RESEARCH METHODS GUIDE

Modelling animal network data in R using STRAND

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Abstract

1. There have been recent calls for wider application of generative modelling approaches in applied social network analysis. At present, however, it remains difficult for typical end users—for example, field researchers—to implement generative network models, as there is a dearth of openly available software packages that make application of such models as simple as other, permutation-based approaches.

2. Here, we outline the `STRAND` R package, which provides a suite of generative models for Bayesian analysis of animal social network data that can be implemented using simple, base R syntax.

3. To facilitate ease of use, we provide a tutorial demonstrating how `STRAND` can be used to model proportion, count or binary network data using stochastic block models, social relation models or a combination of the two modelling frameworks.

4. `STRAND` facilitates the application of generative network models to a broad range of data found in the animal social networks literature.

KEYWORDS
animal networks, generative models, R software, social networks, social relations

1 | INTRODUCTION

The application of theory and methods from network science (i.e. social network analysis) to ethological data has led to important advances in our understanding of the structural features of animal societies (Krause et al., 2009; Wey et al., 2008). Similarly, the role that sociality—broadly conceived—plays in the differential success and survival of individuals and groups (e.g. Clutton-Brock, 2009) has been a topic of perennial interest across the social, behavioural and biological sciences. By quantifying the social interactions (i.e. ties or edges) that are observed between individual animals (i.e. nodes or vertices), researchers can more formally study how various dyadic phenomena are related to one another (e.g. Smith-Aguilar et al., 2019) and to key individual-level properties (e.g. Pike et al., 2008; Pisor et al., 2020).

Recent network-based research has, for example, advanced theory on how social relationships—both positive (e.g. food sharing and grooming) and negative (e.g. agonistic behaviours)—guide the emergence and maintenance of social hierarchies (Kawakatsu et al., 2021; Redhead & Power, 2022), influence the spread of disease (Read et al., 2008; Silk et al., 2017) and adaptive information (Hobaiter et al., 2014; Waters & Fewell, 2012), and explain how individual actions culminate in group-wide movement patterns (Jacoby & Freeman, 2016; Strandburg-Peshkin et al., 2015). To address these topics, and many others, network data are rapidly being compiled across a broad range of taxa (Sah et al., 2019). Given the flexibility of network-based frameworks for understanding behaviour, social network analysis has become one of the most popular areas of research in animal behaviour, behavioural ecology and the quantitative evolutionary and social sciences more broadly (Webber & Vander Wal, 2019).

1.1 | Inferential concerns and potential solutions

While network analytical tools have great potential for advancing our understanding of social behaviour across taxa, there are many statistical complexities inherent in such approaches. Network data are highly interdependent, and theorists generally argue that they cannot be appropriately modelled using standard statistical approaches that assume uncorrelated errors (Back & Kenny, 2010). Nevertheless, in much empirical work, standard regression tools are applied to network data. Beyond issues of statistical interdependence, non-human animal network data often feature variation in reciprocity levels, variation in sampling intensity, censoring issues and a variety of other features that make data analysis challenging. While some work-arounds for these issues have been developed, solutions are often incomplete.

For example, it is common for researchers to regress outgoing ties on incoming ties to estimate reciprocity (e.g. Carter & Wilkinson, 2013), but such regressions have been shown to be affected by residual confounding bias (see Koster & Leckie, 2014). Similarly, it is common to correct for variation in sampling effort by creating a Simple Ratio Index (SRI; Cairns & Schwager, 1987; Farine & Whitehead, 2015; Whitehead & James, 2015), but such indices divide out sample size and give the weakest data points disproportionate weight in downstream analyses (Hart, Weiss, Franks, et al., 2021). Additionally, permutation-based methods—such as the quadratic assignment procedure (Dekker et al., 2003; Hubert & Schultz, 1976; Krackardt, 1987) and conceptually related approaches—have been used to model network data on animal behaviour (see also Croft et al., 2011; Farine & Carter, 2022; Farine & Whitehead, 2015; Sosa et al., 2021); however, permutation-based methods can only generate data expected from a given null hypothesis—they do not permit researchers to estimate unbiased effects conditional on observed data, or to parametrically simulate data from non-null models of interest (see Farine & Carter, 2022; Hart, Weiss, Brent, et al., 2021; Weiss et al., 2021).

By raising these issues, we do not seek to critique any work in particular. Instead, we highlight that solutions to many common inferential problems already exist inside of a unified Bayesian approach to data analysis. For example, dyadic reciprocity can be estimated using correlated random effects rather than including the transposed outcome as a predictor (Koster & Leckie, 2014), the usefulness of the simple ratio index approach can be improved through the use of binomial outcome models to propagate uncertainty (Hart, Weiss, Franks, et al., 2021), and generative network models can be deployed to *actively* account for non-independence of data points via integration of correlated random effects at both the node and dyad level (see Back & Kenny, 2010; Kenny & La Voie, 1984; Snijders & Kenny, 1999 for classic derivations; and McElreath, 2020 for accessible textbook examples).

Although Bayesian approaches to network data analysis are well suited to resolving known challenges in the animal behaviour literature, Bayesian methods are used much less frequently than other, often permutation-based methods. We argue that the reasons for this are largely historical, as correlated random-effects models were difficult to fit using early computer software and required end users to define bespoke statistical models by-hand. In fact, nuanced generative models of social networks have been described for decades (e.g. see Kenny & La Voie, 1984), but estimation of these models remained computationally intractable until only recently, with the advent of powerful and fast Markov Chain Monte Carlo engines, like Stan (Stan Development Team, 2021b). As such, there is still a dearth of freely available open-source software for implementing such generative modelling approaches as network analysis tools.

