The evolution of matrilineal kinship organization
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Matrilineal kinship organization is a human social system that emphasizes interactions between matrilineal kin, i.e. individuals related only through females. The ‘matrilineal puzzle’ refers to the potential for tension characteristic of this social system, owing to the conflict between the interests and responsibilities of men in their roles as brother/uncle versus husband/father. From an evolutionary perspective, matrilineal kinship organization is puzzling when it diverts investment of resources from the individuals who provide the potentially highest reproductive returns. I use a game-theoretic framework to investigate a particular form of matrilineal inheritance—the transfer of property from a maternal uncle to a sororal nephew. The analysis reveals two mechanisms that may make this strategy a stable evolutionary outcome. First, a polygynous male has multiple wives, and hence multiple brothers-in-law; with matrilineal inheritance, each additional brother-in-law may transfer resources to the male’s wife’s offspring, thus potentially contributing to the male’s inclusive fitness. Second, the husband of a polyandrous female is effectively ‘sharing’ paternity with other men; depending on the number of husbands, he may be better off investing in his sister’s offspring. I conclude by discussing how these results address the challenges posed by the occurrence of matrilineal kinship organization.

Keywords: matrilineal kinship organization; mother’s brother–sister’s son inheritance; paternity threshold; kinship; kin-biased investment; human social behaviour

1. INTRODUCTION

(a) The matrilineal puzzle

Compared with other species, humans show a remarkable degree of variation in social organization across groups [1]. Explaining particular facets of this variation has proved especially difficult, however. One challenge is the occurrence of matrilineal kinship organization, a social system that emphasizes interactions between matrilineal kin, i.e. individuals related only through females [2, pp. 43–44]. In a given society, the emphasis on matrilineal kin may be expressed in one or more social domains, including the norms regulating inheritance, succession to office, marital residence, authority within the family, and descent [3, p. 207].

In each of these domains, matrilineal kinship may be used as one of the criteria for the allocation of rights and duties among individuals [4, p. 47]; other possible criteria include age, gender or status. Unlike alternative arrangements (e.g. allocation based on patrilineal kinship), matrilineal kinship organization may involve conflict between the interests and responsibilities of men in their roles as brother/uncle versus husband/father, especially where men hold control of the resources (i.e. resources proceed between males, but via females). The notion of the ‘matrilineal puzzle’ [3, p. 246] captures the potential for tension inherent in the matrilineal arrangement. This social system has been the focus of extensive anthropological research since the late nineteenth century [5], yet the puzzle is still unsolved.

(b) The paternity threshold model

In evolutionary terms, different social arrangements can be viewed as biases in investment towards particular sets of kin. The question then becomes whether these biases can be understood as the outcome of the strategic behaviour of individuals in the allocation of resources to their relatives. Within this framework, matrilineal kinship organization is puzzling when it diverts investment of resources from the individuals who provide the potentially highest reproductive returns. For example, in a particular form of matrilineal inheritance, mother’s brother–sister’s son inheritance, property is transferred from a maternal uncle to a sororal nephew, although a man’s own children likely provide higher reproductive returns. This form of matrilineal inheritance is a rare but recurrent practice across human societies: in the Standard Cross-Cultural Sample [6], it occurs in 8 per cent of societies for land and in 9 per cent of societies for movable property.

Evolutionary approaches to matrilineal kinship organization view investment in matrilineal kin as an accommodation to low probability of paternity—essentially a form of ‘insurance’ against cuckoldry [7]. With mother’s brother–sister’s son inheritance, the key is that a man’s wife’s children are not necessarily his own children; in other words, a man may or may not be related to his wife’s offspring. By contrast, he is always related to his sister, through his mother if not through his father; consequently, he is always related to his sister’s offspring. This implies that he may be better off investing in his sister’s children if the probability that he fathered his wife’s children is low.

The ‘paternity threshold model’ [8, p. 155] formalizes this line of reasoning within the context of inclusive fitness theory [9]. In its simplest formulation, the model rests on comparison of the coefficients of relatedness...
between a man and wife’s versus sister’s offspring, as a function of the probability of paternity. The comparison sets at $2 - \sqrt{3} \approx 0.268$ the paternity threshold, i.e. the probability of paternity below which a man is better off investing in his sister’s children rather than in his wife’s ([10]; see Rogers [11] for critical discussion).

