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BaYaka forager food sharing networks in the Congo Basin: The roles of gender homophily and kin sharing

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Abstract

Objectives: Food sharing is a costly form of cooperation that was likely critical to human evolutionary success, including the emergence of human's life history strategy. Food sharing in human communities may be maintained through a number of pathways, including direct dyadic reciprocity, reputation-based processes, and kinbiased exchange. Differences in reproductive demands, labor, and cultural norms may also result in gendered differences in cooperative networks. Here, we examine cooperative networks in egalitarian BaYaka foragers from the Congo Basin.

Materials and Methods: We collected social network data from 112 adults in 41 households in this subsistence community. We implement a Bayesian latent network model to assess individual-, dyadic-, and block-level predictors of food sharing partners.

Results: Conditioning on covariates, we found limited evidence for direct dyadic reciprocity in food sharing. Despite local norms regarding prestige avoidance, we found statusbased homophily. High-status individuals-council members and local healers-were more likely to share with one another. Importantly, our results highlight gender differences in patterns of food sharing, interacting with genetic relatedness. Women were more likely to share with one another, especially with kin as genetic relatedness increased.

Discussion: Our results align with evolutionary framing emphasizing kin selection in costly cooperation. The results showing that women cooperate with other women, particularly kin, also complement sex-based patterns in some other mammalian species, potentially reflecting the social support necessary to manage reproductive costs and childcare. BaYaka women's subsistence productivity and local cultural dynamics for autonomy and egalitarianism may likewise help facilitate women's preferential cooperation with one another.

KEYWORDS

kin selection, resource sharing, sex differences, social networks, social status

INTRODUCTION 1

support-and thus greater social integration into groups-has been linked to lower mortality risks, better health, and higher reproductive fitness across a range of species (Silk, 2007; Snyder-Mackler

The benefits of sociality have been extensively theorized and researched across a range of taxa. The receipt of social and material et al., 2020). Potential barriers to the evolution of costly sociality may This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

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be overcome through pathways involving kin selection (Hamilton, 1964), direct reciprocity (Axelrod & Hamilton, 1981), indirect reciprocity (Nowak & Sigmund, 2005; Redhead et al., 2021), and reputation-based partner choice (Roberts et al., 2021), yielding selective benefits via assortment of cooperators. Human cooperation comparatively stands out for its range of domains and coordination as well as its integration and expansion into cultural norms and institutions that allow larger-scale expression, including in societies where population growth reduces possibilities for direct reciprocity (Boyd & Richerson, 2009; Dyble et al., 2016; Glowacki & Lew-Levy, 2022; Henrich & Muthukrishna, 2020).

Food sharing is a specific form of costly cooperation given the importance of energetic resources to health, survival, and reproduction (Gurven, 2004; Jaeggi & Gurven, 2013; Kramer & Ellison, 2010). Food sharing is widespread among humans, and may have been critical to human evolutionary success, including aspects of human's life history strategy (i.e., the stacking of dependency periods for slow developing, energetically costly young; Gurven, 2004; Kaplan et al., 2000; Kramer & Ellison, 2010). In immediate-return forager societies, the circulation of food is considered an important mechanism for maintaining egalitarian social relations, alongside free and equal access to resources and mobility practices (Lewis et al., 2014; von Rueden et al., 2019; Woodburn, 1982). The pooling of energetic resources through food sharing serves a critical risk reduction role in communities where individual subsistence returns can be highly variable (Ember et al., 2018; Ringen et al., 2019), including those that rely on foraging (Gurven, 2004; Jaeggi & Gurven, 2013).

Risk reduction strategies (e.g., reciprocity, need-based sharing) and allocation of resources to kin are considered evolved tendencies that help maintain widespread food sharing among human communities (Gurven, 2004). Depending on the resource, food sharing may also be shaped by costly signaling, status seeking, and coalition building (Apicella & Silk, 2019; Hawkes & Bird, 2002; von Rueden et al., 2019). Specifically, individuals may be motivated to share their resources to improve their relative standing within the community (i.e., their social status). This is because having high status provides a multitude of benefits-with, for example, individuals being more likely to cooperate with those in good standing (e.g., through processes of indirect reciprocity; Alexander, 1974; Redhead & von Rueden, 2021; Roberts et al., 2021)---and status in human communities commonly rests upon perceptions of an individual's ability and willingness to confer benefits to others (Redhead et al., 2019; Redhead & Power, 2022). There may also be gender-based differences in positions in certain types of social networks, and in the formation and maintenance of cooperative relations (von Rueden et al., 2018). These differences may be influenced by evolved dimensions of reproductive strategies in humans and other mammals and likely also intersect with local social norms and culturally evolved conventions regarding gendered group formation in humans (Gurven, 2004; Redhead & Power, 2022; Smith et al., 2021).

