Kinship, Distance, and Reciprocity Underpin Economic Support in the Pantanal Wetland

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The behavioural phenomenon of cooperation has been a focus of study in a variety of disciplines. Evolutionary anthropologists often use quantitative methods to test hypotheses on cooperation, grounded in theories such as kinship and reciprocal altruism: people are more likely to help those to whom they are related and who repay the cost of the altruistic act. That said, empirical results are somewhat mixed; numerous factors may cause social structures to vary across contexts. Here, we advance this line of inquiry in an underexplored freshwater fishery of the 179,300 km² Pantanal region in Brazil. In doing so, we examine the underlying structures of sociality within an economic-based support system at the household level (N = 55). Exponential random graph models reveal that households tend to engage in support with kin, nearby neighbours, and reciprocal partners across the network. These results affirm longstanding evolutionary theories of cooperation while challenging preconceived assumptions regarding wealth differentials in offering and requesting aid; they also inform debates on inequitable nature-based solutions in conservation, the practical implications of which could lead to better-adapted local policy interventions and feedback to communities to support regional initiatives.

Keywords: kin selection, Pantanal wetland, reciprocal altruism, small-scale fisheries, social support networks

1. Introduction

Among humans, kinship is one of the most widely studied determinants of cooperation. Cooperation towards related individuals is studied within the theoretical framework of kin selection. This theory assumes that natural selection supports helping relatives when the benefit to them is greater than the cost to the actor, taking into account how closely they are related (Hamilton, 1963; Maynard Smith, 1964).

There is extensive evidence to show that individuals are more likely to support relatives (e.g., Dyble et al., 2015; Du et al., 2019; Gurven, 2000; Madsen et al., 2007; Sear et al., 2002; Sear and Mace, 2008; Smith et al., 1987; Thomas et al., 2018). Affinities towards kin tend to manifest in observations of parental investment (Lawson and Mace, 2011; Lycett and Dunbar, 1999; Marlowe, 1999) and allocaring, which is investment by anyone other than the individual's biological parents (Arnot and Mace, 2021; Euler and Weitzel, 1996; Gaulin et al., 1997; Prall and Scelza, 2020).

Cooperation with kin is aided by mechanisms, such as kin recognition and limited dispersal (West et al., 2007). Yet, there may be circumstances where related individuals compete, influenced by the effect of family size and birth order (Lawson and Mace, 2011; Mysterud, 2006). Kinship, therefore, is not a rigid predictor of sociality, but rather a flexible variable influenced by ecological context, reproductive potential, perceived relatedness, and family structure – both within and between households – all of which can interact to shape patterns of altruistic behaviour among kin.

Cooperative behaviours between non-kin are arguably less intuitive from an evolutionary perspective. Direct reciprocity, commonly known as reciprocal altruism (Trivers, 1971), is thought to be an evolutionary mechanism that promotes cooperative behaviour based on bidirectional exchanges between individuals. Geographic proximity between individuals or households is a well-documented proxy for social bondedness in a variety of societal structures (Apicella et al., 2012; Axelrod and Hamilton, 1981; Thomas et al., 2018; Ready and Power, 2018; Nowak et al., 2006). Being in close proximity to another individual increases the likelihood of interaction, which reinforces accountability and, in turn, promotes adherence to social norms (Nowak, 2006; Onnela et al., 2011).

Although both kinship and proximity are consistently linked to cooperative behaviour, empirical findings reveal that support can diverge from these patterns, owing to the array of predictors at play – such as mate choice and cultural factors, to name just a couple (Allen-Arave et al., 2008; Kaplan and Hill, 1985; Widlok, 2016). This is particularly apparent in modern Western societies, where market integration, urbanisation, and Catholic doctrine encourage individualism and neolocal residencies, giving rise to "nuclear families" that are physically dispersed from both close and extended kin (Schulz et al., 2019), which have shown a correlation to less kin-dense networks over time (Colleran, 2020; Henrich, 2020).

Among non-Western networks of small-scale societies, social structures are influenced to some extent by the interplay between kinship relations, cultural norms of sharing, social status roles, and the rapid transmission of reputation (via distance and third-party policing) (Schnegg, 2015). These factors have been explored in a breadth of societies, covering hunter-gatherers (Apicella, 2012; Dyble et al., 2016), pastoralists, and forager-horticulturists (Du et al., 2019; Mattison et al., 2021, 2022; Thomas et al., 2015, 2018), among other rural and traditional groups (Colleran and Mace, 2015; Power et al., 2017a; 2017b). Such populations are typically characterised by frequent face-to-face contact, limited dispersal, dependence on natural resources, and close family networks, and they typically experience harsher environmental conditions than those from more industrialised societies (Borgerhoff Mulder et al., 2009). These features are thought to be similar to those of ancestral *Homo sapiens* living during the Pleistocene epoch, an arguably critical period of time for evolutionary change in the hominin lineage, dating from around 2.58 million to 11,700 years ago (Cohen et al. 2013; Harvati and Reyes-Centeno, 2022). Contemporary small-scale societies therefore provide a unique lens through which to test evolutionary hypotheses of the adaptive origins of human cognitive evolution, such as cooperation (Pontzer et al., 2018; West et al., 2007).

Here, we employ ego-centric social network analysis using exponential random graph models (ERGMs) at the household level on a small-scale society of fishers. The data are ethnographically informed and derived from semi-structured interviews with household representatives. We aim to understand the social, demographic, and structural factors associated with the presence of giving and receiving support in a population residing on the western border of the Pantanal wetland, Brazil, focusing on one type of support network: economic (material).

In doing so, we build ERGMs around the following research questions: (i) what is the relative importance of consanguineal (i.e., blood-related) kinship and residency patterns in predicting cooperative decision-making between households, and (ii) what other structural, demographic, and socioeconomic factors influence the propensity to form support ties?

Based on the existing literature, we derive several evolutionarily grounded hypotheses for the network (See Table 1). We predict that households actively engaged in economic-based support will likely form ties with genealogically related households (H1). This prediction is based on kin selection theory (Hamilton, 1964), which suggests that there are inclusive fitness benefits to helping and receiving help from related individuals. Households will likely form ties with those closer in distance (H2) and who reciprocate (H3). H2 and H3 are based on the theoretical concept of reciprocal altruism, which suggests that neighbours who are closer in distance will tend to have more frequent opportunities for interactions, promoting behavioural accountability and subsequently the enforcement of social norms (Trivers, 1971). Furthermore, we predict that wealthier households are less likely to engage in support than poorer households (H4).

2. Materials and Methods

2.1 The Pantanal Wetland

The Pantanal wetland serves as the socioecological[1] context for the study. It is the world's largest tropical wetland, spanning approximately 179,300 km² across parts of Brazil, Bolivia, and Paraguay (Chiaravalloti et al., 2025). In Brazil, the Pantanal partially covers the states of Mato Grosso and Mato Grosso do Sul.

[1] A socioecological system is a term introduced by Berkes and Folke (1998) to describe the embeddedness of human systems (as individuals, groups, and institutions) with nature.

The seasonality of the Pantanal is characterised by annual yet stochastic flood pulses. Heavy rainfall, which can cover up to 110,000 km² and last three to four months, shapes the floodplain and its surrounding landscape (Junk et al., 2011). The timing of flooding varies annually in onset and duration, disrupting the economic viability of populations dependent on rivers (e.g., whether and to what extent fish are present in a given location varies significantly year to year) (Chiaravalloti and Dyble, 2019). The unpredictable ecology of the Pantanal wetland ultimately affects those who are dependent on natural resources.

The *Pantaneiros* ("residents of the Pantanal") comprise local farmers, fishers, and ranchers (Wantzen et al., 2023). *Ribeirinhos* ("people of the river") are small-scale freshwater fishers who eat and sell catches of mainly large Pintado *(Pseudoplatystoma corruscan*s) and Cashara (*Ancistrus tamboensis*), using smaller fish for bait. Fishing is the main livelihood for approximately 70% of the riverine population (Chiaravalloti, 2019; ECOA, 2013). While fishers already face temporal variability in fish stock turnover due to episodic flooding, accelerating temperature rise, and severe droughts resulting from anthropogenic climate change, these factors exacerbate the disruption (Wantzen et al., 2023).

