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# Does gender structure social networks across domains of cooperation? An exploration of gendered networks among matrilineal and patrilineal Mosuo

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Cooperative networks are essential features of human society. Evolutionary theory hypothesizes that networks are used differently by men and women, yet the bulk of evidence supporting this hypothesis is based on studies conducted in a limited range of contexts and on few domains of cooperation. In this paper, we compare individual-level cooperative networks from two communities in Southwest China that differ systematically in kinship norms and institutions—one matrilineal and one patrilineal—while sharing an ethnic identity. Specifically, we investigate whether network structures differ based on prevailing kinship norms and type of gendered cooperative activity, one woman-centred (preparation of community meals) and one man-centred (farm equipment lending). Our descriptive results show a mixture of 'feminine' and 'masculine' features in all four networks. The matrilineal meals network stands out in terms of high degree skew. Exponential random graph models reveal a stronger role for geographical proximity in patriliny and a limited role of affinal relatedness across all networks. Our results point to the need to consider domains of cooperative activity alongside gender and cultural context to fully understand variation in how women and men leverage social relationships toward different ends.

This article is part of the theme issue 'Cooperation among women: evolutionary and cross-cultural perspectives'.

#### 1. Introduction

Humans rely on social relationships to accomplish far-ranging tasks, from mundane, day-to-day activities, to intermittent, but critical forms of help during acute periods of need [1]. The structure and content of social relationships are expected to differ based on attributes of relationship partners (see [2,3]), the type of activities involved, and the hierarchical level (e.g. individual, household, community) at which relationships are expressed. Among such variables, gender has long been held to play a key role in explaining variation in human social relationships (see [2,3]). This follows from sexual selection theory [4,5], which anticipates divergence in male and female reproductive interests and therefore the activities, including social relationships, that support those interests. We [6], along with many others (e.g. [4-8]), have argued previously that such divergences are more likely to be expressed in some contexts than in others, and, more specifically, that strong differences in men's and women's social networks are less likely in contexts that support women's autonomy. In this paper, we leverage variation in kinship and gender norms among the matrilineal and patrilineal Mosuo of China to investigate the associations between gender and social networks that

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vary in type of activity and expectation for male versus female participation. We consider two networks in each kinship ecology: (i) a community meals network oriented around women's labour; and (ii) a farm equipment lending network oriented more strongly around men. We ask whether gendered networks in two domains of cooperative activity diverge in ways consistent with sexual selection theory and whether these differences are modulated by predominant kinship norms (i.e. matrilineal versus patrilineal). Finally, we investigate classic behavioural ecology influences [9] of relatedness, reciprocity and geographical proximity on the probability of a tie and how such influences differ across kinship ecologies.

#### (a) Sexual selection and gendered networks

Social networks offer fundamental sources of support that contribute to fitness [1]. Interestingly, while social network analysis has for some time been a key empirical means to assess inter-individual cooperation [10] and its effects on fitness among actors with different characteristics, there has been very limited research in behavioral ecology tying gender to social network analysis to understand differences in cooperation among women and men (see [6]). Sexual selection theory posits that, due to differences in their reproductive biology, men and women pursue different strategies to secure reproductive success [4,5,11,12]. This is premised on the observation that men's reproductive success is frequently limited by access to reproductive partners, whereas women's is frequently limited by access to resources and allocare of children. Extensions of this framework generally anticipate men engaging in riskier behaviours that are more focused on status enhancement and mating opportunities, and women being more risk averse and focused on securing the resources necessary to support their children. These anticipated differences are further extended to social relationships, expecting men (and boys) to have relatively large (diffuse), hierarchical and unstable social networks compared to women (and girls) [13-18]. In other words, cooperative networks among men are expected to differ substantively (oriented around status and mating) from cooperative networks among women (oriented around childcare).

There is significant empirical support for these general expectations (although remarkable inconsistency in specific findings) in industrialized settings, typically in relation to affective networks such as friendship, with some researchers going so far as to conclude that associated patterns 'constitute strong direct evidence for biological gender-specific differences in networking behaviour' [19]. For example, women had higher node degree (network size) and clustering coefficients (i.e. greater tendencies to interact with women who interacted with each other) in agonistic interactions in an online gaming universe, and were also more likely to reciprocate [19]. Other studies have shown women treating friends more like kin and men treating friends more like strangers [20], boys having more friendship connections than girls [13], and men exhibiting larger networks than women [15,21]. Women are often expected to have stronger, more stable, dyadic relationships: in a study of Dutch and American participants, Peperkoorn et al. [22] found that women engaged more in cooperative activities in dyads, for example (see also [15]).