From a comparative perspective, mammalian females may be more apt to cooperate, particularly with kin, to manage the energetic costs of reproduction. This is because female mammals incur the costs of gestation/lactation and often bear the primary responsibility of parental care.

Moreover, compared with males, female mammals also more commonly remain in their natal group or range (female philopatry), increasing opportunities for repeated interactions and relationships with kin. According to sexual selection perspectives, mammalian males may be more motivated by forms of social status/rank (e.g., dominance) and coalitionary support that aid in access to contested resources and increase sexual opportunities with potential mates, as males are not similarly constrained by offspring care (Mattison et al., 2019; Silk, 2007; Smith et al., 2021; Sterck et al., 1997; von Rueden et al., 2018). Consequently, these sex differences may shape subsistence and social activities, and by extension orientation toward cooperation/sharing partners. Evidence from a broad range of long-lived mammalian species provides some support for these tenets. Although patterns do vary, females more frequently form more stable, stronger ties and cooperative relationships with their female kin and males often form weaker, less stable ties or engage in coalition formation that helps facilitate mating opportunities (Carter et al., 2013; Langergraber et al., 2009; Lettevall et al., 2011; Mitani & Watts. 2001: Murphy et al., 2020: Packer et al., 1991: Pearson, 2011; Silk, Alberts, & Altmann, 2006; Silk, Altmann, & Alberts, 2006; Whitehead et al., 2012; Wittemyer et al., 2005).

In species that have evolved bi-parental care, these differences may be more muted. While costly forms of human paternal care likely emerged in the evolutionary past (Gettler, 2010; Gettler, Boyette, & Rosenbaum, 2020; Gray & Anderson, 2010; Kaplan et al., 2000), such care is facultative and may relate to gendered variation in patterns of cooperative networks. This may occur through cultural and ecological differences in divisions of labor, alongside other local ecological dynamics and social norms, such as locality and availability of kin (Bird & Codding, 2015; Gettler, Lew-Levy, et al., 2020; Marlowe, 2007: Mattison et al., 2019: Mattison et al., 2021: Scelza & Bird, 2008). For example, among Tsimane forager-horticulturalist communities in Bolivia, men had a greater number of cooperation partners, especially among non-kin, than did women. Divisions of labor within families may have helped explain this, as men spent more time on cooperative subsistence/labor activities outside the home while women's networking was more constrained by intrahousehold tasks, such as childcare and food processing (von Rueden et al., 2018). In comparisons of Mosuo agriculturalist villages in China, women tended to have larger friendship networks than men in matrilineal villages, whereas this pattern was not found in patrilineal Mosuo settings (Mattison et al., 2021). The authors point to the importance of local socio-ecological conditions in shaping these network dynamics. Mosuo men's reproductive opportunities are likely constrained by monogamous practices and in matrilineal communities women and men remain in their natal groups, enhancing access to kin and other well-established relationships for support. Mattison et al. (2019) proposed a specific conceptual model-the Expendable Male Hypothesis-to help explain the evolutionary emergence of matrilineal systems that bias investment toward maternal kin.

Pertinent to our analysis here, Mattison et al. (2019) argue that when ecological conditions and subsistence practices coincide to enable women's independent ability to meet the needs of their families, they will often focus their cooperative and resource sharing efforts on other women, particularly kin (Mattison et al., 2019). They suggest this can co-occur with inconsistent or minimal paternal investment and possibly also disincentivize men's parenting and care. In addition to their findings from Mosuo communities (Mattison et al., 2021), research elsewhere can likewise be considered through this framework. For example, among Martu Aborigines in Australia, women's hunting plays an important role in community subsistence and it has been shown that women cooperate more in hunting and also strategically maintain residence with their mothers and sisters to facilitate gendered care and foraging networks (Bird et al., 2012; Scelza & Bird, 2008).