The riverine foragers of the Pantanal thus face the challenge of adapting to extreme seasonal shifts; some even argue that the fishers' social network structures are crucial to their resilience (Chiaravalloti et al., 2021; Chiaravalloti and Dyble, 2019).

Table 1. Hypotheses tested in the study. See main text for context.

Hypotheses	Economic Support Network	Supported?
H1	Households will be more likely to form ties with kin	Yes
H2	Households will form support ties with neighbours closer in distance	Yes
H3	Households will engage with those who reciprocate	Yes
H4	Wealthier households will be more likely to support poorer households	No

2.2 Study Site and Participants

The study site spans ~150,000 hectares along the western border of the Pantanal in the state of Mato Grosso do Sul, Brazil. The participants living in the area comprise two distinct settlements that differ in their spatial organisation along the river floodplain (Chiaravalloti, 2019). Community 1 resides in the south of the region, at the intersection between the Paraguay River and the Paraguay Mirim River, whereas Community 2 resides in the north, on the left bank of the

Paraguay River in a location referred to as Barra do São Lourenço (Costa et al., 2022; ECOA, 2024). At the time of data collection in 2019, approximately 600 people were living in 70 households in this area (Chiaravalloti, 2019).

2.3 Data Collection

The data collected are part of a broader academic study called the ENDOW project ("The Effect of Social Networks on Inequality: A Longitudinal Cross-Cultural Investigation"), whose members designed the questionnaire. Interviews were conducted face-to-face at the interviewees' homes. Information was collected at the node level, these being individual attributes, e.g., locality and material wealth, and the edge level, which are social network attributes (who nominates whom), e.g., kin-relatedness between two individuals. The questionnaire respondent – hereby referred to as an "ego" – answered the questionnaire on behalf of family members of the same household. The ego and those they nominated in the social network portion of the survey – hereby referred to as "alters" – were assigned anonymised identification to protect identities.

A sharing unit, distinct from a household, can encompass multiple households in the same locality; multiple egos may exist within a single unit. Egos were not always household heads: responses were sometimes provided by spouses or, occasionally, by other family members.

At the household level, key demographic information was collected on age, gender, wealth, and the sharing unit's geographic coordinates (longitude and latitude). A Global Positioning System (GPS) assigned geographic coordinates to the sharing unit localities. Gender was recorded as binary, reflecting the participants' self-identification as either male or female.

Using a second survey, the quantity and economic value of the sharing unit's material possessions were recorded, including electronics, machinery, kitchen appliances, livestock, and fishing equipment. The 2019 local cost estimates, expressed in the local currency, BRL, were calculated for all items listed above and later converted to USD as an approximation of material wealth, a proxy for annual income. A third survey collected genealogical information based on the identification of each node's mother and father.

Following this, the ego was asked to list individuals from whom they would likely receive economic support and to whom they would likely provide economic support under specific scenarios (see Table 2). This heuristic method of social support is widely used in other social network studies in the field as a proxy for cooperative decision-making (e.g., Apicella, 2012; Dyble et al., 2015; Ge et al., 2024; Nolin, 2010; Power, 2017b; Redhead et al., 2023). That said, it should be clarified that these measures likely capture perceived support rather than direct evidence of cooperation. Structurally, questions 1–4 concerned economic support; the ego could nominate up to 10 alters, who could be anyone outside their own household and sharing unit (see Table 2). Under the ENDOW project's research protocol, nominations were capped at 10 people to minimise major inconsistencies between individuals' responses without eliminating node-level variance altogether.

2.4 Data Preparation

A single long list of dyadic nominations (ego → alter pairings and the survey questions they pertained to) was created, hereafter referred to as the “edge data frame.” RStudio (version 4.4.3) and QGIS (version 3.42) were used in the data manipulation.

Pedigrees were created using the *kinship2* package in RStudio (R Core Team, 2012). The metric of kinship is the relatedness coefficient (r), which is an approximation of the proportion of genes shared between two individuals, based on shared ancestry.

Manipulating the data also involved calculating the difference in geographic distance (in metres) between the ego and the alter; this was done using QGIS software and the coordinates of longitude and latitude.

In order to create networks in RStudio, the edge data frame of economic support was combined with the corresponding nodal attributes. This transformation was done using the following packages: *network*, *statnet*, and *dplyr* (R Core Team, 2012).

Table 2. Economic-based survey questions.

1	When you have an urgent and unexpected need, perhaps related to a medical emergency, from whom could you borrow the equivalent of one week's wages? [25 litres of gas]
2	In the event of an urgent need, to whom would you lend the equivalent of a week's wages? [25 litres of gas]
3	In the last month, from whom did you borrow day-to-day things, such as mate tea, a hoe, or pliers?
4	Who do you sell fish and bait to?

2.5 Statistical Analysis

The statistical framework required the additional use of *ergm*, *ggplot2*, *sna*, and *statnet* packages (R Core Team, 2012). Before analysis, data exploration and preliminary diagnostic tests were conducted, using the protocol outlined by Zuur et al. (2010). This was an essential step to eliminate multicollinearity between covariates, while also removing outliers that could skew the data, both of which could lead to spurious results (misleading relationships between predictors and outcomes).

Exponential random graph models (ERGMs) were chosen over a standard regression model, which would have been limited in that it could not explore the effect of covariates on tie outcomes independent of the network in which they are a part. ERGMs consider each possible tie configuration between nodes in a network matrix (n x (n-1)), along with associated node and edge attributes, similar to those expected in real-world social networks (Stanford Human

Evolutionary Ecology and Health, 2026; Hunter et al., 2008), and it is therefore a commonly used method in social network studies (e.g., Bond and Gaoue, 2020; Ge et al., 2024; Mattison et al., 2023; Nolin et al., 2010; Power and Ready, 2019).

Following the methodological framework of Goodreau et al. (2008), candidate models were constructed by first fitting a baseline in model one (M1), then added groups of covariates at intervals to create cumulative models that increased in complexity: in general, structural attributes were added to the baseline to create model two (M2), such as reciprocity, dyad-wise and edge-wise shared partnerships, then covariates of age and gender were added to create model three (M3), then wealth attributes (M4), and, finally, the main predictors to create model five (M5). Markov Chain Monte Carlo (MCMC) tests model convergence. Akaike Information Criterion (AIC) are used as a point of comparison: lower AIC and higher logarithmic likelihood (LogLik) indicate simpler models.

3. Results

3.1 Descriptives

The economic network comprises 55 nodes and 143 unique edges; it is inclusive of both those who made nominations and those who were nominated but did not make nominations (see Figure 1).

Node Attributes: 38 out of 55 nodes (69%) belong to Community 1, and the remaining 17 (31%) belong to Community 2. The mean age of the household representative is 42 years old (SD: 15), and the median annual income per household is 5612 USD (IQR: 3893). There are more males than females in the network: 32 males (58%) compared to 23 females (42%).

Edge Attributes: the median distance between dyads is 1490 metres (IQR: 8563). Relatedness coefficients range from 0 to 0.25 (see Table 4 for a categorical breakdown of kin relatedness). A non-parametric Spearman's rank test indicates a moderate yet significant negative correlation between distance and relatedness (rho = -0.31, p-value < 0.001), so households tend to live near close kin.

Network and Matrix-level Descriptives: 59 of the 143 ties are reciprocated, 14 nodes (~25%) receive zero incoming ties, whereas 13 nodes receive exactly one nomination. In terms of outgoing ties, three nodes do not nominate at all, but 12 have one outgoing tie. 2,979 possible pairs (55 x 54) of economic support comprised the matrix that was simulated in the ERGM, resulting in a network density of 0.047 (4.7%). (See Table 3 for summary of network.)

