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| 16 | Abstract | Matriliny has long been debated by anthropologists positing either its primitive or its puzzling nature. More recently, evolutionary anthropologists have attempted to recast matriliny as an adaptive solution to modern social and ecological environments, tying together much of what was known to be associated with matriliny. This paper briefly reviews the major anthropological currents in studies of matriliny and discusses the contribution of evolutionary anthropology to this body of literature. It discusses the utility of an evolutionary framework in the context of the first independent test of Holden et al.'s 2003 model of matriliny as daughter-biased investment. It finds that historical daughter-biased transmission of land among the Mosuo is consistent with the model, whereas current income transmission is not. In both cases, resources had equivalent impacts on male and female reproduction, which should be associated with daughter-biased resource transmission given any non-zero level of paternity uncertainty. However, whereas land was transmitted traditionally to daughters, income today is invested in both sexes. Possible reasons for this discrepancy are discussed. | |
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# Evolutionary Contributions to Solving the "Matrilineal Puzzle"

## A Test of Holden, Sear, and Mace's Model

**Siobhán M. Mattison**



**Abstract** Matriliny has long been debated by anthropologists positing either its primitive or its puzzling nature. More recently, evolutionary anthropologists have attempted to recast matriliny as an adaptive solution to modern social and ecological environments, tying together much of what was known to be associated with matriliny. This paper briefly reviews the major anthropological currents in studies of matriliny and discusses the contribution of evolutionary anthropology to this body of literature. It discusses the utility of an evolutionary framework in the context of the first independent test of Holden et al.'s 2003 model of matriliny as daughter-biased investment. It finds that historical daughter-biased transmission of land among the Mosuo is consistent with the model, whereas current income transmission is not. In both cases, resources had equivalent impacts on male and female reproduction, which should be associated with daughter-biased resource transmission given any non-zero level of paternity uncertainty. However, whereas land was transmitted traditionally to daughters, income today is invested in both sexes. Possible reasons for this discrepancy are discussed.

**Keywords** Mosuo · Evolution · Kinship · Matriliny · Sex-biased parental investment · Intergenerational transmission of wealth

In matrilineal kinship systems, descent and inheritance are directed toward kin related through females. Postmarital residence is variable but is often with the bride's mother (uxorilocal), the groom's mother's brother (avunculocal), or, somewhat less commonly, involves separate residences for the bride and groom (nata- or duolocal; Driver and Schuessler 1967; Gough 1961a; Murdock 1949). Furthermore, because certain forms of altruism are directed toward and received from kin related through females in matrilineal kinship systems, the role of the father and other affinal

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relations is often diminished relative to their roles in patrilineal or bilateral societies; instead, the mother's brother often assumes the highest status in the family.

The special position of the mother's brother has been the subject of much puzzlement and debate in anthropology: its occurrence in patrilineal societies has been said to defy normative unilineal principles (e.g., see Bloch and Sperber 2002 for a review) and its emphasis in matrilineal societies to undermine the principle of a male's authority over his offspring (e.g., Richards 1950; Schneider 1961; Schneider and Gough 1961). Explanations for this have been sought on a variety of theoretical grounds, from unilineal evolutionist (e.g., Bachofen 1967; Morgan 1964) to functional (e.g., Malinowski 1930; Radcliffe-Brown 1924), to structural-functional (e.g., Fox 1983; Murdock1949; Richards 1950; Schneider and Gough 1961), to evolutionary (e.g., Alexander 1974, 1977; Flinn 1981; Hartung 1976, 1981, 1985; Holden and Mace 2003; Holden et al. 2003). This paper briefly reviews the rationale underlying various statements of what has become known as the "matrilineal puzzle" (Richards 1950) and the attempts to "solve" it. In line with the purpose of this special issue, it focuses on the contributions of quantitative evolutionary anthropologists by way of testing a recent model explaining the evolution of matriliny as daughter-biased investment (Holden et al. 2003) among the matrilineal Mosuo of Southwest China. As the first independent test of this model, this paper verifies the model's main predictions in a new setting, while highlighting some nuances in its application in contemporary contexts, thereby adding to the empirical foundations of our understanding of matrilineal kinship.

## The "Matrilineal Puzzle": Inception and Conception

The study of matriliny has a long history in anthropology and yet one that may be largely unfamiliar to students of evolutionary anthropology (Knight 2008). With the publication of *Das Mutterrecht* (Mother Right) in 1861, Bachofen (1967) was the first anthropologist to theorize about the nature of matrilineal kinship (Divale 1974). In 1877, Lewis Henry Morgan (1964), struck by similarities in classificatory kinship terminology among matrilineal Native American tribes, pioneered (along with E. B. Tylor, and followed by McLennan, Engels, and others) the school of "evolutionism," which described kinship systems as evolving in a unilineal fashion whereby matriliny, which was thought to be associated with group marriage, was seen as a primitive stage of evolution experienced by all societies on their route toward civilized monogamy. In so doing, Morgan helped to establish social anthropology as its own discipline (Knight 2008) and incited generations of subsequent debate about the primacy of matrilineal kinship and the universality of human kinship elements and structure.

The arguments of early evolutionists undoubtedly impacted the framing of the matrilineal puzzle as it was conceived in the mid-twentieth century. According to the unilineal evolutionists, when kinship elements of a given society mirrored those expected in matrilineal societies, for example, they were deemed "survivals"—vestiges of previous matriliny and evidence of unilineal evolution. Analogously, the relative rarity of matrilineal kinship, which was found in only 17% of a worldwide sample of societies (Murdock and White 1969), has been used as evidence of its

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impending doom (see Douglas 1969) and contributed to the notion that matriliny is inconsistent with modernization (Gough 1961b). Moreover, the presumed universality of stages in human kinship gave way to the search for elementary kinship structures (e.g., Lévi-Strauss 1969) and universal kinship principles (e.g., Radcliffe-Brown 1924). Both of these notions—the modern incongruence of matriliny and the search for kinship universals—shaped the initial framing of the matrilineal puzzle, arguably hindering our ability to understand systematically the adaptive features of matriliny until modern evolutionary anthropology provided a theory embracing the variation inherent in human kinship systems.

Though matriliny had already been central to the study of anthropology for more than half a century, the first modern systematic attempts to understand its functions were made by functionalists such as Malinowski (1932) and structural-functionalists pursuing cross-cultural study, beginning with Murdock (1949) and culminating with the publication of Schneider and Gough's (1961) edited volume, *Matrilineal Kinship,* before the study of kinship fell out of favor among anthropologists during the latter part of the twentieth century. These attempts were associated with what has been dubbed the "matrilineal puzzle": "the difficulty of combining recognition of descent through the woman with the rule of exogamous marriage" (Richards 1950:246). Put differently, matrilineal kinship, by vesting authority in men and tracing descent through women, splits a man's allegiance between his own natal kin, with whom he is reared, and those of his wife and children, whom he desires to control (e.g., Schneider 1961).

Lacking any particular unifying theory about the nature of matriliny, the structural-functionalists embarked on numerous comparative studies to yield insights into the associations between matriliny and other social and ecological variables. Though rare, matriliny (or its corollary, matrilocal residence) was consistently found in association with horticulture (Aberle 1961; Keesing 1975) or where agricultural yields were low (Douglas 1969); in the presence of warfare, especially external warfare (Divale 1974; Ember and Ember 1971; Jones 2011; see also Ember 1974); and when men were otherwise absent (Keegan and Maclachlan 1989). Matriliny was rarely found in association with plow agriculture or with significant animal husbandry or pastoralism (Aberle 1961) and was thought to erode under conditions of economic prosperity (e.g., Goody 1962; Gough 1961b; Murdock 1949). Finally, matriliny was associated with high frequencies of divorce (e.g., Gluckman 1950; Poewe 1978) and low levels of paternity certainty (Aberle 1961; Murdock 1949).

