential to the traditional Mosuo as the men are more likely to nurture and raise their sisters' children than their own. Mosuo women are indifferent to a potential mate's social status or resources, do not expect their romantic partners to commit to the relationship, and are open to having multiple sexual partners. Wealth and resources are held by the matriarch and handed down through daughters. By posing a significant challenge to mainstream beliefs about mating and family structure, the unconventional practices of the Mosuo present a valuable opportunity to think about human mating dynamics beyond those common to WEIRD cultures and expand our knowledge of how evolutionary pressures shape sex and reproduction.

TRADITIONAL MOSUO PRACTICES AS SOLUTIONS TO ADAPTIVE PROBLEMS

Upon closer examination, the behaviors of the traditional Mosuo, however unorthodox they may seem, are well

underscored by adaptive logic and thus provide strong support for evolutionary principles. By doing away with the need for paternal investment and keeping the lineage within the maternal side, Mosuo familial and relationship practices appear to overcome a range of adaptive problems that often arise in other mating arrangements. We consider several adaptive solutions afforded by traditional Mosuo practices:

Solution to women's problem of assessing the commitment and resource-provisioning quality of mates

Mainstream perspectives of mating suggest that women would face the adaptive challenge of assessing prospective partners' willingness to commit and ability to provide protection and resources, primarily because the survival prospects of a woman and her offspring hinge critically on a male partner's commitment and provisioning (Lu et al., 2015; Symons, 1979). In traditional Mosuo contexts, however, childbearing or childrearing women have their needs met through the resources, protection, and nurturance provided by their natal households (Cai, 2001; Shih, 2010). Such cooperative breeding arrangements may even be superior to having fathers provide for offspring, as suggested by a study of 45 societies which found that investments from alloparents, such as maternal grandmothers and siblings, more consistently improved offspring outcomes than investments from fathers did (Sear & Mace, 2008). With her and her childrens' welfare ensured by kin, a Mosuo woman will be guaranteed reliable help while avoiding the costs associated with partner desertion or the selection of an inept mate. Moreover, she can avert the hassle of having to determine whether potential mates are deceptive about their commitment or mate quality (Tooke & Camire, 1991). Consequently, Mosuo women are relatively freer to make relationship choices based on factors other than economic bonds (Walsh, 2005). As one Mosuo tourist host put it, "The criteria according to which we choose our partner is very simple: we don't take into consideration the possession of a house or a car, neither do we care about other material goods. We instead pay attention to our partner's character and personality. Therefore, our judgment parameters are different to those of the people from the city. People from big cities are looking for a partner to spend their lives with, while we are looking for a soul mate" (cited in Renda & Kanenawa, 2021, p. 73).

Solution to men's problem of demonstrating mate quality and intrasexual competition through wealth and status

Conversely, because Mosuo women can afford to be less stringent in mate selection compared to women from other cultures who must carefully assess the commitment and resource-provisioning ability of prospective partners, Mosuo men need not incur the costs associated with accumulating and displaying wealth and status to court mates (Buss, 1988). This has positive consequences not only for men but also for society more broadly.

In general, male intrasexual competition carries harms both to men and to the social environment wherein these men compete. Among males vying for female attention, the motive to compete produces a preoccupation with gaining resources, status, and power, which can translate into a variety of outcomes ranging from injuring or killing mating rivals (Wilson & Daly, 1985) to increased risk-taking (Ronay & von Hippel, 2010) or an acute obsession with work and income (Yong, Li, Jonason, & Tan, 2019), all of which put men's wellbeing at risk. At a societal level, the male desire to accrue resources in the name of intrasexual competition exacerbates status disparities between men who have resources (and are thus capable of accruing even more resources) and men who do not, leading to a host of problems associated with socioeconomic inequality (Wilkinson & Pickett, 2009). In particular, the inherently aggressive nature of male intrasexual competition has been argued to be an underlying cause of societal instability, such as gang violence (Wilson & Daly, 1985), homicide (Daly & Wilson, 1988), and even terrorism (Kanazawa, 2007). While studies have not directly examined whether Mosuo men are disinclined toward competition, there is some evidence suggesting that matrilineal men are indeed less competitive than matrilineal women and patriarchal men (Gneezy, Leonard, & List, 2009), and that Mosuo girls score higher than Mosuo boys in the closely related trait of risk-taking (though this sex difference became reversed after prolonged interaction with Han children; Liu & Zuo, 2019). Thus, traditional Mosuo practices may diminish men's need to compete for mates on the basis of wealth and status, in turn reducing men's exposure to harm while promoting societal stability.