3.2 ERGM

Multicollinearity among all covariates in the best-fitted model was assessed using variance inflation factors (VIF). VIF values are all close to 1.0, indicating that the variables are independent of each other (not highly correlated). The ERGM output of the economic-based support network reveals that the propensity for households to form a tie is strongly influenced by kinship, distance, and reciprocity. (See Table 5 for candidate models and Table 6 for best-fitted model output summary.)

The predicted odds of a support tie forming in the baseline group are 0.018 (95% CI = [0.0089, 0.037]), corresponding to an expected 1.8% chance that any two individuals in the network will form a tie with each other, in the absence of the model predictors.

People tend to nominate kin (OR = 1.82, 95% CI = [1.478, 2.229], $p < 0.001$). Because relatedness was scaled such that one unit represents a 0.1 increase in relatedness coefficient, this means that for every unit increase in genetic relatedness, the odds of forming an economic support tie almost double. This finding supports H1, and we can thus reject the null hypothesis that economic support tie formation is not affected by relatedness among households.

As expected in H2, geographic distance has a negative effect on the propensity to form ties (OR = 0.999, 95% CI = [0.994, 0.9997], $p < 0.001$). One unit increase in distance represents one metre, so for every unit increase in distance, the odds of requesting aid decrease by approximately 0.1%. This effect accumulates over longer distances: a 100-metre increase corresponds to approximately 9.5% reduction in the odds of tie formation, in consideration of the other covariates in the model. Mutuality is another significant predictor of economic-based support (OR = 2.95, 95% CI = [1.537, 5.644], $p = 0.000113$).

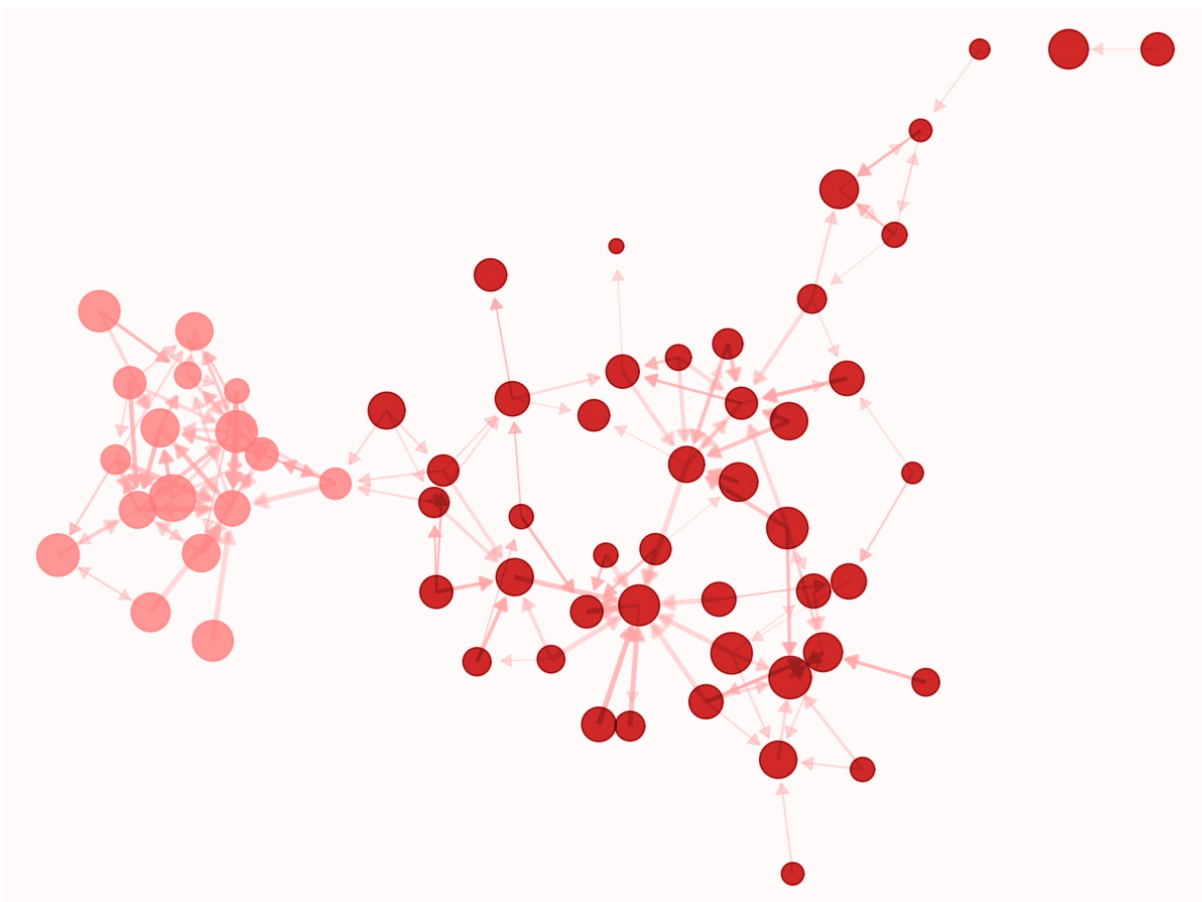

Figure 1. Economic support network. Edges represent nominations of economic support from one household to another; they are unidirectional and weighted based on tie frequency (only unique ties are analysed). Nodes (N = 55) indicate households and are sized based on the ego's age (bigger = older). Networks are coloured by community: darker red represents Community 1, while lighter red represents Community 2.

Table 3. Summary of network descriptives

Density	0.047
Matrix Size	2,979
Network Size	55
Reciprocity	59 (41%)
Unique edges	143

Table 4. Categorical breakdown of relatedness among dyads

r	Relationship	N (%)
0.50	Parent-Child; Full Siblings	0 (0%)
0.25	Grandparent-Grandchild; Half Siblings; Uncle/Aunt-Nephew/Niece	41 (29%)
0.125	First Cousins; Great Grandparent-Great Grandchild	7 (6%)
0.0625	First Cousins Once Removed	1 (1%)
0.03125	Second Cousins	0 (0%)
0.00	Unrelated	94 (64%)
NA	Unknown	0 (0%)

Note: ***r*** *is the average relatedness coefficient between an ego and alter who have formed a tie in their associated networks, rounded to at least one significant figure (1 s.f.). Unknown relatedness among dyads was removed prior to network formation.*

This means that if a household nominates another, the likelihood that the nominated household reciprocates by nominating the first as a support partner is nearly three times higher than expected by chance. The model output on reciprocity therefore supports H3.

Other influential predictors in the economic network included the following: ego's age (OR = 1.01, 95% CI = [1.003, 1.017], p = 0.00492), edge-wise shared partnerships (OR = 3.68, 95% CI = [2.699, 5.030], p < 0.001), and dyad-wise shared partnerships (OR = 0.77, 95% CI = [0.697, 0.842], p < 0.001). This suggests that older household representatives are more likely to nominate others than younger ones – a significant result, but not majorly so ($p < 0.05$). For edge-wise shared partnerships (existing connections), each additional shared mutual connection between households multiplies the odds of a tie occurring by 3.68. This is a strong indication of triadic closures: people are more likely to be connected in this particular network if they already have mutual contacts. For dyad-wise shared partnerships (connections that don't yet exist), more indirect connections is associated with a lower likelihood of forming a direct tie.

The following covariates do not show any effect on tie formation in the network: gender homophily (OR = 1.27, 95% CI = [0.896, 1.785], p = 0.182), wealth homophily (OR = 1.00, 95% CI = [0.9996, 1.00006], p = 0.691), alter's wealth (OR = 1.00, 95% CI = [0.9995, 1.00520], p = 0.960), ego's wealth (OR = 1.00, 95% CI = [0.99997, 1.00005], p = 0.607), and ego's gender (OR = 1.24, 95% CI = [0.937, 1.632], p = 0.134). In particular, the odds-ratio of forming ties with the same gender is positive but non-significant, while wealth-related factors and ego gender had odds-ratios very close to one, indicating no meaningful effect. In other words, neither similarity in gender nor wealth, nor the individual attributes of wealth and gender, strongly determines the tendency to form or request economically based support ties.

