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One piece of the matrilineal puzzle: the socioecology of maternal uncle investment

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Maternal uncle relationships in which men invest resources (usually in the form of inheritance of material wealth) into their sisters' children are characteristic of matrilineal systems and hypothesized to arise under certain socioecological circumstances, but little research has systematically investigated conditions that are associated with this type of investment. We quantify relationships between household-level socioeconomic variables and different types of maternal uncle investment (direct care and indirect resource investment) within a bilateral, semi-nomadic population. Shodagor people of Bangladesh allow us to consider matrilineal behaviours in an evolutionary framework owing to their flexible social structure in which 39% of families receive some investment from a maternal uncle. Variables associated with direct maternal uncle care reflect the significance of maintaining consistent residence throughout the year and an increased need for childcare in families residing on boats versus those living on the land. Informative predictors of indirect investment indicate that a mother's birth history corresponds with more tangible contributions such as food and clothing. These results identify household-level variables specific to direct versus indirect maternal uncle investment, whereas having more older brothers or being firstborn increased the odds of a mother receiving any investment from brothers at all. Exploring these social and ecological associations in a bilateral, relatively flexible population unveils household circumstances that may lead to the development of female-biased kinship.

This article is part of the theme issue 'The evolution of female-biased kinship in humans and other mammals'.

1. Introduction

The role of men in the lives of their sisters and sisters' children varies across all levels of social organization and kinship systems, but the status and inheritance rules ascribed to maternal uncles in matrilineal kinship systems have been deemed particularly puzzling by anthropologists and is referred to as the 'matrilineal puzzle' [1]. Matrilineal kinship organization could require men to split their allegiances between their natal and marital households and create a conflict between their roles as brother/uncle and husband/father, which is pronounced when men hold control of the resources. When resources are controlled by men, but passed through the female line, investment by maternal uncles in their sister's sons leads evolutionary researchers to question the adaptive nature of this type of investment [2–11]. Theory has attempted to explain the evolutionary circumstances that could lead to the role of maternal uncles in matrilineal inheritance systems, but more empirical work is needed to assess whether theory matches observed patterns of human behaviour. A flexible social structure, high levels of direct investment from men and unique ecology inhabited by semi-nomadic, boat-dwelling, Shodagor people in rural Bangladesh present an opportunity to consider matrilineal behaviours in an evolutionary context. While Shodagor communities recognize bilateral

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inheritance rules, with Shodagor identity passing from fathers and property from mother and father to children of both sexes, families generally own very little heritable property, and adherence to expected patterns of investment is often flexible. Residence patterns are also flexible: postmarital residence and household movability associated with boat-dwelling allow families access to matrilineal and patrilineal kin throughout the year. Thus, we address an evolutionary question of the matrilineal puzzle by examining maternal uncle investment patterns among Shodagor people of rural Bangladesh: what are the socioecological and economic conditions under which maternal uncles invest directly and indirectly in their sisters' children? Results reveal circumstances that could aid in the development of female-biased kinship systems and have implications for future work on the evolution of matriliny.

(a) The matrilineal puzzle

In matrilineal kinship systems, descent and inheritance are traced through the female line. In some cases, inherited property is passed from mother to daughter (e.g. [12–14]), but more commonly, property is vested in males and passed from mother's brother to sister's son(s) (e.g. [15]). Matriliny is often associated with a particular suite of socioecological variables, many of which we expect to shape Shodagor maternal uncle investment.

First, the specific rules about who inherits are somewhat consistent across matrilineal societies with the majority adopting a form of matrilineal primogeniture, in which the eldest sister's eldest son inherits property from her eldest brother [16]. There is variation in inheritance rules, though. In some cases, matrilineal ultimogeniture is recognized, in which the youngest daughter in a family inherits property from her mother (e.g. [13]). Other times, rules are more flexible and all of a mother's children (or all children of one sex) inherit property from her or one of her brothers [8]. Hrdy & Judge [17] indicate a link between variation in rules of primo- and ultimogeniture and changing ecological circumstances in patrilineal societies and give an evolutionary rationale for the role that birth order plays in investment patterns across cultures. While we do not have an *a priori* reason to expect Shodagor families with maternal uncle investment to follow one type of inheritance rule over another, we do expect a Shodagor woman's birth order to play a role in maternal uncle allocations of investment.

Second, most matrilineal groups have uxorilocal postmarital residence rules in which a newly married couple is expected to live near the bride's family [1]. As with inheritance rules, Shodagor residence patterns are relatively flexible. In 2014, 63% of families reported living virilocally after marriage, 35% uxorilocally (with some families living near both husband's and wife's family) and 15% neolocally [18]. Given the near-ubiquity of the cross-cultural co-occurrence of matrilineal inheritance systems with uxorilocal postmarital residence, we expect the trend to hold for Shodagor families as well, with those who live uxorilocally after marriage being more likely to report investment from a mother's brother. Also, about half of all families live a semi-nomadic lifestyle. Those who do so moved their houseboats between communities an average of 2.5 times per year in 2013. While most reported their reason for moving was for work, some also said they moved in order to be near family, and nearly all reported moving into communities in which extended family lived. Even when postmarital residence is not uxorilocal, movement between groups would allow families to spend at least part of the year living near the wife's relatives, including her brothers, and we expect that more frequent contact with maternal uncles should increase the chances of those uncles providing care for their sisters' children. So, in addition to postmarital residence, variables related to Shodagor movement patterns—including number of movements per year and boat-dwelling (as opposed to land-dwelling)—should also be associated with maternal uncle investment.