Here, we examine how direct dyadic reciprocity, indirect reciprocity via status hierarchy (e.g., where choices to cooperate are based on an individual's relative standing in a community; Leimar & Hammerstein, 2001; Milinski et al., 2001; Panchanathan & Boyd, 2003), and kin-biased exchange characterize food sharing networks among BaYaka foragers in the Congo Basin. We also evaluate whether BaYaka food sharing patterns are consistent with predictions about comparative (cross-species) sex differences in forming cooperative relations. BaYaka are an excellent fit to examine these predictions. They have cultural practices that mitigate status seeking (Lewis, 2008), which may limit some of the bidirectional links between cooperation and status (von Rueden et al., 2019). Moreover, their gender-based divisions of labor are more attenuated compare to many other subsistence societies (Hewlett, 1991; Marlowe, 2007; Thomas & Bahuchet, 1991; see Section 2). Finally, BaYaka communities practice demand sharing (Kitanishi, 1998), which likely also contributes to the dynamics of food sharing networks.

2 | METHODS

2.1 | Ethnographic setting

In their rainforest ecology, BaYaka women and men's contributions to household and community pooled energetic resources are often comparable and not heavily skewed (Hewlett, 1987, 1991; Marlowe, 2007). Women specialize in collecting fruit, yams, nuts, greens, mushrooms, and fish (Kitanishi, 1995), usually in larger groups with children and adolescents. Men hunt, trap, and collect honey, typically alone or in small groups (Kitanishi, 1995). BaYaka families also practice modest levels of swidden agriculture, with women primarily responsible for planting and cultivating garden plots for crops such as cassava. Reflecting somewhat attenuated divisions of labor, both men and women engage in fishing, gathering, and gardening activities. Fathers are also frequently involved in day-to-day direct caregiving (e.g., infant care and teaching) (Boyette et al., 2020; Hewlett, 1991; Sarma et al., 2020; Thomas & Bahuchet, 1991). While spouses sometimes forage together, women and men spend much of the day in segregated groups (Hewlett, 1992; Lewis, 2008).

Like other forager societies, resource sharing is strongly valued among BaYaka, and helps maintain egalitarian and cooperative social relationships (Kitanishi, 1998; Lewis, 2002). Because it is an unpredictable resource and often comes in surplus (e.g., a large animal kill), any meat captured is widely shared (Kitanishi, 1998). At the kill site, raw meat is shared among the hunters according to their roles in the hunt. Upon return to the settlement, hunters share raw meat with cohabitants and visitors, who then redistribute it to women to cook. Raw plant food transfers between women are usually needs-based (Kitanishi, 1998), except in the cases of surplus yams, agricultural products from the village, and excess fruit. Women redistribute up to 80% of cooked food to other households. Settlement size structures the sharing of cooked food (Kitanishi, 1998). In small settlements, cooked food is shared with all present. In larger settlements, cooked food is shared with neighbors and close kin.

BaYaka also participate in communal activities that foster cooperation and information sharing including telling fables (*gano*) and public speaking (*mosambo*), during which a community member may air their grievance, sharing norms are enforced, and labor is organized (Bombjaková, 2018). More informally, the evening is spent in conversation. Women usually aggregate near their hearths and men around the *mbandjo* sitting area. Conversations often focus on techniques for finding resources, recollections of foraging trips, gossip, and discussions of upcoming feasts, commemoration ceremonies, and spirit plays (Bombjaková, 2018; Lewis, 2002, 2008).

2.2 | Study site

We collected data from adults in a remote multiethnic village along the Motaba river in Likouala Department (province) in the northern Republic of the Congo. Fieldwork took place in June and July 2018 in the larger of two BaYaka neighborhoods. All adults were invited to participate in the study. In total, 112 adults (aged 18 or over; 65% women) from 41 households—representing 77% of the total neighborhood population—provided social network data. Those who did not participate in the study were generally ill, newly postpartum, in the forest for extended hunting trips, or otherwise engaged in labor for neighboring farmers. Because BaYaka do not record age, we estimated approximate age in years for adults following the methods outlined in Diekmann et al. (2017), and adjusted for a minimum parentchild difference of 16 years. The average estimated age of participants was 40.9 years of age (SD 14.5 years) (Table S1).

