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Preface

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The evolution of female-biased kinship in humans and other mammals

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Female-biased kinship (FBK) arises in numerous species and in diverse human cultures, suggesting deep evolutionary roots to female-oriented social structures. The significance of FBK has been debated for centuries in human studies, where it has often been described as difficult to explain. At the same time, studies of FBK in non-human animals point to its apparent benefits for longevity, social complexity and reproduction. Are female-biased social systems evolutionarily stable and under what circumstances? What are the causes and consequences of FBK? The purpose of this theme issue is to consolidate efforts towards understanding the evolutionary significance and stability of FBK in humans and other mammals. The issue includes broad theoretical and empirical reviews as well as specific case studies addressing the social and ecological correlates of FBK across taxa, time and space. It leverages a comparative approach to test existing hypotheses and presents novel arguments that aim to expand our understanding of how males and females negotiate kinship across diverse contexts in ways that lead to the expression of female biases in kinship behaviour and social structure.

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

1. Introduction

Kinship plays a fundamental role in how animals interact with one another and often forms the foundation on which social groups are built [1]. While there is considerable diversity in mammalian social structures, most species are socially organized around sets of maternally related females (e.g. [2]). Female-biased kinship (FBK)—family groups or structures oriented more strongly around related females than around related males—is comparatively rare in humans [3,4]. This has led to centuries of speculation as to FBK's evolutionary and social origins, especially among scholars working on human kinship (see discussion in [5]). An enduring framework characterizing this effort is known as the matrilineal puzzle, which posits that matrilineal descent (effectively, a cultural and/or social emphasis on kinship relationships traced through the mother) may result in tension among men's allocation of authority between their natal and spousal kin [6,7]. As evolutionary anthropologists, we return to this puzzle, harnessing the power of the comparative approach to recast the question of FBK to focus on how different manifestations of FBK emerge and how they operate across varying social and ecological contexts. We strive for an integrative framework that will push this field of inquiry forward, embracing tools and perspectives from theoretical biology, animal behaviour, evolutionary ecology, and evolutionary and sociocultural anthropology.

Within this issue, we consider any cases in which behaviour or social structure reflect biases towards maternal kin as instances of FBK. We provide at the end of this preface definitions and a table of kinship terms that serve as a starting point to facilitate comparisons between humans and other species. This avoids the pitfalls associated with glossing disparate behaviours (e.g. inheritance, descent, cooperation) generically as 'matriliny' (see [8]). Many of our contributing authors elaborate on the functional aspects of these comparisons (e.g. [8,9]) by delineating the domains of kinship relevant to a given analysis and explicitly considering the ways in which these domains interact. This allows us to ask: (i) to what extent sex biases in behaviour and organization are correlated across different domains of kinship; and (ii) how strongly ecological correlates are tied to various domains of FBK within and across species.

In addressing these issues, we extend previous perspectives that have often focused more narrowly on matrilineal kinship. To this end, we include empirical analyses informed by theoretical models derived from the study of kinship across species [10,11], including articles describing taxa and circumstances under which FBK emerges as most prominent [9,12,13]. As highlighted below, these articles describe hypotheses that are novel to, yet could be fruitfully tested in, humans. We also include articles drawing on individual-level variables to examine the proximate determinants [14–16] and consequences [17] of prioritizing different kin as targets of cooperation or investment. This type of evidence reveals the micro-level influences on individual behaviour that may be obscured by group-level classifications of behaviour as male- or female-biased [18]. Indeed, several case studies in the issue reveal how normative patterns of descent group membership, intergenerational inheritance and post-marital residence conceal the strategic decisions of individuals to align their interests and investments in ways that secure fitness benefits. Finally, cross-cultural work suggests that, although no definitive explanation of FBK emerges across taxa and contexts, considerable patterning in relation to various hypothesized socio-ecological drivers is apparent [19,20], providing important targets for ongoing empirical and theoretical work.