Matrilineal kinship is also more likely to be associated with horticulture than with other modes of economic production [19,20]. A woman's coresidence and ability to cooperate with her female family members may partially account for this relationship, because horticulture—unlike plough agriculture or some other subsistence systems—relies mostly on female labour [21,22]. Among Shodagor people, fishing is men's main subsistence practice, while there are three occupations available to women: trading (40%), fishing (39%) and housewife (21%). Women who fish almost always do so with their husbands or sons, rarely with other male relatives, and almost never with other women. By contrast, cooperation among women is a key characteristic of trading. Women who trade carry heavy loads of household wares, clothes or jewellery on their heads while walking for several hours per day, selling and trading with women in non-Shodagor households. They often travel in groups of between two and six women, many of whom are related [18]. While different from horticulture in that women are not cooperating to produce a communally shared resource, they coordinate with one another to determine location, duration and mode of travel each day, with the intention of protecting against physical harm and reputational damage that may be associated with women travelling alone within Bangladesh. Trading is also associated with a suite of characteristics unusual for women's work, including incompatibility with childcare, high-variance returns and the ability to out-earn men [18], thus women traders report higher levels of autonomy than those who fish or are housewives. Given the association between matriliny and subsistence practices that require female–female cooperation as well as greater levels of female autonomy [23,24], we expect that Shodagor women's trading should be associated with a higher likelihood of maternal uncle investment. Uxorilocality, female cooperation in subsistence work and higher levels of female autonomy, along with lower levels of marital stability and paternity confidence [4,19,25], may diminish the importance of paternal roles and subsequently elevate the position of mothers' brothers, thus creating a conflict for men who must decide between investing in their sisters' or their wives' children.

Evolutionary theory suggests that a man should only invest in his sister's children when he stands to gain greater reproductive fitness payoffs than he would if he invested in his wife's children. Because men are only half as related to their sisters' children as they are to their own, matrilineal investment patterns are in conflict with the expectations of kin selection theory [2,26,27]. Therefore, circumstances under which men are unlikely to be related to their wives' children (i.e. in cases of divorce and remarriage) or are unsure of the paternity of their wives' children (i.e. in cases of female promiscuity) may also be those under which men choose to invest in their sisters' children, for whom

relatedness is guaranteed [2,4,8,28–31]. The paternity threshold model formalizes the role of paternity uncertainty as an adaptive explanation for matriliny [32]. Although the suggested level of certainty necessary to produce such investment patterns is probably unrealistically low [4,5,10,33], and these low levels may be unnecessary to produce evolutionarily stable investment patterns between mother's brother and sister's son, multiple empirical studies have shown a relationship between paternity confidence and paternal investment (e.g. [4,28–30,34]).

While there are no estimates of paternity uncertainty calculated among Shodagor people, there are a number of reasons to expect the rate to be very low. First, paternity uncertainty is expected to be low among the agricultural Bangladeshi population, which accounts for the majority population in the country. Purdah, the practice of female seclusion, remains a common practice and functions to closely guard women's sexual reputations [35]. In Bangladesh, purdah is expressed through practices like covering of one's body to varying degrees and largely relegating women to private spaces, avoiding work or interactions outside of the home. While some Shodagor women follow these practices more closely than others, female autonomy is generally higher among Shodagor than it is among the land-dwelling, non-Shodagor Bangladeshis [36]. However, as noted above, when women work outside of the home, they are almost always accompanied by their husbands or male relatives when fishing or by other women when trading. Women are rarely alone outside of the Shodagor communities, so there are relatively few opportunities for female promiscuity to occur. Next, divorce among Shodagor (one measure used by Flinn [4] to estimate paternity uncertainty) is somewhat less common than in other societies of similar size and social structure. For example, 11% of Shodagor interviewed in 2014 reported ever being divorced, while 25% of all Ache children grew up with a divorced parent [37] and dissolution of marriage is notoriously high among all foragers [38]. Finally, in qualitative interviewing, several Shodagor men and women stated that infidelity is uncommon [18]. Even with a low expected paternity uncertainty rate, we still expect measures associated with lowered paternity confidence (remarriage after husband's death or divorce and husband absence) to be associated with increased investment from maternal uncles.

Other attempts to model the adaptive value of matriliny have emerged. The daughter-biased investment model emphasizes the reproductive fitness benefits for grandparents investing in their daughters' children and incorporates wealth inheritance with paternity confidence [10]. Empirical studies have shown some support for this model (e.g. [10,11]), and a large body of literature demonstrates the commonality of matrilateral (versus patrilateral) investment in grandchildren, which offers tangential support for the premise of the model (e.g. [39–42]). Fortunato [5] showed that both polygynous and polyandrous marriage could present the necessary conditions for matrilineal inheritance patterns to benefit the reproductive fitness of individual men, although polygyny is rare among the Shodagor and they do not practice polyandry, therefore, we do not make any specific predictions referencing multiple marriage and maternal uncle investment.

When matrilineal inheritance is discussed as a puzzle, it is almost always in reference to inheritance of larger, more difficult to divide resources like land. In reality, men have been known to invest even these resources in both their sisters' children and their own (e.g. [43]), and also to invest smaller, more easily divisible resources (like food, money or time—in the form of direct care of children) in their nieces and nephews as well as their wives' children. In these cases, matriliny is less puzzling, but also presents the following question: what are the circumstances under which men invest different types of resources in their sisters' children?