### (b) Type of activity and network structure

Less is known about how the type of cooperative activity relates to gender divergences in network structure, despite the obvious constraints that different types of cooperative activities place on, for example, the number of ties or the distance over which ties might be pursued (see [23]). Yet it is clear that the type of network is associated with its structure [24-27] and also the opportunity to observe differences between men and women (e.g. [28]). Indeed, the extent to which men's and women's activities diverge differs considerably across societies ([29], see also [30]). This suggests the need to evaluate whether gender exerts different influences on network structure across a range of cooperative or affiliative activities and more generally to uncouple (deconflate) gender from activity in drawing inferences about patterns in network structure. For example, a recent study of gendered movement among the Hadza revealed more clustering among women gathering together and more solitary activity among men hunting for game [31]. In this context, male networks appeared smaller than female networks, but this may have more to do with activity (hunting versus gathering) than with gender, per se. Women's clustering in the context of gathering may facilitate cooperation in different ways than activities pursued in a more solitary, temporally disconnected fashion [32], even when nodes and ties are similar, reinforcing the need to know how activity and gender together drive network structure in different socio-cultural contexts. Here, we investigate two different types of networks, both inclusive of women and men, but each normatively oriented around one gender, to see whether these gendered expectations are associated with feminine versus masculine network characteristics predicted from sexual selection theory.

#### (c) Kinship socio-ecology and gendered networks

Finally, it is reasonable to expect that social-ecological contexts shape differences in gendered networks (e.g. [33,34]). This is because differences in socio-ecologies affect the payoffs to male and female reproductive strategies, especially by limiting payoffs associated with men's pursuit of status and reproductive opportunities [7,35–40]. Specifically, sexual selection theory relies on a set of assumptions that are met to varying degrees across human societies [41], including lower caps to the number of children produced by females, compared to males, higher variance in male reproductive success, and a steeper association between mating effort and reproductive success among males than among females. In contexts where these assumptions are not met or met only weakly, the rationale for sexual selection theory, including differences in gendered networks, may be lost or significantly muted [6].

In this paper, we ask whether and how gender predicts the characteristics of two different types of cooperative networks among matrilineal versus patrilineal Mosuo in Southwest China. The first is a community meals (CM) network that characterizes helping among individuals during festivals, funerals or other community events [42]. These meal preparation activities do not exclude men but are normatively oriented around women, who work together to prepare food and serve it during these events. Anecdotally, the networks appear diffuse, with few obvious constraints in terms of size (meals can be prepared and served in large courtyards) or other aspects of network structure. The second is a farm equipment lending (EL) network that typically, but not exclusively, involves men providing access to equipment to help with agricultural activities. In the context of patriliny, where the terrain is steep and plots are smaller, equipment is less mechanized and less expensive than in the context of matriliny, where equipment is highly mechanized and expensive, such that purchasing ability is limited to relatively few individuals. Thus, the EL networks may be more constrained in terms of ownership in matrilineal contexts and arguably more likely to be centralized as a result. EL networks in patrilineal contexts might be more concentrated in terms of geographical proximity and more clustered. Gender differences in patrilineal EL networks might also be relatively muted, given regular labour contributions of both genders to household agricultural activities [43]. While imperfect in terms of absolute comparability (e.g. because equipment lent in patrilineal communities differs from what is lent in matrilineal ones), our analysis allows us to begin to tease out how gender, the type of network, and socio-ecological context intersect to affect gendered differences in network size, transitivity and important predictors of ties.

Specifically, we examine the following predictions from a gendered-differences hypothesis to investigate whether gender-oriented networks display the following differences in network structure:

- (i) the CM networks will show female-oriented network properties and EL networks will show male-oriented network properties; i.e. we expect smaller degree (smaller networks) and more transitivity (shared partners) in CM networks; and
- (ii) these differences will be more pronounced in the patrilineal community than in the matrilineal community.

Tests of related hypotheses have largely been relegated to affective networks such as friendship networks (see [6] for review). Such networks are arguably less goal-oriented than instrumental networks that form around particular types of activities. Still, if sexual selection drives differences in female versus male assortment across a range of cooperative activities, as commonly proposed (e.g. [5,44]), then we should anticipate women and men using any given network to support divergent reproductive goals. In other words, if women and men are using instrumental networks in ways that reflect their reproductive strategies, then we should see, across network types, a female or male 'signature'. If, however, activity type supersedes gender in driving network structure, then we should see that type of activity leaves a stronger signature.

This test is perhaps less strong than one that investigates the differences in gendered use of non-goal-directed networks such as friendship or religious networks. Yet, both men and women participate in both types of networks investigated here, allowing us to query whether expectations associated with gender orientation in the networks produce a signature anticipated by gendered-differences hypotheses despite representation of men and women in both types of network. If we find that CM networks have female signatures and EL networks have male signatures, then we have evidence consistent with the idea that the gendered-differences hypothesis generalizes to goal-directed networks across domains of activity. The socio-ecological context provides an additional means of assessing differences in gender by normatively reinforcing pre-existing gender biases (see [45]). However, if we fail to find female or male signatures in a given network, we cannot reject the gendered-differences hypothesis because, in this test, the type of activity could constrain network observables in ways that limit the expression of gender differences. We have no a priori reason to expect such constraints, but we acknowledge that the test is less strong than one investigating male versus female networks across a range of overlapping activities.