In tying together these associations, mid-twentieth-century anthropologists problematized matriliny. In its original conception, the matrilineal puzzle emphasized the difficulty inherent to male members of matrilineal systems. Men were expected to cope with matriliny only under conditions of poverty or low productivity or when their absence owing to warfare or other reasons prevented them from governing their households. If conditions changed such that men acquired more resources or otherwise improved their lots, they would desire to regain authority over their wife and children and would push the kinship system away from matriliny. The emphasis on men and universal male authority overlooked to some extent women's contributions to kinship governance (cf. Murdock's 1949 argument that the sexual division of labor was responsible for kinship arrangements), however, and assumptions of universal male authority absent theoretical justification made

understanding the benefits of matriliny elusive. The rarity of matriliny and high frequencies of divorce were cited as evidence of the problematic nature of matriliny against a background in which nuclear families were held to be the universal building blocks of kinship systems.

## The Adaptive Value of Matriliny

Modern evolutionary anthropologists picked up the question of matriliny more or less where the structural-functionalists left off, adding to what was known in at least three important ways: (1) by tying together existing particulate associations under a common theoretical framework; (2) in formalizing predictions based on theory through quantification; and (3) by asking whether matriliny could be understood as an adaptation, rather than as a tenuous, problematic solution, to certain socio-ecological circumstances. In attempting to understand matriliny as an adaptation, evolutionary anthropologists invoked the theory of natural selection, predicting that matriliny would evolve under circumstances where it benefitted individual reproductive success (i.e., genetic representation in future generations). Rather than assuming a universal desire by males to control their reproductive partners and biological children, evolutionary anthropologists asked when it would benefit men to invest in their matrilateral nieces and nephews.

Paternity certainty formed the basis of initial attempts by evolutionary anthropologists to explain the adaptive functions of matriliny. Kin selection theory (Hamilton 1964; Maynard Smith 1964) predicts that, for a given net benefit, costly investment in others will be proportionate to their level of genetic relatedness, *r*. Under conditions of certain paternity, a man's maternal nieces and nephews are only half as closely related to him ($r=0.25$) as are his own offspring ($r=0.50$). Whereas a mother's parentage is virtually certain, a father is rarely entirely sure of his paternity. Thus, if paternity certainty were low enough, it could be in a man's best interest to invest in matrilateral nieces and nephews, to whom his relatedness is assured, rather than to raise offspring to whom he might be unrelated (Alexander 1974, 1977; Anderson 2006; Flinn 1981; Gaulin and Schlegel 1980; Greene 1978; Kurland 1979; Lancaster and Kaplan 2000; Trivers 1972).

Though several empirical studies indicate that paternity confidence is associated with the level of paternal investment (e.g., Anderson 2006; Anderson et al. 2006; Gaulin and Schlegel 1980; Huber and Breedlove 2007; Flinn 1981; Lancaster and Kaplan 2000; Marlowe 1999),[1] the level of paternity certainty necessary to produce conditions under which men are likely to be more related to their matrilateral nieces and nephews is probably unrealistically low (Flinn 1981; Holden et al. 2003), ranging from a probability of paternity (*P*—the level of certainty under which a man is more related to his sister's children than to his own putative offspring) of 0.268 (Greene 1978) to 0.33 (Alexander 1974, 1977:320; Kurland 1979) in the short-term,

[1] Paternity confidence refers to a man's assessment of the likelihood that he is the genetic father of a given child. The studies referred to here may include other people's assessments of likely parentage rather than the putative father's per se. Paternity certainty as used in this paper refers to the actual probability of paternity, which may differ from paternity confidence (e.g., Anderson 2006).

to 0.46 if the compounding geometric effects of paternity on relatedness over several generations are included (Hartung 1985). These levels are well below certainty rates of 0.9 cited by most researchers (usually cited in terms of uncertainty at 10%; e.g., Alfred 2002; Cervino and Hill 2000; Stewart 1989; all cited in Anderson 2006), and the observed certainty levels both in "high paternity confidence" societies (0.981) and "low paternity confidence" societies (0.702; all figures from Anderson 2006).

Given that unrealistically low levels of paternity certainty are necessary to favor men who choose to invest in their nieces and nephews over their own putative children, paternity certainty cannot fully explain the evolution of matriliny. Recently, evolutionary anthropologists have modified hypotheses concerned solely with paternity certainty to incorporate another variable known to be associated with matriliny and to affect investment in daughters versus sons: wealth (Holden et al. 2003). The matriliny-as-daughter-biased-investment hypothesis (MDBI) recognizes and incorporates the variable effects of wealth on men's and women's reproductive success. Following the logic of the Trivers-Willard hypothesis, the model recognizes that it should benefit parents to invest wealth in the sex whose reproduction stands to gain most from such investments (e.g., Cronk 1989; Hartung 1976, 1982; Holden et al. 2003; Mace 1996; Trivers and Willard 1973). Many forms of heritable wealth are thought to impact male reproductive success more than female: both livestock and productive land are usually more beneficial to males than to females, for example, owing to their greater impacts on males' ability to acquire partners (Holden et al. 2003). Thus, there are reasonable premises for incorporating wealth into a model that attempts to explain the evolution of matriliny.

It is worth noting here that the MDBI hypothesis, while adequately incorporating the effects of wealth on the reproductive success of women versus men, is perhaps misnamed and/or not applicable in its narrowest form (described below) to all matrilineal societies. Importantly, whereas in a number of matrilineal societies, parents together confer inheritance on their offspring, in others, inheritance is transferred from mother's brother to sister's son or, as in the Mosuo case, collectively from one generation of matrilineally related relatives to the next. Acknowledging variation in transmission pathways, Holden et al. speculate that daughter-biased investment of resources is still key:

> In other matrilineal societies, property is transferred from the mother's brother to his sister's son (Schneider and Gough 1961). For grandparents, this is equivalent to inheritance by their daughters' offspring. This type of inheritance allows sons to use inherited resources during their lifetime, while ensuring that those resources are ultimately transferred to the daughters' children (Holden et al. 2003:102).

A simple diagram clarifies the mistake in this reasoning (Fig. 1): In societies where men's property is controlled separately from women's property, there is no direct transmission of men's property to their daughters, nor to their daughters' offspring. Either men inherit from their maternal uncles (panel a) or one generation of matrilineal relatives inherits collectively from another (panel b). Indeed, the only case in which matrilineal transmission can be considered daughter-biased or granddaughter-biased is in societies that practice pooling of parental resources (panel c).