(b) Maternal uncle investment

There are two main categories of investment that children may receive: direct and indirect. Direct investment refers to any direct interaction with a child, including holding, feeding, soothing and grooming, among other caregiving activities. Indirect investment refers to provisioning of children [44], as well as activities that contribute to a child's social status or other measures of quality, such as paying for education [45], buying clothing or household goods, arranging a marriage [46,47], or facilitating rites of passage necessary for marriage and parenthood [48]. The amount and type of investment typically provided by males varies across societies [44]. Levels of paternal investment are associated with a number of factors, including need [49,50], necessity for survival (e.g. [51]), subsistence mode, mating system and male resource control and contribution [44], as well as paternity certainty [52]. Empirical data show that direct investment in young children is rarely provided by non-paternal males (e.g. [53,54]) and indirect investment from grandfathers and uncles is more likely to be given facultatively or when fathers are unavailable to provide it (e.g. [48]). However, maternal uncles may present an exception in some cases (see also [55]).

Regardless of formal inheritance rules, postmarital residence patterns, subsistence practices or societal levels of paternity certainty, maternal uncles support and care for their sisters' children in a number of ways. For example, in patrilineal, virilocal societies, children often have more informal, affectionate relationships with their maternal uncles than with their paternal uncles (e.g. [56,57]). This type of relationship has been well documented in the land-owning, agricultural population in Bangladesh (e.g. [58]) and is often reflected types of uncle/niece/nephew interactions (e.g. [58]) and visiting patterns (e.g. [59]). In other cases, maternal uncles have more formal roles in relation to their sisters' children. They may be expected to play the role of disciplinarian or teacher (e.g. [60,61]) or to pay for education (e.g. [62]), they may have important ritualistic roles (e.g. [63]), and sometimes even become the primary carer of a child, taking in a sister's son for a number of years (e.g. [64]). Maternal uncle investment has been documented in modern societies as well (e.g. [65]), and appears to be independent of presumed societal levels of paternity certainty (e.g. [66]).

Shodagor fathers provide an unusually high amount of direct investment for their children, and some fathers stay at home as the primary carer of young children for half of the year while mothers work away from home [36]. Other Shodagor men also seem to invest in direct care at unusually high rates; for example, preliminary observational and qualitative data indicate that older sons and grandfathers often care for children [18]. Shodagor fathers and grandfathers are also involved in many aspects of indirect investment, including

provisioning, buying clothes, paying for education and arranging marriages, although this pattern is common across cultures [67,68]. While there are no expressed formal roles or societal-level expectations for maternal uncles, 25% of Shodagor families in Matlab received direct care and 18% received some form of indirect investment from maternal uncles (table 1). Given these trends in male care, we expect that general availability of allocarers should impact investment from maternal uncles. Specifically, we expect that women who have more brothers should have a higher likelihood of receiving any investment from at least one brother. We also expect that availability of other alloparents (e.g. when women have more sisters, or when a family has a higher total number of available alloparents) will associate with a lower likelihood of receiving investment from a maternal uncle.

Cross-cultural patterns of maternal uncle investment are in line with a large body of literature that emphasizes the importance of matrilateral investment—usually focused on maternal grandmothers (e.g. [39–42]), but grandfathers, aunts and uncles may follow suit (e.g. [65,66,69]). The presence and care provided by maternal relatives have been associated with measures of higher fertility for mothers, such as increased child survival [42], better health and nutritional measures for children [70,71], earlier first births [72], lower interbirth intervals (IBI) and higher numbers of surviving children [73] for mothers. Evolutionary theorists again put forward paternity uncertainty as an important driver in the adaptiveness of matrilateral investment [65,74–78], though broader inclusive fitness benefits are also probably at play [79]. Of course, in a society without conscribed rules about maternal uncle investment, we would not expect a women's reproductive decision-making to be systematically shaped by the promise of future investment from their brothers. We also do not predict a causal relationship in either direction between care or investment given by mother's brothers and particular aspects of her fitness (i.e. does care from a maternal uncle lead a woman to have more children or does a greater number of children increase the likelihood that her brother will help care for or provide for those children?). But, given the importance of alloparents in responding to needs related to a woman's reproductive history, and their relationship to a woman's reproductive strategies, we expect measures indicating higher reproductive fitness for mothers (more children, fewer child deaths, shorter IBIs) to be associated with investment from maternal uncles.

2. Methods

(a) Shodagor people of Matlab, Bangladesh

Matlab is a mostly rural subdistrict in Bangladesh, located approximately 59 km southeast of the capitol city of Dhaka, and bisected by the Donagoda River—a tributary of the Meghna River, which is one of the three largest rivers in the country. Matlab is home to approximately 200 000 people [80,81], including around 200 Shodagor families, most of whom live on small, wooden boats—while others live in makeshift houses—in small communities on or near the banks of the Donagoda [36]. Matlab Shodagor observe bilateral inheritance rules: Shodagor identity is inherited from fathers, and property is passed from both mother and father to children. As is common among nomadic and semi-nomadic groups [82], Shodagor postmarital residence patterns are multilocal, with families in Matlab living virilocally, uxorilocally, near both spouses' families or neolocally after marriage. Residence patterns change approximately twice per year after marriage. Most marriages are monogamous unions with only occasional polygyny, and most families live in nuclear family households in which the majority of economic and childcare responsibilities are concentrated.

(b) Data collection

This study is based on interview data that were collected over nine months in 2014, resulting in an almost complete population sample of Matlab Shodagor. Quantitative survey interviews were conducted in two rounds, between May and July 2014, and again in September and October 2014. This research was reviewed and approved by the University of Missouri's Institutional Review Board as well as the Ethical Review Committee at the International Centre for Diarrhoeal Disease Research, Bangladesh (ICDDR,B). All members of the Shodagor group in Matlab were eligible to participate in this study and only five declined, for an initial sample of 178 adults from 92 households. The sample size for this maternal uncle analysis is 61 households and only includes households for whom there is at least one maternal uncle and no missing data.