## 2. Population and cooperative activities

The Mosuo are an ethnic minority population of Tibetandescended high-altitude [46] agriculturalists residing in the Hengduan Mountains on the border of Sichuan and Yunnan Provinces in Southwest China [42,47]. They consist of two subpopulations, one matrilineal and one patrilineal, that share language, identity, and numerous customs, but differ substantially in norms and institutions surrounding kinship, as well as in certain aspects of subsistence [43,48,49]. The matrilineal Mosuo live in the expansive Yongning Basin (figure 1), where they tend irrigated fields producing a variety of crops, including buckwheat, corn, potatoes and vegetables, and keep numerous livestock and fowl, including water buffalo, cattle, pigs (a traditional symbol of wealth), chicken, ducks and geese. Among the matrilineal Mosuo, inheritance, including the homestead, is passed from one senior generation of co-inhabitants to the next; normatively, only women's children belong to a given household, resulting in matrilineal inheritance of shared resources. Marriage is less common than traditional forms of non-contractual partnerships known as sese, in which a woman and her reproductive partner(s) maintain residence in their natal households (i.e. residence is natalocal), but visit each other at night [50]. The patrilineal Mosuo reside in steeper terrain at lower altitudes to the west of Yongning. They keep smaller farms with more limited use of plows and different livestock and crop composition than in the basin, including greater reliance on tobacco and rice, sheep and goats, and more limited reliance on bovids. Inheritance among the patrilineal Mosuo is from a senior male to one son (typically the oldest or youngest). Residence is patrilocal stem, where the inheriting son and his wife reside together with the son's parents. Marriage is normative and sese rare [43].

Instrumental and affective social networks are relatively sparse overall among the Mosuo, especially the matrilineal Mosuo, despite a normative emphasis placed on intra- and inter-household cooperation [42,43,49,51]. Economic autonomy, especially in matriliny (see [45] EHS), may limit the need for significant inter-household exchange [9,52]. Correspondingly, cooperation is more extensive in activities that are traditionally community-oriented, such as preparing meals for communal feasts, compared to domestically oriented activities such as childcare [6]. Gender is associated with different patterns of social relationships among the Mosuo, though in different ways than many other populations. Our previous work has shown gender reversals in certain metrics of friendship networks, including network size (degree), such that matrilineal women reported higher numbers of friendships, on average, than matrilineal men [6]. How gender differences extend to other sorts of networks remains unknown and is the crux of our investigation here.

Community meals (figure 2*a*) are commonplace across Mosuo villages and arise in conjunction with major life or household events, such as weddings, funerals, coming-of-age ceremonies and opening or refurbishing a guest house [48,49]. As in many parts of China, both men and women participate in community meals, but in normatively different ways. Women frequently do much of the cooking, while men slaughter animals for the feast and assist with background tasks such as preparing the space for cooking and moving cookware or heavy bags of rice, as





**Figure 1.** The matrilineal community of Mosuo (a) lives in expansive, flat basins of the Hengduan mountains, whereas the patrilineal community lives in much steeper terrain (b), albeit at lower altitude. (Online version in colour.)



Figure 2. Community meals (a) involve significant preparation, here for the Chinese New Year, and are oriented around women but inclusive of men. Equipment lending (b) often involves men providing access to expensive (in matrilineal villages) or routine (in patrilineal villages) equipment through dyadic transactions that need not involve overlapping participation given temporal disjunctures in borrowing and lending. (Online version in colour.)

well as serving and clearing food. These normative expectations are only partially met, as both men and women can be seen engaging in any of the tasks involved in meal preparation. Chefs are visible during preparation and widely known to community members. There are no obvious limits to the number of participants in these festivities; cooking spaces are often bustling with as many as a dozen or more individuals at once helping with preparations. These activities are undertaken in similar ways in both matrilineal and patrilineal contexts.

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Equipment lending (figure 2b) is oriented around men in both patrilineal and matrilineal contexts, although to different degrees. In matrilineal villages, men have historically been called upon to carry out the more strenuous activities associated with agriculture, including yoking cattle and preparing the land for planting [43]. Nowadays, some of this labour has been transitioned to mechanized equipment, purchased initially by wealthy families under the stewardship of men (not without women's input). Equipment lending is sporadic, but relatively common in matrilineal contexts compared to patrilineal ones, as mechanized equipment is still sparsely owned yet highly desirable. In patrilineal areas where terrain is steeper, there is more limited use of mechanized equipment. Instead, equipment is shared more regularly when e.g. a scythe or hoe is misplaced or needs repair. Because both men and women participate in all activities associated with agriculture in the patrilineal communities, there is less expectation of strong gender divergences in these equipment lending networks. At the same time, our ethnographic work underscores that these activities are more strongly oriented around men, as the equipment lending network was suggested to us by participants as an appropriate male domain when we were piloting our social network instrument.

