

Opinion piece



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Lineal kinship organization in cross-specific perspective

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I draw on insights from anthropology to outline a framework for the study of kinship systems that applies across animal species with biparental sexual reproduction. In particular, I define lineal kinship organization as a social system that emphasizes interactions among lineally related kin—that is, individuals related through females only, if the emphasis is towards matrilineal kin, and individuals related through males only, if the emphasis is towards patrilineal kin. In a given population, the emphasis may be expressed in one or more social domains, corresponding to pathways for the transmission of different resources across generations (e.g. the allocation of food, the transfer of access to the natal territory or household). A lineal bias in any domain can be viewed as a bias in investment towards a particular set of kin—specifically, towards the offspring of daughters if the bias is matrilineal, and towards the offspring of sons if the bias is patrilineal. Effectively, investment is restricted to the offspring of the females in the population in one case, and to the offspring of the males in the other. This is distinct from a bias in investment towards daughters and towards sons, respectively. Overall, I propose a shift in focus—from viewing matrilineal and patrilineal kinship as unitary phenomena, to consideration of the different aspects of the social system featuring a bias towards lineally related kin.

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

1. Introduction

In his now classic *Kinship and marriage: an anthropological perspective*, Fox [1, p. 50] lamented that ‘anyone trying to understand the subject has to fight his way through half a dozen conflicting taxonomies each with its patchy, *ad hoc* terminology’. Against this background, what follows may appear as a long-winded attempt to define ‘matriliny’ and related concepts, and in particular to disentangle descent from other aspects of matrilineal kinship in humans. In some ways, perhaps, it is. Yet extensive sleuthing through anthropological sources, old and new, suggests that terminological clarity is the key to conceptual progress in this area. It is also a critical first step towards development of a cross-specific perspective, bridging the persistent divide between the study of human and non-human kinship systems.

Calls to clarify relevant terms and concepts have appeared periodically in the anthropological literature, as interest in matriliny waxed and waned over the course of a century, from the early 1860s through to the 1960s (e.g. [2–4]; see [5,6] for historical overviews). The topic enjoyed a brief resurgence during the 1970s and early 1980s in the context of feminist analysis, which focused on understanding the roles of women at the intersection of gender construction and family organization [6]. In a parallel development, at around the same time researchers interested in the evolution of human social behaviour turned to matriliny as a test case for the application of kin selection theory (e.g. [7–14]; see [15–17] for critical discussion). Many of the insights that had been gained over

a century of anthropological enquiry were lost in this context—including an understanding of what matriliney is, and what it is not.

Faced with multiple and ambiguous definitions, evolutionarily minded anthropologists have recently taken a pragmatic stance, replacing ‘matrilineal kinship’ with biologically inspired labels, such as ‘female-biased/based/centred kinship’ (e.g. [18] and other articles in the theme issue). Underlying this trend is the belief that, if we move past seemingly trivial debates about terminology, we can turn to hypotheses, data and analyses of ever-increasing sophistication. However, this approach simply sidesteps the issue, compounding conceptual blindspots that had been at least partly addressed in anthropology over the course of the twentieth century.

I aim to show that, perhaps counterintuitively, exposing the ambiguity in terminology goes a long way towards resolving the conceptual confusion. It then becomes possible to outline a framework for the study of kinship systems that applies across animal species with biparental sexual reproduction. Reasoning from first principles, I develop such a framework in the abstract, without reference to the social organization of specific human or non-human populations. This is a deliberate strategy, to avoid conflict with established interpretations of relevant patterns. I begin by providing explicit definitions of key terms and concepts (§2). Next, I derive the logical implications of the definitions in cross-specific perspective (§3). The insights that emerge are then applied in cross-cultural perspective (§4). In particular, I corroborate these insights by (i) examining the distribution of two relevant features of human social organization (§4a), (ii) briefly summarizing related conclusions obtained through anthropological analysis in the twentieth century (§4b), and (iii) reframing lineal kinship organization in terms of biases in investment towards specific sets of kin (§4b). I conclude by outlining how this framework applies across species (§5). Readers interested exclusively in non-human social behaviour can skip §§2 and 4, focusing on §§3 and 5 instead.

2. Kinship versus descent

Let us begin by drawing a distinction between the notions of kinship and descent, which is central to related discussions in anthropology. My aim here is twofold: first, to explicitly define key terms and concepts, in order to address the confusion surrounding their use; second, to provide a minimal compendium, for reference, which reconciles the multitude of definitions found in the literature. Relevant terms and concepts are then applied in cross-specific perspective in §3.

Across human societies, kinship is ‘culturally reckoned and socially important’ [19, p. 24]. Furthermore, kinship reckoning is always *bilateral*—that is, all societies recognize relationships on both ‘sides’ ([19]; see discussion below). Relatives on the mother’s side are *matrilateral* (also *maternal*; [5]). Relatives on the father’s side are *patrilateral* (also *paternal*; [5]).

Some societies also reckon descent, meaning that they attach social and cultural significance to subsets of these relationships, based on links of relatedness among people descended from an ancestral individual in a particular way. Effectively, the reckoning of descent emphasizes a ‘chain’ of parent–child links between the ancestral individual and their descendants, and this sequence is socially and culturally salient [5,19].

Where the emphasis is restricted to either the mother’s line or the father’s line, descent is said to be *unilineal*. Specifically, it is termed *matrilineal* (also *uterine*; [5]) if traced along the *matriline*—from ancestral individual to descendants via a series of female links, i.e. from mother to daughter to daughter’s daughter, etc. Conversely, it is termed *patrilineal* (also *agnatic*; [5]) if traced along the *patriline*—from ancestral individual to descendants via a series of male links, i.e. from father to son to son’s son, etc.