(c) Analysis

We explored relationships between household-level socioeconomic variables and three binary measures of maternal uncle investment (direct, indirect and any), also at the household level (table 1), using Bayesian generalized linear models (GLMs). 'Direct' investment indicates that the mother's brother provided direct care (i.e. watching, holding, playing, feeding) to one or more children in the household, whereas 'indirect' investment includes providing food, clothing, treats or a marriage payment for one or more children in the household. 'Any' investment denotes whether or not the mother's brother provided either direct or indirect investment (or both) to one or more children in the household. These maternal uncle investment variables reflect whether a maternal uncle provided investment to any child in the mother's household at any point in time, thus all results are generalized to the household level ($n = 61$ households).

Given the exploratory nature of our aims, we examined a combination of household socioeconomic measures as well as characteristics of the mother's life history and her natal family as potential predictor variables (table 1). Summary statistics are reported from the raw variables, but household income was log-transformed and all other non-binary variables were z-scored prior to all analyses. We screened predictor variables in clusters in order to systematically determine which variables have directional relationships with each of the three investment outcomes in a targeted manner, given that some of our variables measure overlapping or related aspects of the household. Two variables were included as controls in all screened clusters: mother's age as a measure of cohort effect and household income as a socioeconomic marker indicative of differences in household resources.

The residential cluster includes variables related to the family's residence pattern, indicating whether they now live or did live near the husband's family after marriage, the wife's family, or neither, as well as the number of times the household moved locations during the 2014 year and whether they live on a boat or the land (table 1). The socioeconomic cluster has two variables indicating whether or not the mother sells goods to earn income and whether or not she has any education. The paternity cluster has two variables related to marital status: dummy variables that reflect whether or not the mother has been married more than once—all mothers in the sample have been married at least once, with seven married twice, as well as whether a

Table 1. Household-level summary statistics for maternal uncle (MU) investment variables and all screened predictors. $n = 61$.

cluster	variable	min	Q1	median	Q3	max	mean	s.d.
all	mother's age (years)[a,b,c]	15.0	24.0	30.0	40.0	68.0	33.0	12.8
all	household income (taka)[a,b,c]	0.0	54 720.0	109 200.0	192 000.0	520 000.0	142 371.0	112 890.9
residential	number of annual movements[b]	0.0	0.0	0.0	2.0	3.0	0.8	1.1
reproductive	mother's no. of living children	1.0	2.0	3.0	4.0	9.0	3.1	2.0
reproductive	mother's age at first birth	13.5	15.0	17.0	18.5	26.4	17.1	3.6
reproductive	IBI after first birth (years)[a,c]	0.7	1.8	3.0	5.0	34.0	4.1	4.7
natal	mother's total no. of siblings	2.0	5.0	7.0	8.0	13.0	6.7	2.2
natal	mother's no. of sisters	0.0	3.0	4.0	5.0	9.0	3.8	1.6
natal	mother's total no. of brothers	1.0	2.0	3.0	4.0	6.0	2.9	1.3
natal	mother's no. of older brothers[a,b]	0.0	0.0	1.0	2.0	5.0	1.4	1.3
natal	mother's no. of younger brothers	0.0	1.0	1.0	2.0	5.0	1.5	1.3
natal	number of available alloparents	0.0	0.0	1.0	1.0	7.0	0.9	1.2
		yes	no					
—	received any MU investment	24	37					
—	received direct MU investment	15	46					
—	received indirect MU investment	11	50					
residential	matrilocal residence after marriage	21	40					
residential	patrilocal residence after marriage	22	39					
residential	other residence after marriage	21	40					
residential	household lives on a boat[a,b]	37	24					
socioeconomic	mother sells goods[a,b]	28	33					
socioeconomic	mother has any education	7	54					
paternity	father is present	56	5					
paternity	mother married more than once	7	54					
reproductive	mother has lost a child[c]	23	38					
natal	mother was firstborn[a,c]	8	53					

[a]Predictor retained in 'any investment' model.
[b]Predictor retained in 'direct investment' model.
[c]Predictor retained in 'indirect investment' model.

woman's husband is currently present in the household. The reproductive history cluster has variables capturing the mother's birth history, including the IBI in years between her first and second births, and whether or not any of her children have died. The natal family cluster includes variables that characterize the composition of the mother's natal family such as whether or not she is firstborn among her siblings and how many alloparents are available to provide direct care to her children if needed (although alloparents are not limited to only members of the mother's family).