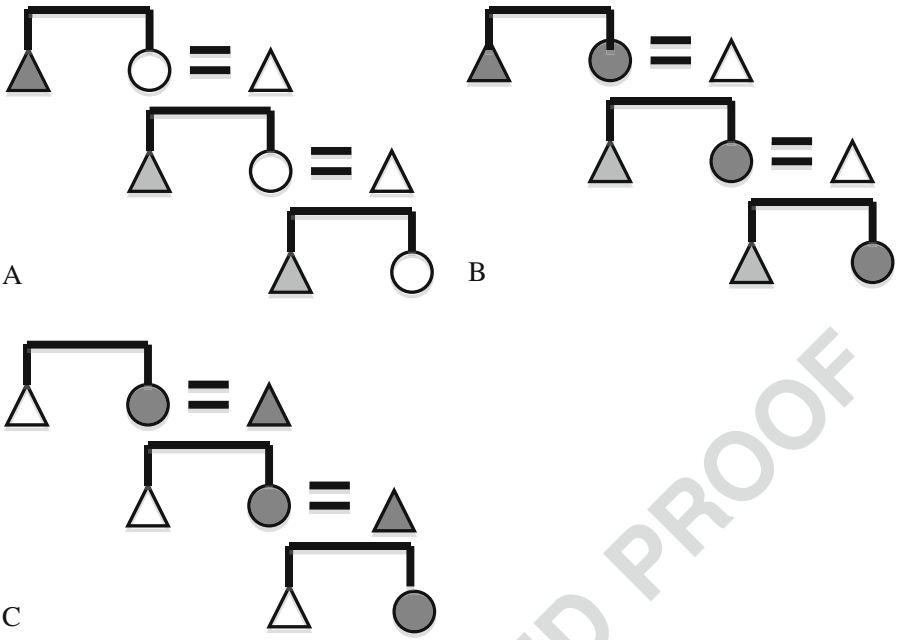




**Fig. 1** Diagrammatic representations of the flow of resources according to the type of matrilineal transmission. In A (upper left), mother's brother transmits to sister's son such that, while women are never stewards of property, their daughters nonetheless effectively stand to inherit the resources from her matrilineal household. Men in A do not practice daughter-biased investment because their resources are transferred to sisters' children, not their own. Panel B (upper right) corresponds to transmission of resources as traditionally occurs among the Mosuo. The situation is similar to A, except that women are also stewards over property and men temporarily are able to use property even though their sisters' children inherit over the long-term. Panel C (lower left) shows the only type of inheritance structure that corresponds in name to daughter-biased or granddaughter-biased inheritance. In this case, a child's biological father must also confer property to his own children, rather than to those of his sisters. NB: Triangles represent males; circles, females; equal signs, marriages or reproductive unions; and overarching bars, sibships. Shading indicates who transmits property in each generation

How, then, do we reconcile the model's main predictions and empirical correspondence to at least one matrilineal society with variance in the rules of inheritance that seem to undermine the process by which the model operates? The key lies in the relative impacts of the resources on male and female reproduction. If resources have equal or lower impacts on male reproduction relative to female, the nominal transmission mechanisms are moot because the household's resources primarily support reproduction by (resident) daughters. Among the Mosuo, for example, though men nominally are partial stewards of economic resources, and are said to play a role in decisions related to financial expenditures (e.g., Weng 1993), they are rarely in complete control of household resources. This point is critical because it means that men in such situations effectively do not use a household's resources to promote their own reproductive interests. If substantial household resources support men's reproduction, and men devote these to their sisters' offspring, then Holden et al.'s model cannot account for transmission dynamics because the model is based on parental decision-making (i.e., the certainty parents have over sons' offspring). If men are effectively without property, on the other

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hand, then the question of who inherits is still a question of daughters or sons—only, as theorized by Hartung (1985) and formalized by Holden et al. (2003), one faced by mothers but not by fathers.

## The Model

The MDBI hypothesis examines the effects of the probability of paternity (*P*) and the inheritance of wealth on the benefits to parents of investing wealth in daughters versus sons.[2] It begins with the straightforward premise that parents should invest wealth equally in daughters and sons when the inclusive fitness benefits of doing so are equal, or when BS = BD (where BS is the benefit of wealth to sons' reproductive success and BD to daughters'). Because paternity in sons' offspring is not assured, the benefit of investing in sons must be devalued by P: PBS = BD. Rearranging, the model predicts that the benefits of investing in sons and daughters are equal when

$$\mathrm{BS}/\mathrm{BD} = 1/\mathrm{P}.$$

This relationship is depicted in Fig. 2: when BS/BD > 1/P, it is more beneficial to invest in sons; when this benefit ratio falls below 1/P, it is more beneficial to invest in daughters.

Though simple, this model potentially explains many of the features associated with matriliny once used to support the premise that matrilineal inheritance was somehow "puzzling" or a "cumbersome dinosaur" (Douglas 1969:123) doomed for extinction. In particular, the model's fundamental prediction is that matriliny evolves when the increased impact of resources on men's reproduction does not outweigh the risk of non-paternity in sons' offspring. Regardless of whether inheritance is transmitted primarily from women to their daughters (with men as temporary stewards) or from parents in matrilocal marriages to their daughters, the prediction is the same and thus the model is applicable to the forms of matrilineal wealth transmission considered in this paper and by Holden et al. The inclusion of paternity certainty explains links between matriliny and high rates of divorce and protracted absences, including warfare, while the term reflecting differential impacts of wealth on men's and women's reproduction explains links to resource scarcity and horticulture. Moreover, in contrast to the viewpoints of unilineal evolutionists (and currently favored by certain former Soviet countries and China; e.g., see Divale 1974; Pusey 2009), this hypothesis predicts transitions from other forms of kinship to matrilineal if conditions change to make daughter-biased investment beneficial to parents. Quantitative model specification makes sense of variation in the factors associated with matrilineal kinship, contributing to our understanding of matriliny without appealing to unfounded and unexplained universals in human kinship. I turn

[2] I retain Holden et al.'s explanation here, but throughout the paper, when I say "parents," "mothers" would be more appropriate to the Mosuo context, as explained above. Note that in their test of MDBI, Holden et al. compare the matrilineal Chewa to the patrilineal Gabbra. According to Holden et al., among the Chewa, 75% of land is inherited directly from mother to daughter. Moreover, marriage among the Chewa was historically uxorilocal (Phiri 2009). Thus, the Chewa correspond to panel C of Fig. 1, satisfying the conditions of Holden et al.'s transmission process.

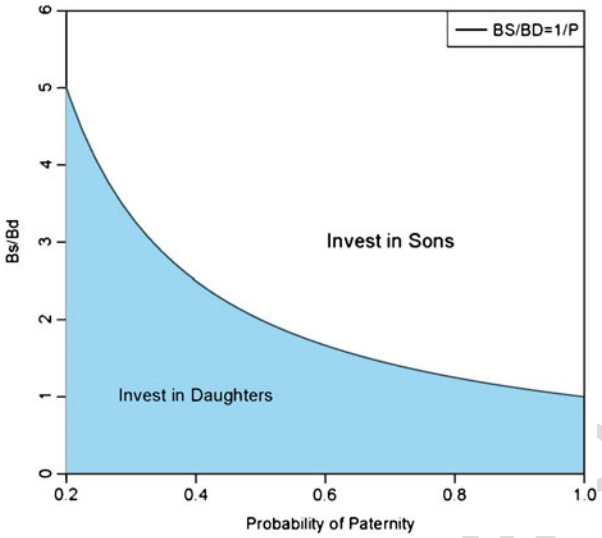


**Fig. 2** The MDBI model depicting the direction of sex-biased investment. The *y*-axis depicts the ratio of the benefit of investing wealth in sons versus the benefit of investing the same wealth in daughters (BS/BD). The *x*-axis is the probability of paternity (*P*) in sons' offspring. The line (BS/BD=1/*P*) represents the values of the benefit ratio and the probability of paternity for which equal investment in sons and daughters is predicted. Above this line, parents are expected to invest in sons because the benefit of wealth to sons outweighs the risk of non-paternity in their offspring. Below the line, parents are expected to invest in daughters. (Modified from Holden et al. 2003)

now to testing this model to evaluate whether it can explain matrilineal inheritance among the Mosuo of Southwest China.