This value seems, however, unrealistically low. For example, among the Himba of the Omuhabga basin in the Kunene region of Namibia, women attribute 17.6 per cent of marital births to extra-pair matings (ranging from 0% of marital births within ‘love match’ marriages to 23.2% within arranged marriages) [12]. Even though this is the highest rate of extra-pair paternity reported for a small-scale, natural fertility human population, it corresponds to a probability of paternity substantially higher than the threshold value ($\approx 0.8$ versus $\approx 0.3$). In this population, inheritance of cattle is matrilineal, down lines of maternally related brothers and maternal related sororal nephews [13, pp. 53–54]. In an idealized scenario, upon death of a man, his cattle are inherited by the eldest of his surviving full brothers (i.e. brothers by the same mother; the man’s father may have multiple wives). When there are no surviving brothers in this line, the cattle are transferred to the eldest son of the eldest full sister and, upon his death, to his brother(s). When there are no surviving brothers in this line, the cattle are transferred to the eldest son of the second-eldest sister, and so on.

Assuming that comparable (or higher) probabilities of paternity characterize mating behaviour across human populations [14], the paternity threshold model seems implausible in its simplest formulation. This has spurred the development of several extensions to the model, in an attempt to find scenarios that yield realistic threshold values (e.g. [7,8,15–17]). More recently, Rogers [11] showed that all formulations of the model make restrictive assumptions in the estimation of the coefficients of relatedness, such as even allocation of sexual access among extra-pair mates. Each of these assumptions reduces the probability that two sibs share a father and, consequently, the estimated relatedness of men to sister’s offspring. Relaxing one or more of the assumptions, the threshold value increases within a region delimited by the lower bound of 0.268 and an upper bound of $\frac{1}{2}$. Thus, even under the conditions most favourable to the model (i.e. when all assumptions are relaxed), the paternity threshold is substantially lower than observed probabilities of paternity.

(c) Objective

While appealing for its intuitive simplicity, the paternity threshold model fails to explain biases in investment towards matrilineal kin, as in mother’s brother–sister’s son inheritance. This suggests that we move beyond the quest for plausible threshold values and explore the interaction of inheritance strategies with known social and ecological influences (reviewed in recent studies [18,19]).

Fortunato & Archetti [20] developed a game-theoretic framework to investigate the interplay between behavioural strategies relating to marriage, property transfer and level of paternity. Addressing the question of the evolution of monogamous marriage, they showed that this marriage strategy may be advantageous over polygynous marriage because it ‘concentrates’ resources in a limited number of heirs. It may also be advantageous because a woman may grant her husband higher levels of paternity if he marries monogamously, leading to exclusive investment of his resources in her offspring. One prediction of the analysis was the positive association between monogamous marriage and the transfer of property to wife’s offspring, as opposed to alternative inheritance strategies [21].

Here, I apply the framework developed in Fortunato & Archetti [20] to explore a complementary question: under which conditions does the transfer of property to sister’s offspring represent a stable evolutionary outcome? Like the paternity threshold model, this framework captures the notion of strategic male behaviour in response to paternity level. Additionally, it includes all possible marriage strategies, strategic male behaviour in response to the marriage strategy of females, strategic female behaviour in response to the marriage strategy of males, and the effect of resource types characteristic of different subsistence systems. None of these factors have been explored in previous theoretical work.

2. THEORETICAL FRAMEWORK

The framework developed in Fortunato & Archetti [20] focuses on the decisions faced by both males and females with respect to marriage strategy, by males with respect to transfer strategy, and by females with respect to paternity strategy. Here, I outline the rationale for each of these components of the framework and how they are implemented; additional details are in the electronic supplementary material, section S1.

(a) Marriage strategy

(i) Rationale

Through the implicit assumption of monogamous marriage, all formulations of the paternity threshold model overlook the potential interaction between marriage and transfer strategies.

The marriage strategy of males seems relevant because it affects the optimal pathway in the transfer of property [20]. For example, where the value of resources is depleted through division among multiple heirs, it may be advantageous to concentrate resources in a single heir (§2c). Where males marry polygynously, investment in a single heir may be easier to implement among the children of sisters than among the children of wives (e.g. the eldest son of the eldest sister, as in the Himba case described in §1b, versus the eldest son of the first wife). This is because each wife is likely to ‘demand’ a share of the husband’s resources as a condition of marriage, whereas sisters come without such demands.