To address this gap in the software space, we draw upon classic generative modelling approaches for network data—like stochastic block models (SBMs) (Pearl & Schulman, 1983) and the social relations model (SRM) (Kenny & La Voie, 1984), and integrate them with contemporary tools for Bayesian model fitting (Stan Development Team, 2021b). In doing this, we have developed an R package, `STRAND`, that allows end users to build complex network analysis models using simple `lm`-style syntax in base R, simplifying the process of modelling empirical network data.

1.2 | Generative modelling approaches

It is widely agreed upon that empirical data are best analysed using scientifically informed *generative models* (Reilly & Zeringue, 2005)—that is, models that can be used to forward-simulate data with specific, biologically realistic features. In the case of modelling animal social networks as outcome variables, such features might include: (1) dyadic reciprocity (i.e. the correlated tendency of animal i to perform some action to animal j when animal j performs the same action to animal i); (2) correlated variation in out-degree (i.e. the tendency of given animals to act on other animals) and in-degree (i.e. the tendency of given animals to be acted upon by other animals); and (3) group structure (i.e. the tendency of some animals to form tight-knit subgroups), as well as (4) a variety of other features than can be controlled parametrically (e.g. as a function of covariate data).

There are a wide range of generative network models that have been developed to represent complex data generating procedures (see Hobson et al., 2021; Newman, 2018, for reviews), including biased reporting (De Bacco et al., 2023; Redhead et al., 2023; Young et al., 2020). Through Bayesian inversion (Allmaras et al., 2013), these models can be used as analytic tools that support statistical inference on the basis of empirical data. One such model that holds particular promise for research on animal social networks is the SRM (Kenny & La Voie, 1984; Snijders & Kenny, 1999), which examines and accounts for correlations in node-level and dyad-level random effects. Across many contexts, animal social networks may further be partitioned into observable subgroups—such as

coalitions (Kajokaite et al., 2019), matrilines (Ilany et al., 2021) and groupings based on identity or physical location (De Dreu & Triki, 2022). These groupings may create gross community structure in networks, whereby individuals preferentially interact with those in their own subgroups (i.e. 'blocks'). Given this, *SBMs* may be especially useful in animal social network analysis (Pearl & Schulman, 1983), as they capture these higher order structures (Peixoto, 2019), and allow the probability of network ties to vary within and between subgroups. Together, these approaches (SRMs and SBMs) provide a framework for a more direct analysis of the mechanisms involved in the data generating process of animal social relationships (see also mathematical derivations in the Supporting Information).

1.3 | Our contribution

In order to address the concerns outlined in previous sections, our R package for Bayesian social network analysis deploys generative network modelling approaches. The STRAND package currently supports SBMs, SRMs and more complex latent network models (see Redhead et al., 2023).

Social network analysis is a large field, with a wide range of models and approaches (Pinter-Wollman et al., 2014); `STRAND` focuses only on modelling networks as outcome/response variables as a function of individual and dyadic covariates (which might include other networks). In this paper, we outline specifically how SBMs and SRMs can be fit to non-human animal network data—for example, as collected by focal observation, GPS tracking or proximity detection—to answer key research questions. By presenting a tutorial for fitting these models to each of the three most commonly collected types of outcome data used in studies of animal behaviour and behavioural ecology—that is, proportion data (e.g. counts of behavioural observations where the sampling rate is variable across possible dyads), count data (e.g. through behavioural observations over a standardised time window) and binary tie data (e.g. via binary classification of relationship types)—we hope to inspire more widespread application of generative network models in empirical research.

Our approach to network modelling here complements that of the `BISoN` team (Hart, Weiss, Franks, et al., 2021), who have also developed a suite of network analysis models using Bayesian methods. Our R package provides additional functionality to typical end users; however, in that, it integrates Bayesian network analysis models with a user-friendly interface that allows even casual R users to specify complex network models (which may include a variety of block-level, individual-level and dyad-level covariate data), using nothing more than base R syntax. In the supporting information, we detail the mathematical foundations of each of the models described in the tutorial and demonstrate that each of these models performs well on unit tests, recovering the parameters of generative models used to simulate realistic network data with known properties.

2 | MATERIALS AND METHODS

The `STRAND` package is designed specifically to model *directed* networks—that is, network data that describe flows or actions from individual *i* to individual *j*. Nevertheless, `STRAND` models can be applied to *undirected* networks as well, as such networks can be thought of as special cases of directed networks with maximally high reciprocity (Meyers et al., 2006), but more care is needed in parameter interpretation. Additionally, the `STRAND` package is designed to be applied in cases where networks are accurately observed; if substantial sampling biases are present, users may need to build bespoke models of the data generation and observation process directly in Stan. This being said, `STRAND` is appropriate for modelling data where there is variation in the sampling rate of different dyads, as long as variation in exposure to risk of observation is accounted for—for example, through the use of binomial outcome models, as we discuss below.

Much of the functionality of `STRAND` is made possible by `Stan` (Stan Development Team, 2021b) and `CmdStanR` (Stan Development Team, 2021a). Users must install these programs prior to installing `STRAND`. Installation and loading of `STRAND` is then simple: just run three lines of code from R:

library(devtools)
install_github("ctross/STRAND")
library(STRAND)

All of the tutorial code elaborated on below can also be found online at: https://github.com/ctross/STRAND, where the package will be maintained.

2.1 | Building data objects

The first step in building any `STRAND` model is to organise the data. Social network data are normally complex, with some variables being reported at the level of the individual and others being reported at the level of the dyad. The `make strand data` function serves to organise all of these data into a unified format that can be read by later functions. After data are compiled, they can then be analysed with simple, `lm-style` function calls, as we discuss below.