## Study Population

The Mosuo are a population of approximately 40,000 minority Chinese living on the border of Sichuan and Yunnan provinces in the Himalayan Mountains (Walsh 2005). The Mosuo may be subdivided into two distinct subpopulations according to kinship practices: patrilineal and matrilineal (see Shih 1993). Discussion in this paper will focus on the matrilineal Mosuo residing near Yongning, their cultural center and township seat, and Lugu Lake, the center of tourism, both in Yunnan Province (Fig. 3).

The majority of Mosuo until recently were subsistence agriculturalists, raising such crops as buckwheat, corn, wheat, potatoes, and garden vegetables for their own subsistence, and engaging in animal husbandry of livestock, including cattle,[3] as a significant sideline (Cai 2001; Shih 1993, 2010). Beginning in the 1980s and increasingly since the mid-1990s, a subset of the Mosuo residing primarily along Lugu Lake have earned their living from profits driven by a thriving tourism industry (Mattison 2010a, 2010b; Walsh 2001, 2005). These profits are distributed to some

[3] Cattle are rare among matrilineal societies. Though the Mosuo keep cattle, they do so in insignificant numbers, such that one head of cattle is often shared among multiple households. Moreover, cattle apparently are not used as bridewealth payments or for consumption, but as draft animals.

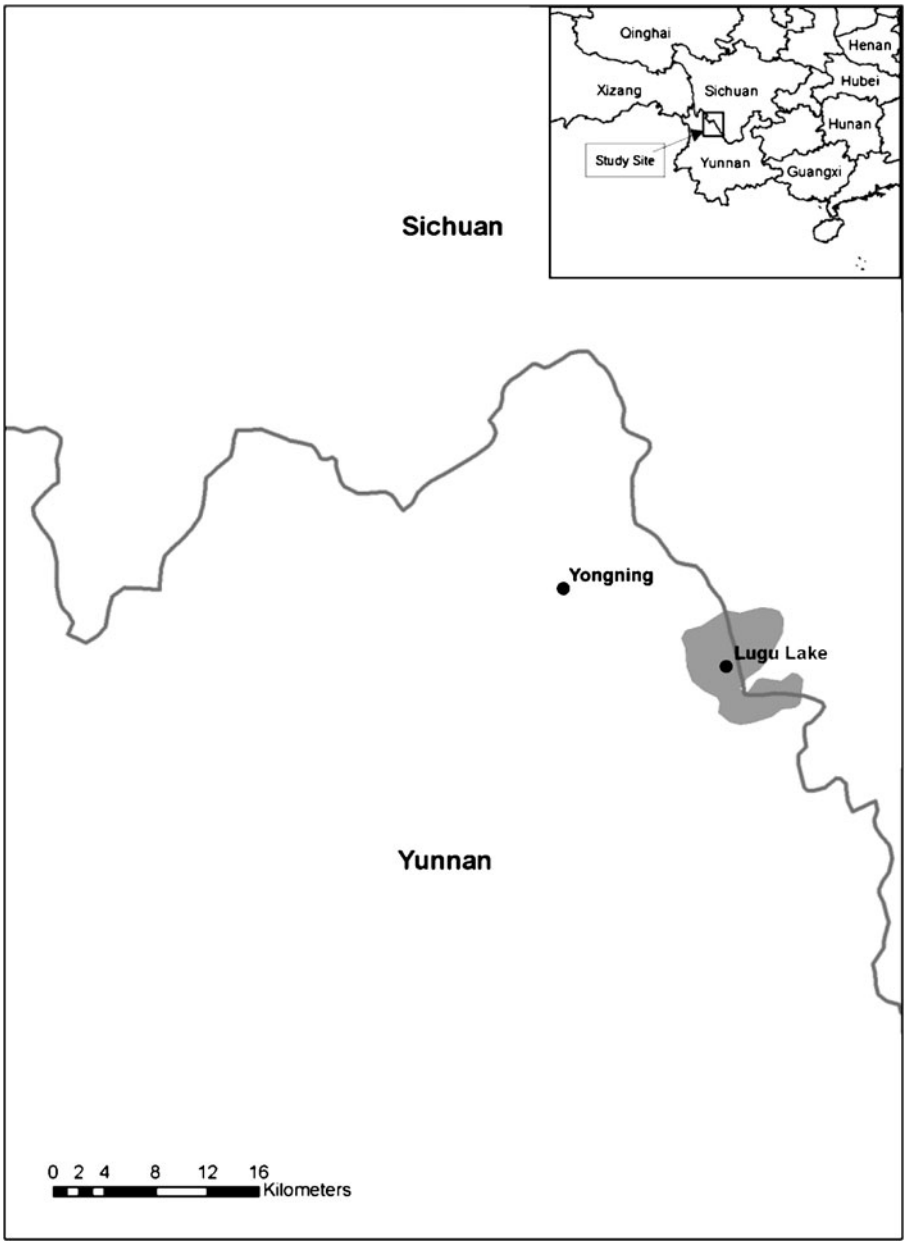


**Fig. 3** Map of study site. The matrilineal Mosuo reside along the border of Sichuan and Yunnan provinces in southwestern China (from Mattison 2010a)

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extent communally, with each family sending one representative to assist in community-based tourism ventures such as public dance displays and boating excursions to destinations inside the lake (e.g., Xing et al. 2009). Family-owned hotels and shops have nonetheless resulted in substantial income variation among households (Mattison

2010a), and incomes are such that most individuals in areas where tourism is prevalent live entirely off of associated profits (Mattison 2006). Most families residing in areas away from the lake have retained agricultural traditions as the major source of subsistence, though individuals in many of these families have salaried occupations ranging from wage laborers engaged in physical activities to television anchors.

Among traditional Mosuo, women effectively transmit property to their daughters and their daughters' offspring while Mosuo men act as temporary co-stewards of property, which is transmitted to their sisters' offspring (Fig. 1b). All offspring of matrilineally related women in a household have usufruct access to household property, but only offspring of female descendants stand to pass property to subsequent generations. Labor is supposedly dedicated to a man's natal household rather than to his partner's household, but historical participation in caravans would have led to prolonged absences and, correspondingly, low male contributions to any household labor. Whatever rights men have to property, nominal or real, are transferred to their sisters' children. Lineage affiliation among the Mosuo is also matrilineal: children of both sexes belong to their mother's lineage and normally 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 now become more important, especially in areas where tourism is prevalent.

Men's authoritative roles among the Mosuo were traditionally relegated to their natal lineages (Cai 2001; Shih 1993, 2000, 2010). Practicing a system of pairing known as "walking marriage" (*sese*), most men traditionally visited their lovers at night, retaining separate residences throughout the duration of their unions. According to ethnographers of the Mosuo (Cai 2001; Shih 1993, 2000, 2010), walking marriages involve no contract between lovers, paternity is not assured and is unimportant, and multiple concurrent unions are possible and do not incite jealously. Men engaging in sese are thus expected to refrain from active participation in their partners' lineages under most circumstances, as this may cause tension between a woman's affinal and consanguineal relatives. Anecdotal field evidence and reports from ethnographers of the Mosuo (e.g., Cai 2001; Shih 2010) indirectly support the nominal nature of men's historical participation in decision-making: when men were in control of resources (e.g., they were paid individual incomes), they were likely to expend them as individuals (e.g., as gifts to lovers) rather than through normative communal mechanisms.