The marriage strategy of females seems relevant because it affects the relatedness of men to wife’s and sister’s offspring. The paternity threshold model focuses instead on how relatedness varies with the probability of paternity (as determined by the rate of extra-pair paternity). Crucially, however, in a polyandrous marriage, multiple men effectively ‘share’ one wife. For example, even in a population with no extra-pair paternity, the relatedness of a man to his wife’s children depends on whether the wife has any additional husbands, and how many.

(ii) Implementation

In a population of $n$ males and $n$ females, individuals marry monogamously or polygynously, with $n \geq 1$ wives for
males and $h \geq 1$ husbands for females; they have perfect knowledge of the marriage strategy of their spouse(s).

(b) Transfer and paternity strategies

(i) Rationale

The paternity threshold model hinges on the notion of strategic male behaviour in the allocation of resources: males invest in wife's or sister's offspring, opting for one or the other strategy based on the probability of paternity. In all formulations of the model, females play a passive role.

The framework developed in Fortunato & Archetti [20] extends the reasoning in two ways. First, in addition to responding strategically to the level of paternity, males may respond strategically to the marriage strategy of females (§2a). Second, the framework includes the notion of strategic female behaviour in the allocation of paternity to males, based on the level of male investment in a female's offspring (as determined by the marriage strategy of males).

(ii) Implementation

Individuals in the population have one sibling of the opposite sex. Males transfer resources to the next generation 'vertically' to their wife's (or wives') offspring or 'diagonally' to their sister's offspring. The resources of married females are controlled by their husbands, i.e. a male controls his own resources $\delta_m$ and a share $1/h$ of the resources $\delta_i$ of each of his $w$ wives. Unmarried females transfer resources to their own offspring, whereas unmarried males transfer resources to their sister's offspring (see the electronic supplementary material, figure S1).

Females give their husbands 'high' paternity $p_L$ or 'low' paternity $p_H$, with $0 < p_L < p_H \leq 1$. They obtain an advantage $0 < \alpha < \frac{1}{2}$ from mating with other males besides their husbands, i.e. $\alpha_L$ for low-paternity females and $\alpha_H$ for high-paternity females, with $\alpha_L > \alpha_H$. $\alpha_H = 0$ for $p_H = 1$. This reflects the incentive for females to engage in extra pair mating, which may be, for example, in the form of genetic benefits or resource contributions [22]. Males can infer their level of paternity $p_L$ or $p_H$ from direct phenotypic or indirect behavioural cues; in humans, the latter include the conformity of females to cultural norms regulating their sexual behaviour.

The game set-up also includes male and female strategies that are conditional upon the behaviour of individuals of the opposite sex. The transfer strategy of males may be conditional upon the marriage and paternity strategies of females: a 'suspicious' male transfers vertically if his wives are monogamous and provide paternity $p_{1L}$, diagonally otherwise; an 'ingenious' male transfers diagonally if his wives are monogamous and provide paternity $p_{1H}$, vertically otherwise. The paternity strategy of females may be conditional only upon the marriage strategy of males: an 'astute' female provides paternity $p_{1H}$ if her husbands marry monogamously, $p_L$ otherwise; a 'naive' female provides paternity $p_L$ if her husbands marry monogamously, $p_{1H}$ otherwise.

(c) The effect of inherited resources on fitness

(i) Rationale

The effect of concentrating resources in a single heir versus dividing them among multiple heirs likely depends on the type of resources transferred (§2a); in the transfer of property, this is closely linked to the subsistence system [18–20]. A useful distinction is between subsistence systems where productive resources are scarce and those where they are not: scarcity provides an incentive to concentrate resources in a single heir, as their value may be depleted through division among multiple heirs. The first category includes intensive agriculture (i.e. plough or irrigation agriculture): high productivity results in land scarcity, with division among multiple heirs leading to plots of land that are too small to sustain a household. The second category includes extensive agriculture (or horticulture, i.e. hoe agriculture) and pastoralism. In horticulture, scarcity of land is unlikely because productivity is low. Pastoralism is characterized by the self-generating property of the resources (i.e. livestock reproduce), which acts as a buffer against scarcity: for example, two halves of a herd can each potentially grow back to the original herd size.

(ii) Implementation

Each female produces one male and one female offspring. Each sibling pair in the offspring generation inherits resources $\delta$. For example, $\delta = \delta_h + \delta_i = 1$ in a population where males and females marry monogamously and males transfer vertically, with $0 \leq \delta_h \leq 1$ and $0 \leq \delta_i \leq 1$ the male and female contributions to $\delta$.