Table 5. Candidate Models

Economic Social Network						
Model No.	**Cumulative Parameters**	**Total No. Parameters**	**LogLik**	**AIC**	**ΔAIC**	**Description**
1	~ edges	1	-565	1131	323	Baseline (intercept only) added
2	+ reciprocity + gwesp + gwdsp	4	-547	1102	294	Structural attributes added
3	+ ego age + alter age + ego gender + gender homophily	8	-469	949	141	Controls added
4	+ ego wealth + wealth homophily	10	-439	891	83	Covariates added
5	+ relatedness + distance	12	-392	808	0	Key predictors added

Note: Models 1–5 are ordered by ascending cumulative parameter complexity and their corresponding fit to the data. Model 5 is the relatively best-fitting model – indicated by least negative LogLik and lowest AIC values – and is the one analysed in the main text. The model of best-fit includes measures of relatedness, distance between households, ego attributes, alter attributes, and a number of structural covariates. LogLik, log-likelihood; AIC, Akaike's Information

Criterion; ΔAIC, difference between AIC of best-fitted models and other candidate model. This statistical framework was in accordance with that of Goodreau et al (2008).

A goodness-of-fit test reveals that the economic support model accurately captures the observed features of the network. All estimations of model statistics indicate a good fit across all covariates (i.e., high p-values, ranging from 0.84 to 1.00). Results from the MCMC simulation show that the model achieves good convergence (Geweke, $p = 0.487$).

Table 6. Summary of ERGM output (Model 5)

	Full Model			
Variables (unit)	**Coefficient (β)**	**OR**	**95% CI**	**P-Value**
Baseline	-4.003	0.018	0.0089, 0.037	p < 0.001
Edge attributes				
Distance (metres)	-4.06e-05	0.99995	0.9994, 0.9997	p < 0.001
Gender Homophily	0.23	1.27	0.896, 1.785	0.182
Relatedness	0.60	1.82	1.478, 2.229	p < 0.001
Wealth Homophily	1.02e-05	1.00	0.9996, 1.00006	0.691
Node attributes				
Alter's Wealth (USD)	-1.36e-06	1.00	0.9995, 1.00520	0.960
Ego's Age (years)	0.0098	1.01	1.003, 1.017	0.00492
Ego's Gender (Male; ref: Female)	0.21	1.24	0.937, 1.632	0.134
Ego's Wealth (USD)	1.03e-05	1.00	0.99997, 1.00005	0.607
Structural attributes				
Dyad-wise Shared Partnerships (α = 0.5)	-0.27	0.77	0.697, 0.842	p < 0.001

	Full Model			
Variables (unit)	**Coefficient (β)**	**OR**	**95% CI**	**P-Value**
Baseline	-4.003	0.018	0.0089, 0.037	p < 0.001
Edge attributes				
Distance (metres)	-4.06e-05	0.99995	0.9994, 0.9997	p < 0.001
Gender Homophily	0.23	1.27	0.896, 1.785	0.182
Relatedness	0.60	1.82	1.478, 2.229	p < 0.001
Wealth Homophily	1.02e-05	1.00	0.9996, 1.00006	0.691
Node attributes				
Edgewise Shared Partnerships (α = 0.5)	1.30	3.68	2.699, 5.030	p < 0.001
Reciprocity	1.08	2.95	1.537, 5.644	0.00113

Note: OR, odds ratio; CI, confidence interval; exponential notation e = 10^; Dyad-wise Shared Partnerships = Indirect connections (D does not form a tie with F, but both D and F are friends with E); Edgewise Shared Partnerships = Direct connections: friends of friends (mutual ties where A→B, B→C, so A→C). Values rounded to at least two significant figures.

Table 7. Summary of significant p-values for key covariates

Variable	Significant P-Value
Relatedness	✓
Distance	✓
Reciprocity	✓
Ego's Wealth	X

*Note: an **X** represents non-significant effects of the key predictors on the social network outcomes; a ✓ indicates a strongly significant influence (p < 0.001).*

4. Discussion

First, it is important to consider the proportion of households included in the final network relative to the entire population and the potential implications for interpreting the results. The total household representation (observed vs. actual) was 79%: 55 households across both communities comprised the network out of the 70 households living in the area at the time of data collection in 2019 (Chiaravalloti, 2019). While this represents a substantial proportion of both communities, the findings should be interpreted with the understanding that the observed network may not fully capture all economic interactions.

The results of the exponential random graph models (ERGMs) indicate that kin-relatedness plays a significant role in predicting who is nominated by whom across the economic network. This behaviour is widely observed in human populations across societies worldwide (e.g., Aktipis et al., 2016; Burton-Chellew and Dunbar, 2015; Du et al., 2019; Gettler et al., 2023; Koster, 2018; Koster et al., 2019; Thomas et al., 2015, 2018; Power and Ready, 2019).

To our knowledge, the population consists mainly of nuclear families; there are no strict kinship rules governing marriage, heritable wealth, and residency patterns among the Pantaneiros (such as matrilineal organisation) (Chiaravalloti, 2019; Wantzen et al., 2023). Such structures can privilege certain family members over others, often distributing resources and parental investment unequally; as a result, they tend to exacerbate sibling rivalry and foster competition among both immediate and extended kin (Gibson and Gurmu, 2010; Gibson and Sear, 2010). The lack of culturally prescriptive rules in the Pantanal may facilitate the strong kin-directed nominations of support we observe across the floodplain.

While kin are important when choosing support ties, the proximity of households across the floodplain is also significant. As expected, geographic distance is negatively associated with the formation of economic support. Findings of increased sociality with geographic proximity are consistent in the literature. For example, Ready and Power's (2018) ERGM analysis on Inuit households of Kangiqsujuaq, Nunavik, Canada revealed that the probability of the existence of a sharing tie is strongly predicted by decreasing distance between households – a relationship supported by many other studies such as Acipella, 2012; Nolin, 2010; Kasper and Borgerhoff Mulder, 2015; Koster and Leckie, 2014; and Thomas et al., 2018.

This could also be the case in the Pantanal, where neighbouring households likely interact more frequently than more distantly spaced ones because reciprocated exchanges and relative needs of neighbours are easier to monitor, and the transaction costs of exchanges (i.e., time and effort to maintain relationships) are low. These findings are consistent with the principles of reciprocal altruism proposed by Trivers (1971).

As the descriptive statistics indicated moderate negative correlations between distance and relatedness in all three networks, the ERGM results may reflect the interdependence of distance and kinship: people tend to live closer to family members, so distance and kinship are likely not mutually exclusive variables (Jaeggi and Gurven, 2013b; Ready and Power, 2018). Drawing on historical records and ethnographic work on the Ribeirinhos, households are often established near relatives along the riverbank, rather than being randomly dispersed (Chiaravalloti, 2019). This pattern may provide practical benefits by facilitating the sharing of resources, like fishing equipment and food, while ensuring close access to various forms of support, including care for children and elders, as well as emotional assistance during periods of need. Consequently, these intentional clusters of extended family support the argument that kinship and geographical proximity are not independent dimensions of social life in the region.

One would be remiss not to interpret these findings in the political context of the last several decades (Chiaravalloti, 2019). Evidence-based work (including fieldwork and participant observations) and NGOs' records show that the Ribeirinhos have suffered varying levels of displacement and restricted access to natural resources (ECOA, 2024; Costa et al., 2022; Chiaravalloti, 2019; Siqueira et al., 2018). The conservation agenda in the Pantanal from the 1970s onwards led to a “forced exodus” of local residents due to the overlap between conservation-protected areas and Ribeirinhos’ territories (ECOA, 2024; Franco et al., 2013). This expulsion from the newly introduced private and state reserves led to people living in denser living arrangements, thereby reducing the geographical distance between households (ECOA, 2024; Siqueira et al., 2018). Although the reduced geographical distance between households may have increased opportunities for interaction and support exchange, longitudinal data on the communities are needed in order to infer causality.