We will illustrate how `STRAND` data objects are built, using Guinea baboon (*Papio papio*) grooming network data from Gelardi et al. (2019, 2020). First, outcome data and dyad-level predictors (both structured as adjacency matrices) are stored as labelled lists:

# Load package data
data(Baboon_Data)
# Organize outcome & exposure measures
outcome = list(
 Grooming=Baboon_Data$Grooming)
exposure = list(

```
Exposure = Baboon_Data$Exposure)
```

```
# Organize dyadic predictors
dyad=list(
Presenting=t(Baboon_Data$Presenting),
Threatening=t(Baboon_Data$Threatening)
)
```

The outcome data (here, the grooming network) must be either binary data or integers. The exposure variable (here, the number of times each individual was scan sampled to assess which behaviour they were doing to whom) must be integers. As we are applying a binomial model, the outcome at each cell in the grooming matrix must be less than or equal to the corresponding cell in the exposure matrix. The dyadic covariate data can include numeric variables, indicator variables or even categorical variables. These dyadic covariate data can be used to estimate associations between dyad-level characteristics—such as genetic relatedness or physical proximity—and the likelihood of a tie in the outcome network.

Next, the individual-level covariates are stored in a data frame:

```
# Organize individual measures
indiv = data.frame(
Age=Baboon_Data$Age,
Sex=Baboon_Data$Sex)
```

The individual-level covariate data can also include numeric variables, indicator variables or categorical variables. Individual-level covariate data can be used to estimate associations between individual-level characteristics and the likelihood of either sending or receiving a tie.

Finally, individual-level covariates that govern group/block structure are stored in a separate data frame:

```
# Organize blocking measures
block = data.frame(
Sex=as.factor(Baboon_Data$Sex))
```

Although these block-structuring variables are also individual-level data, they are treated differently than other variables by STRAND; these variables must be factors and are used to create random intercept offsets unique to the interaction of focal/sender and alter/receiver block IDs. Note that we have stored 'Sex' both as a blocking variable and as an individual variable. Later, when defining models, sex can be used either as a predictor of block structure *or* as a predictor of in-degree and out-degree.

Once all covariate data are organised as above, they can be compiled into a single STRAND object:

```
# Create the STRAND data object
dat = make_strand_data(
outcome = outcome ,
block_covariates = block,
individual_covariates = indiv,
```

```
dyadic_covariates = dyad,
outcome_mode = "binomial",
exposure = exposure)
```

At this point, the user must define which outcome model to use. The STRAND package supports three outcome modes for each model type: 'binomial' for proportion data (e.g. if the outcome variable is a matrix containing a count of grooming events between each dyad, and the exposure variable is matrix containing a count of the number of scans in which grooming events between each dyad could have been observed), 'poisson' for raw count data (e.g. the number of times constant-time-interval GPS trackers were within 5 m of each other over a fixed 1-week period), or finally 'bernoulli' for binary tie data (e.g. for human self-report/name-generator data, or similar binary tie data from non-human animals). If the outcome mode is set to 'binomial', then the exposure variable must be provided. The exposure variable is a labelled list containing a matrix of sample sizes—that is, counts of the number of times some dyadic tie could have possibly been observed given the sampling protocol.

2.2 | Example model with binomial data

The most common type of data encountered in studies of animal sociality represents tie strength as a weighted social association matrix (e.g. Brask et al., 2019). These measures are typically created by applying a simple ratio association index (SRI; Cairns & Schwager, 1987; Farine & Whitehead, 2015), where, for example, the edge weight of each dyad is calculated as the ratio of the number of scans/observations in which the dyad is observed together divided by the number of scans/observations in which at least one of them was observed.

While this approach of weighting counts by an exposure variable is significantly better than ignoring variation in risk of observation (Farine & Whitehead, 2015), construction of a simple ratio divides out sample size information, leading dyadic observations based on little data to carry disproportionate weight in downstream analyses (see Hart, Weiss, Franks, et al., 2021; McElreath, 2020, for a review of this issue). Moreover, zeros arising from censoring (i.e. due to members of a dyad being unavailable) are sometimes confounded with true zeros (i.e. members of a dyad being present but not interacting). A better approach involves modelling the actual *count* of the number of scans/observations that each dyad is observed together using a binomial model, in which the sample size/exposure parameter is—for example—the number of scans/observations where at least one member of the dyad was observed. Note, however, that when association is measured automatically using GPS or proximity detectors, the dyad-level sample size/exposure data should only count cases in which GPS/proximity readings were simultaneously available for both members of the dyad (see; He et al., 2023, for a detailed guide on using GPS-based data in studies of animal networks).

To demonstrate how to fit a binomial model in STRAND, we again draw on the grooming data (see Figure 1) from captive Guinea
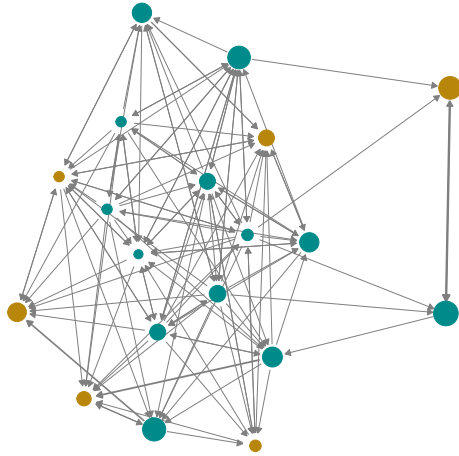
FIGURE 1 Grooming data in captive Guinea baboons published by Gelardi et al. (2020). Nodes are coloured by sex (males in goldenrod and females in dark cyan) and scaled by age. Edge weights are scaled by grooming rate. Variance in node out- and in-degree is estimated using random effects on the probability of providing and receiving grooming respectively.