2.3 | Social network interview

Social network interviews were collected as part of the Economic Networks and the Dynamics of Wealth Inequality project (https://endowproject.github.io/), which aims to understand the effects of network structure on material wealth inequality. We elicited networks at the individual level. To do this, all participating adult and adolescent men and women were asked to free list individuals with whom they maintained a variety of relationships during a 20–30 min interview. In the present paper, we focus on responses to a subset of four questions: (1) who do you share food with?, (2) who shares food with you?,

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(3) who do you forage with?, and (4) who do you converse with in the evenings?.

After each person named, the researcher asked "who else?" until the participant indicated that their list was complete. Participants were free to name anyone, including household members, village inhabitants, or external alters. We did not seek a minimum number of nominations, nor were nominations capped to an upper limit. As shown by questions 1 and 2 above, our food sharing networks were double-sampled (Nolin, 2008; Ready & Power, 2021)-meaning that we asked all participants questions about both directions of the relationship (i.e., who they shared food with, and who shared food with them). To avoid biases introduced from missing data in network models, only individuals who participated in the study were included in the analyses (Kossinets, 2006).

2.4 Social status

Members of the village council and healers within the community were considered to have high social status; 13% of the participants were classified as being high in status. Men and women on the village council act as spokespeople (kombeti or mokonji) for BaYaka during village affairs (Hewlett, 1987). Nganga are healers who provide traditional medicine for BaYaka and neighboring Bantu farmers. Both council members and nganga are considered highly skilled within their respective domains of influence and are frequently turned to for advice (Hewlett, 1987).

2.5 Genetic relatedness and household distance

Genetic relatedness was determined using genealogical interviews (Boyette et al., 2020). We calculated genetic relatedness using the kinship2 package (v.1.8.5; Sinnwell et al., 2014). We collected GPS points for the front doors of all village households. Using the package geosphere (v.1.5-10; Hijmans et al., 2017), we estimated the interhousehold distance in meters.

2.6 Data analysis

We implemented a Bayesian latent network model that jointly assesses the factors that guide food sharing and the possible biases associated with self-reported social networks (Redhead, McElreath, & Ross, 2022) using the STRAND package (Redhead, McElreath, & Ross, 2022; Ross et al., 2022) in R (v.4.0.4.; R Core Team, 2017).

In our model, these estimated and adjusted for (a) whether individuals were prone to forget to report certain ties, (b) whether individuals had a tendency to falsely report ties that did not exist, and (c) whether individuals tended to report the same names across our double-sampled food sharing network items asked because they were in sequential order

"question duplication": see Redhead, McElreath, (i.e., æ Ross, 2022, for further details). We modeled individual-level (estimated age), dyad-level (gender, genetic relatedness, physical distance, foraging ties, conversational ties), and block-level (social status) covariates that may be related to the probability of network ties using a generalization of the Social Relations Model (Snijders & Kenny, 1999), which integrates block-level random effects (i.e., a stochastic block model; see Redhead, McElreath, & Ross, 2022, for technical outlines and tutorials).

By using this modeling framework, we are able to parse the individual characteristics (e.g., age) that may be associated with sharing or receiving food, with attributes of a dyad (i.e., two individuals), such as whether food is shared more often between two women, as opposed to between individuals of the different genders. Alongside this, we are able to assess whether individuals were more likely to reciprocate ties (i.e., dyadic reciprocity), and whether individuals who shared food with a greater number of partners also received food from a greater number of partners (i.e., the correlation between sending and receiving food, often referred to as generalized reciprocity).

Here, "block-level" covariates, are considered observed attributes that individuals can be meaningfully grouped into (e.g., gender or ethnic group; Contisciani et al., 2020; Redhead, McElreath, & Ross, 2022). Choice of treating covariates at the block-level, as opposed to being individual-level or dyadic-level covariates, needs careful consideration and ultimately depends on the research question that is being addressed.

We consider our measure of status-a binary indicator of whether or not an individual is a member of the village council or a healer-as a meaningful grouping variable for the community (i.e., a group of individuals with high status, as opposed to a group of individuals with low status). Including social status as a block-level covariate allowed us to examine whether food sharing was likely observed between individuals of different, or the same, status. In doing so, we were able to answer questions as to whether cooperation flowed to or from higher-status individuals.