In sum, anecdotal evidence suggests that community meals can support large, diffuse networks, yet are normatively oriented around women in both patrilineal and matrilineal communities; there are no obvious size constraints on equipment lending networks, though they might be expected to be sparser and more centralized in matrilineal communities than in patrilineal ones.

# 3. Data and analysis

We carried out social network interviews as part of the Santa Fe Institute Economic Network Dynamics and the Origins of Wealth (ENDOW) project in an attempt to capture full networks of households in one matrilineal (N = 40 households) and one patrilineal (N = 30 households) community of Mosuo in the summers of 2017 and 2018. We walked from house to house and selected any available adult member of the household, man or woman, as respondent. This respondent typically answered questions about their own relationships, but occasionally was asked to comment on relationships of an opposite-gender

adult in the household. The respondent was frequently attended by other members of the household, who assisted in answering questions. We explained the study to potential participants and addressed their questions before obtaining their informed consent for the interview (UNM IRB 06915). Other co-resident adults often assisted in answering interview questions. We used a name generator approach, asking respondents to free list individuals with whom they had various kinds of social ties [53]. Here, we analyze responses to questions about: (i) who helps to prepare a meal for a community event like a wedding or funeral and (ii) a double-sampled question on lending and borrowing farm equipment. Relatedness, both genetic and affinal, was determined from genealogies collected alongside social network data. GPS coordinates allowed computation of geographical distance between nodes.

#### (a) Analysis

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An individual was included in a network (MCM, matrilineal community meals; PCM, patrilineal community meals; MEL, matrilineal equipment lending; PEL, patrilineal equipment lending) if (i) the individual was a respondent who nominated an alter in response to the relevant question, or (ii) the individual was nominated by a respondent, resided in the surveyed community, and was associated with enough additional information (e.g. gender and an identifiable household) for our analysis. Some respondents appear as isolated nodes if they only nominated individuals outside the surveyed community [54,55] outside the surveyed community. By focusing on heads of households, these inclusion criteria preferentially sample individuals who are likely to be central to the network as a whole, minimizing bias in the estimation of network statistics [55,56]. However, it is certain that precise network statistics would differ in a more complete sample; additionally, our sampling strategy systematically underrepresents adults who are not heads of households, some of whom may be important in the network structures we investigate.

Edges in each analysed network point toward the source of help. For CM networks, the respondent nominated alters who helped them with community meals. For EL networks, responses to two different questions were included. Edges for the 'equipment to' question were therefore reversed (from the 'direction' of the name generator) for consistency. Responses to both questions were included in an attempt to capture more of the actual lending network, but we acknowledge that by so doing we may overestimate reciprocity in the EL networks [56]. We operationalize the 'size' of an individual's network by their in-degree, the number of edges pointing towards an individual's corresponding node. Two nodes form a reciprocal dyad if there is an edge from i to jand from j to i. The transitivity of a node reflects the number of a node's neighbours that are connected to each other. We use the motif- or triad-based operationalization of transitivity for directed networks: a group of three nodes is transitive if and only if  $i \rightarrow j \rightarrow k$  then  $i \rightarrow k$  for all i, j and k [57].

Differences in the central tendencies of degree distributions were assessed with a Kruskal-Wallis test, followed by Wilcoxon post-hoc pairwise comparisons. Similarly, straightforward methods to test for differences in degree skewness  $(r_1)$ , reciprocity  $(r_2)$  and transitivity  $(r_3)$  between the small number of networks studied here, to the best of our knowledge, are not readily available. For example, methods that compare distributions of counts of network components have been criticized on the grounds that nonnetwork variables, such as physical proximity, can strongly influence observed network structures [58].

We, therefore, built what we call a fundamental model that expands on Artzy-Randrup et al. [58] to include additional variables that may define the 'space' in which human relationships form. In this model, we propose that observed features of a given empirical network can be explained by a control for the number of observed edges  $(s_1)$ , genetic relatedness  $(s_2)$ , affinal relatedness ( $s_3$ ) and geographical distance ( $s_4$ ). These variables are not drawn from the observed networks, but rather are expected to constrain the possible observed networks: farm equipment may be more likely lent to a geographical neighbour than an individual several kilometers away, and family members more likely to be asked to help with meal preparation. If an observed network is similar on some dimension (e.g. the frequency of a certain structure) to random networks generated from the fundamental model, then we cannot rule out the possibility that these spatial variables may explain the frequency of the observed network structure. If, on the other hand, the counts differ significantly, we reject the idea that the fundamental model is a good model for the observed network on this dimension. We can compare several networks by noting whether each network is similar to or different from its ensemble. However, this is a qualitative comparison: we cannot quantify the amount by which the observed network differs from its proposed fundamental model, nor can we compare the observed networks directly.