baboons published by Gelardi et al. (2019, 2020). We investigate three questions—controlling for age and sex—here: (1) Do individuals who groom others more also receive more grooming in general (i.e. is there generalised reciprocity)?, (2) accounting for individual-level differences in the probability of grooming, does the probability of individual i grooming individual j increase with the probability that individual j grooms individual i (i.e. is there dyadic reciprocity)? and (3) is the probability of individual i grooming individual j associated with whether individual j 'presents' to individual i? (Presenting is defined as: '*another individual gently with or without lipsmacks and grunts and presenting the rear*'; Gelardi et al., 2020).

To model the data, we use a hybrid of the SBM and SRM (see Supporting Information for full mathematical details). The STRAND syntax is based on standard lm syntax from base R. To model the data, we write out equations for block effects, focal/sender effects, target/receiver effects and dyadic effects:

```
fit =
fit_block_plus_social_relations_model(
 data=dat,
 block_regression = ~ Sex,
 focal_regression = ~ Age,
 target_regression = ~ Age,
 dyad_regression = ~ Presenting ,
 mode="mcmc",
 stan_mcmc_parameters = list(
 chains = 1,
 iter_warmup = 1500,
 iter_sampling = 1500))
```

In this model, we estimate block-level effects for sex using the argument: block_regression = ~ Sex. These effects are indicative of how the likelihood of a directed grooming relationship varies as a function of block categories—that is, we can measure if male to male ties are more or less likely than male to female ties, female to male ties or female to female ties. If the interaction of focal and target sex is not of interest, sex could be included as a predictor of in-degree and out-degree instead.

Next, the focal regression model, focal_regression = ~ Age, explores how the age of a given individual is related to that individual's propensity to groom others (i.e. it measures the effects of individual-level covariates on *out-degree*). Similarly, the target regression model, target_regression = ~ Age, explores how the age of a given individual is related to that individual's propensity to be groomed by others (i.e. it measures the effects of individual-level covariates on *in-degree*). Finally, the dyad regression model, dyad_regression = ~ Presenting, explores how the likelihood of grooming ties is associated with the (transposed) rate of 'presenting' behaviour (i.e. how likely is individual i to groom individual j, given the rate at which individual j 'presents' to individual i).

Additional parameters can be supplied to control MCMC performance. Stan is much more efficient than earlier MCMC samplers: 1500 iterations each for warmup and sampling on a single chain is normal sufficient for exploratory model testing. We recommend slightly longer runs using several chains for final inferences. Users should also check traceplots, $\hat{r}$ values and number of effective samples to ensure good model fit. Example code for such performance checks can be found in the tutorial titled 'Binomial Example.R' on the STRAND GitHub page. See McElreath (2020, sections 8.3–8.4) for further guidance.

When the model has finished running, the MCMC samples can be processed and summarised using convenience functions:

```
# Summarize results
res = summarize_strand_results(fit)

# Plot slopes
vis = strand_caterpillar_plot(res,
 normalized=TRUE, only_slopes=TRUE)
vis
```
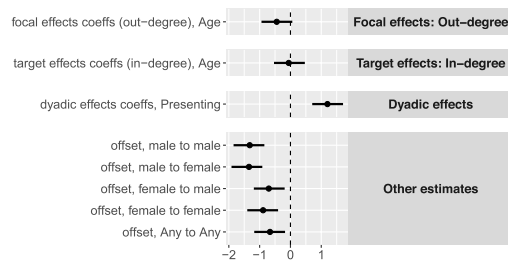
The results are presented in Table 1 and Figure 2. We note that the correlation, ρ, of focal and target effects is negative. This indicates that baboons who frequently groom others are actually less likely to be groomed themselves by others. Such unidirectional behavioural propensities are consistent with dominance hierarchies (e.g. Gullstrand et al., 2021), in which unbalanced benefits are tolerated. However, after accounting for this individual-level variation in grooming propensity, there is evidence of dyadic reciprocation, as indicated by the strong correlation, ρ, in dyadic random effects. Finally, in this sample of Guinea baboons, individuals appear more likely to groom conspecifics who regularly 'present' to them.

We find no strong effect of age on the probability of sending or receiving grooming ties. Additionally, at first glance, it looks like the
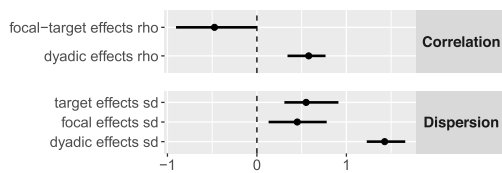
TABLE 1 Analysis of grooming in captive baboons.

Type	Variable	Median	HPDI:L	HPDI:H	Mean	SD
Random	Focal σ	0.451	0.131	0.78	0.46	0.194
Random	Target σ	0.55	0.307	0.911	0.568	0.19
Random	Dyadic σ	1.428	1.228	1.658	1.434	0.138
Random	Focal-target ρ	−0.474	−0.904	0.00	−0.426	0.289
Random	Dyadic ρ	0.579	0.342	0.767	0.567	0.136
Focal	Age	−0.037	−0.078	0.005	−0.038	0.026
Target	Age	−0.005	−0.048	0.042	−0.005	0.028
Dyadic	Presenting	0.377	0.222	0.536	0.379	0.097
Block	Intercept	−2.694	−4.769	−0.71	−2.652	1.246
Block	Female-to-female	−3.475	−5.484	−1.57	−3.496	1.189
Block	Female-to-male	−2.751	−4.646	−0.735	−2.725	1.197
Block	Male-to-female	−5.417	−7.704	−3.677	−5.432	1.209
Block	Male-to-male	−5.283	−7.38	−3.383	−5.27	1.226

Note: HPDI:L and HPDI:H show the low and high endpoints of the highest 90% posterior density intervals. *Focal*, *target* and *dyadic* effects are interpreted as slopes. *Block* effects are interpreted as intercept offsets. *Random* effects include terms that control the variance of random effects, σ, and terms that control the correlation of random effects, ρ.