The fitness of each sibling pair in the offspring generation is given by $z$, where $z > 0$ is a parameter determining the relationship between the amount of resources and their fitness value to the heirs. Specifically, $z = 1$ gives linear returns to scale in fitness, $z < 1$ decreasing returns to scale and $z > 1$ increasing returns to scale. For example, consider the case of a male transferring two units of resources to one heir (e.g. one sibling pair, the offspring of one wife) versus one unit each to two heirs (e.g. two sibling pairs, the offspring of two wives). With linear returns to scale (i.e. $z = 1$), the two strategies are equivalent. With decreasing returns to scale (i.e. $z < 1$), the fitness value of an additional unit of resources declines with each unit invested; consequently, the male is better off transferring one unit each to two heirs. With increasing returns to scale (i.e. $z > 1$), the fitness value of an additional unit of resources grows with each unit invested; consequently, the male is better off transferring two units to one heir.

(d) Inclusive fitness payoffs and analysis

The possible combinations of male and female strategies differ in inclusive fitness payoffs. The payoffs are used to derive evolutionarily stable equilibria consisting of a pair of strategies, one male and one female, that cannot be invaded by rare mutants playing alternative strategies [23].

The inclusive fitness payoff for a focal male in the parent generation is given by (i) the fitness value of the resources inherited by his wife's (or wives') offspring and (ii) the fitness value of the resources inherited by his sister's offspring. The payoff for a focal female is given by (i) the fitness value of the resources inherited by her brother's wife's (or wives') offspring, (ii) the fitness value of the resources inherited by her own offspring, and (iii) any advantage she obtains from extra-pair mating. Resources are divided equally among the offspring of multiple wives.
In both cases, components (i) and (ii) are scaled by the relevant coefficient of relatedness (see the electronic supplementary material, table S1). The formulations of the coefficients include simplifying assumptions analogous to those analysed by Rogers [11], for example that a female's $h$ husbands have equal probability of fathering her offspring. As discussed in §1b, Rogers [11] showed that each of these assumptions reduces the estimated relatedness between sibs. The implication for the present analysis is that it rests on the lower bound of relatedness between men and sister's offspring; consequently, the relative benefit to men from investing in sister's offspring is understated. In other words, the analysis is conservative [11].

3. RESULTS
I begin by replicating the scenario captured by the paternity threshold model (§3a); I discuss this case in detail to build intuition for the modelling framework. In the remainder of the section, I outline the general qualitative pattern that emerges from the analysis (§3b).

(a) The paternity threshold model scenario
The paternity threshold model scenario can be replicated by restricting the analysis to males who marry monogamously and transfer vertically or diagonally, with females who marry monogamously and provide a generic level of paternity $0 < p \leq 1$, and assuming that fitness is linear in resources (i.e. $z = 1$).

The condition for stability of the resident male strategy is derived by comparing its inclusive fitness payoff to the payoff for the mutant male strategy; these are derived in the electronic supplementary material, section S2.1. In a population of resident males who transfer diagonally, the condition for stability of a resident male against a mutant male who transfers vertically is

$$p^2 + 4(1 - 2^z)p + 1 > 0. \quad (3.1a)$$

In a population of resident males who transfer vertically, the condition for stability of a resident male against a mutant male who transfers diagonally is

$$(1 - 2^z)p^2 + 4p + 1 - 2^z > 0. \quad (3.1b)$$

Equations (3.1a) and (3.1b) are plotted in figure 1; the grey-shaded areas represent the values of $p$, for a given value of $z$, for which resident males are stable in the two cases. The boundaries of the two regions intersect at $z = 1$ and $p = 2 - \sqrt{3}$. This value of $p$ corresponds to the ‘classical’ paternity threshold derived in previous theoretical work (§1b). Put differently, figure 1 shows that the classical threshold is relevant only under the assumption that fitness is linear in resources (i.e. $z = 1$). Relaxing this assumption reveals an interaction between transfer strategy, type of resources transferred and paternity level.