We fitted the fundamental model to each network by maximum pseudolikelihood [59]. We then simulated 2500 random networks from each fitted model such that, across the simulated networks, the average of each spatial variable  $s_i$  is expected to be the same as that calculated from the

term	variable	operationalization	reference
s <sub>1</sub>	number of edges	the number of observed edges in the empirical network	[27]
s <sub>2</sub>	genetic relatedness	estimate of genetic relatedness	[60,61]
<b>S</b> <sub>3</sub>	affinal relatedness	estimate of relatedness through marriage	[61,62]
S <sub>4</sub>	geographical distance	estimated by the research team from the GPS coordinates of each household	
<i>r</i> <sub>1</sub>	degree skew	the skewness of the in-degree distribution	[63]
<i>r</i> <sub>2</sub>	reciprocity	the count of reciprocal dyads	[27]
<i>r</i> <sub>3</sub>	transitivity	the count of transitive triads	[27]

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**Table 1.** Descriptive statistics, network measures.

	community meals		equipment lending	
	matriliny (MCM)	patriliny (PCM)	matriliny (MEL)	patriliny (PEL)
# nodes (women, men)	22, 12	12, 15	11, 10	9, 16
# total (women, men)	33, 14	34, 17	15, 21	14, 30
age (mean, IQR)	48 (39.5, 55.5)	46.8 (35.5, 51.5)	43.16 (36.5, 53.5)	42.18 (34.0, 49.0)
network density	0.025	0.024	0.028	0.036
average in-degree (mean, IQR)	1.09 (0, 1)	1.20 (0, 1)	0.97 (0, 2)	1.55 (0, 2)
in-degree skewness	3.03	1.62	1.21	1.79
# reciprocal dyads	3	1	10	20
# transitive triads	7	4	0	0

observed data. In the empirical value of the count of network structure  $r_k$  was within the upper and lower limits set by 95% of the simulated  $r_k$  values, we considered that  $r_k$  to be explained by chance given the fundamental model; if the value of  $r_k$  was below those limits, we considered the value

All analysis was conducted in R (v. 4.1.2) with standard repository packages, including *statnet* (v. 4.5.0) and *igraph* (v. 1.2.11) [64]. The fundamental models were fitted and simulated with *ergm* (v. 4.1.2) [65].

#### 4. Results

All four networks were similar in number of nodes (range: 36–51; table 1, figure 3) and density (0.024–0.036). Individual ages were similar across the networks, and the proportions of women and men were similar within network types (i.e. CM and EL). However, the MCM network stands out for having high in-degree skewness and number of transitive triads, whereas the two EL networks have relatively large numbers of reciprocal dyads (figure 3).

The average in-degree is different between the four networks we analysed (Kruskal-Wallis test,  $\chi^2 = 10.014$ , d.f. = 3, p = 0.018). *Post-hoc* pairwise comparisons suggest that nodes in the matrilineal CM network tend to have lower in-degree than the patrilineal EL network (p = 0.024) but that the other comparisons (e.g. MCM and MEL or PCM and MEL) are not meaningfully different.

The fitted fundamental models are presented in table 2. Genetic relatedness is an important predictor of the existence of ties in both matrilineal networks and the patrilineal CM network but not in the patrilineal EL network. On the other hand, geographical distance is a significant predictor of edges in both patrilineal networks and in the matrilineal EL network but not in the matrilineal CM network. Notably, affinal relatedness is not a significant predictor in any of these four models.

Figure 4 shows graphically the results of our simulation approach. Each panel of figure 4 shows the results from the set of simulations for each network (columns) and network observables (rows). Panels contain a histogram of the network observable in the simulated networks (grey bars); 95% of simulated networks had values for the observable within the hashed blue lines. The empirical value is shown by the purple line. For example, the top left panel shows

of  $r_k$  to be 'low' and if above those limits, we considered the value to be 'high'.

We operationalized fundamental model terms  $s_i$  and network observables  $r_k$  as follows:

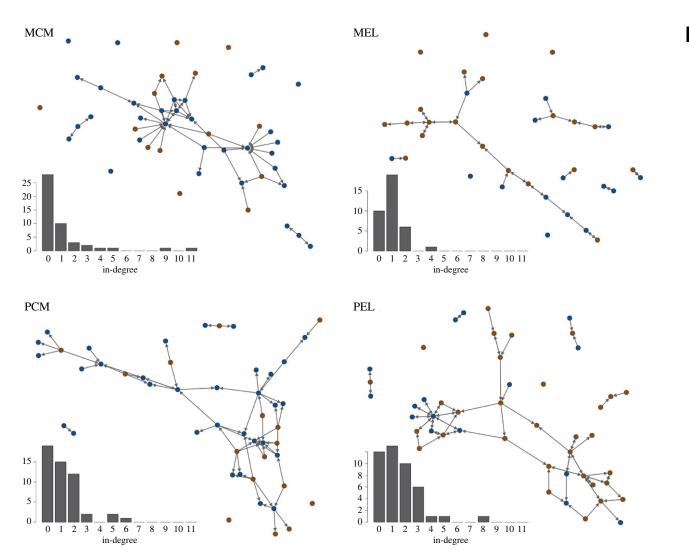
the results for the skewness of the degree distribution of the matrilineal CM network. The majority of networks simulated from the fundamental model of the matrilineal CM network had a degree skewness approximately near 0.75, and 95% of such values were between approximately 0.25 and 1.6. The empirical value was over 3.0, suggesting that the skewness of the degree distribution of the matrilineal network was high compared to networks generated by its fundamental model. In the lower right corner are the results of our analysis of the transitive triads in the patrilineal EL network: the number of transitive triads in this network is low compared to its fundamental model.