As the ERGMs show, there are other foundations on which to form economic-based ties of support. Mutuality of relations is one of the strongest predictors of tie formation across the networks. This could be the case because households may only feel comfortable requesting economic support when trust and reliability are demonstrated through reciprocal exchanges; in turn, the reciprocity that occurs reduces the risk of exploitation and non-repayment of monetary services in an unpredictable environment such as that of the Pantanal (Chiaravalloti and Dyble, 2019). These patterns of reciprocal altruism are also found elsewhere in nature (Nowak, 2006; Wilkinson, 1984, 1988; Power and Ready, 2019).

Surprisingly, the wealth status of ego or alter failed to significantly predict the formation of ties in the economic support network. This suggests that requests for support in this population do not simply stem from resource deficiency, nor are target sources of support chosen based on wealth differentials. Also, the non-significant effect of wealth homophily on support tie formation suggests that material similarity alone does not influence cooperation.

Although our results are contrary to the expectation that wealth predicts support, it is important to note that evolutionary theory does not necessarily predict it would have, and they are not entirely inconsistent with behavioural ecology research. Other studies support unintuitive patterns of relative wealth rank associations; notably, Thomas and colleague’s (2018) study on costly cooperation among the Mosuo pastoralists of southwestern China revealed the unexpected finding that poorer households were more likely to help wealthier households. Also, Chaudhary et al. (2016) demonstrated that access to cooperative partners (i.e., relational wealth) was a more important source of risk buffering than material assets among the BaYaka hunter-gatherers of Congo. Together, these studies stress the importance of social relationships, which may counteract the importance of wealth differentials in predicting support.

So why are nominations of support not linked to one’s material status in the Pantanal? Our findings may support the idea that people rely more on established social ties rather than material status when choosing whom to approach for economic support, challenging notions of the relationship between wealth and perceived cooperation in the field, specifically that requests for material support are principally oriented toward alleviating resource deficiency (Cronk and Aktipis, 2021; Hao et al., 2014). If a distinction had been made between outgoing support and incoming requests for support, we may have been better able to disentangle whether wealth influences the provision of support, the seeking of support, or both.

Other plausible reasons may relate to the strong social norms surrounding support. Households of varying degrees of wealth may provide or request support as a means of reinforcing or legitimising their prestige within the community. Given that reciprocity is a key determinant of sociality in this population, combined with the unpredictable nature of the Pantanal, the act of requesting aid may function as a signal of willingness to reciprocate under future unknown circumstances, thereby strengthening bonds between affluent households and others, irrespective of economic rank.

Alternatively, measurement constraints of the survey may not have accurately captured wealth variation of the population. Households' material wealth was measured based on the cumulative quantity and value of possessions; it therefore fails to capture more nuanced differences in wealth among households, such as access to resources or annual income. If material wealth exists as only a partial proxy for broader socioeconomic status in the first place, then wealth disparity may not be accurately captured, and thus our findings may not hold under alternative measures of wealth. That being said, another study among the same population found the same correlation between wealth and social ties, despite using a different metric of household wealth (Chiaravalloti et al., 2021).

Furthermore, shared partnerships influence tie formation in the economic networks. Pre-existing mutual ties between households that form a tie (i.e., edge-wise partnerships) show the positive effect of triangles, commonly referred to as triadic closures: households are more likely to engage in hypothetical transactions of material support when they already share a mutual tie with the partner household, as noted in other social network studies (Asikainen et al., 2020; Mosleh et al., 2025). This reveals the tight-knit structure of the riverine communities, where households often rely on mutual friends for support or to transmit information about ecological conditions, such as the availability of fish (Chiaravalloti et al., 2021).

Indirect connections between households that do not share a tie (i.e., dyad-wise partnerships) show a negative effect in the same network. This suggests that when households already have multiple indirect pathways through mutual contacts, there is a lower tendency to form an additional direct tie with that household, since assistance is still available through intermediaries. This could indicate that households strategically focus direct requests for support on close and trusted partners, possibly those belonging to the same community, as suggested by Chiaravalloti and Dyble's (2019) study on in-group favouritism and out-group hostility among the Ribeirinhos.

The findings have important implications for the field of human behavioural ecology. First and foremost, we confirm theoretical expectations on evolutionary theory pertaining to kinship and reciprocal altruism in a novel socioecological setting. In doing so, we support the argument that such mechanisms were central to human evolution because they are prominent in contemporary small-scale societies, presumably to manage risk in unpredictable environments (Apicella et al., 2012).

Second, new insights from the Pantanal case emerge that advance the scientific literature. The positive association between relatedness and economic support demonstrates that kinship continues to influence support in spite of increasing market integration and processes of displacement (Chiaravalloti, 2019). This finding extends evidence from the classic behavioural ecology literature, which traditionally focuses on hunter-gatherer and horticultural small-scale groups (Koster, 2018; Koster et al., 2019; Thomas et al., 2015, 2018; Power & Ready, 2019), showing that kin biases persist despite shifts to economic and structural organisation. In other words, there is comparatively less focus on contemporary wetland fishing populations experiencing external pressures.

Also, the insignificant importance wealth plays in the economic network challenges assumptions that such transfers are principally oriented toward alleviating resource deficiency (Cronk and Aktipis, 2021; Hao et al., 2015). Given that reciprocity is a key determinant of sociality in this population, and considering the unpredictable nature of the Pantanal, the act of giving and receiving material aid may serve as a signal of willingness to reciprocate under future, unknown circumstances. This could strengthen bonds between affluent and poorer households, irrespective of economic rank. This points to the potential importance of social networks in managing social capital and prestige dynamics rather than just alleviating resource scarcity and immediate risk.

There are several limitations of this paper within the scope of the research aims. The data concern perceived social support, nominations based on who someone would likely ask to help or be helped by, not actual cooperative interactions. This means that a true cost to the actor has not necessarily been incurred, so the conditions of Hamilton's Rule are not met by definition (Madsen et al., 2007). It therefore limits the extent to which conclusions can be drawn about the evolutionary mechanisms underlying cooperation, as the data reflect potential support based on one's nominations rather than observed costly behaviours.

The data are also not longitudinal – that is, they only reflect social support at one specific point in time – and are at the household level only. This poses two important data quality challenges, respectively: the first being that temporal dynamics of cooperation cannot be captured, meaning changes in one's preferences in support, perhaps due to seasonal or political upheaval, are not captured. As such, and as previously noted, the causality of sociality is not determined or assumed in this study, since this typically requires longitudinal data. The second is that the aggregation of data at the household level obscures individuals' agency, thereby limiting the inferences that can be drawn about sociality to inter-household relations rather than the social network at large, which we know extends beyond the region to nearby towns of Corumbá and Port Amolar as well as cities including Campo Grande and São Paulo.

Future research can extend beyond the scope of this paper by examining the interdependencies and interconnectedness of social and ecological covariates. Rather than considering these factors in isolation, scholars might ask how multiple drivers of cooperation interact to shape social dynamics. Although disentangling reciprocity from kin- and non-kin-based interactions is challenging, a more integrative approach that accounts for the intersections of kinship, spatial proximity, and reciprocity is likely to provide a clearer understanding of the mechanisms underlying nepotism (Power and Ready, 2019; Wilkinson, 1984, 1988).

The findings of this study demonstrate that connectivity among this population of the Pantanal is not random; instead, kinship, residency patterns, and reciprocity, to name a few, all play a role in predicting who supports whom. Bearing in mind the unpredictable nature of the Pantanal, whereby stochastic flooding affects the spatial and temporal availability of fish (Chiaravalloti and Dyble, 2019), this strong affinity among kin, to take just one example, may point to the crucial role of direct familial ties in mitigating competition for scarce resources. More broadly, these results may provide a useful foundation for future research on risk management strategies for resource-sharing along the floodplain, thereby informing environmentalists and policy-makers at all levels about the underlying structures of human social systems.