We used Bayesian GLMs to explore the relationships between each cluster of predictor variables and the three binary investment outcomes (direct, indirect and any) using Markov chain Monte Carlo (MCMC) sampling to characterize posterior probability distributions with the MCMCglmm package in R v. 3.4.3 [83,84]. This method enabled us to incorporate several predictor variables in a multivariable fashion such that the impacts of each variable in a model were measured independently, controlling for the rest. We used prior settings with residual variance fixed at one ($R = \text{list}(V = 1,\ \text{fix} = 1)$) given the binary nature of our outcome variables (residual variance is unidentifiable in logit models), and restricted settings on the predictor (i.e. fixed effect) covariance matrices in order to prevent the model from overfitting and jumping to high parameter values as suggested by the package author ($B = \text{list}(\text{mu} = c(\text{rep}(0,n)),\ V = \text{diag}(n)*(4.3 + \text{pi}^{2/3})$). Bayesian MCMC models update prior probability distributions when given data, producing posterior distributions that reflect the probability of each predictor variable as it impacts a given outcome, controlling for the other variables also included in the model. Logit models produce parameter coefficient estimates on a log-odds scale, reflecting the direction and magnitude of association between each predictor variable and the outcome. Based on our clustered screening, we retained predictors across all clusters that showed clear, directional relationships (90% credible intervals from posterior coefficient distributions did not span zero) with each maternal uncle investment variable (table 1). All resulting final models also included maternal age and household income as controls. Each model ran for 10 500 000 iterations with a burn-in of 500 000 and thin of 10 000 in order to retain 1000 samples of each coefficient estimate from the posteriors. (code and data available at: https://github.com/kstarkweather8/Maternal-Uncle-Phil-Trans.)

GLM coefficients estimate the change in log odds of maternal uncle investment per unit increase in each predictor (figures 1–3). Posterior modes represent the most likely coefficient estimates, and 90% credible intervals encompass 90% of the retained 1000 samples in each posterior distribution, showing how varied or imprecise relationships with large credible intervals are in this household-level data. Regardless of credible interval width, intervals on the log-odds scale that do not span zero indicate clear, directional relationships in which a one unit increase in the predictor consistently corresponds with either an increase or decrease in investment odds. In other words, credible intervals that are entirely positive or negative identify consistently directional relationships between predictors and investment outcomes, and the width of each interval is indicative of the precision in each coefficient estimate for this population of 61 households (figures 1–3).

We report predictor probabilities on an odds ratio scale in the electronic supplementary material (table S4) for our three final models. Electronic supplementary material (tables S1–S3) provide two indicators of model fit for all clustered screening models as well as the final three models for any investment, direct investment and indirect investment. We report marginal R^2 values defined specifically for MCMC results [85] to indicate the proportion of variance explained by each model's combination of predictor variables. We also report deviance information criterion (DIC) for all models as a comparative measure of fit. DIC penalizes increasing model complexity, and smaller values of this statistic indicate better model fit [86].

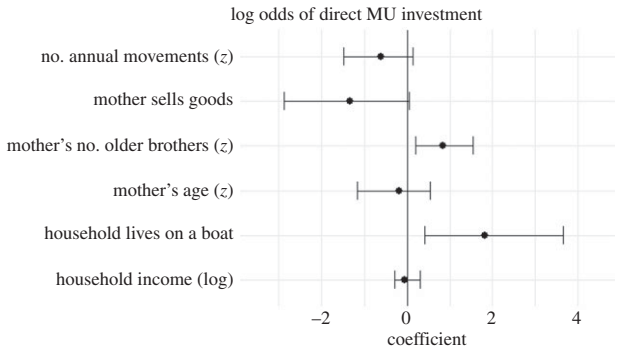

Figure 1. Bayesian posterior modes and 90% credible intervals summarize 1000 retained coefficient samples, showing the relationship of each predictor variable to the outcome of direct maternal uncle (MU) investment on a log-odds scale.

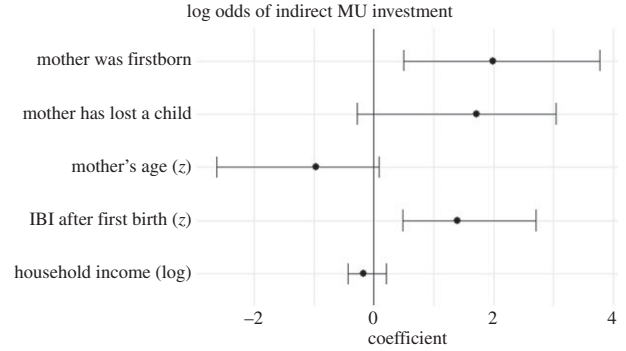

Figure 2. Bayesian posterior modes and 90% credible intervals summarize 1000 retained coefficient samples, showing the relationship of each predictor variable to the outcome of indirect maternal uncle (MU) investment on a log-odds scale.

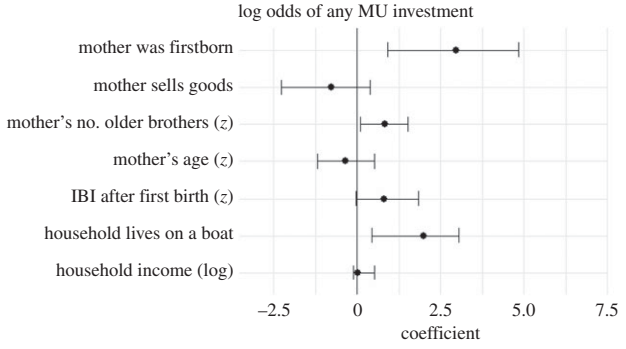

Figure 3. Bayesian posterior modes and 90% credible intervals summarize 1000 retained coefficient samples, showing the relationship of each predictor variable to the outcome of any maternal uncle (MU) investment on a log-odds scale.