(a) Effects of covariates.

(b) Standard deviation and correlation of random effects.

FIGURE 2 Analysis of grooming in captive baboons. Points represent the posterior medians, and bars represent 90% highest posterior density intervals. Guinea baboons appear more likely to groom conspecifics who regularly 'present' to them. Interestingly, the correlation, ρ, of focal and target effects is negative. This indicates that baboons who frequently groom others are less likely to be groomed themselves by others. However, after accounting for this individual-level variation in grooming propensity, there is evidence of dyadic reciprocation, as indicated by the correlation, ρ, in dyadic random effects.

posterior distributions of the effects of sex overlap (Figure 2); however, with block effects, researchers must be sure to calculate posterior contrasts (see McElreath, 2020, section 5). Upon calculating contrasts, the difference in female to male and male to female offsets is strong and reliable: 2.70 (89% HPDI: 1.79, 3.51), with females

grooming males more than vice versa. Example code for computing such contrasts can be found in the tutorial titled 'Binomial Example.R' on the STRAND GitHub page.

2.3 | Example model with Poisson data

In other cases in the animal behaviour literature, network data are recorded using numerical measurements (e.g. the number of times two animals are observed fighting), but exposure time data are assumed to be constant across dyads. As an example of how to analyse such measures, we use data on blood sharing (Figure 3) among vampire bats (*Desmodus rotundus*), published by Carter and Wilkinson (2013), and make the simplifying assumptions that: (1) sampling rates were approximately equal across observed dyads and (2) that some dyads had no opportunity to be observed together (i.e. such outcomes were censored). If these assumptions are not met, then a more complex model with an exposure measure for each dyad might be needed. The bat data include individual-level predictors (i.e. sex) and dyad-level predictors (i.e. genetic relatedness, and whether each dyad had the opportunity to be observed sharing blood). As such, we investigate the following set of research questions: (1) Is blood sharing reciprocal?, (2) is there evidence that kin are more likely to share blood than non-kin? and (3) is there evidence that blood sharing networks are structured by sex?

As before, we start by organising the data:

```
data(Bat_Data)
# Number of minutes of blood licking
nets = list(
  Lick=round(Bat_Data$Lick/60,0))
```
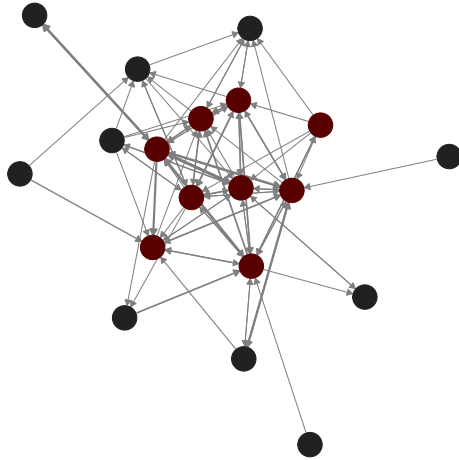
FIGURE 3 Blood sharing network data from vampire bats published by Carter and Wilkinson (2013). Red nodes represent females and dark grey nodes represent males. Group structure is modelled by including sex as a block variable. Variance in node degree is estimated using random effects.

```
# Dyadic variables
dyad = list(
 Relatedness=Bat_Data$Relatedness ,
 NoOpportunity=Bat_Data$NoOpportunity)
# Block variables
group_ids = data.frame(
 Sex=as.factor(Bat_Data$Sex))
```

Then, the data can be compiled into a STRAND data object. This time, we must include the argument: `outcome_mode = "poisson"`, so that STRAND knows to apply the Poisson model. Also, since there are no individual-level covariates other than sex, which is used as a blocking variable here, we can set: `individual_covariates = NULL`.

```
dat = make_strand_data(
 outcome = nets,
 block_covariates = group_ids ,
 individual_covariates = NULL,
 dyadic_covariates = dyad,
 outcome_mode = "poisson"
 )
```

Then, a model can be fit to the data:

```
fit =
fit_block_plus_social_relations_model(
 data=dat,
 block_regression = ~ Sex,
 focal_regression = ~ 1,
 target_regression = ~ 1,
 dyad_regression = ~ NoOpportunity *
Relatedness ,
 mode="mcmc",
```

```
 stan_mcmc_parameters = list(
 chains = 1,
 iter_warmup = 1500,
 iter_sampling = 1500)
)
```

Here, we set the focal and target regression models to be intercept only (as we have no individual-level covariates) using the `lm`-style syntax: `focal_regression = ~1` and `target_regression = ~1`. Additionally, we model the dyadic data using an interaction term: `dyad_regression = ~ NoOpportunity * Relatedness`. This interaction allows us to investigate the relationship between relatedness and blood sharing within the subset of dyads where outcomes were observable (i.e. not censored).

