

# Robust Bayesian modeling of animal networks subject to censoring and sampling biases

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## Abstract

Animal Social Network Analysis (ASNA) has emerged as a crucial approach, leading to significant progress in theoretical and empirical studies of animal social behavior, social development, genetic factors, fitness impact, epidemiology, animal culture, and social structures. This progress owes much to the development of cutting-edge analytical techniques.

## Keywords

social networks, animal networks, social interactions, generative models

## Introduction

Over the past 50 years, graph theory has become a vital tool in studying natural and artificial systems in various fields like anthropology, sociology, economics, ecology, ethology, and animal societies. It applies to both small-scale (e.g., proteomics) and large-scale (e.g., ecosystems) systems. In the realm of animal sociality research, innovative techniques, such as association indices and pre-network permutations, have expanded upon traditional graph theory. These methods help address specific challenges in this field, like variations in sampling efforts. However, recent studies have highlighted significant reliability concerns associated with hypothesis testing protocols developed in Animal Social Network Analysis (ASNA).

These issues involve elevated rates of false negatives (meaning failing to reject a false null hypothesis) and false positives (accepting a false null hypothesis). For instance, in a simulation study by Puga-Gonzalez et al., they considered a scenario with data biases stemming from the data collection process (like oversampling certain individual categories). They found false positive rates ranging from 35.6% to 60.8%, and false positive rates ranging from 36.6% to XXX. Variations in error rates are connected to the different protocols used and will be discussed further. Since very few biological data collected in natural settings are entirely free from biases related to the studied system or limitations in sampling, these findings emphasize a common challenge that urgently needs addressing to ensure the reliability of hypothesis testing in ASNA. Several approaches have been proposed since the issues with rates of false positives and negatives were raised. These new methods can be categorized into two types based on whether they control for bias within the steps of the ASNA hypothesis testing protocol. In ASNA, there are typically two hypothesis testing protocol steps: 1) Estimating social interaction patterns among individuals, which are quantified within a social network. 2) Testing statistical hypotheses about these patterns.

To achieve the first step, researchers calculate a measure of the tendency for individuals to associate (in undirected behavior) or interact (in directed behavior). This measure is referred to as a social index and is computed for each pair of individuals (dyad). These values are used to create a social network, where each individual is a node, and the social index values represent the strength of the connection (edge weight) between dyad members. In addition, social indices have also the goal to control for sampling effort (i.e. heterogeneity in observations between individuals). Currently two main types of social index are used: association indices and interaction index. Association indices have been by behavioral ecologist. Although, many of the existing association indices estimate the proportion of time that a pair of individuals spends together. The higher the index value, the stronger the association within the dyad. The most used association index so far is the simple ratio index (SRI; Eq. 1), designed for data collected in discrete sampling periods (e.g. gambit of the group, scan sampling). The Interaction Index (Eq. 2) is primarily utilized by primatologists for data collected during continuous sampling periods, such as focal sampling. This index estimates the rate of social interactions per unit of time (e.g. the total time of focus), as opposed to association indices that are proportion-based. A higher index value indicates a stronger rate of interaction within the dyad. Currently, there is only one approach that has been suggested for addressing the social interaction patterns among individuals. XXX employs a Bayesian generative network approach to estimate the uncertainty of links related to observations. Also, there hasn't been any testing conducted to assess the reliability of results based on biased data. The lingering question is then whether Bayesian

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generative networks can outperform sociality indices or not.

$$SRI_{ij} = \frac{x_{ij}}{y_i + y_j + y_{ij} + x_{ij}} \quad (1)$$

Where  $x_{ij}$  is the number of sampling periods with  $i$  and  $j$  observed associated,  $y_i$  is the number of sampling periods with only  $i$  identified,  $y_j$  is the number of sampling periods with only  $j$  identified and  $y_{ij}$  is the number of sampling periods with  $i$  and  $j$  identified but not associated.

$$II_{ij} = \frac{x_{ij}}{y_i + y_j} \quad (2)$$

Where  $x_{ij}$  represents the overall frequencies or total interaction time,  $y_i$  and  $y_j$  denote the number of observations or the total observation time for individuals  $i$  and  $j$ , respectively.