To understand the interaction, consider the scenario leading to equation (3.1a). In the case of a resident focal male, two units of resources are allocated to two sets of heirs (i.e. one unit to wife’s offspring, transferred by the wife’s brother, and one unit to sister’s offspring, transferred by the focal male; all males transfer diagonally). In the case of a mutant focal male, two units of resources are allocated to one set of heirs (i.e. two units to wife’s offspring, one transferred by the wife’s brother, who transfers diagonally, and one by the focal male, who transfers vertically). With decreasing returns to scale (i.e. $z < 1$), the fitness value of the resources is greater if they are divided between two sets of heirs (§2c), leading to an increase in inclusive fitness for a resident focal male compared with a mutant male. This counters the effect of the difference in relatedness to wife’s versus sister’s offspring; as a result, the resident male is stable for values of $p > 2 - \sqrt{3}$. Analogous reasoning applies with increasing returns to scale (i.e. $z > 1$). Further details are in the electronic supplementary material, section S2.2.

(b) Stability of diagonal transfer
Table 1 shows which pairs of male and female strategies resulting in diagonal transfer are stable when the analysis is extended to the full set of behavioural strategies; a detailed example is in the electronic supplementary material, section S3. Here, I provide a qualitative account of key mechanisms underlying the stability of diagonal transfer.

(i) Polygynous males
The first insight to emerge from the full analysis relates to the effect of males marrying polygynously. To understand this effect, consider a population of males who marry monogamously or polygynously and transfer diagonally, with females who marry monogamously and provide a generic level of paternity $0 < p \leq 1$; for simplicity, assume that $b_h = 0$ and $z = 1$.

In a population of resident males who marry polygynously, the inclusive fitness payoff for a resident focal male includes the resources transferred to his wives’ offspring by the brother of each wife, and the resources transferred to his sister’s offspring by the focal male himself. The payoff for a mutant focal male who marries monogamously includes the resources transferred to his wife’s offspring by the brother of his only wife, and the resources transferred to his sister’s offspring by the focal
male himself. This implies that with diagonal transfer a focal male benefits from marrying polygynously: each wife comes with a brother who transfers resources to her offspring, i.e. the focal male’s wife’s offspring. Consequently, the resources that potentially contribute to the inclusive fitness payoff for a focal male increase with each additional wife. Note that if \( \delta_t \neq 0 \), there may be a further benefit to males from marrying polygynously, deriving from the resources contributed by each wife.

The advantage of polygynous marriage to males may be modulated by additional factors. For example, males who marry polygynously obtain lower paternity, compared with males who marry monogamously, from astute females (i.e. \( p_L \) versus \( p_{LB} \) [28]). Overall, however, all stable cases involving diagonal transfer also involve polygynous marriage for males (table 1). This implies that a population of males who marry monogamously and transfer diagonally, as in the paternity threshold model scenario (§3a), is not an evolutionarily stable outcome.

(ii) Polyandrous females

The second insight to emerge from the full analysis relates to the effect of females marrying polyandrously. To illustrate this effect, it is useful to compare the coefficients of relatedness between a male and wife’s versus sister’s offspring, in the simplest scenario where females marry \( h \geq 1 \) husbands and provide a generic level of paternity \( 0 < \rho < 1 \). Given these generic values of \( h \) and \( \rho \), and using the notation in the electronic supplementary material, section S1, the coefficients of relatedness for a focal male are \( r_{M\ell} = \rho/(2h) \) to wife’s offspring and \( r_{M\ell} = \left(\frac{h}{2}\right)(1 + \rho^2/h) \) to sister’s offspring (see the electronic supplementary material, table S1).

These are plotted in figure 2 for different values of \( h \). With \( h = 1 \), \( r_{M\ell} > r_{M\ell} \) for \( 0 < \rho < 2 - \sqrt{3} \approx 0.268 \) (figure 2a), corresponding to the range of values captured by the paternity threshold model. The range of values increases to \( 0 < \rho < 2 - \sqrt{2} \approx 0.586 \) with \( h = 2 \) (figure 2b); \( 0 < \rho < 1 \) with \( h = 3 \) (figure 2c); \( 0 < \rho < 1 \) with \( h = 4 \). This is because as \( h \to \infty \), \( r_{M\ell} \to 0 \) while \( r_{M\ell} \to \frac{h}{2} \). As discussed in §2a, the exact values will depend on the specific assumptions made in formulating the coefficients of relatedness [11]. However, the qualitative effect is clear: a growing number of husbands for females reduces the relatedness of males to wife’s and sister’s offspring, with a stronger effect on the former. This may increase the relative benefit to men from investing in sister’s children.