Finally, the results can be summarised and plotted:

```
# Summarize results
res = summarize_strand_results(fit)
# Plot slopes
vis = strand_caterpillar_plot(res,
 normalized=TRUE, only_slopes=TRUE)
vis
```

Table 2 and Figure 4 present the effects of relatedness and sex on the rate of blood sharing transfers. We recover the primary results of Carter and Wilkinson (2013), finding that blood sharing is reciprocal, genetic relatedness is a reliable predictor of blood sharing, and that transfers are reliably more likely between female–female dyads than between male–male or mixed-sex dyads.

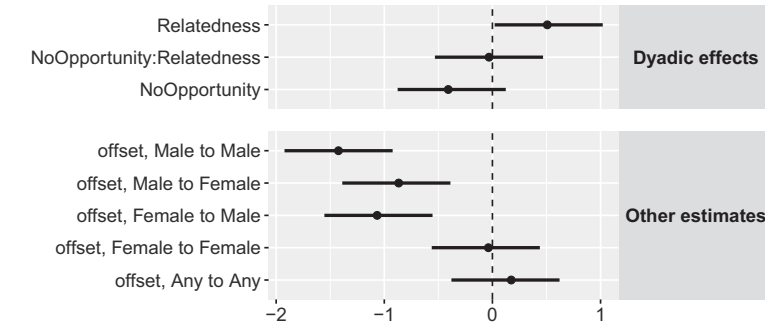## 2.4 | Example model with binary data

In human research, social networks are most frequently represented as a matrix of binary ties (i.e. zeros indicating the absence of ties, and ones indicating the presence of ties). In the non-human literature, such data are less frequent, but are sometimes used to represent dyadic traits like coresidence (DeTroy et al., 2021), pair bonding (Clark et al., 2014; Davis, 2022) or group identity (Murphy et al., 2020). For researchers interested in comparative work, we present an example analysis of human friendship network data in the Supporting Information (see also Redhead et al., 2022).

However, in our main example here, we will explore network structure (Figure 5) in a cooperatively breeding primate—the common marmoset, *Callithrix jacchus*—using data published by De la Fuente et al. (2022). More specifically, we will investigate directed aggression during experimental co-feeding as a function of rank differences. We address four questions: (1) does the difference in rank between individuals *i* and *j* influence the likelihood that individual *i* will aggress individual *j*?, (2) is there any evidence of reciprocal aggression?, (3) is the overall rate of aggression affected by feeding condition, with more intense competition occurring when food is sparse? and (4) are there sex differences in rates of aggressing and being aggressed?
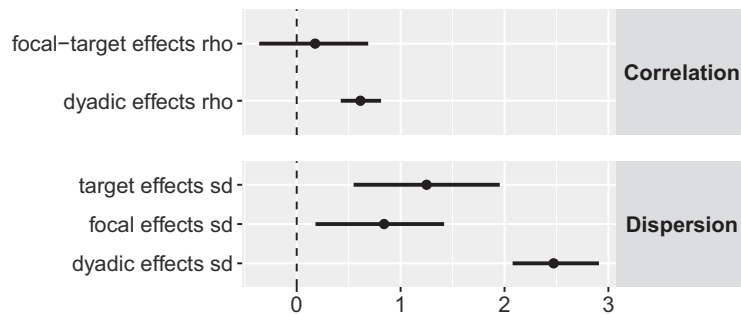
TABLE 2 Analysis of blood sharing among vampire bats.

	Variable	Median	HPDI:L	HPDI:H	Mean	SD
Random	Focal σ	0.841	0.181	1.419	0.845	0.372
Random	Target σ	1.25	0.548	1.954	1.28	0.447
Random	Dyadic σ	2.473	2.078	2.909	2.489	0.262
Random	Focal-target ρ	0.177	−0.361	0.688	0.146	0.331
Random	Dyadic ρ	0.613	0.424	0.812	0.602	0.121
Dyadic	NoOpportunity	−0.948	−2.035	0.287	−0.98	0.696
Dyadic	Relatedness	1.264	0.051	2.542	1.268	0.763
Dyadic	Relatedness:NoOppor.	−0.095	−1.61	1.418	−0.097	0.968
Block	Intercept	0.679	−1.482	2.426	0.658	1.193
Block	Female-to-female	−0.149	−2.247	1.757	−0.216	1.262
Block	Female-to-male	−4.148	−6.046	−2.155	−4.149	1.219
Block	Male-to-female	−3.483	−5.58	−1.561	−3.512	1.244
Block	Male-to-male	−6.257	−8.45	−4.055	−6.315	1.368

Note: HPDI:L and HPDI:H show the low and high endpoints of the highest 90% posterior density intervals.

(a) Effects of covariates.

(b) Variance and correlation of random effects.

FIGURE 4 Analysis of blood sharing among vampire bats. Points represent the posterior medians, and bars represent 90% highest posterior density intervals. Vampire bats are more likely to share blood with relatives than less-related conspecifics. Transfers are also more likely to flow from females to other females than from females to males. Blood sharing is also reciprocal, as indicated by the strong correlation in dyadic random effects.