Solutions to problems of having multiple mates

A problem faced by both men and women in monogamous cultures is the inability to pursue additional mates, as well as the negative consequences of doing so. From an evolutionary perspective, men stand to directly improve their reproductive success by increasing the number of females they can inseminate (Trivers, 1972). Therefore, men may have evolved a preference for sexual variety and to desire multiple partners in noncommittal sexual relationships (Li & Kenrick, 2006; Schmitt, 2005). In general, however, the orthodox female preference for relationship exclusivity and long-term commitment often constrains men's ability to enact a quantity- and variety-driven reproductive strategy (Buss & Schmitt, 1993; Symons, 1979). As relationship commitment is not expected in traditional Mosuo contexts, Mosuo men are free to seek additional mates and satisfy their desire for sexual quantity and variety without fear of repercussions (e.g., physical retaliation from the cheated partner's family or the legal consequences of infidelity) given that the preferences of the opposite sex are not violated.

At the same time, the irrelevance of commitment allows Mosuo women to avoid the problems that women of other cultures face from having multiple partners, such as the stigma of promiscuity and the sexual double standard that regulates women's sexuality in many other parts of the world (Fox,

1983). As females can enhance their reproductive success by engaging in multiple matings, such as through increased sperm competition (Firman & Simmons, 2008; Gerlach, McGlothlin, Parker, & Ketterson, 2012; Shackelford & Goetz, 2007), women under more permissive or conducive circumstances may also be interested in exploring sex with a wider range of partners. For instance, one study found that women increased their receptivity to casual sexual invitations when in a non-threatening environment (Baranowski & Hecht, 2015), which contrasts with previous research showing that women were completely closed to the idea when asked by strangers in a public setting (Clark & Hatfield, 1989). Research has also shown that individuals in the somewhat similar arrangement of consensual nonmonogamous relationships experience less jealousy than do individuals in monogamous relationships (Valentova, de Moraes, & Varella, 2020), and any potential jealousy that arises can even be transformed into sexual arousal toward the partner (Mogilski et al., 2020). More importantly, Mosuo women can avoid the well-documented threat of being seriously harmed by jealous partners, whose aggressive behaviors have been argued to be an adaptive response to prevent cuckoldry (Yong & Li, 2018). We elaborate on this problem next within the broader context of paternity uncertainty.

Solution to problems associated with paternity uncertainty

As human reproductive biology entails internal female fertilization, men face the problem of cuckoldry; that is, investing in children who are actually sired by other men—an adaptive problem not faced by women. The uncertainty over whether offspring are theirs produces an evolutionary incentive for men to prioritize mating over parenting (Geary, 2000). Given the acceptability for Mosuo women to mate freely, Mosuo men's confidence in paternity over children sired through walking marriages is reduced. However, because Mosuo men are not obligated to raise their own putative offspring, paternity is less of a concern (Cai, 2001). Indeed, although Mosuo men may sometimes choose to care for their own offspring (whom they cannot be certainly sure are theirs), they primarily channel caregiving to their sisters' children instead. As women are sure of their own progeny, the brothers of Mosuo women have a higher degree of confidence over the relatedness of the matrilateral nephews and nieces they help to raise (Gaulin, McBurney, & Brakeman-Wartell, 1997), thus reducing the possibility of investing in unrelated children.

Crucially, doing away with the need for relationship commitment allows both Mosuo men and women to avoid issues associated with potential as well as actual infidelity in conventional relationships. For instance, it is less likely that Mosuo individuals would devote serious effort to mate guarding, nor would they be as prone to romantic jealousy as would conventional couples who fear losing the interest of their partners (Yong & Li, 2018). Indeed, Mosuo individuals have been documented to experience lower levels of romantic jealousy compared to individuals from other cultures (Scelza et al., 2020; but see Renda & Kanenawa, 2021 for examples of occasional exceptions). Moreover, a recent paper that reconceptualized the adaptive basis of men's sexual jealousy also suggests that it is not only paternal certainty that jealousy functions to protect, but rather the loss of paternal opportunities (Edlund et al., 2019), which explains why men can feel jealous even when paternity certainty is not stake—such as when a romantically desired person whom they have no relationship with is in an exclusive sexual relationship with someone else. As such, contexts like the traditional Mosuo, where both sexes can mate freely and hence are less limited in their mating opportunities (Shih, 2010), may be ideal for eliminating jealousy. On the flipside, being subjected to intense mate guarding can be extremely harrowing. As men from cultures that practice fatherhood have a strong desire to avoid being cuckolded and raising unrelated children (Smuts, 1992), they have been documented to take extreme actions to deter or punish mates for sexual infidelity, leading to serious injuries or even death (Goetz, Shackelford, Romero, Kaighobadi, & Miner, 2008). These undesirable behaviors and outcomes are all effectively mitigated by the traditional Mosuo.