Ethics. Research ethics were approved by UCL's Department of Anthropology in the Faculty of Social and Historical Sciences (Approval Number: SHSAnth-2324-200-1); local ethics clearance was obtained by the non-governmental organisation (NGO) Ecologia e Ação (ECOA) in Campo Grande, Mato Grosso do Sul, Brazil. Data are not yet available. The original R code for the data preparation and analysis is available for access in the GitHub repository linked: https://github.com/EL564/ANTH0121-PG-Dissertation.git.

Authors' contributions. Conceptualisation by E.L., R.C., and R.M.; literature review by E.L.; data collection by R. C.; methodology by E.L. and R.M.; data manipulation by R.C. and E.L.; data analysis and write-up by E.L.

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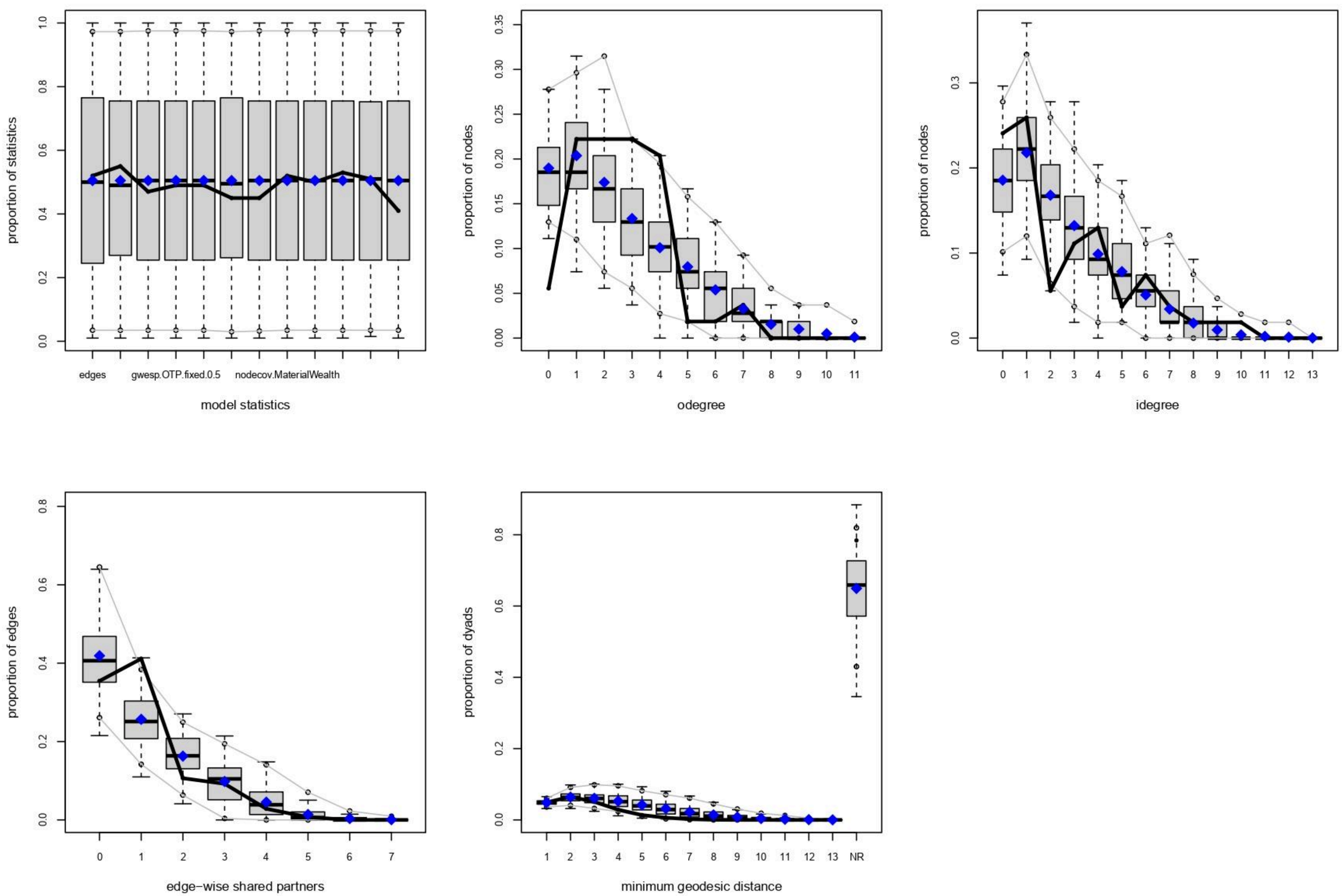
Appendix: Economic Network Goodness-of-fit Plot



References

Aktipis, A., de Aguiar, R., Flaherty, A., Iyer, P., Sonkoi, D. and Cronk, L. (2016) Cooperation in an Uncertain World: For the Maasai of East Africa, Need-Based Transfers Outperform Account-Keeping in Volatile Environments. *Human Ecology*, 44(3), pp. 353–364. https://doi.org/10.1007/s10745-016-9823-z.

Allen-Arave, W., Gurven, M. and Hill, K. (2008) Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an Ache reservation. *Evolution and Human Behavior*, 29(5), pp. 305–318. https://doi.org/10.1016/j.evolhumbehav.2008.03.002.

Apicella, C., Marlowe, F., Fowler, J. and Christakis, N. (2012) Social networks and cooperation in hunter-gatherers. *Nature*, 481(7382), pp. 497–501. https://doi.org/10.1038/nature10736.

Arnot, M. and Mace, R. (2021) An evolutionary perspective on kin care directed up the generations. *Scientific Reports*, 11(1), p. 14163. https://doi.org/10.1038/s41598-021-93652-4.

Asikainen, A., Iñiguez, G., Ureña-Carrión, J., Kaski, K. and Kivelä, M. (2020) Cumulative effects of triadic closure and homophily in social networks. *Science Advances*, 6(19). https://doi.org/10.1126/sciadv.aax7310.

Assine, M. (2015) Brazilian Pantanal: A large pristine tropical wetland. In: B, Carvalho Vieira, A. Rodrigues Salgado and L, Cordeiro Santos, eds. *Landscapes and Landforms of* Brazil. Dordrecht: Springer Science and Business Media, pp. 135–146.

Axelrod, R. and Hamilton, W. (1981) The Evolution of Cooperation. *Science*, 211(4489), pp.
1390–1396.

Berkes, F. and Folke, C. (1998) Linking Social and Ecological Systems: Management Practices and Social Mechanisms for Building Resilience. Cambridge University Press, Cambridge.

Bond, M. and Gaoue, O. (2020) Prestige and homophily predict network structure for social learning of medicinal plant knowledge. *PLOS ONE*, 15(10), p. e0239345. https://doi.org/10.1371/journal.pone.0239345.

Borgerhoff Mulder, M. et al. (2009) Intergenerational Wealth Transmission and the Dynamics of Inequality in Small-Scale Societies. *Science*, 326(5953), pp. 682–688. https://doi.org/10.1126/science.1178336.

Burton-Chellew, M. and Dunbar, R. (2015) Hamilton's rule predicts anticipated social support in humans. *Behavioral Ecology*, 26(1), pp. 130–137. https://doi.org/10.1093/beheco/aru165.

Chaudhary, N., Salali, G., Thompson, J. et al. (2016) Competition for Cooperation: variability, benefits and heritability of relational wealth in hunter-gatherers. *Scientific Reports*, 6, 29120. https://doi.org/10.1038/srep29120.

Chiaravalloti, R. (2019) The Displacement of Insufficiently "Traditional" Communities:Local Fisheries in the Pantanal. *Conservation and Society*, 17(2). http://doi.org/10.4103/cs.cs1858.