To achieve the second step, which involves testing statistical hypotheses about sociality, researchers often use node-based measures computed on the network of association. These measures are derived from the network and help assess various aspects of an individual's position within the network. However, using node-based measures straightforwardly to test hypotheses about individual associations isn't ideal because each association/interaction is counted twice, once for each individual in the dyad, which violates the assumptions of parametric tests. Therefore, much of the methodological work in ASNA has focused on developing techniques to enable valid hypothesis testing. Since 2000, in ASNA permutations have been the main standard coming in three forms: network permutations, pre-network permutations, and double permutations. For more detailed information on the principles of permutation approaches, readers can refer to XXXX. Issues related to false positive and negative rates were originally demonstrated in network permutations and pre-network permutations. To address these issues, double permutations (which combine both) have been developed. Permutations have recently faced criticism for producing permutations that are essentially similar. Moreover, studies that highlighted problems with permutation approaches or propose new methods have been employing the same simulation protocol. As demonstrated in Appendix 1, this simulation has some issues. Firstly, these simulations were designed to generate a specific bias known as the "bias of interaction". This bias pertains to missing associations or interactions while observing individuals. It differs from observation bias, as the heterogeneity of observation among individuals is known by the observer(s) and is used by indices of sociality to control for it. In contrast, bias of interaction is unknown to the observer. However, during simulation, generating bias of interaction inadvertently leads to observation bias. This complicates the separation of the effects of both biases and the estimation of which aspects are controlled by indices and/or permutation approaches.

To tackle these concerns, we developed a new simulation that allows to independently specify sampling bias and interaction bias. Using this simulation, we created various scenarios to assess the reliability of results obtained through different methods: association index, interaction index, Bayesian generative network, pre-network permutation,

network permutation, and double permutation. Through this analytical approach, we have multiple goals. Firstly, we aim to assess whether issues related to false positives and false negatives in ASNA methods are associated with observation or interaction biases. Secondly, we want to determine if Bayesian generative networks outperform traditional ASNA methods in terms of providing accurate estimates and/or differences in hypothesis testing. Lastly, this will help us identify analytical protocols that can produce more reliable results for hypothesis testing in ASNA.

## Methods

### Modeling animal networks

In the vast majority of cases, researchers in animal behavior collect network data in the form of numerical outcomes—i.e., the number of times that ties *were observed*, conditional on the number of times that ties *could have been observed*. For example, researchers may conduct a specific number of observations (scans or focals), and the outcome data  $Y_{[i,j]}$  might reflect the number of observations in which directed (e.g., grooming or aggression events) or undirected (e.g., spatial associations) ties from individual  $i$  to individual  $j$  were observed. In this case, the number of observations is the sampling effort, an *exposure* variable which strongly—indeed, *proportionally*—influences the outcome variable. Thus, we let the variable  $E_{[i,j]}$  be the number of observations in which individuals  $i$  and  $j$  could have observed engaging in the dyadic behavior of interest. As such, a Bayesian model of the network data will generally take the form:

$$Y_{[i,j]} \sim \text{Binomial}(E_{[i,j]}, \phi_{[i,j]}) \quad (3)$$

where  $\phi_{[i,j]}$  is the *true* latent directed connection strength between  $i$  and  $j$ , represented as the probability that a directed tie from  $i$  to  $j$  occurs in a given observation.  $Y_{[i,j]}$  is typically a count of events or duration summed over all scans in the study.  $E_{[i,j]}$  is the number of observations in which ties between  $i$  and  $j$  could have been detected (e.g., the total number of scans or the sum of focals for individuals  $i$  and  $j$ . Farine and Whitehead 2015). Note that in the generative context,  $\phi$  represents a true *biological* phenomenon, whereas the outcome variable,  $Y$ , and the exposure variable,  $E$ , may be strongly affected by the sampling protocol, researcher behavior, and features of animals  $i$  and  $j$  other than sociality (e.g., cryptic coloration might cause the researcher to fail to observe true ties).

The goal of modeling, is to measure  $Y$  and  $E$ , and then recover  $\phi$ . This can be complicated, however, if there are structural biases in  $Y$  and/or  $E$ . Here, we will consider two potential causes of bias: (1) sampling bias, where features of  $i$  and  $j$  influence  $E_{[i,j]}$ , and (2) detection bias, where features of  $i$  and  $j$  influence measurement of  $Y_{[i,j]}$  given  $E_{[i,j]}$  independent of  $\phi_{[i,j]}$ .