Because one of the goals of the issue is to spur a synthesis of work in human and non-human animals, it is important to note that kinship in human societies is differentiated along a larger number of axes than has been typical for non-human animal societies (table 1). Human studies refer to sex biases in the reckoning of descent, intergenerational inheritance, post-marital residence and succession to office/leadership positions; gender-biased cooperation and conflict are clearly relevant to human kinship systems, but they have been less explicitly considered in anthropological studies of kinship. In non-human animals, kinship organization is generally based on grouping and association patterns. In some cases, there are partial analogues between human and non-human terms. For example, post-marital residence and dispersal patterns, succession of office and inheritance of rank, and intergenerational inheritance and aspects of parental investment, are roughly analogous and can show consistent sex biases (table 1). For a more systematic comparison between human and non-human systems, we will need to align our terminologies more closely. Fortunato [8] explores some of these issues, and in this preface, we present some definitions that we propose will help scholars working on human and non-human systems compare their empirical cases more precisely.

2. Significant findings

One clear finding from the diverse set of included papers is that the labels used to describe kinship systems have constricted our thinking. For example, Fortunato [8] shows that, in humans, biases in investment toward matrilineal kin can exist even in societies that do not reckon descent. Yet, in anthropology, the term 'matriliny' and its derivatives (e.g. 'matrilineal society') have come to imply matrilineal descent. To the extent that the reckoning of descent relies on symbolic communication and extensive cultural transmission, it is not easily mapped onto non-human social behaviour. De-emphasizing descent in the study of kinship systems opens up the possibility of drawing parallels between biases towards lineal kin in humans and other species. Several papers in the issue provide evidence speaking to this point. Emery Thompson's [9] examination of FBK in non-human primates suggests that FBK is evident even where male philopatry would ordinarily constrain female–female relationships. Many of the included papers show that, in humans, individuals are extraordinarily facultative, turning for help to individuals related through females, individuals related through males, reproductive partners or others, irrespective of the norms associated with post-marital residence, descent group membership, intergenerational wealth transmission and so on. Indeed, Borgerhoff Mulder *et al.* [17] show that despite the prominence of male-biased kinship institutions, patrilineal inheritance and patrilocality, careful investigations of parent–son and parent–daughter similarities across 15 societies show no clear evidence of son preference. Several papers in this issue focused on human case studies similarly point to 'emergent' FBK within male-biased kinship systems [14,16,21], reinforcing (i) that typologies of kinship often overlook and underemphasize the contributions that females make to their families and social partners and (ii) that FBK is probably more important than often conceived in structuring the content and outcomes of mammalian—and especially human—social interactions. Furthermore, this work illuminates the necessity of moving beyond dichotomous categorizations of kinship systems to understand the influence of FBK in both humans and non-human animals.

The evolutionary drivers of FBK are the focus of several contributions to this issue. Theoretical models in behavioral ecology focus on how factors such as inbreeding avoidance and sex differences in the costs and benefits of dispersal affect which sex stays versus disperses (e.g. [2,22–24]), often emphasizing that the type and distribution of resources determines the distribution of females in space and time, and in turn both the opportunity and need for female kin support and the strategies available for males [25–28]. Resources also play an important role in thinking about FBK in humans [3,29–35]. Specifically, it is hypothesized that moderate-productivity subsistence systems (e.g. horticulture) are conducive to FBK where such systems do not lead to disproportionate fitness returns to men [21,36]. In this issue, Surowiec *et al.* [20] provide additional analysis, within a cross-cultural framework, of the relationship between matrilineal descent and various putative drivers, including aspects of subsistence systems. Via a *de novo* coding of transitions to or from matrilineal descent found in the source material

Table 1. Comparative definitions of relevant kinship terms.

	human	non-human	human/non-human notes
post maturation or post-mating/marital residence	virilocal, uxorilocal, neolocal, ambilocal, duolocal	male/female-(biased) philopatry	In non-humans (NH), the dispersing sex transfers between groups in order to find new mates or avoid inbreeding, whereas in humans, dispersers may have found mates prior to dispersal and there are often other reasons for dispersal.
descent/lineage membership	patrilineal, matrilineal, bilateral, ambilineal, double descent	patrilineal/matrilineal kinship	In humans, patrilineal and matrilineal descent are used to define membership in lineages or corporate descent groups; the equivalent in NH species is whether individuals associate preferentially with matrilineal or patrilineal relatives. This is most likely limited by sex-biased philopatry and constraints on kin recognition.
succession (to status/ office/positions of leadership/rank)	patrilineal, matrilineal, bilateral, ambilineal, double descent	patrilineal/matrilineal hierarchies; matriarchy may be appropriate	For humans, these terms typically apply to rules for the transfer of leadership positions over time. For NH, these terms refer to status hierarchies where rank acquisition depends on the ranks of living relatives. While matrilineally inherited rank is known for many species, it is unclear whether true patrilineal hierarchies exist in NH, though the term has been used loosely to describe systems where hierarchies consist of related males and where 'inheritance' of rank is incidental.
inheritance (of resources/ information)	patrilineal/matrilineal/ bilateral; son/ daughter-biased	son-/daughter-biased	Arises in different domains, e.g. land/structures, movable property and information.
cooperation	matrifocal; patrifocal	female-bonded; male-bonded	In animals, bondedness refers to membership and the 'social relationships within sexes' [21] often including cooperation. Matrifocality and patrifocality in human studies typically refer not to membership but to behaviours that are oriented around a core group of females versus males, respectively.