Matriliny as daughter-biased investment is also adaptive in optimizing resource allocation based on inclusive fitness (Hamilton, 1964; Holden, Sear, & Mace, 2003). Many societies transmit wealth and property to sons because of the higher reproductive potential of males (Kaplan & Lancaster, 2003). However, because Mosuo walking marriages generate uncertainty over paternity, transmitting wealth and property through males would inevitably lead to loss of resources to non-kin. Therefore, paternity uncertainty may have acted as a historical basis for early Mosuo parents to adopt matrilineal practices and bias investment of wealth and property toward daughters (rather than sons) so that resources will be channeled toward actual progeny (we expound further on this when discussing the origins of Mosuo practices in the next section).

Solution to the problem of sexual violence

The high levels of sexual permissiveness in Mosuo culture may also contribute to lowered sex-related violence. According to evolutionary theories of sexual conflict, sexual violence (e.g., rape) may occur when men—typically the more eager sex—force themselves onto unwilling women out of sexual frustration (Li & Yong, 2018). In contrast, Mosuo men (and women) may experience low levels of sexual frustration as their needs for sexual gratification appear fairly unhindered, and rape is reportedly unheard of among the Mosuo (Knoedel, 1997). According to Shih (2010), Mosuo folk have expressed pride in the lack of sexual crime in their community, and they believe "the absolute freedom of sex and ample opportunities" to be a major reason (p. 80).

Critiques of evolutionary accounts of sexual violence have nonetheless argued that sexual desire or frustration as a source of sexual aggression and rape proclivity has only

received equivocal support (e.g., Briere & Malamuth, 1983; Ward & Siegert, 2002), and point instead to attitudes like hostile sexism, prejudice against women, and dislike of women (particularly those seen as violating traditional gender norms; Glick & Fiske, 1996) as stronger predictors (Briere & Malamuth, 1983; Masser, Viki, & Power, 2006). However, as women are held in high esteem given the central role they play in traditional Mosuo culture (Shih, 2000), misogynistic attitudes through which sexual violence may occur are also likely nonexistent.

Solution to the problem of familial instability

In most formalized marriage contexts, people officially marry into families and this often involves the female moving into the male household (Jensen & Thornton, 2003; Perkin, 1989). This practice produces avenues for conflict due to genetic unrelatedness between the household and incoming individuals. For instance, given that the incoming female is non-kin, her in-laws may minimize cooperation with her or even exploit her. When a couple has children, the female may also be inclined to view herself and her children as a genetically related unit distinct from her partner's household, and then value the interests of her unit over those of the household. These misalignments in genetic self-interest can lead to familial instabilities, as evidenced by the numerous instances of infighting among the concubines of imperial families throughout recorded history (Soulliere, 1988). The traditional Mosuo avoid such rifts by not having contractual marriages and emphasizing commitment primarily to one's natal household (Cai, 2001), thereby minimizing the intrusion of non-kin with divergent genetic interests. Indeed, Mosuo individuals have expressed that they prefer to avoid the affinal complications wrought by marriage, with one woman saying: "Who wants a mother-in-law?" (cited in Dawson, 2018). Together, the absence of unrelated individuals in Mosuo households and high degree of relatedness through the maternal line facilitate familial solidarity and strong kin cooperation.

Solution to the problem of conflict over whom to invest in

People in conventional relationship and familial contexts sometimes face the dilemma of having to choose between their natal family or romantic partner (which may include in-laws) in situations of conflict. This dilemma is often difficult to resolve because both parties are usually important in conventional contexts—as the natal family is genetically related, helping them directly benefits inclusive fitness (Hamilton, 1964); at the same time, because the romantic partner is a reproductive mate and co-parent, helping them is directly beneficial for reproductive success and indirectly beneficial for inclusive fitness (Pillsworth & Haselton, 2005). This conflict may manifest, for example, as dilemmas like whom to give one's limited resources to or whom to save in a life-threatening situation. Failure to finesse this quandary can prompt anger and distrust from the shortchanged side (Sell, 2011). Among the traditional Mosuo, the norm of returning to and investing in the natal family makes clear that kin should be prioritized, thereby eliminating such conflicts and the need to make difficult choices that may undermine sensitive relationships.