We will now build up a Bayesian model of the data generating process. We will start by describing the sub-model underlying the true weighted network of ties, and then integrate the sub-models underlying the measurement process.

## Social relations

**Model definition** We begin the process of building up the model described in Eq. 3 by providing a generative model for the *true* latent directed connection strength between individuals  $i$  and  $j$ ,  $\phi_{[i,j]}$ . In order to generate networks with empirically plausible typologies, it is generally necessary to define a model for  $\phi_{[i,j]}$  that includes correlated random effects for the propensity to send and receive ties (nodal random effects), and correlated dyad-level random effects for the propensity of  $i$  to send to  $j$  and  $j$  to send to  $i$ . Additionally, such models should permit inclusion of covariate effects that influence block/group structure, node-level tie propensity, and dyad-level tie propensity. See Fig. 1 for an example network generated under such a model.

Following our prior work (Redhead et al. 2023; Ross et al. 2023), we recommend the use of the social relations model (Kenny and La Voie 1984; Snijders and Kenny 1999; Back and Kenny 2010) with an additional set of stochastic block-model parameters (Holland et al. 1983; Karrer and Newman 2011; Peixoto 2019) to account for group structure when necessary. As such,  $\phi_{[i,j]}$  can be modeled as:

$$\text{logit}(\phi_{[i,j]}) = \alpha + \lambda_{[i]} + \pi_{[j]} + \delta_{[i,j]} + \Gamma(i, j, V) + \dots \quad (4)$$

where  $\alpha$  is an intercept term,  $\lambda$  is a vector of individual-specific focal/sender/nominator effects,  $\pi$  is a vector of individual-specific target/receiver/nominee effects,  $\delta$  is a matrix of dyadic effects,  $\Gamma(i, j, V)$  is a function giving an intercept offset as a function of group/block structuring variables, and the ellipsis signifies any linear model of coefficients and focal, recipient, or dyadic covariates.

For example, if  $S$  is an animal-specific measure, like body size, and  $Q$  is a dyad-specific measure, like a matrix of relatedness ties, then the ellipsis may be replaced with:  $\kappa_{[1]}S_{[i]} + \kappa_{[2]}S_{[j]} + \kappa_{[3]}Q_{[i,j]}$ , to give the effects of body size on the probability of sending ties to any target and receiving ties from any target, and the effects of kinship on the probability of dyadic ties.

To model block structure, we can consider a list of  $V$  categorical variables describing individuals  $i$  and  $j$ . Let  $B_{[v,b_1,b_2]}$  be a three-dimensional parameter array, where  $v$  run over variables, and  $b_1$  and  $b_2$  run over the category levels within variables. Finally, let the function  $b(i, v)$  return the block of individual  $i$  for variable  $v$ . Then, we can then define  $\Gamma(i, j, V)$ , such that:

$$\Gamma(i, j, V) = \left( \sum_{v=1}^V B_{[v,b(i,v),b(j,v)]} \right) \quad (5)$$

where the probability of a tie from individual  $i$  in block  $b(i, v)$  to individual  $j$  in block  $b(j, v)$  for variable  $v$  is controlled by the corresponding entry in the array of block parameters,  $B_{[v,b(i,v),b(j,v)]}$ .

**Priors** To complete the model definition, we define vague priors. We model the sender and receiver effects jointly using a multivariate normal distribution. This allows for generalized correlations at the individual level to be detected—i.e., we can detect if individuals who groom others are also more likely to be groomed by others. For computational efficiency (Stan Development Team 2021; Lewandowski

et al. 2009), it is best to write the multivariate normal as:

$$\begin{pmatrix} \lambda_{[i]} \\ \pi_{[i]} \end{pmatrix} = \begin{pmatrix} \sigma_\lambda \\ \sigma_\pi \end{pmatrix} \circ \left( L * \begin{pmatrix} \hat{\lambda}_{[i,j]} \\ \hat{\pi}_{[i,j]} \end{pmatrix} \right) \quad (6)$$

where  $L$  is a Cholesky factor from the decomposition of the  $2 \times 2$  correlation matrix with  $\rho$  on the off-diagonal, and  $\hat{\lambda}_{[i,j]} \sim \text{Normal}(0, 1)$  and  $\hat{\pi}_{[i,j]} \sim \text{Normal}(0, 1)$  are unit-normal random effects. Weakly informative priors may then be independently specified on the variance and correlation terms (Lewandowski et al. 2009):