The relationship between various forms of wealth and childbearing has not been examined systematically among the Mosuo. Given that land historically was the most important source of subsistence until recently, it is reasonable to expect that it might be associated positively with fertility among postreproductive individuals whose reproduction took place prior to major economic changes. Moreover, although land was a valuable asset to the Mosuo, it has not been particularly scarce in matrilineal areas (Shih 1993, 2010). Land is also not particularly productive, requiring intensive manual labor to work. The plow is used for agriculture, but most other activities are carried out by hand. Thus I anticipate that land will have roughly similar effects on male and female reproduction among postreproductive individuals: where land is neither scarce nor highly productive, men cannot easily translate it into higher marginal reproductive success (Holden et al. 2003).

With recent infrastructural and economic changes, land arguably has ceased to be the most important asset to families reproducing in contemporary contexts.

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Increasingly, parents value education for their children and seek reproductive partners with similar values. Indeed, many young people have abandoned an agricultural lifestyle in pursuit of steady employment, whether as tourism entrepreneurs or as salaried professionals (Mattison 2010a, 2010b). As subsistence and reproduction become increasingly tied to income, the opportunities for each gender to translate resources into reproduction may change. Given that income is fungible and easily defensible, it could result in higher reproductive returns for men relative to women, particularly if men are able to attract more sese partners in connection with higher incomes. Recent evidence (Mattison 2010a, 2010b) points to more marriage than indicated in previous reports, particularly among the wealthy. Given recent tendencies toward monogamy, paternity certainty likely is higher for men reproducing in contemporary contexts compared with postreproductive men. At the same time, the benefits of wealth to sons' and daughters' reproduction may be relatively equal in the context of monogamy, favoring daughter-biased investment if paternity is not assured. Whereas land historically was transmitted to female heirs, ethnographic evidence suggests that income is inherited by both male and female heirs (Mattison2010a, b). In this paper, I examine whether wealth transmission—land among postreproductive Mosuo and income among currently reproductive Mosuo—conforms to predictions based on the MDBI hypothesis.

## Methods

### Data Collection

The data analyzed in this paper were collected from January through October of 2008 (for a description of the complete methods, see Mattison 2010b). Household demographic surveys were conducted in 12 villages in the geographic area between Yongning and Luoshui villages, consisting of 177 unique households. Villages were chosen in order to obtain an accurate representation of current lifestyles, from normatively conservative to progressive and from subsistence-based to income-based. All households claiming Mosuo ethnicity were chosen for several villages; in other cases, households were chosen based on convenience sampling (i.e., an adult member of the household was home during the first attempted contact).

For each demographic survey, an adult member of the household (and often several other interested members of the household) acted as respondent and provided information on the household's and each household member's characteristics. In particular, household monthly income and information on land, property, and assets were provided. Each respondent also provided information on household members (including all members who were born in the household, regardless of their current residence) including their roles in the household (i.e., their relation to the household head); their individual incomes, if any; and their approximate age, sex, level of education, occupation, marital status, and number of living children. Household residents who were present during the time of the survey were weighed and their heights measured; these data were not consistently available and are not included in these analyses. All surveys were administered orally to respondents by a member of the research

staff in Mandarin Chinese or the local Sichuan dialect, when possible, and otherwise translated into Naru, the Mosuo language, by a local assistant.

## Data Analysis

This paper examines whether MDBI predictions hold for two different forms of wealth in two age-based cohorts of adults: a cohort of postreproductive individuals whose fertility decisions were made under putatively "traditional" circumstances and a cohort of currently reproductive individuals whose fertility decisions have been impacted by fertility policies and whose subsistence has been altered by a recent transition to a market economy. Among postreproductive individuals, a threshold of 58 years old (i.e., birth during or prior to 1950) was used to examine MDBI. This age cutoff aims to limit exploration of MDBI to only those Mosuo whose fertility decisions were relatively unconstrained by the various historical events that have been shown to affect fertility and wealth. Among these events were the incorporation of the Mosuo into the Chinese communist system, which began in 1950, when the People's Government of Ninglang County was established in Yongning (Shih 1993, 2010); the Great Leap Forward, which impacted fertility through famine and its effects on marital practices (Shih and Jenike 2002); and the various birth planning policies that were implemented in China beginning in the early 1970s. The precise moment at which such policies actually began to affect fertility decisions in rural China is highly variable (e.g., Harrell et al. 2011; Lavely and Freedman 1990; Skinner et al. 2000); thus, examination of actual fertility data among the Mosuo may be insightful. Figure 4 shows the distribution of number of living children reported



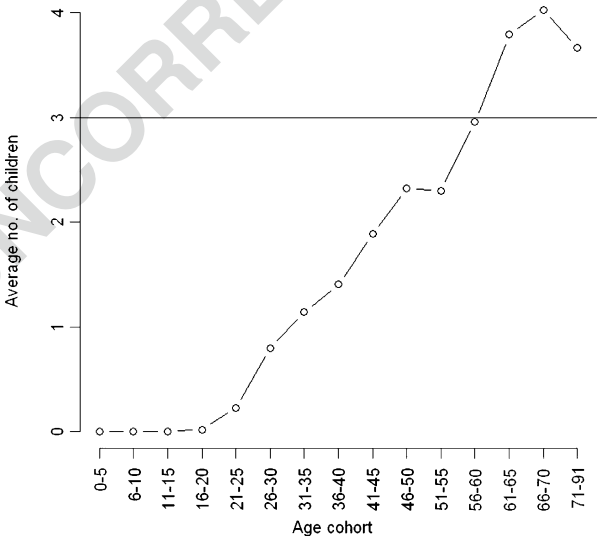


**Fig. 4** Average number of live children reported by Mosuo individuals in each age cohort. The horizontal line at an average of 3 children shows a point of transition between relatively low completed fertility (for those aged 45 and over) of fewer than 3 children and a relatively high completed fertility of more than 3 children. The cutoff age of 58 was chosen as the midpoint of the transitional cohort in order to determine fertility behavior of individuals in the absence of external influence

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by Mosuo of given age cohorts. There is a clear delineation between those who reported an average of more than three children and those who reported fewer. The transition seems to occur among individuals aged 56–60; 58 was the midpoint of this age range and thus deemed a suitable threshold for depicting changes in fertility decisions (see also Zhang 1990, Table 5, which indicates a similar age threshold). Q3

I also assessed the impacts of monetary income on female versus male reproduction among currently reproductive individuals aged 17–45. These age cutoffs were chosen to establish the pattern of parental decision-making in the context of the contemporary economy, where income has become increasingly important to reproduction. A 45-year-old would have been 15 years old in 1978 when the family planning policy was implemented but would not have experienced the effects of a market economy as acutely as a 30-year-old, whose reproduction would have commenced after income from tourism would have become an important resource. To accommodate the nuances in timing of both fertility policies and economic change, I ran the same set of analyses on cohorts of individuals from 17 years of age to anywhere between 30 and 45 years of age, resulting in 16 different regressions (summarized below).