Solution to problems of long-term relationship dissatisfaction and dissolution

Common to married life is the decline of relationship satisfaction over time due to factors like life transitions (e.g., birth of a child), life circumstances (e.g., financial strain), and negative interaction dynamics (e.g., conflict, hostility), which can lead to the breakdown of relationships (Berscheid, 2010). Another corrosive aspect of long-term relationships is boredom, or the loss of excitement associated with the early stages of a relationship (Tsapelas, Aron, & Orbuch, 2009). The negative experiences of dissatisfied couples and their children, including unhappiness, poorer wellbeing, and divorce, are well documented (e.g., Davila, 2001; Fishman & Meyers, 2000). As Mosuo romantic partners are not obligated to live together, not only are the problems associated with long-term coupling avoided, but high levels of relationship excitement and satisfaction are also more easily maintained.

Lending empirical support to this possibility, a neuroimaging study found that when Mosuo participants were asked to view a beloved's face, those who were engaged in *tisese* exhibited responses associated with greater arousal and increased approach motivation relative to those in conventional marriages, which the researchers contend is akin to viewing something novel and appetizing (Wu et al., 2016). Seeing each other sparingly may therefore help to keep their sexual unions fresh and trouble-free. One Mosuo woman, who had been in a walking marriage for 15 years, opined that such marriages are "quite good" and further added: "We do not live together so there is very little quarrelling between us" (cited in Married to the Mob, 1995). Even if disinterest ultimately sets in, relationship dissolution is fairly straightforward and bears minimal consequences. As Mosuo romantic partners do not build a family or home together, terminating a walking marriage does not result in problems with property ownership or custody of children, and children are still cared for by the mother's family (Gatusa, 2005).

In sum, traditional Mosuo practices appear to carry a wide range of adaptive benefits. Engagement in these practices also seems particularly good for women's wellbeing. A study on Mosuo participants found that females living in matrilineal areas enjoyed better health (e.g., lower levels of chronic inflammation and hypertension) when compared to females living in patrilineal areas, as well as when compared to males in general (no difference was found between matrilineal and patrilineal men), even after controlling for age and body mass index (Reynolds et al., 2020). The researchers attribute these gains in health to the greater autonomy, resource control, and social support made available to women by the features of traditional Mosuo culture. Considering the general finding that women tend to have

poorer health than men worldwide (Boerma, Hosseinpoor, Verdes, & Chatterji, 2016), the capacity for traditional Mosuo practices to reverse sex disparities in health outcomes (while also not compromising men's health) is quite remarkable.

POSSIBLE ORIGINS OF TRADITIONAL MOSUO MATING PREFERENCES AND PRACTICES

The current analysis has thus far described the unique practices of the traditional Mosuo and how they can be viewed as alternative ways to solve adaptive problems. A pertinent question, however, is how these different ways may have come about. More specifically, why did many other cultures structure their mating practices and kinship systems in line with those expected from mainstream perspectives on mating (e.g., long-term pair bonds, paternal investment, contractual marriages, courtship marked by male displays of resources to woo females, female demands for resources and relationship commitment, female preferences for monogamy), whereas the traditional Mosuo took such a different approach? Are their practices attributable to sociocultural forces that have overridden evolved preferences such that Mosuo individuals perceive gender roles differently, view fatherhood and formal marriage as irrelevant, and suppress jealousy (cf., Hupka, 1991), or did they evolve a different set of mating-related strategies? Moreover, what environmental conditions did the traditional Mosuo face that may have brought about their practices, whether through cultural forces, adaptive responses, or a combination thereof? The literature is unfortunately quite limited, so we cannot deduce definitive answers. Nonetheless, we review and analyze what is currently known and, in the next section, suggest what future research needs to be done to gain further insights.

Understanding the traditional Mosuo through its matrilineal origins

One means of contemplating the origins of traditional Mosuo practices is to analyze their features in relation to other matrilineal populations and observe what is common versus truly unique. First, we consider the features that are commonplace among matrilineal societies, which may serve as indicators of the factors that have driven or are conducive to their emergence. An extensive body of work by Aberle (1961) showed that matriliny correlates positively with low-intensity horticulture and negatively with intensification of agricultural production, such as plough agriculture, agriculture with complex irrigation works, and pastoralism. In turn, because intensive agriculture supports population growth and gives rise to social stratification, matriliny is also negatively correlated with expanding populations and socioeconomic inequality. Thus, matrilineal societies appear more likely to form and stabilize when population size is small, low-intensity horticulture is sufficient for subsistence, and socioeconomic inequality is low.