Finally, note that while males may be better off transferring diagonally when females marry polyandrously, females obtain no benefit from marrying polyandrously when males transfer diagonally. This is because each additional husband transfers resources to his own sister’s offspring, rather than to the offspring of a focal female. Consequently, all stable cases involving diagonal transfer involve monogamous or polyandrous marriage for females (table 1; technically, females who marry monogamously and polyandrously are neutrally stable).

4. DISCUSSION

Matrilineal kinship organization is a human social system that emphasizes interactions between matrilineal kin, i.e. individuals related only through females. The ‘matrilineal puzzle’ [3, p. 246] refers to the potential for tension characteristic of this social system, owing to the conflict between the interests and responsibilities of men in their roles as brother/uncle versus husband/father (§1a).

From an evolutionary perspective, matrilineal kinship organization is puzzling when it diverts investment of resources from the individuals who provide the potentially highest reproductive returns (§1b).

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Table 1. Pairs of male and female strategies resulting in diagonal transfer and their stability.*

<table>
<thead>
<tr>
<th>Male strategies</th>
<th>Female strategies</th>
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<tbody>
<tr>
<td>MV (MV, ML)</td>
<td>MN (MV, PL)</td>
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<td>MD (MD, ML)</td>
<td>PL (MV, PH)</td>
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<td>MI (MV, ML)</td>
<td>PA (MV, PH)</td>
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<tr>
<td>PV (PV, ML)</td>
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*XY denotes the marriage strategy X and the transfer strategy Y for a male; XZ denotes the marriage strategy X and the paternity strategy Z for a female; (XY, XZ) denotes a pair of male and female strategies (29). XY marriage strategy (§2c): M, monogamous; P, polygamous. Transfer strategy (§2d): V, vertical; D, diagonal; S, suspicious; I, ingenuous. Paternity strategy (§2c): L, low; H, high; A, astute; N, naive. Pairs of strategies resulting in diagonal transfer are in bold; of these, the stable ones are shaded in grey. Note that all stable pairs involving diagonal transfer result in polygynous marriage for males and low paternity for females. This is because all stable cases involve polygynous marriage for males: astute females respond to polygyny by providing low paternity and, in turn, suspicious males respond to low paternity by transferring diagonally (§2b).

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Figure 2. Coefficient of relatedness \( r \) between a male and wife’s offspring (\( r_{M\ell} \), solid line) and between a male and sister’s offspring (\( r_{M\ell} \), dashed line) as a function of paternity \( \rho \) for (a) \( h = 1 \), (b) \( h = 2 \), (c) \( h = 3 \) husbands.
I used the game-theoretic framework developed in Fortunato & Archetti [20] to investigate the evolution of mother's brother–sister's son inheritance, a form of matrilineal inheritance where property is transferred from a maternal uncle to a sororal nephew. The analysis explored under which conditions this arrangement represents a stable evolutionary outcome. Below, I discuss the implications of the results for our understanding of matrilineal kinship organization.

(a) Paternity thresholds
Previous theoretical work aimed at determining the value of the paternity threshold, i.e. the probability of paternity below which a male has higher relatedness to sister's children than to wife's children; below this threshold, natural selection should favour investment in sister's offspring (§1b). This body of work crystallized in the empirical prediction of a one-to-one correspondence between matrilineal kinship organization and behaviours resulting in low probability of paternity, such as widespread promiscuity (e.g. [7,10,15,16,24,25]; see [26–28] for critical discussion).

I extended the scenario captured by previous theoretical work to include the effect of the type of resources transferred (i.e. linear, decreasing or increasing returns to scale in fitness from inherited resources). This extension rests on the widely posted association between inheritance strategies and subsistence systems (reviewed in recent studies [18,19]; see Aberle [29] for an example in the context of matrilineal kinship organization). The extended scenario shows that the classical threshold value applies only under the restrictive assumption that fitness is linear in resources (§3a).

Focusing on the assumptions implicit in the estimation of the coefficients of relatedness, Rogers [11] recently showed that the classical threshold is a lower bound on the relatedness of men to sister's offspring, and that the paternity threshold is expected to vary across populations from this lower bound to an upper bound that is substantially higher (§1b).

Together, these results indicate that there is no single threshold value. This suggests that we move away from the notion of a one-to-one correspondence between matrilineal kinship organization and low probabilities of paternity, to explore general mechanisms that may underlie biases in investment towards matrilineal kin.