The statistical methods used to analyze these predictions closely followed the procedures used by Holden et al. (2003), with some minor modifications. In particular, the impact of wealth (land or income) on reproduction is assessed as the coefficient of the slope of the regression of the number of living children on a given type of wealth, computed separately for males and females via an interaction term that allows for varying effects of wealth on reproductive output based on gender. A significant interaction term is interpreted as evidence that the effects of wealth on reproduction are different for each gender; non-significance indicates that the effects are similar. Thus the first model predicts that the ratio of the benefits of land to sons' reproduction versus daughters' is outweighed by the risk of non-paternity in sons' offspring, such that it benefits parents to invest land in daughters, whereas the second model predicts that this ratio balances such a risk (or is roughly equivalent to the reciprocal of the probability of paternity) such that it benefits parents to invest income in both daughters and sons. The probability of paternity, *P,* is simply the inverse of the ratio of the male to female regression coefficients.

Some features of the variables used in this analysis are important to consider when interpreting the results. First, I am using current estimates of landholdings to estimate prior impacts on reproduction within the postreproductive cohort. There is no way to know definitively how directly this measure correlates to a measure that might have been made during the time these individuals were reproducing. On the one hand, communalization of land and property undoubtedly altered the amount of land held by a given individual over the course of the reproductive period; on the other, many individuals reported that they had not changed residences since birth and that elite families had been able to maintain their status and, eventually, wealth throughout tumultuous periods. Acquisition and maintenance of wealth through this period will be considered in future fieldwork; for now, the current size of land is the best estimate available. Second, both income and land are shared at the household level, though their effects on individuals are considered in the analysis. As described above, wealth is largely shared among household members, and relatively few

individuals report earning individual salaries. To assess the impacts on reproduction of the wealth attributed to individuals, a control for the number of total adults in the household with whom wealth might be shared is included in both models. Households reporting zero income were excluded in Model 2, following Holden et al. and to improve model fit. A control for age is included in the second set of models, but not the first. It had no substantive effect on the first model. A control for land is included in the second set of models to allow for the possibility that it might affect reproduction where individuals continue to pursue an agricultural lifestyle. Finally, education is included in the model of currently reproductive individuals to control for delayed childbearing that may be associated with prolonged education. Data were log transformed as necessary to improve model fit and accommodate assumptions of normality in linear regressions. All analyses were conducted in R (version 2.11.1; R Core Development Team RCDT 2009). Q4

## Summary of Predictions

In summary, the analysis is partitioned into two models. In the first model (M1), I examine the effects of land on postreproductive individuals and predict:

M1.1 The effect of land on reproduction is significant for both sexes; and
M1.2 The ratio of the benefits to sons of land wealth relative to the benefit to daughters is outweighed by hypothetical values of non-paternity in sons' offspring.

The second model (M2) focuses on the effects of earned income on currently reproductive individuals and predicts:

M2.1 The effect of income on reproduction is significant for both sexes; and
M2.2 The ratio of the benefits to sons of income relative to the benefit to daughters balances hypothetical values of non-paternity in sons' offspring.

## Results

### Descriptive Statistics

The demographic surveys resulted in information on 1,156 individuals of known age: 893 adults (over age 17) and 263 children. Table 1 shows descriptive statistics of interest for surveyed individuals according to status of reproduction. There is considerable variation in all variables considered in these analyses. Household-level variables (e.g., wealth) do not differ significantly based on reproductive category (nor would we expect them to), but there are notable differences in the proportion of included individuals who were male (fewer in the older generation), average completed level of education (grade 1 among postreproductives and grade 6.3 among current reproductives), and in the average number of surviving children reported (fewer among individuals currently reproducing).

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t1.1 **Table 1** Descriptive statistics for populations and variables of interest, by reproductive status. Means are reported for continuous variables, with standard deviations in parentheses

| t1.2 | | Postreproductive | Reproductive |
|---|---|---|---|
| t1.3 | Number of children[a] | 3.81 (2.28) | 0.94 (0.93) |
| t1.4 | Log of monthly income (RMB) | 6.06 (2.56) | 6.17 (2.38) |
| t1.5 | Log of land (mu) | 3.01 (0.69) | 2.81 (0.88) |
| t1.6 | Highest educational grade (years) | 1.12 (2.88) | 6.30 (6.99) |
| t1.7 | % male | 35.8 | 46.3 |
| t1.8 | Number of adults in household | 5.13 (1.89) | 4.85 (1.97) |
| t1.9 | *N* | 122 | 656 |

[a] Live children only

*Model 1: Land Effects on Postreproductives*

Table 2 and Fig. 5 show regression results for the effect of land on the number of surviving offspring among postreproductive adults. As predicted (M1.1), land has a positive effect on reproduction for both sexes after controlling for the number of adults in the household. The effect of land on reproduction does not differ between males and females, as the interaction term is not significant. The ratio of the benefits to sons' reproduction relative to the benefit to daughters' is calculated from the regression coefficients. The slope for females (the reference category) is simply the slope for land: 0.9674. The slope for males is calculated by adding the slope for the interaction term (where male=1) to the slope for females (where male=0) and is 0.4489. The ratio of the benefits of land to sons' reproduction is thus 0.4489/0.9674 or 0.4640. Statistically equivalent slopes indicate that the effects of land on reproduction do not differ for males and females. If *P* is less than 1, then it benefits parents to invest land in daughters. Thus, these results are consistent with the MDBI model, and specifically with prediction M1.2: the relative benefit of land to sons versus daughters is outweighed by the risk of non-paternity for any level of paternity lower than absolute certainty, and it benefits parents to invest land in daughters.



t2.1 **Table 2** Regression output for the effect of land on reproduction (number of surviving offspring) for postreproductive individuals over the age of 58 in 2008

| t2.2 | | Estimate | SE | *p* |
|---|---|---|---|---|
| t2.3 | Intercept | 0.4558 | 1.2916 | 0.7248 |
| t2.4 | Log of land | 0.9674 | 0.3902 | 0.0147* |
| t2.5 | Number of adults in household | 0.1567 | 0.1069 | 0.1455 |
| t2.6 | Male | 0.5490 | 1.7917 | 0.7599 |
| t2.7 | Interaction (Male * Log of land) | −0.5185 | 0.5918 | 0.3828 |
| t2.8 | $N$=119 | | | |
| t2.9 | Adjusted $R^2$=0.1238 | | | |

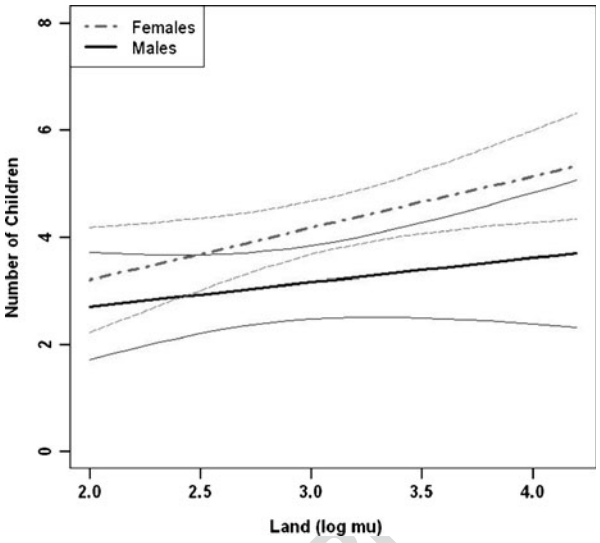


**Fig. 5** The effect of land (log mu) on the number of surviving offspring among postreproductive individuals (more than 58 years old in 2008). The thicker gray dashed line represents the predicted effect based on regression output for females (i.e., controlling for modeled covariates) and the black solid line, for males; thin dashed lines represent 95% confidence intervals for the female regression and the thin solid lines, for the male regression



Importantly, because there was a relative scarcity of men at older ages in the dataset (Table 1), it is possible that, owing to either mortality or migration, men who had reproduced with women in the sample were not, themselves, included in results analyzed here, and men's fertility was consequently biased downward. Results shown elsewhere (Mattison 2010b) have not revealed higher levels of out-migration for men compared with women. It is possible that men suffered higher mortality at older ages, however. To control for this possibility, I performed an additional regression in which individuals over the age of 70, where the female advantage appeared most significant among postreproductives, were excluded. The results (not shown) were not substantively altered; thus, the similarity in male and female reproduction in Model 2 is probably not due to sampling bias.