Unless stated, we interpret the median of the posterior distributions for each parameter included in the model, θ , and the 95% highest posterior density intervals (McElreath, 2020). Please refer to the Supplementary Materials for full descriptive statistics and model results.

RESULTS 3 T

Table 1 presents the descriptive statistics for our food sharing, co-foraging, and conversational networks. Here, we show the raw, doublesampled nominations of food sharing (i.e., Obs. Sharing (out) and Obs. Sharing (in)), along with the food sharing network inferred by our latent network model. Our network follows typical characteristics of previously observed food sharing networks (e.g., Nolin, 2010; Ready & Power, 2018; Redhead, Dalla Ragione, & Ross, 2022; von Rueden et al., 2019). Our networks were relatively sparse, with

TABLE 1 Descriptive statistics for social networks

Network	n ties	Dens. ^a	Recip. ^b	Trans. ^c	Degree	In-deg. ^d	Out-deg. ^d
Est. sharing	763	0.061	0.501	0.429	6.812	0-19	0-18
Obs. sharing (out)	611	0.049	0.347	0.401	5.455	0-15	0-17
Obs. sharing (in)	457	0.037	0.232	0.303	4.08	0-12	0-12
Foraging	366	0.029	0.033	0.095	3.268	0-8	0-12
Gossip	529	0.043	0.054	0.13	4.723	0-13	0-17
Obs. Women's Sharing (out)	333	0.027	0.402	0.489	2.973	0-12	0-14
Obs. Women's Sharing (in)	275	0.022	0.327	0.365	2.455	0-9	0-12
Obs. Men's Sharing (out)	58	0.005	0.207	0.234	0.518	0-5	0-8
Obs. Men's Sharing (in)	46	0.004	0.174	0.288	0.411	0-5	0-7
Obs. Diff. Gender sharing (out)	220	0.018	0.3	0 ^e	1.964	0-7	0-9
Obs. Diff. Gender sharing (in)	136	0.011	0.059	0 ^e	1.214	0-6	0-7

Note: Est. Sharing Network = The predicted sharing network from our latent network model. Obs Sharing out and in are the observed network layers used as data for fitting the latent network model (i.e., in = "who shared food with you" and out = "who did you share food with"). Women's, men's and different gender sharing show the descriptive statistics for sharing between women, between men, and between two individuals of a different gender, respectively.

^aDensity depicts the number nominations, divided by the number of possible ties.

^bReciprocity shows the number of ties that are reciprocated between dyads.

^cTransitivity is the proportion of triads observed (e.g., individuals *i*, *j*, and *h* are all connected in a triangle, regardless of the direction of the connecting ties). ^dHere we present the range of observed in-degree and out-degree. In-degree denotes the number of ties that an individual has received, while out-degree shows the number of ties that an individual has sent.

^eNote that transitivity is impossible in this network given the gender-based coding.



FIGURE 1 Food sharing network inferred from our latent network analyses. Green nodes (circles) represent women, blue nodes represent men. Ties are colored by the probability that they exist, with darker gray suggesting greater certainty.

around 763 ties being inferred, which is around 6% of all potential ties. There was a large range in out-degree and in-degree; individuals were estimated to send between 0-18 ties and receiving between 0-19 ties (Figure 1). Around 50% of the inferred food sharing ties were

reciprocated. Transitivity also patterned the network, with individuals clustering together, and around 43% of all possible triads being observed within the inferred network. Individuals, on average, sent/received food to/from around 6.812 others in the community. Interestingly, when considering descriptive patterns of sharing between women, men, and food sharing between individuals of different genders separately, food sharing between women is the most commonly observed, followed by food sharing between individuals of different genders; food sharing between men was observed much less frequently.

As shown in Figure 2, there was substantial variation in who gave (i.e., sender effects SD) and received food (i.e., receiver effects SD). Figure 2b shows that giving and receiving food were marginally correlated (i.e., there was some evidence of *generalized reciprocity*): individuals who gave more were slightly more likely to receive more. Older individuals were more likely to receive food, but marginally less likely to send food. After conditioning on all covariates, we found no substantial patterns of dyadic reciprocity (i.e., if individual *i* gave to another individual, *j*, that individual *j* was not reliably more or less likely to share food with those who lived closer to them. Individuals tended to share food with their foraging and conversational partners. See Figure 2b for visualizations of all of these dyadic-level effects.