for the Standard Cross-Cultural Sample [4], Shenk *et al.* [19] also provide evidence that subsistence change induces movement to or away from matriliny, alongside evidence of other drivers including social complexity and colonialism.

This theme issue also clarifies the effects of female kin associations on life history and behavioural strategies, facilitating efforts to better understand what evolutionary circumstances favour FBK. For example, Lynch *et al.* [37] describe the beneficial effects of younger maternal sisters on fertility in semi-captive Asian elephants. Rendell *et al.* [13] reveal how FBK in cetaceans serves as a substrate for the evolution of social complexity, longevity and social transmission of migration routes. In their study of South Indian Tamils, Power & Ready [14] describe the importance of female kinship in a patrilineal, patrilocal context, where matrilateral kin often reside in close proximity to each other, provide important forms of support, and avoid the tensions among patrilineally related men competing for access to the same resources. At the same time, men are thought to play significant roles as maternal uncles in both male-biased and female-biased human kinship systems [38,39]; Starkweather & Keith [16] provide some of the first quantitative evidence of avuncular support by uncles of sisters' children in domains that plausibly enhance inclusive fitness without detracting from male investments in the uncle's own children. Matrifocal kinship (see glossary) also structures male social relationships: in Dominica—another nominally male-biased kinship system—matrifocality results in trade-offs between men's investments in conjugal relationships versus male–male support relationships [21]. Borgerhoff Mulder *et al.* [17] find that silver spoon effects are just as likely for daughters as they are for sons, despite the common belief that sons are generally favoured over daughters in so many parts of the world (see also [40]). Finally, Ly *et al.* [41] find support in genetic data for a hypothesis that posits increased endogamy as one means by which the matrilineal puzzle might be solved—by keeping men in close proximity to both their natal *and* spousal kin. Their paper provides a genetic basis for arguments linking sex-biased kinship systems to differences in population and public health (see also [17]).

While there are many potential routes through which kin may benefit one another—e.g. cooperative resource defence, alloparenting and various forms of reciprocal exchange—the costs to such behaviour have less commonly been discussed. In particular, females residing with kin face competition over the resources necessary to produce and support their offspring. Lukas & Huchard's [11] broad phylogenetic comparative analysis across mammals provides compelling support for the hypothesis that resource competition drives infanticide by females. They show that the presence of strong kin networks does not deter infanticide, and that it is not unusual for infanticidal attacks to be perpetrated by close female kin. Resource competition has also been proposed to play a role in the timing of reproductive events (e.g. [42–45]). In particular, an influential model [42] proposes that relatedness to group increases with age, impacting natal versus immigrant community members differently, and affecting willingness to cede reproduction to subsequent generations. In this issue, Koster *et al.* [10] measure the relationship between relatedness to one's community as this changes over the lifespan, in numerous human societies adhering to different norms of locality. Once again, community norms were imperfect predictors of kinship structure, suggesting that facultative dispersal patterns should be considered in models of sex-biased competition for resources among kin.

