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Evolution of polygamous marriage by maximization of inclusive fitness

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HIGHLIGHTS

- Polygyny is often associated with resouce transfer to a male's sister's offspring.
- Polyandry occurs in a few human societies.
- Resources and paternity determine the stability of marriage strategies.
- Resources depletion through division affects evolutionary stability.
- Paternity and co-husband relatedness are less relevant than generally believed

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ABSTRACT

The majority of human societies practice polygynous marriage, in line with the typical mating pattern found in mammals. Polygyny in humans is often associated with the transfer of wealth to a male's sister's offspring, and it has been suggested that this "mother's brother phenomenon" is adaptive when paternity confidence is low. Polyandry, on the other hand, while virtually unknown in mammals, is practiced by a few human societies, and it has been suggested that this is adaptive if the co-husbands are genetically related. The evolution of human marriage strategies, therefore, can be studied in the framework of kin selection and game theory, as strategic transmission of wealth by males and strategic paternity allocation by females can evolve to maximize inclusive fitness. Here I analyse the stability of polygynous and polyandrous marriage using a game theoretical model previously developed to study monogamy. I show that the "mother's brother phenomenon" depends on the degree of resource depletion through division, whereas the paternity threshold commonly discussed in the anthropological literature is largely irrelevant. Resource depletion through division is also the major determinant of the stability of polyandry, whereas relatedness between co-husbands is not essential. Finally, I show that when females control the transfer of their own resources, monogamy is stable under more general conditions than previously believed.

1. Introduction

Interactions between males and females often result in conflict as males and females have intrinsic asymmetries that lead to divergent interests. In mammals, the basic asymmetry is due to internal gestation: while maternity is always certain, paternity is not. On the other hand, females can reproduce only once or a few times per year, while males can potentially have hundreds of offspring per year. As a consequence females invest more than males in their offspring (Trivers, 1972; Alexander et al., 1979; Clutton-Brock and Vincent, 1991). This largely explains the prevalence of polygyny and the virtual absence of polyandry in mammals.

The majority of human societies (about 85%) practice polygynous marriage, while monogamy accounts for most of the remaining 15% and polyandry is very rare (Westermarck, 1921; Murdock and White, 1969). While the prevalence of polygyny may reflect the typical pattern of polygynous mating found in mammals, marriage is not equivalent to mating. Humans are different from most other species in that wealth can be transferred across generations, and marriage defines, among other things, who inherits this wealth. As the resources inherited by the progeny influence their survival and reproduction, strategic transmission of wealth is expected in humans, and preferences about the transmission of wealth can evolve.

Fortunato and Archetti (2010) pointed out that, while males often control the transfer of resources, females can allocate paternity strategically, conditional to marital status, and this may influence the evolution of marriage practices. In other words, males and females have not only different interests but also

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different powers, and under certain conditions monogamy is a rational decision for both males and females. This is the case if monogamy is associated with patrilineal transfer of resources, which is indeed found in about 90% of monogamous societies in the standard cross cultural sample (Murdock and White, 1969).

If this theory based on kinship and strategic inheritance of wealth is correct, it should be able to explain marriage systems other than monogamy. In particular it should be able to explain the diversity of polygynous marriage systems and the existence (and rarity) of polyandry. Here I extend the kinship theory based on the game-theoretical model of Fortunato and Archetti (2010) to polygyny and polyandry. The questions I address are two long-standing debates in the anthropological literature: the importance of the "mother's brother phenomenon" (for polygyny) and the importance of relatedness between co-husbands (for polyandry). Incidentally, this new analysis proves useful to extend previous results about monogamy as well.

1.1. Polygyny: The mother's brother phenomenon and the paternity threshold

While a female has no reason to transfer resources to anybody else than her own offspring, a male can find it profitable to transfer his wealth to his sister's rather than his wife's offspring. This "mother's brother phenomenon" (first described by Junod, 1912), has been reported for other unrelated human societies (Aberle, 1961), and while apparently surprising, it is easily explained in the framework of kin selection: a man is always related to his sister (and therefore to his sister's offspring) through their mother, but he may or may not be related to his wife's offspring. The paternity confidence threshold (Alexander, 1974) below which a man is better off transferring resources to his sister's offspring rather than to his wife's has been calculated to be 0.268 (Greene, 1978; Kurland, 1979; Hartung, 1981, 1985), and the coevolution of paternal investment and cuckoldry in humans has been discussed extensively in anthropology (see also Flinn, 1981; Cronk and Gerkey, 2007; Rogers, 1990; Geary, 2006). The 0.268 threshold is widely believed to be unrealistically low (Hartung, 1981, 1985; Anderson, 2006).