Chiaravalloti, R. (2016) Local communities and conservation in the Pantanal wetland, Brazil. PhD dissertation. University College London, London.

Chiaravalloti, R. and Dyble, M. (2019) Limited open access in socioecological systems: How do communities deal with environmental unpredictability? *Conservation Letters*, 12(2), p. e12616. https://doi.org/10.1111/conl.12616.

Chiaravalloti, R., Freitas, D., de Souza, R., Biswas, S., Markos, A., Manfroi, M. and Dyble, M. (2021) Resilience of social-ecological systems: drastic seasonal change is associated with economic but not social flexibility among fishers in the Brazilian Pantanal. *Ecology and Society*, 26(2). https://doi.org/10.5751/ES-12433-260230.

Chiaravalloti, R., Tomas, T., Leimgruber, P., Akre, T. and Giordano, A. (2025) Conservation Science and Practice in the Pantanal: From crisis to hope. *Conservation Science and Practice*, 7(7), p. e70107. https://doi.org/10.1111/csp2.70107.

Cohen, K., Finney, S., Gibbard, P. and Fan, J. (2013) The ICS International Chronostratigraphic Chart. *Episodes*, 36(3), pp. 199–204. https://doi.org/10.18814/epiiugs/2013/v36i3/002.

Colleran, H. (2020) Market integration reduces kin density in women's ego-networks in rural Poland. *Nature Communications*, 11(1), p. 266. https://doi.org/10.1038/s41467-019-14158-2.

Colleran, H. and Mace, R. (2015) Social network- and community-level influences on contraceptive use: evidence from rural Poland. *Proceedings of the Royal Society B: Biological Sciences*, 282(1807), p. 20150398. https://doi.org/10.1098/rspb.2015.0398.

Costa, A., Manfroi, M. and Chiaravalloti, R. (2022) The impact of Protected Areas on the Well-being of Pantaneiro Riverine Communities. *Ambiente and Sociedade*, 25, p. e00352. https://doi.org/10.1590/1809-4422asoc20210035r2vu2022l4oa.

Cronk, L. and Aktipis, A. (2021) Design principles for risk-pooling systems. *Nature Human Behaviour*, 5(7), pp. 825–833. https://doi.org/10.1038/s41562-021-01121-9.

Du, J., Thomas, M., Bårdsen, B., Mace, R. and Næss, M. (2019) Comparison of social complexity in two independent pastoralist societies. *Behavioral Ecology and Sociobiology*, 73(1), p. 4. https://doi.org/10.1007/s00265-018-2611-6.

Dyble, M. et al. (2016) Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter-Gatherer Groups. *Current Biology*, 26(15), pp. 2017–2021. https://doi.org/10.1016/j.cub.2016.05.064.

Dyble, M., Van Leeuwen, A. and Dunbar, R. (2015) Gender differences in Christmas gift-giving. *Evolutionary Behavioral Sciences*, 9(2), pp. 140–144. https://doi.org/10.1037/ebs0000022.

ECOA (2013) *Ações para o turismo de base comunitária na contenção da degradação do Pantanal*. Campo Grande: ECOA.

ECOA (2024) *Comunidade tradicional Barra do São Lourenço e a RDS: Caminho para a preservação cultural e a conservação ecológica*. Available at: https://ecoa.org.br/comunidade-tradicional-barra-do-sao-lourenco-e-a-rds-caminho-para-a-preservacao-cultural-e-a-conservacao-ecologica/ [Accessed 06 June 2026].

Euler, H. and Weitzel, B. (1996) Discriminative grandparental solicitude as reproductive strategy. *Human Nature*, 7(1), pp. 39–59. https://doi.org/10.1007/BF02733489.

Franco, J., Drummond, J., Gentile, C. and Azevedo, A. (2013) *Biodiversidade e ocupação humana do Pantanal mato-grossense: Conflitos e oportunidades*. 1st edn. Rio de Janeiro: Garamond.

Gaulin, S., McBurney, D. and Brakeman-Wartell, S. (1997) Matrilateral biases in the investment of aunts and uncles: A consequence and measure of paternity uncertainty. *Human Nature*, 8(2), pp. 139–151. https://doi.org/10.1007/s12110-997-1008-4.

Ge, E., DongZhi, C. and Mace, R. (2024) Religiosity and gender bias structure social networks. *Evolutionary Human Sciences*, 6, p. e23. https://doi.org/10.1017/ehs.2024.16.

Gettler, L., Redhead, D., Dzabatou, A. and Lew-Levy, S. (2023) BaYaka forager food sharing networks in the Congo Basin: The roles of gender homophily and kin sharing. *American Journal of Biological Anthropology*, 181(1), pp. 59–69. https://doi.org/10.1002/ajpa.24688.

Gibson, M. and Gurmu, E. (2011) Land inheritance establishes sibling competition for marriage and reproduction in rural Ethiopia. *Proceedings of the National Academy of Sciences*, 108(6), pp. 2200–2204. https://doi.org/10.1073/pnas.1010241108.

Gibson, M. and Sear, R. (2010) Does Wealth Increase Parental Investment Biases in Child Education?: Evidence from Two African Populations on the Cusp of the Fertility Transition. *Current Anthropology*, 51(5), pp. 693–701. https://doi.org/10.1086/655954.

Goodreau, S., Handcock, M., Hunter, D. and Butts, C. (2008) Ergm: A package to fit, simulate and diagnose exponential-family models for networks. *Journal of Statistical Software*, 24(3), pp. 1–29.

Gurven, M. (2000) To give and give not: The evolutionary ecology of hunter–gatherer food transfers. PhD dissertation. University of New Mexico, Albuquerque.

Hamilton, W. (1963) The Evolution of Altruistic Behavior. *The American Naturalist*, 97(896), pp. 354–356.

Hamilton, W. (1964) The genetical evolution of social behaviour. *Journal of Theoretical Biology*, 7(1), pp.17–52. https://doi.org/10.1016/0022-5193(64)90038-4.

Hao, Y., Armbruster, D., Cronk, L. and Aktipis, A. (2015) Need-based transfers on a network: a model of risk-pooling in ecologically volatile environments. *Evolution and Human Behavior*, 36(4), pp. 265–273. https://doi.org/10.1016/j.evolhumbehav.2014.12.003.

Hardin, G. (1968) The Tragedy of the Commons: The population problem has no technical solution; it requires a fundamental extension in morality. *Science*, 162(3859), pp. 1243–1248. https://doi.org/10.1126/science.162.3859.1243.

Harvati, K. and Reyes-Centeno, H. (2022) Evolution of Homo in the Middle and Late Pleistocene. *Journal of Human Evolution*, 173, p. 103279. https://doi.org/10.1016/j.jhevol.2022.103279.

Henrich, J. (2020). *The WEIRDest people in the world: How the West became psychologically peculiar and particularly prosperous*. US: Farrar, Straus and Giroux.

Hunter, D., Goodreau, S. and Handcock, M. (2008) Goodness of Fit of Social Network Models. *Journal of the American Statistical Association*, 103(481), pp. 248–258. https://doi:10.1198/016214507000000446.

Jaeggi, A. and Gurven, M. (2013b) Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, 280(1768), p. 20131615. https://doi.org/10.1098/rspb.2013.1615.

Junk, W., Silva, C., and Cunha, C. (2011) *The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland*. Sofia-Moscow: Pensoft Publishers.

Kasper, C. and Borgerhoff Mulder, M. (2015) Who helps and why? Cooperative networks in Mpimbwe. *Current Anthropology*, 56(5), pp. 701–736. https://doi.org/10.1086/683024.

Koster, J. (2018) Family ties: the multilevel effects of households and kinship on the networks of individuals. *Royal Society Open Science*, 5(4), p. 172159. https://doi.org/10.1098/rsos.172159.

Koster, J. et al. (2019) Kinship ties across the lifespan in human communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(1780), p. 20180069. https://doi.org/10.1098/rstb.2018.0069.