Finally, we find that viewing FBK predominantly through the lens of the matrilineal puzzle deprives the analyst of a host of tools that explain how and why individuals choose to align themselves with different sets of kin. In this issue, Mattison *et al.* [38] argue that parental investment theory undermines key premises of the matrilineal puzzle, and that we should rarely anticipate men investing in nieces and nephews *at the expense* of their own offspring. Humans are considered obligate cooperative breeders by many [46], with mothers relying especially (but not exclusively) on care provided by male reproductive partners [47]. Biparental care is likely to constrain FBK (see also [48,49]), which is notably rare in other taxa with biparental care (e.g. birds), but Mattison *et al.* argue that male involvement in the parenting realm is not simply diverted to nieces and nephews in matrilineal kinship systems. They argue further that the focus on male centrality implied by the matrilineal puzzle is likely to have overemphasized male importance in societies more oriented around females, and the removal of this 'puzzle' opens up variation in inheritance and descent to a broader set of possible explanations. Scholarship in non-human mammals has not been influenced by the matrilineal puzzle and, as discussed below, provides different and useful insights as to the benefits of female-biased social organization that may extend to explanations of human FBK.

3. Concluding thoughts

The evolution of FBK has been a source of significant inquiry in studies of human kinship. This theme issue consolidates and expands on prior inquiry, serving as the first compendium to bring together insights relevant to understanding the patterns, causes and consequences of FBK since Schneider & Gough [7] published their sociological treatment of matriliny in 1961. We expand on prior synthetic attempts by drawing on insights from across mammalian taxa, and using various analytical and theoretical tools to address the broad evolutionary significance of FBK. Together, the papers in this issue reveal significant overlap in the extent to which sex-biases are reflected across broad domains of kinship, while pointing to context- and community-specific variability in the particular behaviours and social structures in which such sex-biases are demonstrated. Despite this heterogeneity, this issue reinforces the central importance of female–female relationships in the evolution of mammalian social systems.

We reiterate here several issues that deserve focused attention as work on the evolution of FBK continues. First, definitions of kinship are notoriously *ad hoc* in both human and non-human scholarship [8]. We provide a glossary here to guide comparative work going forward, but terms will undoubtedly need refinement as they are operationalized within and across studies. Second, we underscore the need to empirically validate assumptions underlying influential evolutionary models of kinship and sociality with quantitative data across multiple levels of organization (i.e. individual, household, community) (see also [50]). Mattison *et al.* [38] make the case that empirical validation of assumptions inherent to the matrilineal puzzle could easily invalidate this influential concept in multiple communities practising matrilineal kinship, for example—a premise that is bolstered by the conspicuous absence of evidence of avuncular support of offspring in mammals. Rendell *et al.* [13] point out that methodological limitations have slowed progress in understanding how female–female relationships structure marine social life and adaptations. Studies of terrestrial species have arguably been more constrained by theoretical perspectives than by methodological limitations. The time is thus ripe to move beyond such constraints to generate new evolutionary insights on the causes and consequences of sex-biases in kinship behaviour.

The papers in this issue demonstrate that human and non-human kinship systems can and should be examined within the lens of behavioural ecology, and that numerous aspects of their patterning are consistent with evolutionary logic. Many of the explanations for FBK in this issue centre on subsistence, even if the precise mechanisms sometimes remain obscure. As discussed above, the best-supported models in humans suggest that relatively low productivity and low male involvement in subsistence are associated with the evolution of FBK, but 'horticulture' is clearly a poor gloss for low productivity and inheritance of cattle does not always spell the demise of FBK [15], contrary to an influential notion suggesting otherwise [29]. We thus need better resolution on the specific impacts of production systems on male versus female reproductive success across species—such work will be facilitated by interdisciplinary teams of researchers poised to address how ecological, economic, sociological and biological factors inter-relate to generate FBK. This endeavour is important to non-human studies, too, where predominant models of dispersal explain generally how females and males become distributed over the landscape in relation to resources, but do not account for all instances of FBK (or its absence), including pelagic matriliny, where the resources supporting life are not patchily distributed nor easily defended [13]. Additionally, non-human studies in this issue point to several explanations of FBK that are under-explored in human studies, including population density and mutualism in cooperative childrearing among matrilineally related females [9,12,13,20,37]. Thus, the issue suggests several fruitful avenues for future research on the evolution of FBK in mammalian societies. Given the importance of kinship to human and non-human society and welfare [1,51,52], such an endeavour will have important consequences for both theory and practice.

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Glossary

Definitions in this glossary are adapted from widely used texts in kinship studies (e.g. [53,54]). There is disagreement over specific use and utility of certain terms; this glossary is presented as a general overview of commonly held meanings.