As shown in the supplementary materials, our results suggest that individuals rarely falsely reported ties in either network layer (i.e., giving or receiving), however the propensity to falsely report ties varied quite substantially across individuals (i.e., some individuals were more likely to falsely report, while others not). Individuals seemed to

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FIGURE 2 (a) Posterior median (log-odds) and 95% credible intervals for all individual-level parameters included in our latent network model. (b) Posterior median (log-odds) and 95% credible intervals for all dyad-level parameters included in our latent network model.



FIGURE 3 The effects of relatedness and gender homophily on food sharing. Posterior predictions of the effects that the interaction between gender homophily and relatedness has on food sharing ties. We present the predicted posterior median (log-odds) and 95% highest posterior density intervals for each combination of genders in a dyad across a plausible range of relatedness values (i.e., from nonrelatives, relatedness = 0, to close kin, relatedness = 0.5).

4 | THE ROLES OF GENDER HOMOPHILY AND GENETIC RELATEDNESS

As shown in Figure 2b, individuals were much more likely to share food with closer kin. Women were much more likely to share with other, unrelated women. Food sharing between unrelated individuals of different genders was marginally less likely to be observed (with man-man food sharing acting as a baseline in our model). Figure 3 **FIGURE 4** The effects of status on food sharing. We present contrast coefficients, and 95% highest posterior density intervals, that indicate the change in probability of sharing ties between and within different levels of status, relative to the probability of low status to low status sharing ties. Negative values that do not encompass 0 indicate that low-low status food-sharing is reliably more likely that the parameter of interest, whereas positive coefficients indicate that they are less likely.



shows simulated model predictions regarding the interaction between gender-based homophily and genetic relatedness. Ties between women were generally most likely to be observed across the range of relatedness values. The probability of any sharing ties within and between genders increased with levels of genetic relatedness. Food sharing between the genders was unlikely to be observed between unrelated individuals, but became much more likely with increased levels of relatedness, which, in turn, was also more likely than observing man to man ties between close kin.

5 | THE EFFECTS OF SOCIAL STATUS

As outlined in detail above, we included social status as a block covariate and generated model predictions about the probability of ties being observed within and between status blocks (i.e., between low and high status individuals). As Figure 4 shows, we found mixed results related to status. After conditioning on all other covariates included in the model (e.g., age), those high in status were reliably more likely to share with high status others. There is a marginal tendency for those low in status to share with those high in status. Those high in status were no more or less likely to share with those low in status, in comparison to those low in status sharing with low status others.

6 | DISCUSSION

Aligning with theory that emphasizes the importance of kin selection to the evolution of cooperation, we found that genetically related individuals were more likely to share with one another (Apicella & Silk, 2019; Gurven, 2004; Jaeggi & Gurven, 2013; Lehmann & Keller, 2006). BaYaka women, especially, were much more likely to share with women and men to whom they were related. In some mammalian species females are often more apt to form bonds with and cooperate intensively with kin, with some limited evidence for related patterns in humans (Carter et al., 2013; Langergraber et al., 2009; Lettevall et al., 2011; Mitani & Watts, 2001; Murphy et al., 2020; Packer et al., 1991; Palchykov et al., 2012; Pearson, 2011; Scelza & Bird, 2008; Silk, Alberts, & Altmann, 2006; Silk, Altmann, & Alberts, 2006; von Rueden et al., 2018; Whitehead et al., 2012; Wittemyer et al., 2005). From a comparative perspective, kin may help females support the costs of reproduction, including their primary role in offspring care. Although these dynamics may also contribute to human networks for costly cooperation, few studies have explored these questions (Palchykov et al., 2012), particularly in energetically demanding ecologies where such support is often imperative (Hawkes et al., 1997; Mattison et al., 2021; Meehan et al., 2013; Scelza & Bird, 2008).