$$\sigma_\lambda \sim \text{Exponential}(1.0) \quad (7)$$

$$\sigma_\pi \sim \text{Exponential}(1.0) \quad (8)$$

$$L \sim \text{LKJ Cholesky}(2.5) \quad (9)$$

We use the above approach to define the dyad-level random effects as well:

$$\begin{pmatrix} \delta_{[i,j]} \\ \hat{\delta}_{[i,j]} \end{pmatrix} = \begin{pmatrix} \sigma_\delta \\ \sigma_\delta \end{pmatrix} \circ \left( L_\delta * \begin{pmatrix} \hat{\delta}_{[i,j]} \\ \hat{\delta}_{[i,j]} \end{pmatrix} \right) \quad (10)$$

where  $\hat{\delta}_{[i,j]} \sim \text{Normal}(0, 1)$  have unit-normal priors, and the variance and correlation terms have weakly informative priors:

$$\sigma_\delta \sim \text{Exponential}(1.0) \quad (11)$$

$$L_\delta \sim \text{LKJ Cholesky}(2.5) \quad (12)$$

Under this model,  $\rho_\delta$  provides a measure of dyadic reciprocity—i.e., whether the probability of focal  $i$  giving to alter  $j$ , increases with the probability that focal  $j$  gives to alter  $i$ .

We recommend standardizing predictor variables. We can then use weakly regularizing priors on the  $\kappa$  terms:

$$\kappa_{[p]} \sim \text{Normal}(0, 1) \quad (13)$$

Lastly, the diagonal elements of  $B_{[v]}$ , which control the frequency of ties within blocks, will generally have slightly higher prior weight than the off-diagonal elements, though other topologies are possible (see Batagelj 1997). For example, we might write:

$$\beta_{k \rightarrow k} \sim \text{Normal}\left(\text{Logit}\left(\frac{0.1}{\sqrt{N_{[k,v]}}}\right), 2.5\right) \quad (14)$$

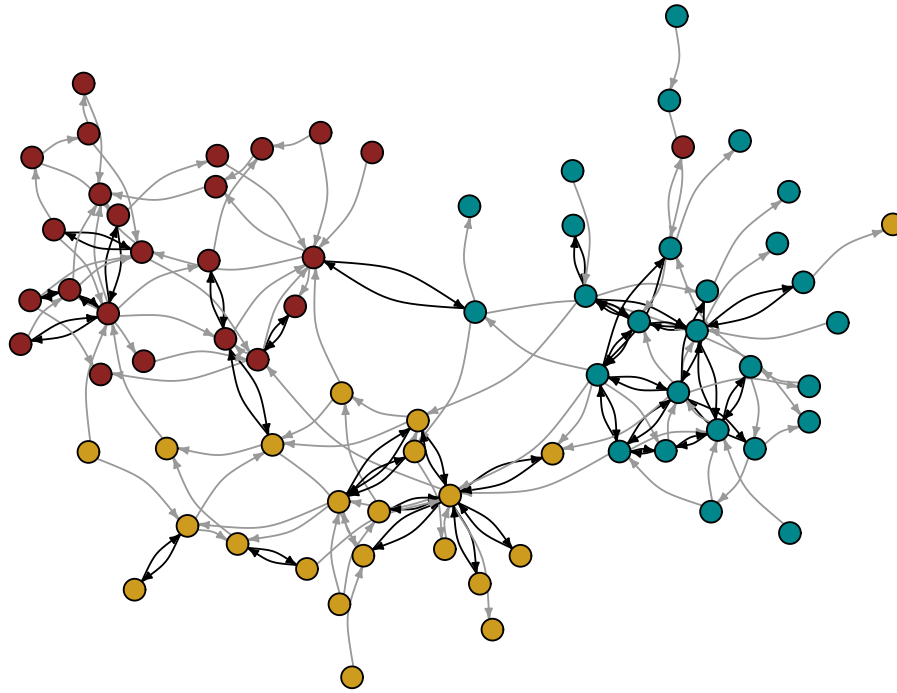
$$\beta_{k \rightarrow \tilde{k}} \sim \text{Normal}\left(\text{Logit}\left(\frac{0.01}{0.5\sqrt{N_{[k,v]}} + 0.5\sqrt{N_{[\tilde{k},v]}}}\right), 2.5\right) \quad (15)$$