*Model 2: Income Effects on Current Reproductives*

Table 3 summarizes the results from 16 linear regressions of the effects of earned income on reproduction among young adults, aged 17–*x*, where the *x* varied from 30 to 45. Controlling for covariates, the effect of income on reproduction was positive, regardless of maximum age, and significant or near significant in most regressions, conforming to prediction M2.1. Interestingly, land seems to have a negative effect on reproduction for individuals reproducing in contemporary contexts, even though the ethnographic evidence suggests that some families have maintained an agrarian lifestyle. Education was negatively associated with reproduction and age was positively associated with reproduction in all regressions. As in M1, the intercepts and slopes for the effect of income on male reproduction were never significant, indicating similar effects of earned income on male and female reproduction.

To exemplify these regressions, Table 4 and Fig. 6 show the effects of various covariates on the number of living children reported by currently reproductive individuals, aged 17–40. Again, differences between the sexes in terms of the effect

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t3.1 **Table 3** Summary statistics of 16 regressions designed to assess the impact of covariates on the number of surviving children among individuals currently reproducing, aged 17–*x*. Age range for cutoff: $x=\{30,45\}$

| | Coefficient | Mean | Range | Number of Regressions in which Variable Was Significant[a] (%) |
|---|---|---|---|---|
| t3.3 | Intercept | −0.885 | −1.101–−0.596 | 16 (100) \| 16 (100) |
| t3.4 | Log of monthly income | 0.048 | 0.037–0.064 | 3 (18.8) \| 12 (75) |
| t3.5 | Log of land | −0.100 | −0.126–−0.064 | 12 (75) \| 14 (87.5) |
| t3.6 | Number adults in household | −0.001 | −0.013–−0.010 | 0 (0) \| 0 (0) |
| t3.7 | Highest educational grade | −0.026 | −0.041–−0.013 | 16 (100) \| 16 (100) |
| t3.8 | Age | 0.065 | 0.056–0.072 | 16 (100) \| 16 (100) |
| t3.9 | Male[b] | −0.040 | −0.157–0.052 | 0 (0) \| 0 (0) |
| t3.10 | Interaction (Male*Income) | −0.040 | −0.055–−0.023 | 0 (0) \| 0 (0) |

*N* ranged from 250 to 600 (increasing with increasing age threshold) across all regressions with a mean of 434.

[a] The number of times a variable was significantly associated with the residual number of children over all regressions; significance is defined as $p\leq 0.05$ and $p\leq 0.1$.

[b] The reference category is female.

of earned income on reproduction are not significant. The scale of the effects is lower than in M1, however, both owing to lower reproduction overall in the younger cohort and as a result of the scales on which land and income were tabulated. The slope for females of the effect of income on reproduction was 0.0537, and for males, 0.0179 (0.0537 + −0.0358). The ratio of BS/BD is thus 0.333, and the probability of paternity necessary to invest equally in sons and daughters is 3. Again, because the difference in slopes is not significant, the probability of paternity necessary to invest equally in sons and daughters is 1. The above illustrate how *P* is calculated for each regression.

t4.1 **Table 4** Regression output for the effect of income and covariates on reproduction (number of surviving offspring) for currently reproductive individuals aged 17–40 in 2008

| | | Estimate | SE | *p* |
|---|---|---|---|---|
| t4.3 | Intercept | −0.9630 | 0.2629 | 0.003*** |
| t4.4 | Log of monthly income | 0.0537 | 0.0270 | 0.0470* |
| t4.5 | Log of land | −0.1019 | 0.0396 | 0.0104* |
| t4.6 | Number of adults in household | −0.0078 | 0.0164 | 0.6350 |
| t4.7 | Highest educational grade | −0.0168 | 0.0050 | 0.009*** |
| t4.8 | Age | 0.0656 | 0.0045 | <0.001*** |
| t4.9 | Male | −0.0760 | 0.2678 | 0.7764 |
| t4.10 | Interaction (Male*Log of income) | −0.0358 | 0.0384 | 0.3517 |
| t4.11 | N=499 | | | |
| t4.12 | Adjusted $R^2=0.3909$ | | | |

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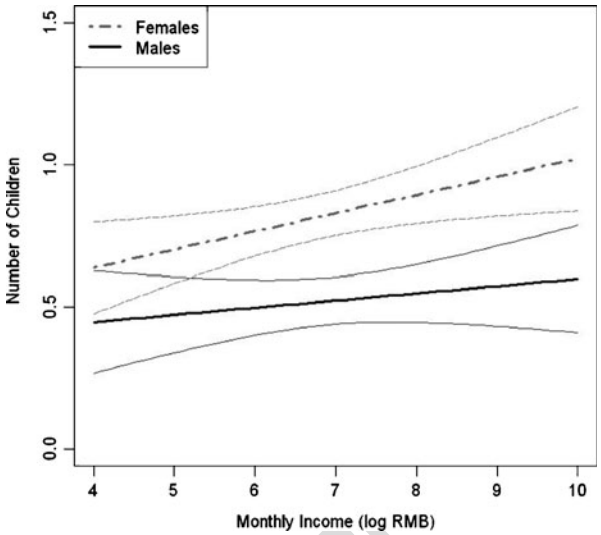


**Fig. 6** The effect of monthly income (log RMB) on the number of surviving offspring among young adults aged 17–38 in 2008. The thicker gray dashed line ?represents the predicted effect based on regression output for females (i.e., controlling for modeled covariates) and the black solid line, for males; thin dashed lines represent 95% confidence intervals for the female regression and the thin solid lines, for the male regression

## Discussion

The MDBI hypothesis explains matriliny as an outcome of daughter-biased wealth investment by parents seeking to optimize allocation of resources in terms of inclusive fitness (Holden et al. 2003). In their paper, Holden and colleagues show evidence that supports their hypothesis in two different societies, one matrilineal and one patrilineal. The patrilineal Gabbra derive nearly three times as much benefit from wealth invested in sons relative to daughters, whereas the benefits of investing wealth do not differ by sex among the matrilineal Chewa. The levels of paternity certainty necessary to make investing in sons beneficial were 0.36 and 0.94, respectively, indicating that paternity certainty can be quite low among the Gabbra before it makes sense to invest in daughters, because the impacts of wealth on male reproduction were much higher than on female reproduction, but not among the Chewa, where it would rarely be beneficial to invest wealth in sons. It is important to note here that according to this model, matriliny derives causally from the type of wealth available to support reproduction in different societies. If the wealth benefits men to such a degree that it outweighs existing levels of non-paternity in their offspring, then mothers and their partners will invest wealth in sons. Patriliny results not only as mothers invest resources in sons but also because sons become freer to pursue their own reproductive interests and as a result begin to invest their resources in their own children. If my explanation of how this model applies to matrilineal societies in which wealth is transferred from mother's brother to sister's son is correct, then men in such societies effectively invest very little in any descendants. When they possess the means to impact reproduction (e.g., because prolonged absences are no longer necessary or the source of wealth changes), men choose to invest in their own children and/or romantic partners and the kinship system shifts away from matriliny.