(b) Polygynous males, polyandrous females
The analysis reveals two mechanisms, both relating to the potential benefits to men of investment in sister's children when marriage is polygamous.

The first mechanism is that matrilineal inheritance may be advantageous for males when males marry polygynously. Additional wives correspond to additional resources potentially contributing to the inclusive fitness of a focal male; the resources may be transferred by the wives themselves and/or by their brothers. A related insight is that transfer to sister's offspring may represent a strategy to concentrate resources in a single heir when males marry polygynously [20]. For example, resources may be inherited by the eldest son of the eldest sister, as in the Himba case described in §1b. The crucial difference between this arrangement and, say, inheritance by the eldest son of the first wife is that a woman's position as eldest or later-born sister is fixed at birth, whereas her position as first or subsequent wife is determined at marriage. Thus, women may 'opt out' of marriage to a married man where inheritance is exclusively by the offspring of the first wife, making polygynous marriage problematic.

The second mechanism to emerge from the analysis is that matrilineal inheritance may also be advantageous for males when females marry polyandrously. This marriage strategy drastically reduces the relatedness of men to wife's and sister's offspring. Because the effect is stronger on relatedness to wife's offspring, men may be better off investing in sister's offspring. At the same time, there is no obvious benefit to females from marrying polyandrously. Additional husbands do not contribute to the inclusive fitness of a focal female, because they transfer resources to the offspring of their own sisters. Whether polyandrous marriage provides less obvious benefits to females, as does polyandrous mating, is unclear [22]; if it does, these benefits may strengthen its interaction with matrilineal inheritance.

To the best of my knowledge, both mechanisms have been overlooked in the extensive literature on matrilineal kinship organization. This may be because polyandrous marriage is exceedingly rare across human societies, while polygynous marriage is exceedingly common (occurring, respectively, in 1% and 82% of societies in the Standard Cross-Cultural Sample [6]). The mechanisms crystallize in the prediction of a cross-cultural association between mother's brother–sister's son inheritance and polygynous marriage for males, coupled with either monogamous or polyandrous marriage for females (table 1). Additionally, they can inform further empirical investigation of the predicted association. For example, is there something peculiar in the workings of matrilineal inheritance (e.g. in the amount of resources or in the timing of the transfer) where it occurs with monogamous marriage for males? If so, how do these peculiarities offset the potential benefits to males from marrying polygynously?

A final insight relates to the interaction of matrilineal inheritance with polyandrous marriage. This suggests that, in addition to the handful of cases of simultaneous polyandry that are described ethnographically (e.g. [30]), we explore the association with sequential forms of polyandry, for example as obtains with frequent divorce and remarriage ([31], pp. 323–325; see Flinn [25], pp. 448–449, for discussion in the context of matrilineal kinship organization).

(c) The matrilineal puzzle recast
The matrilineal puzzle views the conflict that characterizes matrilineal kinship organization from the perspective of kin groups (§1a), i.e. what a man's matrilineal kin 'want' him to do (e.g. his sister and her offspring) versus what his patrilineal kin 'want' him to do (e.g. his wife's offspring, and his wife on their behalf). The present framework suggests viewing the conflict from the perspective of a focal male instead, i.e. what a man 'wants' to do versus what he 'wants' other men to do—including men in his own kin group and men in his wife's kin group. For example, among the Nayars of Kerala in southwest India, matrilineal inheritance gave way to patrilineal inheritance during the first half of the twentieth century. In this process, men supported the transition within their kin groups, while at
the same time opposing it within the kin groups of their wives [30, p. 62]—reflecting, respectively, what a man ‘wanted’ to do and what he ‘wanted’ other men to do.

Recasting the puzzle in these terms provides a more straightforward way to reconcile male control of the resources with the potential for tension inherent in the matrilineal arrangement. Alternative explanations rest on recourse to social pressure by kin groups: even where men hold control of the resources, they ‘succumb’ to the interest of their matrilineal kin, possibly against their own interest (e.g. [7]). Paraphrasing Hartung [7, p. 669], I argue that if pressure to conform to social norms does indeed play a role—and it does, in other human affairs—it is ultimately because each man is likely to be a brother’s son, a brother, a father, and a husband, who wants his own uncle, brother, son, and brother-in-law to follow the principles of matrilineal kinship organization.

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