Here,  $k \rightarrow k$  indicates a diagonal element and  $k \rightarrow \tilde{k}$  indicates an off-diagonal element. The scalar of 0.1 in Eq. 14 places higher prior density on the diagonal of  $B$  (which controls the probability of within-block ties), than the off-diagonal of  $B$  (where the scalar of 0.01 from Eq. 15 generates reduced prior between-block tie probability). The scalars of  $\sqrt{N_k}$  ensure that prior tie probability scales with sample size at roughly the same rate that we see in empirical data sets (Ready and Power 2021). The standard deviation of 2.5 in both equations causes the overall prior to be quite weak, and thus allows the data to dominate the posterior.

## Sampling bias

The next step in building the model described in Eq. 3, is to provide a generative model for the sampling effort between

**Figure 1.** Simulated animal network data under the generative model described in [Ross et al. \(2023\)](#). Nodes are colored by group. The stochastic block model introduces gross substructure, where ties within-groups are more likely than ties between groups. These rates can be varied continuously, producing networks with no group structure on one extreme, to networks fully segmented by group identity on the other. Random effects for sending and receiving ties lead to variable degree. Here, some individuals have small degree and are connected to the network by only a single tie, and others have a high degree and are connected to many other individuals. As with the parameters controlling group structure, the parameters controlling variance (and covariance) in individual-level propensity to send and receive ties can be varied continuously, producing networks with approximately uniform degree on one extreme, to networks with highly unequal degree distributions on the other extreme. Finally, we note that some dyads form reciprocal ties (note the black, bidirectional arrows), while other dyads are linked only by unidirectional ties (note the grey, unidirectional arrows). The parameters controlling variance (and covariance) in dyadic random effects, are continuously variable, and can produce networks with close to no dyadic tie reciprocation on one extreme, and networks with high rates of tie reciprocation on the other.



individuals  $i$  and  $j$ ,  $E_{[i,j]}$ . In most designs, researchers will aim to uniformly sample all dyads, to minimize the potential for bias or censoring issue to confound inferences. That is, there will be some target number of scans,  $\bar{E}$ , per focal individual, and all individuals in the study population will be focal-followed the same number of times, and for the same duration (i.e., number of scans). As such, a simple model of sampling effort can be written as:

$$\hat{E}_{[i]} \sim \text{Binomial}(\bar{E}, \epsilon_{[i]}) \quad (16)$$

where  $\bar{E}$  is maximum number of scans (i.e., the design target),  $\hat{E}_{[i]}$  is the realized number of scans of individual  $i$ , and  $\epsilon_{[i]}$  is the probability that individual  $i$  is observed when the researcher intended to observe individual  $i$ . The parameter  $\epsilon_{[i]}$  might vary as a function of individual-level characteristics, that also influence network structure. For example, an animal with a cryptic phenotype may be more likely to be unobserved—even as the focal in a focal-follow—if their coloration allows them to escape the attention of the researcher performing the behavioral observation. Similarly, individuals with a cryptic phenotype may be under-sampled, because they are less likely to be found on a given day, and

are thus subject to fewer focal follows than desired overall.

$$\text{logit}(\epsilon_{[i]}) = \nu_{[0]} + \dots \quad (17)$$

where  $\nu_{[0]}$  is an intercept, and the ellipsis signifies any linear model of coefficients and individual-level covariates. For example, if  $S$  is an animal-specific measure, like a binary variable for cryptic coloration, then the ellipsis may be replaced with:  $\nu_{[1]}S_{[i]}$ , to give the effects of coloration on number of scans.

Then, following standard approaches (e.g., [Farine and Whitehead 2015](#)), the dyad-level count of scans is given by the formula:

$$E_{[i,j]} = \hat{E}_{[i]} + \hat{E}_{[j]} \quad (18)$$

as ties between  $i$  and  $j$  can be detected either when  $i$  is subject to observation or when  $j$  is subject to observation.

From our formalization, it is obvious that variation in sampling effort should have little to no effect on our ability to identify accurate estimates of  $\phi_{[i,j]}$  from Eq. 3, as long as we apply statistical methods that propagate uncertainty according to the rules of probability theory. A binomial model of  $Y_{[i,j]}$  given  $E_{[i,j]}$  provides information about expected value of  $\phi_{[i,j]}$  that does not depend on  $E_{[i,j]}$ ; however, the narrowness of the posterior distribution of



$\phi_{[i,j]}$  does depend on  $E_{[i,j]}$ , as we can be more confident in estimates of  $\phi_{[i,j]}$  that are based on more observations.