Correspondingly, low socioeconomic inequality diminishes the importance placed on social status which, being a key component of male mate value, has a direct impact on women's assessment of partners and on men's competitiveness (Brooks et al., 2011; Buss & Barnes, 1986). Patriliny is favored when aggressive agricultural production leads to "the development of heritable forms of wealth, such as domesticated animals and improved land", and these forms of wealth confer greater fitness returns on sons than on daughters due to increased inequality and male intrasexual competition (Holden et al., 2003, p. 110). Hence, insofar as inequality and competition could remain low, there would be no incentive to channel resources specifically to male offspring. In line with this view, a comparative study of participants from the Maasai, a patriarchal society in Tanzania, and the Khasi, a matrilineal society in India, found that when participants were given the option to compete in a ball tossing game to win more money, Khasi men opted to compete less than Khasi women and Maasai men did (Gneezy et al., 2009), indicating that matrilineal men may indeed not be particularly inclined toward competition.

Lastly, matrilineal kinship organization may have evolved due to high levels of paternity uncertainty (Fortunato, 2012; Hartung, 1985; Mattison, 2011) as well as the "expendability" of men (Mattison, Quinlan, & Hare, 2019). Because it is adaptive to invest resources in the sex that offers higher reproductive returns, matriliny could prevail if ecological factors cause resource transmission through daughters to become more advantageous (or less disadvantageous) than through sons (Holden et al., 2003). Several of these ecological factors have been identified in matrilineal cultures. High frequencies of divorce where offspring consequently live with the mother have been noted in African matrilineal tribes, such as the Lozi of Northern Rhodesia, the Zulu of Natal (Gluckman, 1950), and the Luapula of Zambia (Poewe, 1978). Regular male absence has also been observed in matrilineal tribes elsewhere, including the Taino in Puerto Rico (Keegan & Maclachlan, 1989) and numerous fishing villages in the Solomon Islands (BenYishay, Grosjean, & Vecci, 2017). Illustrating the impact of protracted male absences, Divale (1974) suggested that marital bonds would become weaker and family life increasingly matrifocal as women increasingly rely on themselves and one another than on male partners. In turn, men would return home to find wives replaced by sisters who, like their wives, have returned to the more secure surroundings offered by their natal households. Eventually, as men depend ever more so on sisters and less on wives to take care of their domestic interests, and as women become increasingly capable of meeting their subsistence and childrearing needs without assistance from men (Mattison et al., 2019), "the situation is resolved in an arrangement whereby women never leave home in the first place, and men divide their time between their natal and conjugal households" (Keegan & Maclachlan, 1989, p. 619). Taken together, the literature suggests the emergence of matriliny when factors underlying low paternity (e.g., prolonged male absences, weak marital bonds) interact with low-intensity production (e.g., low-intensity

agriculture, slow population growth) and low competitive inclination (e.g., low socioeconomic inequality).

The traditional Mosuo share a variety of these features with other matrilineal societies. Apart from facing some hostile pressure by the Chinese government to conform and assimilate into mainstream society in the 1970s (Shih, 2010), the Mosuo have historically had little impetus to accelerate production in response to extrinsic factors such as threats from neighboring tribes or desire for territorial expansion. Their low-intensity agricultural lifestyle has generally satisfied their subsistence needs, and socioeconomic inequality was low only until recently when the tourism sector grew (consistent with the data on shifts to and from matriliny, the profits and economic growth from tourism has led to modernization, loss of matriliny, and greater prevalence of formal marriages for households near the lake; Mattison, 2011; Shih, 2010). A clear reason for husband-wife bonds to be weak and resource transmission to be disadvantageous through sons is the unique practice of walking marriages, which significantly lowers confidence in paternity and reduces the likelihood that wealth and property will be retained through the male line. However, it is unclear whether matriliny led to the practice of walking marriages or vice versa. When viewed against a backdrop of other matrilineal societies, walking marriages are a clearly special custom that has also engendered several other unique traditional Mosuo features which go against mainstream expectations of mating behavior, such as the openness of Mosuo women to multiple sexual partners, the redundancy of paternal investment, and the absence of mate guarding and sexual jealousy. How did this truly unique practice come about?

Origins of walking marriages

Records indicate that the forebears of the present Mosuo descended from the ancient Qiang, a people from the Tibetan plateau that migrated southwards to Minjiang river (currently Sichuan province) and branched into several ethnic groups between the 1st and 8th century AD. Evidence from DNA-sequencing studies suggests that a shift to matriliny (possibly triggered by the emergence of walking marriages) occurred at some point during this period of the Mosuo's development, as the other descended ethnic groups continued practicing patriliny (Lu et al., 2012). However, there is no precise indication as to when walking marriages may have emerged. The little information that exists indicates that the Mosuo have been matrilineal for as long as they have been historically documented (Shih, 2010), and the prevailing view among the Mosuo is that "they and their ancestors have been practicing *tisese* since time immemorial" (Shih, 2000, p. 704).