The existing literature has focused, however, on the strategic allocation of resources by males, whereas the strategic behaviour of females has been ignored. Fortunato and Archetti (2010) introduced female strategic behaviour in the analysis, which was however limited to the evolution of monogamy. In contrast to monogamous societies, polygyny is often associated with the "mother's brother phenomenon". Extending Fortunato and Archetti's framework to polygyny could therefore clarify the issue of the (unrealistically low) paternity threshold.

1.2. Polyandry: Resource depletion and relatedness between co-husbands

Among the few societies that are known to practice or have practiced polyandrous marriage are the Khasas of northern India (Jain, 1948; Majumdar, 1962; Saksena, 1962), the Tibetans of Nepal (Goldstein, 1974; Levine, 1977, 1980, 1988), the Lahul in northern India (Prince Peter, 1963; Parmar, 1975), and Ladak in Kashmir (Prince Peter, 1963), the Todas (Rivers, 1901; Prince Peter, 1963) and the Thandans (Aiyappan, 1935; Prince Peter, 1963) of southwest India, and the Kandyans of Sri Lanka (Prince Peter, 1963; Tambiah, 1966; Hiatt, 1980).

Why are these societies polyandrous? Polyandry is problematic from an evolutionary point of view because it reduces a male's fitness not only by limiting his reproductive success to one wife (like monogamy) but also by sharing the paternity to this wife's offspring with other co-husbands. Polyandry is not known to be prescribed by law. Why should males (who are generally in a position of power and can enforce female monogamy) deliberately choose to enter a polyandrous marriage? Westermarck's early suggestion (1921), that polyandry is an adaptation to limit population growth in environments where resources are scarce, does not explain adaptation from the point of view of the individual. Alexander (1974) proposed that multiple men in a household are an advantage if extensive labour force is necessary, for example in poorly-productive environments like the Tibetan plateau. It has been proposed that polyandry is chosen by males in order to reduce estate taxes, but evidence is scarce (Goldstein, 1971).

On the other hand, it has often been suggested in the literature cited above, that a polyandrous marriage may confer an advantage against a monogamous marriage if (i) the pooled resources inherited by multiple husbands, which individually would have little value, confer synergistic benefits to their household and (ii) if the husbands are related, so that the expected genetic loss associated with polyandry may be offset by sharing a wife with kin. In other words, if the co-husbands are brothers, polyandry allows them to preserve the value of the resources they inherit from their parents and to maintain a reasonable degree of genetic relatedness with their wife's offspring.

There is strong empirical evidence that pooling resources is actually important in polyandry, where land is usually the resource (as observed for monogamy, estates, as opposed to movable property, often leads to decreasing returns when split among multiple heirs; Fortunato and Archetti, 2010). It is also known that in most polyandrous societies co-husbands are indeed usually brothers ("fraternal polyandry"). It is difficult, however, to disentangle the importance of relatedness from the importance of resource depletion, since the co-husbands are both related and the heirs of parts of the same resources.

Furthermore, this can explain why polyandry is stable against monogamy, but it does not solve the main problem: why do males deliberately choose to marry one wife only, rather than being polygynous? That is, even if co-husbands are related and share the resources they inherited, why polyandry rather than polygynandry? In fact, it is known that polyandry is sometimes combined with polygyny: this is generally the case if a family has no male offspring: in this case sisters marry the same husband(s), which move into their household. What we want to explain is, however, not the behaviour of females in the case of an all-female offspring, but the behaviour of males: why should a male deliberately enter a polyandrous marriage rather than a polygynandrous marriage?

2. Model

The strategies of males and females determine how households are formed, how resources are transferred and genetic relatedness across generations; this determines inclusive fitness. Our goal is to describe under what parameters pairs of strategies (one for males and one for females) are stable. While the basic framework is the same as Fortunato and Archetti (2010), further parameters are introduced. Fortunato and Archetti (2010) assumed that a male has total control over the resources of his wives, which is not appropriate for many societies (both monogamous and polygynous) in which a wife's resources (property and labour) belong to her and her lineage (Murdock and White, 1969; Goody, 1976, 1983). Therefore, here I extend the model to allow wives to control their own resources. In addition, in the analysis of polyandry and polygynandry co-husbands can be related and further strategies need to be introduced.