Where the emphasis applies to all descendants of an ancestral individual through both female and male links, or through some combination of these, descent is said to be *cognatic* (also *ambilateral*, *ambilineal*, *bilateral*, *non-unilineal*; [5]; see discussion below). This is distinct from the co-occurrence of both types of unilineal descent, termed *bilineal* (also *double* or *double unilineal*; [5,19]). Note that the parental line through which descent is traced need not match the gender of the ancestral individual. For example, patrilineal descent may be traced back to an ancestress [5].

A society is said to have a *rule of descent* if a person’s descent status determines membership in a socially or culturally defined category. In particular, a *descent group* is a kin group whose members share appropriate status, as specified by the society’s descent rule ([19]; see discussion below). This does not imply that the individuals belonging to such a group reside together—indeed, they may never even meet as a group. In fact, the reckoning of descent need not lead to the formation of descent groups [5]. These tend to be found where there is group property to manage (e.g. joint ownership of impartible land) or some group obligation to fulfil (e.g. worship of ancestral individuals) [1].

To summarize, some societies recognize one or more modes of descent; in others, descent is only minimally salient, or not at all. Unlike kinship reckoning, then, descent reckoning is not universal [19]. Quoting Keesing [19, p. 22]

[i]n societies where descent groupings are culturally relevant, bilateral kinship is also always recognized and always important. Kinship reckoning creates a network of relationships between a great many individuals. A rule of descent gives special meaning to a limited subset of these relationships; it thus carves out pieces of this network and gives them some special social significance.

The analytical distinction between kinship and descent is tied to major theoretical developments that occurred in anthropology over the course of the twentieth century (see [5,20,21] for related discussion). In part, the terminological confusion lamented by Fox [1], noted in §1, likely reflects divergent positions linked to these developments. A case in point is the multitude of terms used for different modes of descent, only a subset of which is given above! Another example relates to the terms used to designate descent groups. Generally, members of a descent group are said to form a *lineage* and, in some cases, a *clan*. The term ‘lineage’ is used when the links among members are known and traceable to an actual ancestral individual, implying that the sequence of parent–child links from this person to their descendants is relatively shallow. Deeper sequences are not always recognized. Where they are, they may be traced back to a long-deceased ancestral individual (or even to a mythical entity, which need not be human), with links among members assumed, rather than known. The term ‘clan’ is used to designate the group at this level. It follows that a clan may comprise multiple lineages [1,5,19].

A potential point of confusion is that some authors reserve the two terms for unilineal descent groups, distinguishing between *matrilineages/matriclans*, if the descent rule is matrilineal, and *patrilineages/patriclans*, if the descent rule is patrilineal (e.g. [5,19]). Other authors eschew the reference to unilineality, adding cognatic lineages/clans to the mix (e.g. [1]). A historical account of the theoretical developments underlying such variation in terminology is beyond the scope of my contribution, and of the theme issue more generally. At the same time, highlighting that variation exists may aid interpretation of relevant ethnographic materials, and of related discussions in anthropology more broadly [5].

For completeness, then, note that the terms ‘bilateral’ and ‘cognatic’ are sometimes used interchangeably, as we saw above in the context of descent—that is, ‘cognatic descent’, as defined above, can also be referred to as ‘bilateral descent’ [5]. Similarly, ‘bilateral kinship’, as defined above, can also be referred to as ‘cognatic kinship’ [19]. The latter usage reflects the distinction between relatives by blood, collectively termed *cognates*, and relatives by marriage, collectively termed *affines* [5]. To complicate matters, however, ‘bilateral descent’ has also been used to indicate the absence of a rule of descent, with relatives aggregated only by blood and/or by marriage (e.g. [22]; see §4a).

3. Lineal kinship in cross-specific perspective

A number of principles stem from the distinction between lateral and lineal kinship introduced in §2. Phrased in abstract terms, these apply generally to any animal species with biparental sexual reproduction. My aim here is to highlight the logical implications of relevant definitions given in §2; I demonstrate the analytic utility of the definitions in §4. For clarity, I focus on the matrilineal case; the patrilineal case is simply reversed.

We saw in §2 that relatives on the mother’s side are matrilineal kin. A subset of these are matrilineal kin—namely, those related through the mother’s line. It follows that matrilineal kin of either sex are related through females only. Males are included, but individuals related through males are not. Thus, the relationship between males who are related matrilineally is mediated by females. More broadly, if we were to trace out the relationships between any two individuals who are matrilineal kin, all the connecting links would be females [1].

Membership in a set of matrilineally related kin is gained through the mother, and the relationships between any two members of the set involve one or more female links. Membership applies to individuals of either sex, but it is restricted to the offspring of the females in the set. That is, membership passes from the females in the set onto their female and male offspring, and then, in turn, from the female offspring onto theirs, and so on. Assuming that the male offspring mate with females belonging to other sets of matrilineally related kin, their offspring will gain membership in those sets instead [1].

A key implication here is that matrilineal kinship delimits discrete, non-overlapping sets of individuals. Individuals belong to only one set of matrilineally related kin, as determined at birth. An individual’s status in relation to any such set is absolute and exclusive—they either belong to the set or not, and membership in one set precludes membership in another. Of course, they belong simultaneously to a set of

patrilineally related kin, with analogous properties. In and of itself, kinship does not partition populations into discrete, non-overlapping sets—rather, it connects individuals into a wider network of relationships (see §2). Status in this network is relative, not absolute, in the sense that, for example, one is an offspring with respect to a given individual, and a sibling with respect to another [1,19].

Membership in sets of lineally related kin is often conflated with the lineal transmission of resources across generations (defined broadly to include the allocation of food, information, etc.). The underlying assumption is that a bias in membership towards one set over the other imposes a corresponding lineal bias in transmission. Generally, however, resources tend to cross the boundaries of any such set, extending to the wider kinship network, with different resources following different routes across generations (see §4). Therefore, the concepts of membership and transmission are best kept distinct [1].