We can ponder the preconditions for walking marriages by comparing their functional differences with formal marriages, which they appear in contrast with and—if ecological conditions permit—are potentially an improvement from. Marriage is a legal institution that lends the involved parties explicit claims and binds them with understood obligations (Fox, 1983; Shih, 2000). In many cultures, formal marriage functions to bind a romantic couple to one another (and sometimes to children) in light of the risk that partners may renege on their relationship obligations, such as when an irresponsible husband and father shirks his role as a provider and diverts his resources away from the family. Many traditional cultures treat women as property in the marriage contract to grant husbands control over sexual resources and prevent cuckoldry (Geary, Winegard, & Winegard, 2014; Perkin, 1989). For the unique non-contractual, non-obligatory, and non-exclusive practice of walking marriages to exist, romantic partners must lack the risks that formal marriages function to deal with. Perhaps the early Mosuo, like other matrilineal societies, found it unnecessary or unprofitable to depend on romantic partners for resources, either because agricultural yields for subsistence were already sufficient, families were close-knit and cooperative (Thomas et al., 2018), or men's activities made them unable to commit and thus expendable. Indeed, some scholars have speculated that matriliny in the Mosuo arose because men were absent for long periods due to frequent mercantile travels (Liu, 2004). Or perhaps it was realized that the attachment of a mother to her children would be strong enough that no contract would be needed to ensure that offspring are cared for. Shih (2000) wrote that Mosuo matrilineal ideology holds mothers, females, and the bond between matrilineal kin in such high regard that they are treated with spiritual reverence. Such attitudes may also serve as important prerequisites to walking marriages.

Although at best speculative, our comparative approach provides a way to think about how matriliny and the unique preferences and practices of the traditional Mosuo may have originated. Importantly, because these practices facilitate reproductive success, they can persist. Highly optimized kinship norms and arrangements enable mating behaviors to be coordinated such that constituent individuals can pursue their survival and reproductive goals without violating the interests of other group members. For instance, the evolved female preference for resources to raise offspring and the evolved male eagerness for sexual quantity and variety (which may also be an evolved female preference, only that it is hindered in other cultural contexts) are very much facilitated by traditional Mosuo practices. In fact, walking marriages coupled with strong matrilineal family relations appear to be a remarkably optimal way to simultaneously satisfy these needs, which are often at odds and thus an unavoidable source of conflict between the sexes in other marriage arrangements (Li & Yong, 2018). In addition, although the redundancy of fatherhood in Mosuo culture seems to contradict the purported adaptive benefits of paternal investment (Geary, 2000), a comprehensive review of 45 societies found that care provided by fathers improved offspring outcomes in only about a third of those societies (Sear & Mace, 2008). Moreover, males that can successfully enact a mating-only strategy, such as polygynous men or the alpha males of many animal species (Yong & Li, 2016), also show that paternal investment is not necessarily the best route to increasing reproductive gains and enhancing fitness. At the same time, Mosuo fathers are still free to care for their

own children if they wish (Mattison et al., 2014), so long as their involvement is not overly intrusive in the mother's household.

Flexibility of adaptive mechanisms

Mosuo practices also reveal the flexibility of adaptive behavior. For example, it is often expected that women prefer the commitment of a single partner and correspondingly have little desire for multiple partners (Buss & Schmitt, 1993). In contrast, Mosuo women have been documented to have multiple partners over the lifetime and do not expect commitment (Yan & Song, 1983)—behaviors that are enabled because they do not require resources from committed partners and are safe to pursue mates primarily for sexual relations. Such facultative adjustments show that our evolved preferences (e.g., the female desire for sexual variety) may be contingent on environmental affordances and elucidate interesting possibilities (e.g., the redundancy of paternal investment) that conventional kinship arrangements obscure. A culturally distinct example that illustrates this point is the highly unique incidence of wife sharing in polygynous systems (Hughes, 1982; Muller, 1980). While the reproductive efficiency of polygyny is well documented, one downside to polygynous arrangements is the high risk of cuckoldry. To cope with this problem, a polygynous man may sometimes share his wives with male relatives as a form of wife-guarding and to increase the relatedness of his wives' offspring to himself, thereby leading to the formation of polyandrous trios in the harem (Hughes, 1982). The emergence of such unique practices ultimately reflects how evolved traits, environmental conditions, and group-wide patterns mutually constrain and influence one another to allow individuals, Mosuo or otherwise, to maximize reproductive fitness within the affordances of their kinship and mating systems (Kenrick, Li, & Butner, 2003).

In sum, while we cannot conclusively determine which specific ecological conditions (e.g., low-intensity agriculture, low socioeconomic inequality, low competition, male expendability, low paternity certainty) came first, the unique practices and preferences of the traditional Mosuo reflect adjustment to those conditions in ways that ultimately facilitate survival and reproductive success. As such, no matter how unorthodox the Mosuo may be, they still fundamentally adhere to deep evolutionary logic.