Applying this framework to the Mosuo revealed that the MDBI hypothesis is generally consistent with inheritance transmission in this population, while

highlighting some interesting nuances of this data set. Among postreproductive individuals whose childbearing occurred prior to the implementation of the birth planning policy, the impacts of land on reproduction were similar for men and women, such that parents would need complete certainty over paternity in sons' offspring in order to invest land equally in sons and daughters. Given that paternity certainty was likely to have been relatively low among postreproductive individuals engaging in sese, the model predicts daughter-biased investment of land, which was indeed the norm among traditional Mosuo.

The effects of earned income on reproduction among young adults currently reproducing must be interpreted within the socioecological context in which reproductive decision-making occurs. As with the first model, the second set of models showed that the relationships between earned income and reproduction were similar for men and women. Here, too, parents would need complete certainty in sons' offspring in order to invest income equally in sons and daughters. Given the increasing prevalence of marriage and monogamy among young Mosuo (Mattison 2010a), it is likely that paternity certainty is higher among recent age cohorts relative to previous generations. Opportunities for employment close to home may also lead to higher paternity certainty as men can spend more time in close proximity to their affines. At the same time, limits on childbearing for rural and ethnic Chinese of two or three children leaves relatively little variation in reproductive outcomes, decreasing the relative advantage of investing wealth in sons that might normally be expected with respect to income. When parents can be assured of paternity, it may indeed benefit them to invest income in both sons and daughters. If actual paternity is lower than 100%, however, parents are expected to bias investment of income toward daughters. Without knowing prevailing levels of paternity confidence, it is impossible to say whether income is distributed in ways consistent with the MDBI model. Future studies of MDBI could incorporate internal variation in inheritance practices to examine whether, for example, married individuals are more likely to invest equally in sons and daughters relative to individuals engaged in non-marital unions.

The MDBI model can be used to analyze variable practices among societies (e.g., Holden et al. 2003), but it is also flexible enough to analyze transmission of different forms of wealth within the same society, as has been done here (see e.g., Keegan and Maclachlan 1989; Pelto and Pelto 1975; Poewe 1978 for discussion of the importance of intrasocietal variation). This flexibility is important because sex-biased parental investment rarely involves binary decisions of whether to invest in just daughters or just sons, but rather responds to the variable effects of each type and increment of investment on a child's reproductive success (Sieff 1990). Indeed, the model's ability to capture variation in sex-biased investment could be expanded to incorporate the differential returns of other types of investment to parental reproductive success, such as those accruing directly to parents through their children's help (e.g., Borgerhoff Mulder 1998; Smith and Smith 1994; Turke 1988).

Another interesting modification of the model could incorporate the synergistic effects of paternity certainty and wealth. Evolutionary theory predicts that men will seek fidelity from reproductive partners as a requirement for substantial paternal investment (e.g., Fortunato and Archetti 2009; Marlowe 2000). If this is the case,

increased levels of wealth might be positively correlated with increased paternity certainty in offspring when paternal investment is significant and men exert control over resources important to reproduction. The empirical significance of paternity certainty or confidence in affecting paternal investment in offspring (e.g., Anderson et al. 2006; Flinn 1981; Gaulin and Schlegel 1980; Greene 1978; Kurland 1979) and wealth in impacting sex-biased transmission of resources (e.g., Cronk 1989; Mace 1996; Trivers and Willard 1973) is well-established. Because these are currently modeled as separate, independent effects on sex-biased transmission of wealth, the MDBI model probably underestimates the synergistic effects of these two variables when acting together.

Finally, when considering the rules and causes of sex-biased intergenerational wealth transmission in places like China, it is important to acknowledge the very real possibility that women's and men's reproduction may not be impacted equally by resources; rather, women's reproduction may be impacted more than men's. Given large female deficits in China's population and corresponding impacts on the marriage market (e.g., Coale and Banister 1994), it is possible that in many locales, women achieve higher average reproductive success than do men. This is because excess males from populations not counted in surveys such as mine may remove a portion of reproductive opportunities from local men. Under such circumstances, parents of local girls may always derive higher benefits from investing certain types of wealth in daughters. In these cases, $P$ takes on values greater than 1 and is no longer interpretable strictly as a probability. Modifications to the model that allow for higher impacts of resources on female reproduction may be called for, and researchers employing the model must take into account the dynamics of wealth and reproduction specific to each population under study.

I began this article by reviewing the historical anthropological arguments associated with matriliny and by arguing that the evolutionary, quantitative perspective added to our understanding of the forces producing matriliny by providing a singular rationale for a variable outcome in kinship behavior. I hope to have shown the utility of an evolutionary framework in tying together what was already known about matrilineal kinship, including the factors that lower $P$, such as warfare and prolonged male absences, and the connections between matriliny, unstable reproductive unions, and its nuanced relationship with resource availability and subsistence base. Because unilineal evolutionism is still the dominant perspective in the geographic area where this work was conducted, it is worth mentioning that the evolutionary framework employed here is at odds with the theoretical rationale of the Chinese state (e.g., Pusey 2009). Instead of viewing matriliny as a fossil-like vestige of some primitive stage in human evolution (Yan 1984), I analyze it as an adaptation to contemporary environments. This perspective is consistent with recent evidence that associates matrifocality with a lack of male contributions to their households (e.g., Quinlan 2006; Stack 1974) and transitions away from matriliny with economic development (e.g., Holden and Mace 2003; Mattison 2010a; Sear 2008), illustrating once again the relative flexibility in responses envisioned by some modern evolutionary perspectives.

Our understanding of matriliny is important not only to kinship studies but also to our understanding of human evolution in general (Knight 2008). Because the human life history is so different than those of our ape ancestors, (e.g., Hill

1993; Mace 1996; Voland 1998), one of the central questions of evolutionary anthropology involves the extent to which different family members contributed to women's fertility, allowing for our unique life history (e.g., Hawkes et al. 1998; Hrdy 1999; Kaplan et al. 2000; Kramer 2005; Leonetti et al. 2005; Sear and Mace 2008). The MDBI hypothesis provides some insights into the types of environments that might have been conducive to different classes of kin in assisting with a woman's reproduction. In order for paternal care to become critical, either paternity certainty must have been relatively assured or the benefits of wealth to sons must have exceeded its benefits to daughters.

## Conclusion

The MDBI hypothesis adds to our understanding of matriliny by tying together variation in inheritance practices among and within societies under a simple yet elegant and precise mathematical model. It explains various features previously known to be associated with matriliny, such as its incompatibility with economic development (Douglas 1969; Goody 1962; Gough 1961a, Gough 1961b; Holden et al. 2003; Murdock 1949), its association with warfare (Divale 1974; Ember and Ember 1971; Holden et al. 2003), and its association with low paternity certainty (Alexander 1974, 1977; Flinn 1981; Greene 1978; Holden et al. 2003; Kurland 1979) and divorce (Gluckman 1950; Poewe 1978), providing an ultimate reason for variation in inheritance via evolutionary theory. My data support the utility of this model in explaining the sex-biased transmission of two types of wealth, land and income, among two reproductive cohorts of the matrilineal Mosuo of Southwest China, while highlighting the importance of local socioecological contexts in shaping transmission dynamics. It is the first independent empirical test of Holden et al.'s model, as well as an application of evolutionary theory to a geographic area in which unilineal evolutionism still drives theoretical understanding of kinship practices.

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