Take, for example, a hypothetical species in which females stay in the natal territory, whereas males disperse as juveniles. For simplicity, assume that populations in this species comprise adult females and their offspring, and that the two generations do not overlap—that is, reproduction begins in one generation only after it has ceased in the other. Adult females mate with unrelated adult males from other populations, interacting briefly and exclusively for this purpose, and adult males are solitary at all other times. Each mating pair produces one daughter and one son.

In this scenario, a population corresponds to a set of matrilineally related kin, comprising females of any age and pre-juvenile males. All of the properties outlined above relating to membership in such a set extend to the population as a whole. Additionally, an individual in the population interacts only with matrilineal kin, to the exclusion of (i) any other kin—that is, other matrilineal kin (specifically, those related through males), their father, and any patrilineal kin, and (ii) any unrelated individuals, except their mate. This is because the population is effectively isolated from other populations, and thus from other sets of matrilineally related kin.

As a result, the properties relating to membership extend also to transmission. Say, for instance, that foraging skills are learnt from the mother. Thus, they pass from an adult female in the population onto both her offspring, then from her daughter onto hers, and so on. In each case, the son’s offspring are born into another population (i.e. his mate’s/their mother’s), and they acquire foraging skills from their mother instead. In this scenario, then, all resources follow the matrilineal route within populations, and there is no transfer of resources between populations.

Now consider a slightly modified scenario, in which unrelated adult males join the population to mate with the adult females, and both parents are then involved in rearing of the offspring. Membership in the ‘resident’ set of matrilineally related kin is as above, but transmission is not. Even if adult males are still solitary at all other times, biparental care and male dispersal, combined, add several routes for the transfer of resources across generations—both within and between populations. Within populations, resources can be transferred directly between females (from mother to daughter to daughter’s daughter, etc.), and/or between males via females (from father to daughter to daughter’s son, etc.). Between populations, resources can be transferred directly between males (from father to son to son’s son,

etc.), and/or between females via males (from mother to son to son's daughter, etc.).

Assuming that, in this scenario, foraging skills are learnt from both parents, they can follow multiple routes across generations—along either the mother's line or the father's line, or some combination of these. Other resources may be transferred predominantly, or exclusively, matrilineally. For instance, the pattern of female philopatry and male dispersal characteristic of the species implies that access to the natal territory follows this route, passing from mother to daughter to daughter's daughter, etc. (see §4a).

To summarize, then, both scenarios feature a matrilineal bias in membership, resulting in the physical aggregation of matrilineally related kin. This bias maps onto a corresponding bias in transmission in the first scenario, but not in the second, reflecting other aspects of the social system. Crucially, in the second scenario different resources follow different routes across generations.

The example illustrates the distinction between the concepts of membership and transmission. Yet the two are implicitly conflated when we designate a kinship system—and, by extension, a whole species, or a population within it—as 'matrilineal' or 'patrilineal'. For example, 'matrilineal kinship' signals a bias towards matrilineally related kin. But is it a bias in membership, in transmission or both? And does it apply to the transfer of all resources across generations, or do different resources follow different routes from one generation to another within and/or between populations?

Such lack of precision fuels the common misconception that it is not possible to define key terms and concepts unambiguously, and in a way that they apply across species (e.g. [18] and other articles in the theme issue). The example above and the preceding discussion show that this is clearly not the case. Framed as generically as they are, the two scenarios in the example provide plausible high-level descriptions for populations in a number of species—including our own.

This observation implies that the principles outlined above apply generally to any human society, irrespective of the degree of emphasis placed on descent from a common ancestor (see §2). That is, a lineal bias in membership and/or transmission may exist even in societies in which descent has only minimal social and cultural significance, or none. In these societies, any such bias is likely to involve closely related kin, and/or kin who interact on a regular basis. The reckoning of descent effectively extends the reach of the bias beyond this subset of kin. For example, shared descent status may be used to justify the transfer of resources between individuals who are only distantly related, do not reside together and rarely interact.

It follows that the reckoning of descent is not intrinsic to lineal kinship organization in humans (see §4). This insight is at odds with current practice in anthropology, in which the terms 'matriliny', 'patriliny' and their derivatives (e.g. 'matrilineal kinship', 'patrilineal society') have come to indicate, more or less explicitly, matrilineal or patrilineal descent (e.g. [5]). The discrepancy generates considerable confusion, contributing to the misconception outlined above. By definition, descent reckoning involves the tracing of relationships beyond the subset of closely related kin, and/or kin who interact on a regular basis (see §2). Therefore, it relies on the combination of symbolic language and cumulative cultural transmission that uniquely characterizes much of human social behaviour. The scope to develop a cross-specific framework for the study of lineal

kinship organization appears limited as a result—a view that has historically prevailed in anthropology, persisting to this day (e.g. [5]; see [23] for related discussion).

Resolving this impasse requires clarity in the definition of key terms and concepts—minimally, as I have done here, by separating out lateral and lineal kinship, a lineal bias in membership from a corresponding bias in transmission, and, specifically for humans, lineal kinship organization from the reckoning of descent (see §§2 and 4).

4. Lineal kinship in cross-cultural perspective

Ironically, the conflation of lineal kinship organization and descent reckoning, outlined in §3, is as problematic in anthropology as it is in cross-specific perspective. The need to distinguish between descent and other aspects of the social system has been long and widely recognized—from early writings on kinship in the nineteenth century (e.g. [24]) through to recent specialist texts (e.g. [5,25]; see [26] for related discussion).