There are two data objects to create—one for each experimental condition—but we only show one here—that is, the concentrated, low-food condition (the C− condition in De la Fuente et al., 2022). See the package GitHub page for full tutorial code.

```
# Load data
data(Callithrix_Data)
# Indicator of i aggressing j
```

```
outcome = list(Aggressed =
  Callithrix_Data[[1]]$Aggressed)
dyad = list(
  RankDiff = Callithrix_Data[[1]]$
  RankDiff ,
  NoOpportunity = Callithrix_Data[[1]]$
  NoOpportunity)
indiv = data.frame(Female =
```
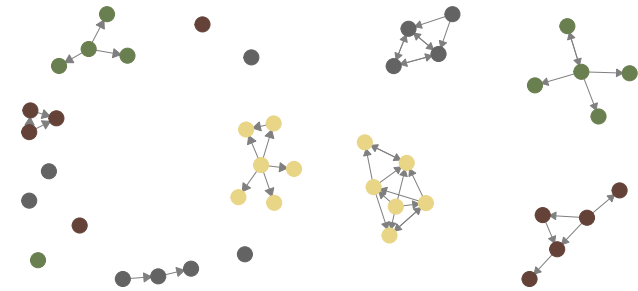
Callithrix_Data[[1]]$Female)

Then, the data can be compiled into a `STRAND` data object:

model_dat_cm = make_strand_data(
outcome = outcome ,
individual_covariates = indiv,

(a) High food productivity   (b) Low food productivity

FIGURE 5 Binarized aggression event networks in marmosets, derived from data in De la Fuente et al. (2022). Directed ties indicate if a focal individual aggressed a target individual at least once every three feeding sessions. Nodes are coloured by group. Feeding was conducted in multiple conditions, of which two are explored here: high food productivity (scattered) and low food productivity (concentrated).

block_covariates = NULL,
dyadic_covariates = dyad,
outcome_mode = "bernoulli")

This time, we must include the argument: `outcome_mode="bernoulli"`, so that `STRAND` treats the outcome data as binary indicators. Also, since there are no block covariates, we can set: `block_covariates=NULL`, and we run the model using the command `fit_social_relations_model`:

fit_cm = fit_social_relations_model(
 data=model_dat_cm ,
 focal_regression = ~ Female,
 target_regression = ~ Female,
 dyad_regression = ~ RankDiff *
 NoOpportunity ,
 mode="mcmc",
 stan_mcmc_parameters = list(chains =
 1, iter_warmup = 1500,
 iter_sampling = 1500))

Here, we set the focal and target regression models to estimate the effects of being female on aggressing: `focal_regression = ~ Female`, and being aggressed: `target_regression = ~`

TABLE 3 Analysis of interspecific aggression in four groups of marmosets.

Type	Variable	Median	HPDI:L	HPDI:H	Mean	SD
(a) Low food						
Random	Focal σ	0.225	0.002	0.602	0.278	0.225
Random	Target σ	0.245	0.001	0.673	0.301	0.242
Random	Dyadic σ	0.269	0	0.727	0.334	0.264
Random	Focal-target ρ	0.043	−0.746	0.663	0.04	0.425
Random	Dyadic ρ	0.017	−0.597	0.673	0.016	0.399
Focal	Female	1.424	0.644	2.178	1.437	0.463
Target	Female	0.672	−0.082	1.372	0.682	0.452
Dyadic	RankDiff	1.722	0.915	2.537	1.725	0.508
Dyadic	NoOpportunity	−4.035	−4.961	−3.256	−4.043	0.515
Dyadic	RankDiff:No_Oppor.	−0.761	−1.943	0.559	−0.771	0.777
Block	Intercept	−1.968	−2.657	−1.189	−1.966	0.457
(b) High food						
Random	Focal σ	1.375	0.097	2.447	1.441	0.768
Random	Target σ	0.377	0.001	0.986	0.464	0.389
Random	Dyadic σ	0.315	0	0.918	0.411	0.343
Random	Focal-target ρ	−0.027	−0.609	0.643	−0.017	0.385
Random	Dyadic ρ	−0.008	−0.659	0.662	0.001	0.406
Focal	Female	0.651	−0.609	1.804	0.64	0.736
Target	Female	−0.354	−1.394	0.625	−0.365	0.632
Dyadic	RankDiff	1.409	0.366	2.579	1.407	0.697
Dyadic	NoOpportunity	−2.936	−3.972	−1.958	−2.972	0.619
Dyadic	RankDiff:No_Oppor.	−0.862	−2.25	0.323	−0.862	0.824
Block	Intercept	−3.606	−4.931	−2.2	−3.683	0.853

Note: HPDI:L and HPDI:H show the low and high endpoints of the highest 90% posterior density intervals.

`Female`. We model the dyadic predictors using an interaction term: `dyad_regression = ~ RankDiff * NoOpportunity`. Here, the variable `NoOpportunity` is 1 if individuals i and j are in different, non-interacting groups, and 0 otherwise. This interaction allows us to investigate the relationship between directed rank difference and aggression within the subset of dyads where outcomes are observable (i.e. not censored). The same workflow is repeated for the scattered, high-food productivity condition (i.e. the S++ condition in De la Fuente et al., 2022), and the results are presented jointly below (e.g. see Table 3; Figure 6).

As suggested by De la Fuente et al. (2022), our analysis shows that the directed difference in rank between individuals i and j is strongly predictive of the tendency that individual i will aggress individual j. In contrast to the other examples, we find no evidence of generalised or dyadic reciprocity in aggression; this is consistent with aggression being directed primarily unilaterally, from higher ranked individuals towards lower ranked ones. The overall rate of aggression is affected by feeding condition, with more intense competition occurring when food is sparse and concentrated; the intercept in the low-food condition is higher than in the high-food condition, and the variance in focal random effects is lower—consistent with higher and more uniform rates of aggression as feeding competition increases. Lastly, as described qualitatively by De la Fuente et al. (2022), we find that females are more likely to aggress conspecifics than are males, especially when feeding competition is high.
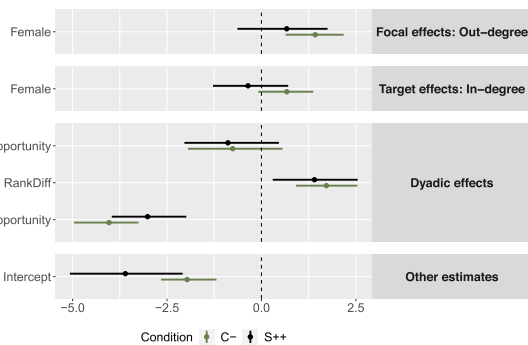
(a) Effects of covariates.
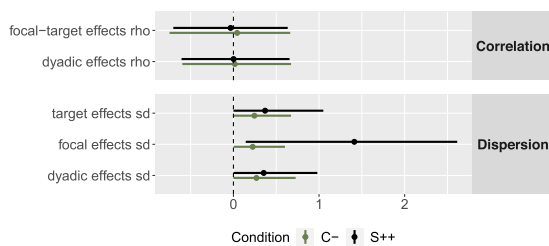
**(b)** Variance and correlation of random effects.