When compared to the associated network ensemble, the MCM and PEL networks have high degree skewness, whereas the degree skewness for the PCM and MEL networks are predictable from the null models (figure 4). Reciprocity is high in the MCM, MEL and PEL networks but not in the PCM network. Transitivity is high in the MCM network and low in the MEL and PEL networks.

All in all, there is not a consistent pattern of purportedly masculine or feminine features across all networks (table 3). Although we used quantitative methods to support our comparisons, the comparisons remain essentially qualitative—and, given our limited sample, of potentially limited generalizability. For example, the MCM network appears masculine (high degree skew) or feminine (low average degree) with respect only to our proposed fundamental model, not with respect to other networks. Additionally, the lack of significance of affinal relatedness seems worthy of further study not supportable by our current data. Even so, the analysis we have presented does not seem to align well with predictions stemming from sexual selection theory as applied to goal-oriented networks.

#### 5. Discussion

In this paper, we aimed to extend prior investigations of gender differences in networks to incorporate effects of the type of gendered cooperative network. Specifically, we



**Figure 3.** Networks and their in-degree distributions. Networks are (top) the matrilineal community meals network (MCM) and equipment lending network (MEL), and (bottom) the patrilineal community meals network (PCM) and equipment lending network (PEL). Women are marked with blue nodes and men with brown. (Online version in colour.)

compared networks oriented around men's activities (equipment lending networks) to networks oriented around women's activities (preparing meals for community events). We set up this comparison as an exploration that might illuswhether prevailing gender norms attending matriliny versus patriliny), or the gendered expectations associated with specific activities, or both, would predict differences in network structure. In general, we found few differences in basic metrics across the four networks. However, the matrilineal community meals network stood out as both more strongly transitive (a 'feminine' trait) and more highly skewed in node degree (a 'masculine' trait). Visually, the equipment lending networks are sparser than the community meals networks. They are also more similar to each other than either is to its kinship system counterpart. In other words, the network activity appears to be important, perhaps more so than prevailing kinship norms, in driving network structure. Finally, exponential random graph models (ERGMs) revealed that genetic relatedness and geographical distance were important predictors of ties in most networks, but that importance was not equal across networks. Affinal relatedness was not associated with ties in any network.

Theory surrounding gender differences in network structure and behaviour is based on sexual selection theory and

the biological adaptedness of 'the' sexual division of labour [66]. If the premises of this theory hold universally, as anticipated by many (see [6]), then the properties of networks that are oriented around one gender, such as men's hunting, should be fundamentally different to those oriented around another gender, such as women's gathering. Such differences could arise because men and women take on activities that reflect divergent social strategies (e.g. men prefer tasks that allow them to show off whereas women prefer tasks that support childcare) or because men and women engage in a given task in fundamentally different ways. Tests of sexual selection theory are clearest in contexts where the content of networks is overlapping, such as in friendship networks, and observed differences can be inferred to be due to gender (e.g. [5,13,15]), and the most opaque when gender and activity are fully conflated (e.g. if men always hunt and women always gather). The test we offer here is somewhere in between-networks are, a priori, 'gendered', in the sense that they are normatively oriented around one gender, yet women and men participate in both types of networks. Thus, we extended sexual selection theory to networks that vary in content, anticipating that 'male' networks (here, equipment lending) would appear unequal and skewed, large (i.e. high node degree) and not particularly transitive [19]. Whereas prior research in wealthy industrialized contexts often supports general

Table 2. Fundamental models for simulation. Model results marked by an asterisk were dropped by the ERGM estimating algorithm because the algorithm could not estimate a coefficient; the other terms in the same model were estimated as if the term marked by an asterisk had not been included. b, coefficient value; z, z-score for that coefficient.

	b	std error	z	p
MCM				
network density	-3.546	0.277	-12.822	0.000
genetic relatedness	3.916	1.049	3.735	0.000
affinal relatedness	*	*	*	*
distance (km)	-0.499	0.497	-1.003	0.316
PCM				
network density	-2.903	0.257	-11.315	0.000
genetic relatedness	2.971	0.903	3.290	0.001
affinal relatedness	1.183	1.449	0.817	0.414
distance (km)	-0.165	0.040	-4.153	0.000
MEL				
network density	-2.719	0.310	-8.771	0.000
genetic relatedness	4.106	1.429	2.873	0.004
affinal relatedness	0.944	2.752	0.343	0.731
distance (km)	-2.436	0.764	-3.187	0.001
PEL				
network density	-1.371	0.229	-5.995	0.000
genetic relatedness	0.629	0.905	0.695	0.487
affinal relatedness	-3.129	2.293	-1.364	0.173
distance (km)	-0.394	0.053	<b>—7.459</b>	0.000

divergences between men's and women's networks [13-15,67], such differences did not extend across the board to gendered Mosuo networks examined here; rather a mix of characteristics putatively associated with a given gender is found in each network (table 3), with type of network appearing to drive the structure more than kinship socioecology (i.e. patriliny versus matriliny).