For instance, Tylor [24, p. 258] emphasizes that 'the maternal and paternal systems are not each a definite institution, but combinations in which more or less strictly the authority, descent, succession, inheritance follow the female or the male side'. Writing over a century later, Parkin [5, p. 23] notes that 'it is rarely appropriate to characterize a whole society in terms of any particular mode of descent, for example, as "patrilineal" or "matrilineal" or "cognatic", despite a widespread tendency to do so'. At the same time, Harrell [25, p. 19] suggests that such designations can be used as 'a convenient shorthand' to describe a kinship system, with different labels capturing whether there is 'a predominant route', or 'an obvious mixture of routes', for the transmission of rights and duties across generations. This suggestion rests on the assumption that [25, p. 18]

[i]n practice, there is a strong tendency for certain directions of transmission of rights and duties (succession to office, descent, and inheritance) to be associated with corresponding systems of residence, so that those in line to inherit or succeed live with those they expect to inherit from or succeed to.

It should be clear from the discussion in §3 why such a suggestion is problematic at a conceptual level. For example, 'matrilineal kinship' signals a bias towards matrilineally related kin, but it fails to specify (i) whether the bias applies to membership, to transmission or both, and (ii) in the case of transmission, whether different resources follow different routes across generations. Furthermore, 'matrilineal kinship' would likely be taken to imply matrilineal descent, because in current anthropological practice 'matriliny' and derived terms have effectively come to indicate this specific aspect of the social system (e.g. [27]). However, as discussed in §3, the reckoning of descent is not intrinsic to lineal kinship organization in humans—thus, a matrilineal bias in membership and/or transmission may exist even in societies that place no emphasis on descent from a common ancestor. Conceptually, then, the use of shorthand such as 'matrilineal kinship' is imprecise and potentially misleading.

A related issue is that, at a practical level, any such designation is arbitrary. In particular, it is not clear what exact criteria must be met to establish that, in a given society, there is a predominant route for the transmission of rights and duties from one generation to another. In fact, the cross-cultural data reveal a complex pattern, challenging

Table 1. Cross-tabulation of modes of descent and residence in the *Standard Cross-Cultural Sample*.^a

		descent (<i>n</i>) ^b					total	
		ambilineal	double	matrilineal	no rule	patrilineal	<i>n</i>	%
residence (<i>n</i>) ^c	ambilocal	0	0	0	11	1	12	6
	avunculocal	0	1	7	0	0	8	4
	neolocal	0	0	0	7	2	9	5
	uxorilocal	0	0	18	18	2	38	21
	virilocal	6	9	1	32	70	118	64
	n.a.	0	0	0	1	0	1	—
total	<i>n</i>	6	10	26	69	75	186	
	%	3	5	14	37	40		

^aModified from table 2 in [22]. Minor discrepancies between the percentages reported here and in [22] arise from inconsistency in the rounding of figures in the latter.

^bThe corresponding variable is data column 10 in [22]. I changed 'bilateral descent' in the original to 'no rule'; see §4a for details.

^cThe corresponding variable is data column 9 in [22], focusing here on 'the prevailing practice of residence after marriage' (i.e. excluding information on 'an alternative but less frequent residential pattern or one confined to a particular phase of the developmental cycle') [22, p. 261]. I changed 'matrilocal' in the original to 'uxorilocal', and 'patrilocal' to 'virilocal'; see §4a for details. One society (Botocudo, #178) lacks data for this variable; percentages in the right-most column relate to the remaining 185 societies.

the underlying assumption that descent, succession, inheritance and residence tend to feature a consistent bias—in this case, towards matrilineally related kin.

I give a concrete example below, focusing on the distribution of modes of descent and residence across societies (§4a). Building on insights gleaned from this example, I then outline an approach to reframing lineal kinship organization in terms of biases in investment towards lineally related kin (§4b).

(a) A cross-cultural example: the association between descent and residence

The association between descent and residence has received considerable attention in anthropology (see [5] for related discussion). Investigation of the relationship between these aspects of the social system occupied the field in the late nineteenth century and for a good part of the twentieth. In particular, early debates focused on the relative primacy, or 'priority', of different forms of social organization—both temporally (e.g. did 'matriliny' precede 'patriliny?') and in terms of importance (i.e. do changes in descent drive changes in residence, or *vice versa*?). Within the prevailing theoretical paradigm of the late nineteenth century, now known as 'classical evolutionism', the aim was to establish specific historical sequences, leading to the discovery of general laws of cultural development (see [26,28] for related discussion).

I do not intend to rehash these debates here. Rather, I turn to the cross-cultural data to evaluate the pervasive assumption of a 'strong tendency' for descent to be associated with 'corresponding systems of residence' [25, p. 18]. In the process I indulge in some technical detail about the data and underlying definitions, both for accurate interpretation and to illustrate the nuance required in drawing inferences from the ethnographic record. Finally, I introduce the notion that descent, residence and other aspects of the social system

represent pathways for the transmission of different resources across generations (see §4b).

The cross-tabulation of relevant variables for the 186 societies in the *Standard Cross-Cultural Sample* (SCCS) [29] is in table 1 (modified from table 2 in [22]). Data for this sample provide the most accurate estimates of the distribution of cultural practices across human societies (e.g. compared to estimates based on equivalent data for its 'parent' sample, the *Ethnographic Atlas*; [30,31]). The increase in accuracy derives from (i) specific considerations underlying the sampling strategy, (ii) explicit criteria for the inclusion of societies, based on the quality of the ethnographic materials, and (iii) refinement of the code definitions and corresponding data (see [28,32] for related discussion).