DISCUSSION

The traditional Mosuo present an illuminating case study of kinship and mating arrangements that go against mainstream (i.e., WEIRD) expectations of mating behavior (e.g., Buss & Schmitt, 1993). Beneath the surface peculiarities, however, the Mosuo practices of matriliny and walking marriages indeed conform to evolutionary principles. In particular, a significant number of adaptive outcomes are achieved, including offspring care and investment, sexual gratification, low levels of sexual conflict, and improved wellbeing. Hence, studies of atypical cultures like the Mosuo can bring into question the practices and preferences that we take for granted as relatively universal (e.g., formal marriages, fatherhood) while revealing avenues for further inquiry into our evolved mating behaviors, strategies, and systems.

Implications and future research

Our analysis highlights how evolution, culture, and ecological factors may interact to produce unique cultural practices and social organizational structures (Sng et al., 2018). On the one hand, there may be a variety of expressions of mating and kinship practices, but those that do not well serve reproductive fitness will not last. On the other hand, and consistent with sexual strategies theory (Buss & Schmitt, 1993), humans evolved a multitude of traits and preferences that adjust or express differently according to local conditions. The Mosuo and other such cultures with atypical mating systems suggest that some basic practices and preferences assumed to have evolved in one way may actually be flexible or facultatively responsive to the environment (Jonason & Schmitt, 2017; Tooby & Cosmides, 1992).

With that said, many of the behaviors exhibited by Mosuo individuals run counter to evolved tendencies for which a lot of theory and evidence exists, such as mate guarding and jealousy (Buss, Larsen, Westen, & Semmelroth, 1992; Yong & Li, 2018), female desire for male commitment and investment, and male desire for sexual fidelity (Buss & Barnes, 1986; Buss & Schmitt, 1993; Geher et al., 2004; Lu et al., 2015; Schmitt, 2005). As evidenced by the failure of free-love communes (Shey, 1977) and the joint raising of children in Kibbutz communities (Shepher, 1983), there are limits to how flexible our preferences and behaviors can be. In addition, although our analysis supports an "evoked culture" view of facultative mechanisms responding to different environmental situations, we cannot rule out the possibility that unorthodox cultures like the traditional Mosuo reflect new strategies that evolved in a relatively short amount of time in response to environments differing from those found in most other locales, or that their unique cultural practices are the result of social meme selection and transmission (Cavalli-Sforza & Feldman, 1981). Hence, we suggest that further investigations, particularly those involving DNA studies that can establish the genetic uniqueness of populations as well as the recentness of particular adaptive features (Marciniak & Perry, 2017; Mathieson, 2020; Mulindwa et al., 2020), are needed to ascertain how these preferences evolved and the specific conditions in which they will be expressed.

The unique mate selection criteria and familial arrangements of the traditional Mosuo also inspire novel predictions and investigations. For instance, given that Mosuo men need not attract women using status and resources, Mosuo women may select men based on other traits such as physical attractiveness (Gangestad & Simpson, 2000). Correspondingly, we may predict high levels of physical attractiveness in Mosuo men due to the selection pressure exerted by women on this trait. A key question that future research can aim to address is what Mosuo women's

mate preferences are, which will afford insights into the mate preferences of women from cultures where resources are controlled and transmitted through female lineage. In a similar vein, studies have not looked into whether intrasexual competition among Mosuo men exists, and how it might look like if it does. For instance, do the well-documented effects of operational sex ratios (Kokko & Jennions, 2008) also apply to Mosuo men (and women), leading to oft-expected variabilities in competitiveness and selectiveness between the sexes? Studying these phenomena with under-explored populations like the traditional Mosuo will help to validate and extend current theories on mating preferences and strategies.

Another interesting line of inquiry concerns the impact of variable fatherhood in traditional Mosuo culture. Given that multiple studies have raised important implications of father absence for child development and sociosexual outcomes later in life (e.g., Gangestad & Simpson, 1990; Kanazawa, 2020), it is pertinent to consider how Mosuo children might be affected by fathers being non-essential. Initial work in this area has shown that Mosuo paternal investment (e.g., direct care, financial support) can indeed improve the educational and reproductive outcomes of putative children (Mattison et al., 2014), which is noteworthy considering the relatively low impact that fatherhood has on offspring outcomes across societies (Sear & Mace, 2008) and suggests that Mosuo practices can bring the best out of fathers. However, questions remain over what makes some Mosuo men want to care for offspring more than others do. For instance, do paternity cues (e.g., facial resemblance, co-residence with spouse), which have been documented to influence rates of paternal investment (Apicella & Marlowe, 2004) as well as violence toward offspring (Alexandre et al., 2011), similarly affect Mosuo men's involvement with their children? Are there biased preferences for daughters or sons? It is also worthwhile to explore whether the significant paternal role played by maternal uncles in matrilineal cultures like the Mosuo is comparable to that of actual fathers in other cultural contexts, which will allow us to probe further the role of fatherhood in offspring development, sociosexuality, and wellbeing across the lifespan.