FIGURE 6 Analysis of interspecific aggression in four groups of marmosets. Points represent the posterior medians, and bars represent 90% highest posterior density intervals. Rank difference predicts aggressive events, and females are more aggressive than males, especially in the low-food condition.

2.5 | Additional details

For interested readers, we include a detailed mathematical description of each of our statistical models in the Supporting Information, Section 1. There, we also walk readers through model specification, default prior settings, parameter interpretation and model validation procedures. In `STRAND`, all default priors are set to be weak—so that the likelihood principally determines the posterior—and/or weakly regularising—to prevent over-fitting (McElreath, 2020). Most users will not need to modify the default priors, but should they need to, we provide a function `make_priors()`, which lets users update any priors they choose before fitting models. See details in Supporting Information, Section 1.4.

2.6 | Validating the models with simulated data

In the Supporting Information, Section 2, we test each statistical model, for each outcome mode (Binomial, Poisson, and Bernoulli) using a suite of unit tests (see also Redhead et al., 2023). Specifically, we first generate network data using forward simulations from an SBM, an SRM or
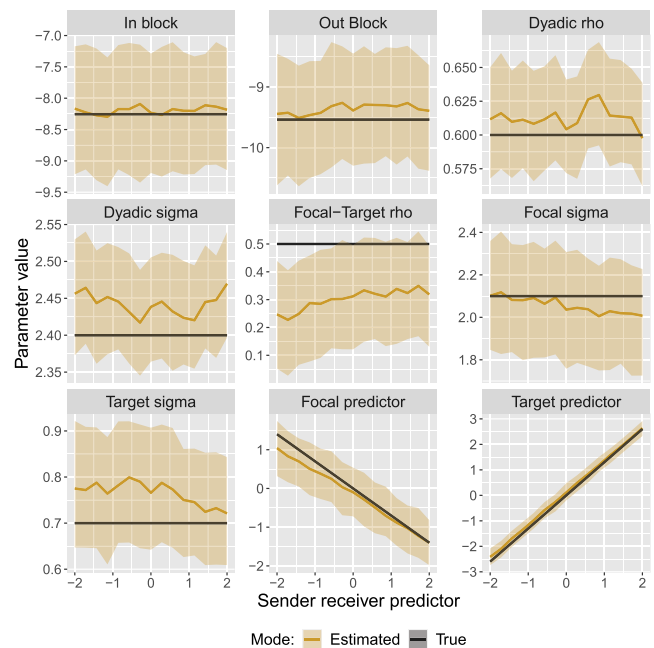
FIGURE 7 Example of model validation results for a binomial outcome model. In this case, we vary one predictor of nodal out-degree (focal predictor) and one predictor of nodal in-degree (target predictor) of a generative network model and simulate a range of artificial data sets. We then use `STRAND` to estimate the model parameters for each simulated data set. Black lines represent the true generative parameter values. Yellow regions represent estimated posterior distributions of the same parameters. We find that our model accurately recovers all generative parameters; this is indicated by the posterior distribution capturing the true generative parameter values. We repeat this process for all combinations of network models and outcome modes, varying all key model parameters for each test case. See Supporting Information for details.

the combined model, which includes both SBM and SRM parameters. We then use the corresponding inferential statistical models to analyse the simulated data sets and ensure that we can recover the generative parameter values. In each simulation experiment, we generally vary only a single generative parameter (e.g. the dyadic reciprocity coefficient) across a broad parameter space that contains realistic values, while fixing all other parameters in the model to empirically plausible values. See Figure 7 for an example, and the Supporting Information for the full suite of unit tests, which all indicate that our models accurately recover generative parameters. We also compare `STRAND` and `asnipe` models applied to the same data, finding that both approaches lead to similar inference concerning statistical significance/reliability. See details in Supporting Information, Section 3.

3 | CONCLUSIONS

The tools included in `STRAND` provide easy to use and efficient methods for generative modelling of human and animal social networks. Here, we have outlined the functionality of `STRAND`, defined the suite of models that are included and provided detailed unit tests to show that the software performs correctly. Using openly available example data sets, we have provided tutorials for end users interested in running network analysis models in R using `STRAND`. We hope that this software will help end users with limited programming experience easily deploy otherwise complex statistical models and investigate fundamental research questions in their fields of interest. End users can find a complete index of—and full documentations for—all functions included in `STRAND` by visiting: https://github.com/ctross/STRAND or by calling `?STRAND` from R. Additional R examples are provided on GitHub as well.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Archived code and data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.z8w9ghxk4 (Ross et al., 2023). The live version of the package will be maintained at: https://github.com/ctross/STRAND.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Code and data used in this paper.

Data S2: Supplemental appendix.

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