For example, the code definitions for descent and residence were developed specifically for the SCCS focusing on the community as 'a unit of significant social interaction beyond the family' [22, p. 255]. The corresponding data set the frequency of matrilineal descent in the SCCS at 14% [22]. An earlier estimate for this sample was based on code definitions originally developed for the *Ethnographic Atlas*, and the corresponding data set the frequency of matrilineal descent at 17% instead [29]. The latter figure is more often cited (e.g. [33]), but it is likely less accurate than the former, for the reasons outlined above. Estimates of the frequency of different modes of descent and residence in the SCCS, based on the code definitions and corresponding data in [22], are included in table 1.

The SCCS code for descent (data column 10 in [22]) maps onto the definitions in §2 relatively straightforwardly. The one exception is the 'bilateral descent' category, which indicates 'more properly the absence of any rule affiliating an individual with the kin group or groups of an ancestor' [22, p. 274] (see §2). For clarity, this category is reported as 'no rule' in table 1.

The SCCS code for residence (data column 9 in [22]) presents some peculiarities compared to other definitions found

in the literature. These peculiarities reflect the terminological and conceptual confusion that has historically characterized efforts to classify residence modes, persisting to this day (see [26,34,35] for related discussion). Here I highlight specific features of the SCCS code relevant to interpretation of table 1.

Focusing on the location of men and women after marriage, or *post-marital residence*, the simplest classification comprises *neolocality*, i.e. residence of the married couple apart from the kin of either spouse, *uxorilocality*, i.e. residence of the married couple with or near the wife's kin, and *virilocality*, i.e. residence of the married couple with or near the husband's kin [19]. The latter two terms are 'unobjectionable from both the etymological and logical points of view' [36, p. 678]—unlike their more commonly used counterparts, *matrilocality* and *patrilocality* (see [5] for related discussion). The SCCS code gives both sets of terms as alternatives, but defined more narrowly as residence with or near, respectively, the wife's female matrilineal kin and the husband's male patrilineal kin.

In addition to neolocality, uxorilocality and virilocality, the SCCS code includes *ambilocality*, defined as residence optionally with or near the parents of either spouse, depending on personal choice or circumstances, and *avunculocality*, defined as residence with or near the husband's mother's brother or other male matrilineal kin, including cases where men customarily marry a mother's brother's daughter and thus reside with wife's kin. Notable for its absence is *duolocality*, in which the spouses live apart [5]—effectively, the SCCS code assumes co-residence of the spouses.

To aid interpretation, following Harrell [25] it is useful to view the different modes of residence as different routes for the transfer of access to the natal household across generations. The emphasis is on cooperation in activities relating to the family (e.g. sex, socialization, the procuring and processing of food and other material resources), rather than on physical proximity—a distinction that generally excludes other types of co-residence, such as lodging in shared accommodation. If a married couple is to live together and cooperate in these activities, one option is that both spouses leave the natal household to set up a separate place of residence. This scenario results in neolocality. The other option is that only one of the spouses leaves the natal household. This scenario results in the other modes listed above, depending on which spouse tends to retain access to the natal household. In cross-specific perspective, then, residence is analogous to the transfer of access to the natal territory across generations, as captured by the pattern of philopatry and dispersal (see §3).

Mapping this framework onto the SCCS code [22], in neolocality there is no transfer of access to the natal household across generations [25]. The transfer is matrilineal in avunculocality and uxorilocality—respectively, between matrilineally related males (i.e. from maternal brother to sororal nephew) and between matrilineally related females (e.g. from mother to daughter, if residence is with the wife's parents) [25]. Similarly, the transfer is patrilineal in virilocality (e.g. from father to son, if residence is with the husband's parents). In ambilocality the transfer is matrilineal or patrilineal with approximately equal frequency [22].

Having established a framework for interpretation, we can finally turn to table 1 and evaluate the assumption of association between matrilineal/patrilineal descent and matrilineal/patrilineal transfer of access to the natal household across generations (e.g. [25]). In line with the assumption,

matrilineal descent occurs almost exclusively with avunculocal and uxorilocal residence (specifically, 25 of 26 societies with matrilineal descent, or 96%). Similarly, patrilineal descent occurs almost exclusively with virilocal residence (specifically, 70 of 75 societies with patrilineal descent, or 93%). The reverse does not hold quite as neatly, however. Notably, the majority of societies with no descent rule feature uxorilocal or virilocal residence (specifically, 50 of 68 societies with no descent rule, or 74%, focusing on entries with data for both variables). Thus, more often than not, societies that do not reckon descent present a clear bias towards lineally related kin in the transfer of access to the natal household across generations. For example, there are as many societies featuring uxorilocal residence with no descent rule, as there are societies featuring uxorilocal residence and matrilineal descent (for each combination, 18 of 38 societies with uxorilocal residence, or 47%).

To make sense of this pattern, it is useful to view different aspects of the social system as pathways for the transmission of different resources across generations (defined broadly to include the allocation of material wealth, such as land, livestock and household goods; embodied wealth, such as practical skills and the determinants of physical condition; and relational wealth, such as position and links in social support networks; [37]). Thus, as discussed above, residence can be viewed as the transfer of access to the natal household. Similarly, descent can be viewed as the transfer of social ties. In the many 'discrepant' cases in table 1, these resources follow different routes from one generation to another, such that residence may present a bias towards one set of lineally related kin and descent towards the other set, or such that a lineal bias in residence may exist even in societies in which descent has no social and cultural significance. Overall, then, the pattern in table 1 is consistent with key insights derived from first principles in §3.

The available cross-cultural data suggest that this pattern extends to other aspects the social system, including inheritance of property (e.g. [38]) and succession to office (e.g. [39]). It thus becomes clear that it is not at all straightforward to determine whether, in any society, there is a predominant route for the transmission of rights and duties across generations. This highlights the ambiguity involved in designating a kinship system—and, by extension, a whole society, or a population within it—as 'matrilineal' or 'patrilineal' (see §3).