Koster, J. and Leckie, G. (2014) Food sharing networks in lowland Nicaragua: An application of the social relations model to count data. *Social Networks*, 38, pp. 100–110. https://doi.org/10.1016/j.socnet.2014.02.002.

Lawson, D. and Mace, R. (2011) Parental investment and the optimization of human family size. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1563), pp. 333–343. https://doi.org/10.1098/rstb.2010.0297.

Lycett, J. and Dunbar, R. (1999) Abortion rates reflect the optimization of parental investment strategies. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1436), pp. 2355–2358. https://doi.org/10.1098/rspb.1999.0931.

Madsen, E., Tunney, R., Fieldman, G., Plotkin, H., Dunbar, R., Richardson, J. and McFarland, D. (2007) Kinship and altruism: A cross-cultural experimental study. *British Journal of Psychology*, 98(2), pp. 339–359. https://doi.org/10.1348/000712606X129213.

Marlowe, F. (1999) Showoffs or providers? The parenting effort of Hadza men. *Evolution and Human Behavior*, 20(6), pp. 391–404. https://doi.org/10.1016/S1090-5138(99)0021-5.

Mattison, S. et al. (2021) Gender Differences in Social Networks Based on Prevailing Kinship Norms in the Mosuo of China. *Social Sciences*, 10(7), p. 253. https://doi.org/10.3390/socsci10070253.

Mattison, S., MacLaren, N., Sum, C., Shenk, M., Blumenfield, T. and Wander, K. (2023) Does gender structure social networks across domains of cooperation? An exploration of gendered networks among matrilineal and patrilineal Mosuo. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 378(1868), p. 20210436. https://doi.org/10.1098/rstb.2021.0436.

Maynard Smith, J. (1964) Group Selection and Kin Selection. Nature, 201, pp. 1145–1147. https://doi.org/10.1038/2011145a0.

Mosleh, M., Eckles, D. and Rand, D. (2025) Tendencies toward triadic closure: Field experimental evidence. *Proceedings of the National Academy of Sciences*, 122(27), p. e2404590122. https://doi.org/10.1073/pnas.2404590122.

Mysterud, I., Drevon, T. and Slagsvold, T. (2006) An Evolutionary Interpretation of Gift-Giving Behavior in Modern Norwegian Society. *Evolutionary Psychology*, 4(1), p. 147470490600400132. https://doi.org/10.1177/147470490600400132.

Nolin, D. (2010) Food-Sharing Networks in Lamalera, Indonesia: Reciprocity, Kinship, and Distance. *Human Nature*, 21(3), pp. 243–268. https://doi.org/10.1007/s12110-010-9091-3.

Nowak, M. (2006) Five Rules for the Evolution of Cooperation, *Science*, 314(5805), pp. 1560–1563. https://doi.org/10.1126/science.1133755.

Pontzer, H., Wood, B. and Raichlen, D. (2018) Hunter-gatherers as models in public health. *Obesity Reviews: An Official Journal of the International Association for the Study of Obesity*, pp. 24–35. https://doi.org/10.1111/obr.12785.

Power, E. (2017a) Discerning devotion: Testing the signaling theory of religion. *Evolution and Human Behavior*, 38(1), pp. 82–91. https://doi.org/10.1016/j.evolhumbehav.2016.07.003.

Power, E. (2017b) Social support networks and religiosity in rural South India. *Nature Human Behaviour*, 1(3), p. 0057. https://doi.org/10.1038/s41562-017-0057.

Power, E. (2018) Collective ritual and social support networks in rural South India. *Proceedings of the Royal Society B: Biological Sciences*, 285(1879), p. 20180023. https://doi.org/10.1098/rspb.2018.0023.

Power E. and Ready E. (2019) Cooperation beyond consanguinity: post-marital residence, delineations of kin and social support among South Indian Tamils. *Philos Trans R Soc*, 374(1780). https://doi.org/10.1098/rstb.2018.0070.

Prall, S. and Scelza, B. (2020) Why men invest in non-biological offspring: paternal care and paternity confidence among Himba pastoralists. *Proceedings of the Royal Society B: Biological Sciences*, 287(1922), p. 20192890. https://doi.org/10.1098/rspb.2019.2890.

R Core Team (2012) *R: A language and environment for statistical computing*. Vienna: The R Foundation for Statistical Computing.

Ready, E. and Power, E. (2018) Why Wage Earners Hunt: Food Sharing, Social Structure, and Influence in an Arctic Mixed Economy. *Current Anthropology*, 59(1), pp. 74–97. https://doi.org/10.1086/696018.

Redhead, D., Maliti, E., Andrews, J. and Borgerhoff Mulder, M. (2023) The interdependence of relational and material wealth inequality in Pemba, Zanzibar. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 378(1883), p. 20220288. https://doi.org/10.1098/rstb.2022.0288.

Schnegg, M. (2015) Reciprocity on demand: sharing and exchanging food in Northwestern Namibia. *Human Nature*, 26(3), pp. 313–330. https://doi.org/10.1007/s12110-015-9236-5.

Schulz, J., Bahrami-Rad, D., Beauchamp, J. and Henrich, J. (2019) The Church, intensive kinship, and global psychological variation. *Science*, 66(6466). https://www.science.org/doi/10.1126/science.aau5141.

Sear, R. and Mace, R. (2008) Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior*, 29(1), pp. 1–18. https://doi.org/10.1016/j.evolhumbehav.2007.10.001.

Sear R., Steele F., McGregor, I. and Mace R. (2002) The effects of kin on child mortality in rural Gambia. *Demography*, 39(1), pp. 43–63. https://doi.org/10.1353/dem.2002.0010.

Siqueira, A., Silva, A. and Lima de Paula Silva, B. (2018) Protected Areas In The Pantanal: Traditional Community Of Barra Do São Lourenço On The Brazil/Bolivia Border - Corumbá-Ms Region. *Raega*, 45(1). pp. 74–90.

Smith, M., Kish, B. and Crawford, C. (1987) Inheritance of wealth as human kin investment. *Ethology and Sociobiology*, 8(3), pp. 171–182. https://doi.org/10.1016/0162-3095(87)90042-2.

Stanford Human Evolutionary Ecology and Health (2026) *SNA workshop: ERGM introduction*. Available at: https://eehh-stanford.github.io/SNA-workshop/ergm-intro.html#why-not-use-standard-regression-methods [Accessed 05 June 2026].

Thomas, M., Næss, M., Bårdsen, B. and Mace, R. (2015) Saami reindeer herders cooperate with social group members and genetic kin. *Behavioral Ecology*, 26(6), pp. 1495–1501. https://doi.org/10.1093/beheco/arv106.

Thomas, M., Ji, T., Wu, J., He, Q., Tao, Y. and Mace, R. (2018) Kinship underlies costly cooperation in Mosuo villages. *Royal Society Open Science*, 5(2), p. 171535. https://doi.org/10.1098/rsos.171535.

Trivers, R. (1971) The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology*, 46(1), pp. 35–57. https://doi.org/10.1086/406755.

Wantzen, K. et al. (2023) The Pantanal: How long will there be life in the rhythm of the waters? In: K. M., Wantzen, ed. *River Culture – Life as a Dance to the Rhythm of the Waters*. Paris: UNESCO Publishing, pp. 497–536. https://doi.org/10.54677/DYRD730421.

West, S., Griffin, A. and Gardner, A. (2007) Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20(2), pp. 415–432. https://doi.org/10.1111/j.1420-9101.2006.01258.x.

Widlok, T. (2016) *Anthropology and the Economy of Sharing*. London: Routledge.

Wilkinson, G. (1984) Reciprocal food sharing in the vampire bat. *Nature*, 308(5955), pp. 181–184. https://doi.org/10.1038/308181a0.

Zuur, A., Leno, E. and Elphick, C. (2010) A protocol for data exploration to avoid common statistical problems: *Data exploration*. *Methods in Ecology and Evolution*, 1(1), pp. 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.