As noted, BaYaka gendered labor divisions are somewhat muted compared with many subsistence societies, with fathers often being involved in childcare and husbands and wives overlapping and cooperating in some subsistence activities (Boyette et al., 2020; Fouts, 2008; Hewlett, 1991; Noss & Hewlett, 2001). Nonetheless, women often spend much of the daytime with their young children and women to whom they are related, and women's subsistence and food sharing provide stable nutrition for children and families. In comparison, BaYaka men may be less likely to routinely share with men who are kin because they engage in solitary or small group hunting and the game they acquire is more widely shared, which benefits the community and builds their reputations (Gettler, Lew-Levy, et al., 2020; Hewlett, 1991; Kitanishi, 1995; Kitanishi, 1998). Given the wider sharing of hunted game across the community (Kitanishi, 1998), one could expect that men would be nominated more often as food sharing partners by non-kin, compared with women. This type of pattern would complement findings from Tsimane communities in Bolivia showing that men had more non-kin cooperation partners, especially among non-kin, than did women (von Rueden et al., 2018). However, our results do not align with these findings, which could be due to several factors. First, hunting is an

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unpredictable activity, which varies considerably in importance across seasons (Kitanishi, 1995). As a result, men's meat sharing with the wider community may also be more sporadic, which could attenuate their nominations as food sharing partners. Second, when men return to camp with game, these resources are ultimately handed over to women, who have responsibility for preparing, cooking, and redistributing food for others, including kin and non-kin (Kitanishi, 1998). Thus, women may be viewed as the main sharers of food, even as they share resources collected by both men and women. In total, BaYaka women and men's sharing networks are likely patterned by the gendered dynamics of their routine subsistence and in-camp activities, which are, themselves, shaped by local cultural and ecological conditions. This aligns with the suggestion that the activity inherent to the focal network itself (e.g., resource sharing) and activities contributing to and shaped by the network (e.g., subsistence, food prep/ distribution roles) should be considered and emphasized alongside "gender" as a predictor and interpretive lens (Mattison et al., 2022). Patterns of gendered network structures will likely vary not only across cultural and ecological contexts but also within local communities depending on the network activity (Mattison et al., 2022)e.g., BaYaka men and women's social information networks might look more similar in structure than the food sharing networks we focused on here.

Our findings for gendered food sharing networks, including among non-kin, do share some similarities with results among Mosuo communities in China, where women tended to have larger friendship networks than men in matrilineal villages (Mattison et al., 2021). Mattison et al. (2021) suggest that with greater access to social support and resources in matrilineal contexts Mosuo women's social strategies can resemble those more often attributed to men in other settings. Although BaYaka are not matrilineal (Lewis, 2002), our results may provide some parallels due to local cultural and ecological dynamics. BaYaka cultural norms and practices emphasize gender egalitarianism, individual autonomy, and lack of coercion/control over others (Boyette & Hewlett, 2017; Lewis, 2008), such as in their formation of social/cooperative relationships. Moreover, women also play a critical role in providing stable resources, making them socially and productively central in these communities in the absence of patriarchal constraints and without women's over-reliance on men's foraging returns. Although BaYaka men/fathers are generally consequential and valued for their roles in families (Boyette et al., n.d.; Boyette et al., 2020; Gettler et al., 2021; Gettler, Lew-Levy, et al., 2020; Hewlett, 1991), these results nonetheless complement aspects of Mattison and colleagues' "Expendable Male Hypothesis" framework, highlighting a further context in which women seem to preferentially form beneficial cooperative networks with one another when local conditions are favorable to do so. Moreover, past Aka/BaYaka results have shown the importance of women's network centrality to their reproductive success and child outcomes (Page et al., 2017) and the imperative support role that grandmothers play for their daughters and grandchildren (Meehan et al., 2013).

While our model predictions suggest that around half of all ties were reciprocated, there was no meaningful tendency toward dyadic