(b) Reframing lineal kinship organization as lineal biases in kin investment

The conceptual confusion underlying the ambiguity in terminology highlighted in §4a was first recognized in anthropology in the first half of the twentieth century (e.g. [38,40–43]). Separation of the different aspects of the social system that may feature a bias towards lineally related kin represented a major advance in the study of matrilineal kinship (see [26] for related discussion). Indeed, the notion was considered received wisdom by the middle of the century, with Richards [44, p. 207] stating, for example, that

[...] it is generally recognized that no society is entirely matrilineal or patrilineal as regards descent, inheritance, succession, and authority, but that the family system provides a balance of interests and rights between the two sides of the family with a predominant emphasis on one side or the other [...].

Divergent theoretical positions elaborated over the course of the century emphasized this notion to different degrees, however (see [5,20,21] for related discussion). In any case, it

appears to have been largely lost in current practice—likely in the transition that began around the 1970s when, as noted in §1, matriliney, and kinship more generally, were displaced from the core of anthropological enquiry, at the same time as researchers from other fields turned their attention to the topic. The recent introduction of biologically inspired labels, such as ‘female-biased/centred kinship’, is symptomatic of the latter development. These labels are no less ambiguous than those they are intended to replace, with conceptual and practical issues analogous to those outlined above with reference to the use of ‘matrilineal kinship’ as shorthand. Additionally, labels such as ‘female-biased/centred kinship’ gloss over the distinction between lateral and lineal kin (see §§2 and 3). This is a potentially fatal oversight for explanations that rely on specific assumptions about relatedness in determining the relative costs and benefits of different strategies (see [45,46] for discussion of relevant assumptions in the case of matrilineal inheritance).

The solution I propose here effectively recapitulates the earlier notion, reframing it in terms of biases in investment towards lineally related kin. In this context, the term ‘investment’ simply indicates the transfer of resources to one or more individuals, to the exclusion of other individuals. It does not imply that the transfer is driven by personal choice, rather than by adherence to a social norm—that is, there is no implicit statement about agency (see [47] for related discussion).

Building on the premise that ‘no society is entirely matrilineal’ [44, p. 207], in [45] I define *matrilineal kinship organization* as a social system that emphasizes interactions among matrilineally related kin, and thus individuals related through females only (see §§2 and 3). In a given society, the emphasis may be expressed in one or more social domains, including descent reckoning, inheritance of property, succession to office, post-marital residence, and authority within the family [43]. In each domain, matrilineal kinship may serve as one of the criteria used to allocate rights and duties among individuals. Other relevant criteria are age and gender, for example.

By extension, here I define *lineal kinship organization* as a social system that emphasizes interactions among lineally related kin (see §§2 and 3). In a given society, the emphasis may be towards matrilineal kin in some social domains, and towards patrilineal kin in others; other domains still may present no such emphasis. A lineal bias in any domain can be viewed as a bias in investment towards a particular set of kin—specifically, towards the children of daughters if the bias is matrilineal, and towards the children of sons if the bias is patrilineal. Effectively, investment is restricted to the children of the ‘women of the group’ [1, p. 42] in one case, and to the children of the ‘men of the group’ [1, p. 42] in the other [1]. Crucially, this is distinct from a bias in investment towards daughters and towards sons, respectively. For example, in the matrilineal case investment may be restricted to the sons of the women, to the exclusion of the women’s daughters. A clear illustration is the transfer of property from a man to his sororal nephew, in which resources flow between matrilineally related males (i.e. between males via females). This form of matrilineal inheritance, termed *mother’s brother–sister’s son inheritance*, is distinct from the transfer of property from mother to daughter, in which resources flow between matrilineally related females (i.e. directly between females). The distinction highlights the confusion that may arise from framing matriliney as daughter-biased investment [33,48].

Viewing different aspects of the social system as pathways for the transmission of different resources across generations, as suggested in §4a, it follows that the relative costs and benefits of investment in matrilineal versus patrilineal kin may vary across social domains. For example, the costs and benefits to a man of investing in sister’s versus wife’s offspring may differ for material, embodied and relational wealth. In fact, they may differ also for different forms of wealth of the same type, such as land and livestock [45].

Conceptually, a key implication is that explanations for biases towards lineally related kin must not be confounded across social domains. Clearly, the factors leading to a bias towards a particular set of kin in one domain may have analogous effects in others, and there will likely be feedback across domains. For example, a bias towards matrilineal kin in assigning group membership may favour the physical aggregation of matrilineally related women and their dependants, and/or *vice versa*. At the same time, there is no reason to assume that the factors leading to matrilineal descent will inevitably result in matrilineal transfer of access to the natal household (see [1] for related discussion).

The approach to defining lineal kinship organization I propose here is consistent with the cross-cultural pattern examined in §4a. Furthermore, it resolves the ambiguity implicit in current usage of ‘matriliney’, ‘patriliney’ and derived terms (e.g. ‘matrilineal kinship’, ‘patrilineal society’), as well as biologically inspired labels (e.g. ‘female-biased/centred kinship’), by separating out lateral and lineal kinship, a lineal bias in membership from a corresponding bias in transmission, and lineal kinship organization from the reckoning of descent (see §§2 and 3). In particular, it corroborates the insight that descent reckoning is not intrinsic to lineal kinship organization in humans—rather, it is only one of many social domains in which an emphasis towards lineally related kin may be expressed in a given society.

5. Conclusion

I conclude by briefly outlining how the framework introduced in §4b applies in cross-specific perspective. To this end, I simply reiterate the key relevant points, eschewing references to features of social organization that are exclusive to humans (e.g. descent reckoning, post-marital residence).