More empirical research is also needed to validate the numerous adaptive benefits we proposed and uncover how such unorthodox practices facilitate adaptive outcomes. For instance, as different Mosuo subpopulations may vary in their combinations of features (e.g., those further inland may be fully traditional whereas others practice a hybrid of matriliny and monogamous marriages), studies that compare between these different subpopulations on mating-related dimensions such as sociosexuality, mating preferences, and jealousy will likely prove useful in assessing how traditional Mosuo practices help to fine-tune reproductive behaviors and strategies. In addition, few if any systematic studies exist on the psychological experience of Mosuo individuals engaging in walking marriages. For example, do Mosuo individuals anticipate romantic unions similarly or differently to individuals engaging in mainstream forms of courtship? When one party loses interest in the relationship, how does the other party react? What constitutes mate preferences amongst the Mosuo? Do Mosuo men and women have similar or divergent preferences? This endeavor will not only enlarge our perspective on the possibilities for human kinship arrangements—including their various pros and cons—but also contribute more broadly to our understanding of mating psychology and behavior.

It is sometimes assumed that matricentric social organizations shift the balance of power in favor of females and thus offer more benefits to females than to males (cf., Eller, 2000; Wu et al., 2016). The current analysis, however, highlights how males might benefit from matrilineal arrangements that reduce the need for intense intrasexual competition. These insights also correspond with other findings that lower levels of societal patriarchy and greater social empowerment of women correlate with reduced competition and mortality risk for men (Kruger, Fisher, & Wright, 2014). Consequently, the reduced need for men to be competitive or aggressive in mate acquisition appears beneficial for everyone as women also get to enjoy being free of harassment from sexually frustrated or jealous men. Moreover, the reverence paid to females in Mosuo culture ensures that violence against women arising from misogyny is unlikely. Taken together, these findings shed light on how conventional or modern familial and relationship structures may be modified to benefit both sexes while drawing attention to the need for more research on the trade-offs inherent to alternative mating structures.

We primarily highlighted the ways by which matriliny (in general) and traditional Mosuo practices (more specifically) are instrumental to reproductive success. However, we would be remiss not to consider their potential drawbacks. For instance, conflict between communally breeding sisters can arise as reproductive success decreases with an increasing number of co-residing female kin (Ji et al., 2013). In addition, given that matrilineal societies are a minority in the world, there clearly are limits to the benefits afforded by their social organization (Douglas, 1969). Although traditional matrilinies such as the Mosuo may be self-sufficient and comfortable in the absence of external threats, their relatively lower levels of productivity and competitiveness may put them at a disadvantage (e.g., lack of technological prowess, small population size) when confronted by other formidable groups with aggressive or expansionist inclinations (cf., Gneezy et al., 2009). The fact that matriliny numbers are dwindling also suggests that their practices can be easily eroded by modernizing factors, thus indicating that the utopian promise of matrilinies, while idyllic, may be less robust to a rapidly changing and technologically advancing world (Shenk, Begley, Nolin, & Swiatek, 2019). Relatedly, a longitudinal study of school populations comprising children of the matrilineal Mosuo (the minority) and the patriarchal Han (the majority) found that although the two groups had distinct risk attitudes initially (Mosuo girls were less risk averse than Mosuo boys, whereas Han children followed the more typical sex difference of girls being more risk averse than boys), long-term intermingling resulted in Mosuo children's attitudes becoming more like those of Han

children (Liu & Zuo, 2019). This finding indicates that traits like risk preferences and potentially other attitudes can be shaped by exposure to other cultures, especially when those cultures exert majority influence. Therefore, a fuller treatment of the traditional Mosuo should assess their vulnerabilities alongside their strengths.

Conclusion

The current paper demonstrates the utility of the traditional Mosuo as an important case study of alternative mating behaviors and invites an appreciation of reproductive arrangements beyond those typically adopted by WEIRD cultures. Such examples also show that even if a culture appears unusually different on the surface, deep-seated adaptive logic continues to underlie their functioning, hence serving as compelling support for evolutionary principles. Our analysis brings to light many of the costs that may be incurred in conventional marriages and expands our understanding of the adaptive functionality of alternative kinship structures.

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