Female-biased kinship (FBK)—family structures more strongly oriented around related females than related males. This term is meant to broadly incorporate all forms of human and non-human kinship to be discussed in this issue where ties of kinship through females are important for residence, subsistence, inheritance, succession, descent and/or cooperation.

Human Kinship Terminology

Residence aka post-marital residence—where a couple resides after 'marriage' (or establishing a pair bond)

- **Virilocal**[1] (aka patrilocal): residence with or near the husband's family
- **Uxorilocal** (aka matrilocal): residence with or near the wife's family
- **Avunculocal**: the couple resides with the husband's (often eldest) maternal uncle
- **Ambilocal**[2]: the couple may reside with or near the wife's or husband's kin (common pattern in hunter–gatherer communities [55])
- **Neolocal**: the couple establishes an independent residence away from either the husband's or wife's family (common in European and descendant societies, market economies)
- **Natalocal/Duolocal**[3]: the couple continues to reside with their own kin groups after marriage

Descent—descent is the entire series of links based on filiation (i.e. links between parent and child), going into preceding generations and forward into future generations.

- **Patrilineal** (agnatic) descent is inclusion in a *descent group* through only male links
- **Matrilineal** (uterine) descent is inclusion in a *descent group* through only female links
- **Bilateral** descent (e.g. common European pattern) is descent traced through both parents; generally not considered a descent *group* unless it involves the formation of corporate groups that jointly own property, resources, or rights
- **Cognatic** descent (rarer pattern, found, e.g. in Austronesia), involves descent *groups* created through both parents (aka ambilateral, ambilineal, non-unilineal)
- **Bilineal** descent—descent through *both* male and female lines, each serving separate purposes simultaneously (aka **double unilineal descent**)

Descent group (corporate descent group)—a descent group that collectively owns and organizes property, resources or rights. Descent is not unique to humans, but descent groups may be.

- **Clans** are unilineal descent groups whose members have some known but also many *unknown, untraceable* relationships to an often mythical common ancestor
- **Lineages** are unilineal descent groups whose members have *known, traceable* relationships to a common ancestor

Inheritance—acquisition of property, resources, territory, status or information (or rights of access thereto) through kin ties

- **Primogeniture**—inheritance/succession by the eldest child (often of a particular gender)
- **Ultimogeniture**—inheritance/succession by the youngest child (often of a particular gender)
- **Unigeniture**—inheritance/succession by a single child

Succession—acquisition of formal office through kin ties

Matri*focal*ity is a cultural complex in which women co-reside and/or cooperate extensively, regardless of nominal descent system, i.e. strong female–female bonds can arise even in systems that are nominally *patrilineal* or *patrilocal*

Matri*arch*al implies that *authority* is vested in women.

Affines are kin relationships created through *marriage* (or long-term, stable pair-bonds in societies that do not practice institutionalized marriage).

Non-Human Kinship Terminology

Philopatry is the closest analogue to residence in the animal behaviour literature, referring to the propensity to remain with the natal group. Philopatry is often sex-biased, i.e. female-biased philopatry is analogous to uxorilocal post-marital residence, though not involving affinal relationships.

Dispersal is emigration from the natal group, which is often sex-biased, e.g. female-biased dispersal in bonobos.

Matriarchal mammals include whales and some carnivores in which leadership positions are held by females and their relations (potentially of both sexes).

Female-dominant species occur when females are systematically dominant to males.

Female-bonded species are those where group membership is based on a core of resident females. **Male-bonded** species are those where group membership is based on a core of resident males.

Endnotes

[1] Authors may be more familiar with the terms 'matrilocal' and 'patrilocal', but we prefer 'uxorilocal' and 'virilocal' as these terms capture the couple's movement, rather than being based on the vantage point of children resulting from the marriage.

[2] Multilocal is often used as a synonym for ambilocal, but we prefer the latter term as it better encapsulates the flexibility inherent to locality in relevant contexts.

[3] Strictly speaking, 'natalocal' arises when each member of the couple maintains primary residence with the natal family (e.g. among the Mosuo of China). 'Duolocal' is a more general term that would encompass a variety of residential arrangements where husband and wife live apart. Bilocal has been used in the literature synonymously with natalocal or with ambilocal. We believe it is more ambiguous than any of the terms employed here and prefer to avoid its use.

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