Lineal kinship organization is a social system that emphasizes interactions among lineally related kin—that is, individuals related through females only, if the emphasis is towards matrilineal kin, and individuals related through males only, if the emphasis is towards patrilineal kin (see §3). In a given population, the emphasis may be expressed in one or more social domains, corresponding to pathways for the transmission of different resources across generations (e.g. the allocation of food, information, and so on, or the transfer of access to the natal territory). The relative costs and benefits of investment in matrilineal versus patrilineal kin may vary for different resources, leading to an emphasis towards matrilineal kin in some domains and towards patrilineal kin in others, with other domains still presenting no such emphasis.

A lineal bias in any domain can be viewed as a bias in investment towards a particular set of kin—specifically, towards the offspring of daughters if the bias is matrilineal, and towards the offspring of sons if the bias is patrilineal.

Thus, investment is directed to the offspring of the females in the population in one case, and to the offspring of the males in the other. This is distinct from a bias in investment towards daughters and towards sons, respectively. For example, in the matrilineal case investment may be restricted to the sons of the females in the population, to the exclusion of the females' daughters. Resources are transferred matrilineally in both scenarios, but they flow between males via females in the first, and directly between females in the second (see §3).

Across species, then, it is important to specify which social domains the bias applies to, if any (e.g. the allocation of food or the transfer of access to the natal territory) and the precise route that different resources follow across generations (e.g. between males via females or directly between females). More broadly, explanations for biases towards lineally related kin must not be confounded across domains. Of course, the same factors may lead to a bias towards a particular set of kin in more than one domain, and feedback across domains seems likely. For example, the physical aggregation of matrilineally related females and their dependants may facilitate the transfer of, say, foraging skills from mother to offspring. Similarly, the transfer of foraging skills from mother to offspring may favour the physical aggregation of matrilineally related females

and their dependants. However, there is no reason to assume that the same factors are at play in the two domains, nor that a bias towards matrilineally related females in one domain will inevitably lead to a corresponding bias in the other (see §3).

The overall implication is that viewing matriline and patriline as unitary phenomena may hinder understanding of variation in social behaviour within and across species. In particular, the underlying variation is masked by the common practice of designating a species, a population, or a kinship system as 'matrilineal' or 'patrilial'. Recourse to alternative labels such as 'female-biased kinship' does not address this issue. Rather, what is required is precision in the definition of key terms and concepts, with separation of the different aspects of the social system that may feature a bias towards lineally related kin.

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References

1. Fox R. 1983 *Kinship and marriage: an anthropological perspective*. New York, NY: Cambridge University Press. (Originally published by Penguin Books Ltd, 1967; reissued with a new Preface.)
2. Bachofen JJ. 1861 *Das Mutterrecht: eine Untersuchung über die Gynaiokratie der alten Welt nach ihrer religiösen und rechtlichen Natur*. Stuttgart, Germany: Kraus & Hoffmann.
3. Douglas M. 1969 Is matriliney doomed in Africa? In *Man in Africa* (eds M Douglas, PM Kaberry), pp. 121–135. London, UK: Tavistock Publications.
4. Schneider DM, Gough K (eds). 1961 *Matrilineal kinship*. Berkeley, CA: University of California Press.
5. Parkin R. 1997 *Kinship: an introduction to basic concepts*. Oxford, UK: Blackwell Publishers Ltd.
6. Peters PE. 1997 Introduction. *Crit. Anthropol.* **17**, 125–146. (doi:10.1177/0308275X9701700202)
7. Alexander RD. 1974 The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383. (doi:10.1146/annurev.es.05.110174.001545)
8. Alexander RD. 1977 Natural selection and the analysis of human sociality. In *Changing scenes in the natural sciences, 1776–1976* (ed. CE Goulden), pp. 283–337. Philadelphia, PA: Academy of Natural Sciences.
9. Flinn M. 1981 Uterine vs. agnatic kinship variability and associated cousin marriage preferences: an evolutionary biological analysis. In *Natural selection and social behavior: recent research and new theory* (eds RD Alexander, DW Tinkle), ch. 26, pp. 439–475. New York, NY: Chiron Press.
10. Gaulin SJC, Schlegel A. 1980 Paternal confidence and paternal investment: a cross cultural test of a sociobiological hypothesis. *Ethol. Sociobiol.* **1**, 301–309. (doi:10.1016/0162-3095(80) 90015-1)
11. Greene PJ. 1978 Promiscuity, paternity, and culture. *Am. Ethnol.* **5**, 151–159. (doi:10.1525/ae.1978.5.1.02a00110)
12. Hartung J. 1981 Paternity and inheritance of wealth. *Nature* **291**, 652–654. (doi:10.1038/291652a0)
13. Hartung J. 1985 Matrilineal inheritance: new theory and analysis. *Behav. Brain Sci.* **8**, 661–670. (doi:10.1017/S0140525X00045520)
14. Kurland JA. 1979 Paternity, mother's brother, and human sociality. In *Evolutionary biology and human social behavior: an anthropological perspective* (eds NA Chagnon, W Irons), ch. 6, pp. 145–180. North Scituate, MA: Duxbury Press.
15. Gray JP, Wolfe LD. 1982 A note on brother inheritance. *Ethol. Sociobiol.* **3**, 103–105. (doi:10.1016/0162-3095(82)90006-1)
16. Hartung J. 1982 Comment: reply to Gray and Wolfe. *Ethol. Sociobiol.* **3**, 101. (doi:10.1016/0162-3095(82)90005-X)
17. Wolfe LD, Gray JP. 1981 Comment on Gaulin and Schlegel (1980). *Ethol. Sociobiol.* **2**, 95–98. (doi:10.1016/0162-3095(81)90039-X)
18. Mattison SM, Shenk MK, Thompson ME, Borgerhoff Mulder M, Fortunato L. 2019 The evolution of female-biased kinship in humans and other mammals. *Phil. Trans. R. Soc. B* **374**, 20190007. (doi:10.1098/rstb.2019.0007)
19. Keessing RM. 1975 *Kin groups and social structure*. New York, NY: Holt, Rinehart and Winston.
20. Holy L. 1996 *Anthropological perspectives on kinship*. London, UK: Pluto Press.
21. Kuper A. 1982 Lineage theory: a critical retrospect. *Annu. Rev. Anthropol.* **11**, 71–95. (doi:10.1146/annurev.an.11.100182.000443)
22. Murdock GP, Wilson SF. 1972 Settlement patterns and community organization: cross-cultural codes 3. *Ethnology* **11**, 254–295. (doi:10.2307/3773219)
23. Cronk L, Gerkey D. 2007 Kinship and descent. In *Oxford handbook of evolutionary psychology* (eds RIM Dunbar, L Barrett), ch. 31, pp. 463–478. Oxford, UK: Oxford University Press.
24. Tylor EB. 1889 On a method of investigating the development of institutions; applied to laws of marriage and descent. *J. Anthropol. Inst. Great Britain and Ireland* **18**, 245–272. (doi:10.2307/2842423)
25. Harrell S. 1997 *Human families*. Boulder, CO: Westview Press.
26. Schneider DM. 1961 Preface. In *Matrilineal kinship* (eds DM Schneider, K Gough), ch. 17. pp. vii–xvii. Berkeley, CA: University of California Press.
27. Johnson J. 2016 Matriliney. In *The Cambridge encyclopedia of anthropology* (eds F Stein, S Lazar, M Candea, H Diemberger, J Robbins, A Sanchez, R Stasch). Retrieved on 20 January 2019 from <http://doi.org/10.29164/16matriliney>.
28. Fortunato L. 2018 Systematic comparative approaches to the archaeological record. In *The emergence of pre-modern states: new perspectives on the development of complex societies* (eds JA Sabloff, PLW Sabloff), ch. 3, pp. 33–49. Santa Fe, NM: SFI Press.
29. Murdock GP, White DR. 1969 Standard cross-cultural sample. *Ethnology* **8**, 329–369. (doi:10.2307/3772907)
30. Murdock GP. 1967 *Ethnographic Atlas*. Pittsburgh, PA: University of Pittsburgh Press.
31. Murdock GP. 1967 *Ethnographic Atlas: a summary*. *Ethnology* **6**, 109–236. (doi:10.2307/3772751)