3. Results

Households who reside on boats (in contrast with those living on land) have increased odds of receiving investment from a maternal uncle in the form of direct care (figure 1; electronic supplementary material, table S4). Households

Table 2. Summary statistics for maternal uncles providing any investment. $n = 24$.

variable	min	Q1	median	Q3	max	mean	s.d.
birth order	1.0	2.0	3.0	4.3	6.0	3.1	1.5
age diff. with sister	−30.0	−8.0	−2.0	3.3	8.0	−3.1	9.1
	yes	no					
direct investment	15	9					
indirect investment	11	13					
gave food	4	20					
gave clothes	3	21					
gave treats	10	14					
paid for marriage	2	22					
firstborn	3	21					
midborn	20	4					
lastborn	1	23					
lives near sister	8	16					
lives on a boat	7	17					
married	18	6					
has children	18	6					
older than sister	11	13					

that move more frequently throughout the year and those in which the mother sells goods (requiring her to travel) have decreased odds of direct maternal uncle investment in most cases. Having more older brothers also increases a mother's odds of receiving direct childcare from one of her brothers. Marginal R^2 values show that the combination of modelled predictors accounts for approximately 85% of the variance in whether or not a family receives direct investment from a maternal uncle, and between 62 and 86% of this variance is explained in 90% of our estimates (electronic supplementary material, table S1).

Indirect investment in which a maternal uncle provides food, clothing, treats or pays for marriage shows a cohort effect in which mothers born more recently are more likely to receive these contributions (figure 2; electronic supplementary material, table S4). Other predictors of indirect investment reflect the significance of mothers' birth histories: families in which a child has died have increased investment odds, as do families with longer birth spacing. Firstborn mothers have increased odds of their children receiving indirect investment from a maternal uncle. Our retained predictors explain approximately 79% of the variance in indirect investment outcomes, and between 56 and 86% of this variance in 90% of our estimates (electronic supplementary material, table S2).

Families of mothers who were firstborn in their natal families have increased odds of receiving some (direct and/or indirect) investment from a maternal uncle, and for families in which the mother was not firstborn, a higher number of older brothers corresponds to increased investment odds (figure 3; electronic supplementary material, table S4). Households in which the IBI between the first and second child was longer have increased investment odds, as do households who live on boats rather than land. The predictors included in any investment GLM explain approximately 81% of the variance in this outcome, and between 68 and 87% of the variance in 90% of our estimates (electronic supplementary material, table S3).

We identified the 24 maternal uncles providing some form of investment to at least one of their sisters' children and report summary statistics to characterize this sample of the Shodagor population (table 2). Notably, these men live on the land in a higher proportion than the general population. Two maternal uncles provided both direct care and indirect resources to their sisters' families, and the remaining 22 provided either direct or indirect investments, but not both. Among this sample of investing maternal uncles, first and second-born men provided more indirect resources, whereas men of later birth-orders provided more direct care to their sisters' children (figure 4).

4. Discussion

Investment by maternal uncles in their sisters' children is often discussed anecdotally but has rarely been explored empirically outside of the context of matrilineal inheritance. In our analyses, we examine the conditions under which maternal uncles invest in their matrilateral nieces and nephews through direct care and indirect investment in a society with flexible investment rules and no formal role for mothers' brothers. Results indicate that while direct care is predicted by ecological and economic variables, indirect care is associated with variables related to a mother's life-history strategy. Both types of investment are related to characteristics of a mother's natal family: as expected, more maternal uncles are associated with more direct care and children of a woman who is the firstborn in her family are more likely to receive indirect care. There also appears to be a cohort effect such that children of mothers born more recently are more likely to receive indirect investment from their maternal uncles. Our results also suggest that among

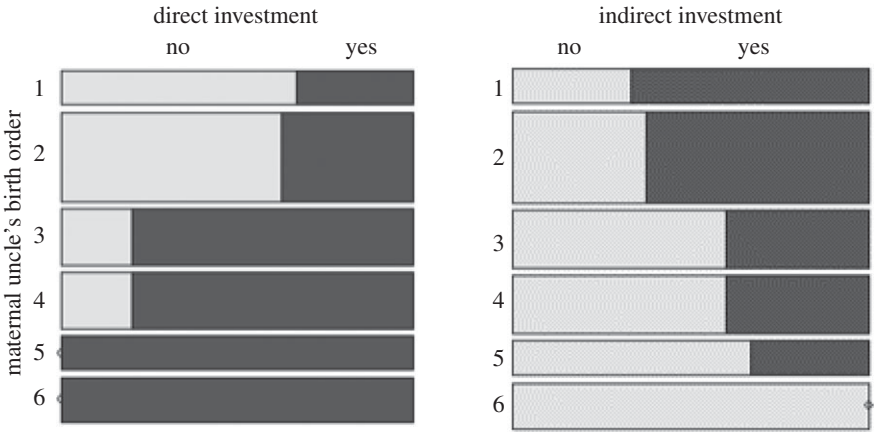

Figure 4. Proportions of maternal uncles providing direct and indirect investment, grouped by birth order (1, firstborn). Two maternal uncles provided both types of investment. $n = 24$.

investing uncles, their own ecological circumstances may be important and their birth order is associated with the type of investment they give. These results emphasize the importance of the Shodagor ecology in organizing male investment towards their matrilateral relatives. They indicate that need for alloparental investment and access to maternal uncles probably work together to determine when an uncle will invest in his sister's children. We suggest a potential mechanism by which investing in sisters' children may enhance a man's reproductive fitness.