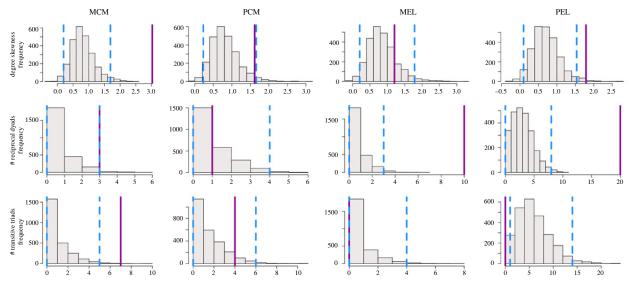
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As we have argued previously [6], stark depictions of universal gender differences downplay the role played by contextual variation in the norms and institutions regulating gender, as well as the (probably considerable) overlap among men and women in reproductive, economic and social goals in many contexts [41,68,69]. They also fail to appreciate constraints a chosen network type (friendship, sharing, cooperating in different tasks) bring to bear on estimated network characteristics, which has rarely been examined [19], yet is critical to structuring network observables. For example, Aktipis and colleagues have shown that need-based livestock transfers among the Maasai are associated with different principles of cooperation than transfers based on 'accountkeeping' [70], even when the item being transferred is the same. This suggests that cooperative activities and their underlying goals exert strong influences on patterns that may be observed in cooperative networks in ways that are (perhaps frequently) likely to supersede the differences attributable to gender, per se.

We attempted to tease some of this out here, by comparing two networks that normatively centre around women (community meals) and men (equipment lending). It is important to note that neither of these networks is relegated to one gender, as women and men can and do participate in both, and both are characterized by 'female' and 'male' network features, as conceptualized in sexual selection theories of human cooperation. Community meals are highly visible (male), for example, and equipment lending less visible (female), but plausibly riskier (male). And, indeed, our results suggest that outcomes associated with both genders are apparent in every network examined here (table 3). Thus, what we conventionally think of as 'female' or 'male' activities are not exclusively so. At the same time, the structure of activities dominated by women (community meals) appears more 'female' on the whole than those of other networks. Node degree is lower, on average, in CM networks, in both patrilineal (not significant) and matrilineal settings, and transitivity higher. This is despite the conspicuousness of community meal preparation. Thus, there may be something more constraining about community meals as an activity than women's friendship networks, which were overall more 'male' among matrilineal women in prior analyses [6]. We suspect it may be related to culinary skills, as respondents frequently attested to preferring a specific set of highly skilled women to assist in meal preparation. Finally, it is worth noting that matrilineal women were also those who stood out in terms of health benefits in our prior analysis of inflammation and hypertension [71]. Thus, while we often think of men as having greater variation in behaviour, health and reproductive success [41], it is interesting that here, women appear to be important levers in terms of driving observed gender differences.

There were few consistent differences in network structure based on prevailing kinship norms (i.e. matriliny versus patriliny), but two stand out: geographical proximity was consistently associated with ties in patriliny and less important in matriliny; and genetic relatedness was less consistently associated with ties in patriliny than in matriliny. The influence of geographical proximity likely has to do both with type of terrain (steeper in patriliny) and access to automobiles (less in patriliny) [43,48], rather than something inherent to how activities are structured under different prevailing kinship systems. Why relatedness across categories was more important in matriliny is unclear. Relatedness has previously been shown to predict cooperation among the Mosuo [51], particularly in the context of high recipient need. Here, we see a positive effect of genetic relatedness on participation in CM networks and no effect of affinal relatedness, which is expected to be more important for women's activities in patrilineal contexts [61,72]. We are uncertain as to why affinal relatedness did not predict ties, but note that the role of affines is downplayed in matriliny [7,73] given frequent absence of institutionalized marital unions [50]. Affines in patriliny often come from relatively nearby villages [49] such that they may already share many relations in common with their spouses; further, such relationships may simply be less important than geographical distance in networks that involve moving equipment and cooking materials over difficult terrain.

This study is subject to limitations. First, the sample size is small, particularly at the level of networks. This hampers our ability to make generalizable inferences. Second, the comparison between patrilineal and matrilineal kinship systems and gender norms is imperfect in the sense that there is more that varies between these communities than just



**Figure 4.** Comparison of empirical networks with the corresponding network ensemble: skewness of the degree distribution (top row), the count of reciprocal dyads (middle), and count of transitive triads (bottom) for each of the four networks (MCM, matrilineal community meals; PCM, patrilineal community meals; MEL, matrilineal equipment lending; PEL, patrilineal equipment lending). The value of each variable from the empirical network is marked with the solid purple vertical line; 95% of the simulated values are between the dashed blue lines. (Online version in colour.)