32. Fortunato L. 2017 Insights from evolutionary anthropology on the (pre)history of the nuclear family. *Cross-Cult. Res.* **51**, 92–116. (doi:10.1177/1069397117691006)
33. Holden CJ, Sear R, Mace R. 2003 Matriliney as daughter-biased investment. *Evol. Human Behav.* **24**, 99–112. (doi:10.1016/S1090-5138(02)00122-8)
34. Alvarez HP. 2004 Residence groups among hunter-gatherers: a view of the claims and evidence for patrilocality. In *Kinship and behavior in primates* (eds B Chapais, CM Berman), ch. 18, pp. 420–442. New York, NY: Oxford University Press.
35. Fortunato L. 2011 Reconstructing the history of residence strategies in Indo-European-speaking societies: neo-, uxori-, and virilocality. *Hum. Biol.* **83**, 107–128. (doi:10.3378/027.083.0107)
36. Adam L. 1947 Virilocal and uxori-local. *Am. Anthropol.* **49**, 678. (doi:10.1525/aa.1947.49.4.02a00220)
37. Borgerhoff Mulder M *et al.* 2009 Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science* **326**, 682–688. (doi:10.1126/science.1178336)
38. Murdock GP. 1949 *Social structure*. New York, NY: The Free Press.
39. Aberle DF. 1961 Matrilineal descent in cross-cultural perspective. In *Matrilineal kinship* (eds DM Schneider, K Gough), ch. 17, pp. 655–727. Berkeley, CA: University of California Press.
40. Lowie RH. 1919 The matrilineal complex. *Univ. Calif. Publ. Am. Archaeol. Ethnol.* **16**, 29–45.
41. Lowie RH. 1920 *Primitive society*. New York, NY: Boni and Liveright.
42. Murdock GP. 1937 Correlations of matrilineal and patrilineal institutions. In *Studies in the science of society* (ed. GP Murdock), pp. 445–470. New Haven, CT: Yale University Press.
43. Rivers WHR. 1924 *Social organization*. London, UK: Kegan Paul, Trench, Trubner & Co., Ltd.
44. Richards AI. 1950 Some types of family structures amongst the Central Bantu: characteristics of matrilineal kinship organizations in Central Africa. In *African systems of kinship and marriage* (eds AR Radcliffe-Brown, D Forde), pp. 207–251. London, UK: Oxford University Press for the International African Institute.
45. Fortunato L. 2012 The evolution of matrilineal kinship organization. *Proc. R. Soc. B* **279**, 4939–4945. (doi:10.1098/rspb.2012.1926)
46. Rogers AR. 2013 Genetic relatedness to sisters' children has been underestimated. *Proc. R. Soc. B* **280**, 20121937. (doi:10.1098/rspb.2012.1937)
47. Smith EA. 2013 Agency and adaptation: new directions in evolutionary anthropology. *Annu. Rev. Anthropol.* **42**, 103–120. (doi:10.1146/annurev-anthro-092412-155447)
48. Mattison S. 2011 Evolutionary contributions to solving the 'matrilineal puzzle': a test of Holden, Sear, and Mace's model. *Hum. Nat.* **22**, 64–88. (doi:10.1007/s12110-011-9107-7)