(a) Ecological variables represent access to maternal uncles

In order for children to receive direct care from a particular set of kin, they must have access to one another throughout the year. Given this and that ecology also plays an important role in parenting and subsistence decisions [36], as well as and nutritional outcomes for all family members [87], it is not surprising that ecological variables representing family residence patterns predict direct care from maternal uncles. It is also not surprising that the more older brothers a woman has, the more likely her children are to receive direct care from one of her brothers. While postmarital residence, itself, was not included in any of the final models in this analysis, it may not be the best indicator of a family's current situation. Boat-dwelling is associated with an increased likelihood of direct care and is indicative of a family's ability to move between Shodagor communities to spend time with a variety of relatives. Results also show that when controlling for boat-dwelling, *fewer* movements throughout the year predict a higher chance of direct care. More data are needed in order to fully understand this relationship. However, we would expect to find that families who receive direct care from maternal uncles spend at least part of the year in the same community as those uncles, and that this would either be achieved by living in the same group and moving infrequently, or by moving the family's houseboat into the same group with one or more uncles throughout the year.

A mother's occupation is also associated with maternal uncle care, although not in the expected direction. Children of women who trade are less likely than women in other occupations to receive direct care from maternal uncles. Therefore, women who fish or are housewives are more likely to have brothers who care for their children. Given that women's occupations are tied closely to ecological circumstances [36] and that 82% of families in which women fish and 65% of families in which women are housewives live on boats, this result may be a part of a suite of results that reflect the importance of a family's ecological circumstances in determining a maternal uncle's investment. A woman's occupation may also reflect a family's need for additional investment from allocarers.

(b) Direct and indirect maternal uncle investment are a response to need

A family's need for allocare—in addition to access to alloparents–should be one of the primary predictors of receiving care. Variables that predict direct and indirect care are indicative of different types of need for Shodagor families. Boat-dwelling presents unique ecological circumstances that pose an acute risk of drowning for young children. A majority of the country of Bangladesh lies in a large river delta, which floods during the rainy season, and drowning is one of the leading causes of death for non-Shodagor, land-dwelling, Bangladeshi children in Matlab [81]. Families who live on boats are surrounded by water year-round, while those in this study who live on the land are only surrounded by water during the rainy season [36]; therefore, boat-dwelling should present an even greater risk of drowning for Shodagor children. Owing to the association between living on a boat and women's occupation, this risk may be compounded for mothers who are housewives, as they are more likely than other women to have very young children [36].

Shodagor families take measures to prevent drowning by teaching children to swim at an early age, having fathers stay at home with children while the mother works, and using mostly adults as allocarers [36]. When examining the characteristics of some of the uncles who invest in their sisters' children, we also find that most of them live on land. This creates a scenario in which most investing uncles live on the land and most families who are recipients of care live on boats. This relationship probably indicates that these men have an increased ability to respond to the caregiving needs of their sisters' families. Our results suggest that maternal uncles may be an important part of a constellation of carers who provide a buffer against the increased drowning risk associated with boat-dwelling.

In contrast with the need for direct care, indirect investment should be associated with financial (or subsistence-based) needs. We might expect this to be reflected in a household's income, but this was not an important predictor of indirect investment from Shodagor maternal uncles. The Shodagor economy is mixed, with around 80% of families regularly practicing subsistence fishing [18], so income may not be the best measure of need. Instead, we suggest that variables associated with a woman's reproductive decision-making may be a better indicator of a family's need for additional investment. For example, a family with more children may need help providing food or clothing for those children. Results show that women who have lost at least one child are more likely to receive indirect investment from their brothers. We do not have the data that would allow us to determine whether or not uncles invested in children prior to their deaths, but we do not suggest that children with more maternal uncle investment are more likely to die. Instead, child loss is probably representative of a family's need for additional help.

Children of women with longer IBIs following their first birth are also more likely to receive indirect investment from their mothers' brothers. A longer IBI could signal need in cases where it is related to lactational amenorrhoea or general inability to conceive owing to nutritional deficiencies (for review, see [88]). A longer IBI can also indicate a family's pursuit of a 'quality' life-history strategy in which parents and alloparents invest more resources into fewer children [88,89]. This strategy is also characterized by longer birth spacing and lower mortality, and is often representative of societies undergoing a demographic transition (e.g. [90]). While children of women born more recently are more likely to receive indirect investment from mother's brothers (which might suggest that a demographic transition is underway), if uncles were contributing to the 'quality' of their nieces and nephews, as opposed to responding to need based on nutritional deficiencies, we might expect them to invest in children's education or marriage. Instead, the data show that treats (which are often chips, cookies, ice cream or other high-calorie, market foods) are the most common type of indirect investment, followed by food and clothing. Although 'treats' may contribute to a child's caloric intake, neither the magnitude nor the function of the contribution is clear and more data are necessary to understand the importance of this type of investment.

(c) Trading, women's autonomy and paternity uncertainty

We expected women's trading to be associated with maternal uncle investment because cooperation among women, women's autonomy, and a potential for higher levels of paternity uncertainty characterize trading and matrilineal kinship systems. Instead, children of mothers who trade are less likely to receive investment from their uncles. This could be owing to the two factors we have already discussed: more than half (54%) of families in which women trade live on the land and may not live near any maternal uncles; and because women's trading can produce higher incomes than fishing and fathers often watch young children while women work [18], these families may have less need for additional investment. It also appears to be the case that paternity certainty is not an important predictor of maternal uncle investment. Our data show that most women in the study have not been divorced and even fewer have been remarried. There are also very few cases of husband absence when children were young. While it is true that these are not the only—or even the best—ways to measure paternity certainty within a society, these results are consistent with our expectations based on cultural factors as well as models which suggest that unrealistically low levels of paternity may not be necessary for matrilineal inheritance patterns to be evolutionarily stable [5,33]. In addition, we suggest that owing to the divisible nature of the types of investment we are exploring in this paper, men are not necessarily required to choose between investing in their sisters' children and their own. In cases where investment is inexpensive and is not 'all-or-nothing', levels of paternity uncertainty should need to be even higher before a man is motivated to cease investment in his own children in favour of his nieces and nephews. Given this, the cooperative nature of women's trading should prevent against necessarily high levels of infidelity and paternity uncertainty.