reciprocity and only a relatively small effect of generalized reciprocity when modeled alongside other predictors. Differences between the latent network modeling framework that we apply here and frameworks implemented in previous studies may help explain discrepancies between the present reciprocity results and those that included Aka/BaYaka reciprocity effects in the past (Jaeggi & Gurven, 2013; Kitanishi, 1998). Our findings suggest that, if reciprocity is observed, it may likely occur, for example, between kin, especially two women, or two individuals of different genders. Furthermore, counter to the widespread theoretical emphasis and empirical support of the role of reciprocity in the evolution of costly cooperation (Axelrod & Hamilton, 1981; Gurven, 2004; Nowak & Sigmund, 2005; Redhead et al., 2021), it is possible that reciprocity beyond that patterned by gendered norms and kin relations is not imperative to the maintenance of sharing in these communities. BaYaka value egalitarianism and community-wide generosity, realized through widespread giving and demand sharing (Hewlett, 1991; Kitanishi, 1998; Lewis, 2002; Sonoda et al., 2018), which may diminish the importance of reciprocity within the BaYaka community. This finding potentially points to the complex interplay between conditions that may be necessary for the biological or cultural evolution of a behavior versus its ongoing expression and variability in local contexts in contemporary communities. However, we note that these data are cross-sectional reciprocal nominations rather than observed resource transfers, which could have implications for the longitudinal patterns as well as the materiality of costly exchanges.

BaYaka who held locally valued roles as members of the village council or as healers were more likely to report food sharing with fellow high status individuals. Given the egalitarian norms and practices among BaYaka, these findings are potentially surprising, as one might predict greater food sharing and redistribution from higher to lower status individuals, rather than status-based homophily. However, the observed status homophily is consistent with past cross-sectional work showing that higher status individuals or households preferentially cooperate with one another among Inuit village residents in western Canada (Ready & Power, 2018) and rural Colombian communities (Redhead, Dalla Ragione, & Ross, 2022). This may help individuals maintain status, as status in such contexts may be closely linked to the perceived ability and willingness to share costly resources (Ready & Power, 2018; Redhead & Power, 2022; von Rueden et al., 2019). There was also some indication that lower status individuals were more likely to share with those of high status (compared with the opposite). This finding aligns with those from recent studies that show that higher status men were preferred as cooperation partners (Smith & Apicella, 2020; von Rueden et al., 2019) and that such partnerships may increase the status for the lower-status counterpart (von Rueden et al., 2019). Note that our results do not suggest that higher status individuals redistribute resources to those who may have greater need, as has been found in some prior work (Gurven, 2004). There are thus potential benefits to positions of high status among BaYaka, despite their overall cultural values of prestige avoidance. In mathematical models focused on the emergence of inequality, it has been shown that such status-based homophily ("elite cliques") can develop when those with higher status seek to monopolize resources and information

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(D'avid-Barrett & Dunbar, 2014). Ethnographically, we do not think these conditions are typically met by the high-status domains we measured here, which are generally oriented toward community health (healing) and benefit (council roles), though the latter could be plausibly leveraged for individual gain.

It is also possible that our finding of status-based homophily reflects long-standing social relationships, rather than status driven preferences. Specifically, the individuals occupying high status roles have generally developed friendships with one another across their lives, so their preferred sharing could reflect these long-term relationships and their maintenance through sitting on councils or performing healing ceremonies together. Furthermore, we do not have additional data on status or prestige. For example, differences in men and women's subsistence productivity are generally known reputationally within the community, despite prestige avoidance. This local form of "status" could plausibly be linked to different food sharing patterns (Redhead & Power, 2022).

To conclude, in this study of food sharing networks in a forager community, our key results show that BaYaka women were more apt to share with other women, particularly if they were genetically related, as well as men who were kin. After inclusion of other predictors, dyadic and generalized reciprocity were not strongly linked to BaYaka food sharing. These patterns align with evolutionary framing emphasizing kin selection in costly cooperation and point to the likely important intersections between divisions of labor, including in childcare and subsistence, women's productivity and autonomy, and food sharing networks in this highly egalitarian setting. Overall, our findings align with theory emphasizing kin selection and gender-based strategies in the evolutionary and biocultural dynamics of costly cooperation.

AUTHOR CONTRIBUTIONS

Lee T. Gettler: conceptualization, writing—original draft, writing review and editing. Daniel Redhead: conceptualization, methodology, formal analysis, visualization, writing—original draft, writing—review and editing. Sheina Lew-Levy: conceptualization, investigation, writing—review and editing. Ardain Dzabatou: verification, writing review and editing. All authors gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The analysis script is available as a supplementary material. Because the study community is small, even anonymized data could lead to identification. Thus, to protect participants, data are available upon request from the corresponding authors.

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SUPPORTING INFORMATION

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