**Table 3.** Summary of results.

MCM	MEL		
high degree skew (masculine)	low transitivity (masculine)		
low average degree (feminine)	high reciprocity (feminine)		
high transitivity (feminine)	genetic relatedness (positive)		
high reciprocity (feminine)	geographical distance (negative)		
genetic relatedness (positive)			
PCM	PEL		
genetic relatedness (positive)	high degree, high skew (masculine)		
geographical distance	low transitivity (masculine)		
(negative)	high reciprocity (feminine)		
	geographical distance (negative)		

gender norms: in addition to differences in gender and kinship norms, these communities differ in topographical characteristics and economic development [45]. Comparing networks that are, a priori, gendered, is less ideal than comparing networks that have similar substance and in which both women and men participate, such as friendship. Nonetheless, the networks we describe include both women and men and would not appear to constrain one or the other on outcomes of interest such as size, transitivity or dyadic frequencies, which still allows us to consider how gendered expectations might yield different network structures, something that has received limited attention to date in studies of human evolution. Comparative studies with sufficient variation on axes of kinship and economic factors as predictors of network structure would allow for more robust hypothesis tests, as would larger samples to facilitate comparison of female versus male networks within each domain of activity, which we were unable to analyze here. Use of two name generator questions to characterize equipment lending may have overstated reciprocity (if respondents were more likely to name a particular alter as someone to whom they lent equipment and from whom they borrowed equipment) compared to a single name generator [56], so our findings with regard to equipment lending reciprocity must be interpreted with caution. Analytically, although it is theoretically possible to conduct our analysis entirely in an ERGM framework [59,74], in practice dependency terms in ERGMs can be difficult to fit [75] and models can suffer from degeneracy and other problems related to statistical theory [76]. The approach we have taken avoids dependency terms in the ERGM itself but does not support the familiar interpretation framework that a purely ERGM approach would have provided. Finally, social network methods were adapted from the ENDOW study design (https://endowproject.github.io). The questions we asked may under-depict nuances of social relationships (e.g. the fact that all households are expected to send one member to prepare community meals) while faithfully representing other aspects (e.g. that some people were preferred as cooks to organize meal preparation).

#### 6. Conclusion and future directions

Does a woman hunt like a man or does she hunt like a hunter? It is difficult to answer this question without analysing the ways that women and men behave across a range of overlapping activities. This exploratory analysis is an explicit, if imperfect, attempt to tease out potentially overlapping effects of gender, cooperative activity, and contextual variation in prevailing gender norms on the structure of social networks. In general, as per our previous results [6], we find little evidence of universality of structures associated with gender, per se. Rather, there are both 'female' and 'male' characteristics among all network structures analysed here. At the same time, we could not fully separate gendered expectations in a given activity from the substance of the activity. More comparative analyses will be necessary before we can tease out those effects with finer resolution. Future research should attend to all of these axes of variation-gender, activity and context-for more nuanced and robust examinations of the causes of variation in cooperative network structures. Such studies would overcome some of the limitations to which this study is subject by comparing networks that are not gendered at the outset, such as friendship, religious networks or certain forms of food sharing networks, over a range of contexts that offer different support for women's and men's reproductive agendas.

Social network analysis remains a powerful tool for investigating the evolution of human cooperation and its consequences [77,78]. The historical interest in food sharing and realms of cooperation dominated by men has given us limited insight into female cooperation across contexts and domains of activity [6,79,80], even though female-female cooperation has long been known to support reproductive success [1]. The Mosuo example continues to provide evidence that the ways in which women operate differ significantly across contexts, including adopting behaviours or patterns frequently deemed 'male' [6,71,81,82]. The comparison of how gendered activities differ in matrilineal versus patrilineal contexts is imperfect, but important for establishing how gender interacts with domains of activity and wider cultural norms to impact behaviour and outcomes [34,43,83], especially if, as many behavioural ecologists have argued, culture ultimately plays a stronger role in driving behavioural variation than evolved biological predispositions to pursue canalized, gender-specific 'strategies' [84-87].

Ethics. Ethical review was conducted by UNM (UNM IRB 06915).

Data accessibility. Partial data are available at the second author's GitHub account (https://github.com/ngmaclaren/ynlb). Data

cannot be fully de-identified—additional variables may be requested via the first author as necessary to validate models.

Authors' contributions. S.M.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing; N.M.: data curation, formal analysis, methodology, visualization, writing—original draft, writing—review and editing; C.S.: data curation, investigation, project administration, writing—review and editing; M.K.S.: writing—review and editing; T.B.: funding acquisition, investigation, project administration, writing—review and editing; K.W.: data curation, formal analysis, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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#### **Endnotes**

<sup>1</sup>Whereas theory refers to biological sex, our data capture what women and men do; thus, we refer to gender rather than sex throughout this manuscript.

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