(d) When does maternal uncle investment make evolutionary sense?

Hrdy & Judge [17] show that ecologically imposed limitations on resources may provide an evolutionary explanation for rules of unigeniture. Shodagor people recognize partible inheritance rules, in which all children (regardless of gender or birth order) are expected to receive investment, and do not have formal rules regarding maternal uncle investment. However, the data show that children of women who are firstborn are more likely to receive indirect investment from their mothers' brothers than those whose mothers were born later in the birth order. Given that nearly all Shodagor families in the study area have very few material resources, it is reasonable to assume that the choice to invest in one sister's children over others may be owing in part to resource limitations and a desire to maximize investment. Additionally, disproportionate investment in the children of a firstborn sibling could result from earlier-born children presenting lowered opportunity costs for uncles (i.e. if they do not yet have children of their own) as lower investment costs should increase inclusive fitness benefits [27]. Patterns in the data on Shodagor men who invest in their sisters' children add support for this scenario.

One of the shortfalls of this study is that the data were not collected for the specific purpose of understanding maternal uncle investment (but for investment from all possible sources), so specific details about all investing uncles are not currently known. Therefore, we are unable to compare investing uncles against those who do not. However, of the 24 uncles we were able to identify who gave some investment, one of the patterns that stands out in the data is that uncles born earlier in the birth order were more likely to invest indirectly, while those born later were more likely to invest directly in their sisters' children (figure 4). It is important to point out that while these trends may appear to oppose model results, the trends show that brothers from a particular end of the birth order are more likely to invest, while the model results inform on where the receiving sister stands in the birth order in relationship to her investing brothers.

A maternal uncle should incur lower costs to investing in nieces and nephews when it does not negatively impact his ability to invest in his own children (see also [55]). For Shodagor uncles, this may be the case under multiple scenarios. First, if older uncles have more resources to invest, they may be able to do so without diverting resources away from their own children. Maternal uncle investment may also come at a lower cost when a man has no children of his own to invest in. This is probably more likely to be the case for uncles born later in the birth order than those born earlier, or when an elder sister reproduces before her younger brothers.

The ecological conditions experienced by recipients of care (who are more likely to live on boats) and caring uncles (who are more likely to live on land) may work together to decrease uncles' opportunity costs and increase inclusive fitness benefits to investment in sisters' children in the following ways. If an uncle lives on land, his own children may face lower risk of drowning than those living on boats. If this is the case, they may require less (or less vigilant) direct care, resulting in more time available to care for his sister's children. Care from maternal uncles living on land could also further reduce his nieces' and nephews' risk of drowning, given that he can watch them in or near his house, rather than on a boat. If chances of niece/nephew survival are increased, maternal uncles have a better chance of reaping inclusive fitness benefits. And if chances of inclusive fitness benefits can be increased without increasing costs to a man's own children, he can maximize individual reproductive fitness.

5. Conclusion

One of the key questions in the 'matrilineal puzzle' is: why would maternal uncles invest in their sisters' children instead of their own? While this question is almost always asked in reference to inheritance of land and other large resources, maternal uncles often invest in other ways as well, both in matrilineal and non-matrilineal societies. Investment of direct care or smaller, more easily divisible resources like food, money and clothing can be invested simultaneously in multiple children, including a man's nieces and nephews as well as his own children. Kin selection theory suggests that men gain an inclusive fitness benefit from investing in their siblings' children [27] and models of daughter-biased investment suggest there is often more to gain from investing matrilaterally than patrilaterally [10,11,79]. Our analyses show that in a semi-nomadic society with bilateral inheritance rules, multilocal postmarital residence patterns, high presumed levels of paternity confidence and no formal role for mother's brothers, maternal uncles appear to be investing in their sisters' children under circumstances that are likely to be important to those children's survival and well-being. We would expect maternal uncles in other societies to make similar investment decisions. While direct investment is probably less common cross-culturally, given the unusually high amount of Shodagor male care, it may be particularly important in cases of extreme need that are associated with difficult and dangerous environments. Indirect investment in the form of more easily divided resources like food or money for clothing should be associated with factors in a sister's reproductive history—whether as a driver of reproductive outcomes or as a response to them—that indicate greater need for material investment (i.e. women who have lost children, women with more children to feed, etc.). We also expect the nature of investment to be based on a maternal uncle's own characteristics. Among the Shodagor, when older brothers invest indirectly and younger brothers directly, neither may face stark trade-offs between investing in sisters' or one's own children, in which case the inclusive fitness benefits make investment less puzzling. Much more empirical work on the investment patterns of maternal uncles needs to be done across societies with different social structures and kinship systems in order to understand the evolutionary implications of such behaviour. In addition, work on downstream consequences of investment on maternal uncles' reproductive fitness, including health and survival outcomes for children receiving investment, are necessary to reveal the adaptive nature of such investment.

Ethics. This research was reviewed and approved by the University of Missouri's Institutional Review Board as well as the Ethical Review Committee at the International Centre for Diarrhoeal Disease Research, Bangladesh (ICDDR,B).

Data accessibility. Code and data available at: https://github.com/kstarkweather8/Maternal-Uncle-Phil-Trans.

Authors' contributions. K.S. designed the study and collected data. M.K. performed analysis. K.S. and M.K. drafted the manuscript.

Competing interests. We declare we have no competing interests.

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