The standard approach in animal behavior of calculating a simple ratio index—e.g., by writing:

$$\hat{\phi}_{[i,j]} = \frac{Y_{[i,j]}}{E_{[i,j]}} \quad (19)$$

and then applying models to the point-estimates  $\hat{\phi}_{[i,j]}$ , does lead to bias, however, especially in small samples. This occurs because Eq. 19 divides out sample size, and gives samples based on sparse evidence disproportionate weight in downstream analysis. These samples based on sparse data typically have values at specific fractions with small denominator—like 0, 1,  $\frac{1}{2}$ ,  $\frac{1}{3}$ ,  $\frac{2}{3}$ ,  $\frac{1}{4}$ , etc—leading to scatter plots like Fig. 2.

### Interaction bias, or censoring

Although we showed that sampling bias does not pose much of a threat to inference, censoring, or “interaction bias” is a more severe problem. In this case, a researcher performed  $E_{[i,j]}$  scans and detected  $\hat{Y}_{[i,j]}$  ties. However, if he or she is following animal  $i$ , and animal  $j$  has a cryptic phenotype, then it is possible that ties from  $i$  to  $j$ , or  $j$  to  $i$ , did occur, but the researcher did not detect them. For a single scan, the indicator of a true tie be  $Q_{[i,j]} \in \{0, 1\}$ , the indicator of a detected tie be  $\hat{Q}_{[i,j]} \in \{0, 1\}$ , and the indicator for individual  $i$  being detectable be  $D_{[i]} \in \{0, 1\}$ . Then, we find that:

$$Pr[\hat{Q}_{[i,j]} = 0] = Pr[(1 - Q_{[i,j]})D_{[i]}D_{[j]}] + Pr[1 - D_{[i]}D_{[j]}] \quad (20)$$

$$Pr[\hat{Q}_{[i,j]} = 1] = Pr[Q_{[i,j]}D_{[i]}D_{[j]}] \quad (21)$$

where zeros arise as a mixture of two process: (1) a process where both  $i$  and  $j$  were detectable, but no tie occurred, and (2) a process where either  $i$  or  $j$  was censored; ones, however, can only occur when both  $i$  and  $j$  were detectable and a true tie occurred.

Let  $\eta_{[i]} = Pr[D_{[i]} = 1]$  describe the detectability of individual  $i$  and  $\phi_{[i,j]} = Pr[(1 - Q_{[i,j]})]$ . We note that Eqs. 20 and 23 define the probability mass function of a Bernoulli random variable, and so we can aggregate over scans,  $E_{[i,j]}$ , to yield a Binomial model. Thus, we can rewrite Eq. 3 as:

$$\hat{Y}_{[i,j]} \sim \text{Binomial}(E_{[i,j]}, \phi_{[i,j]}\eta_{[i]}\eta_{[j]}) \quad (22)$$

We can let  $\eta_{[i]}$  depend on individual-specific covariates:

$$\text{logit}(\eta_{[i]}) = \psi_{[0]} + \dots \quad (23)$$

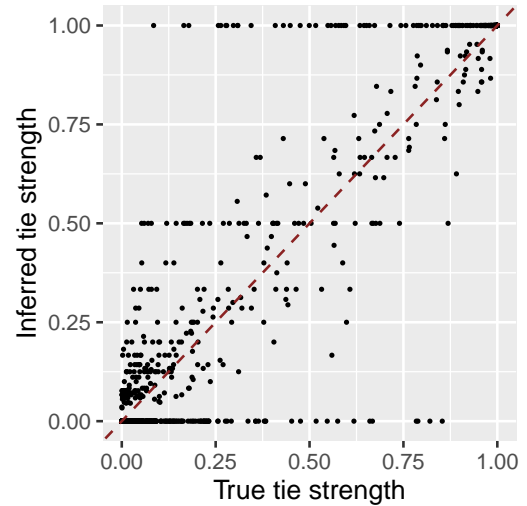
where  $\psi_{[0]}$  is an intercept, and the ellipsis signifies any linear model of coefficients and individual-level covariates. For example, if  $S$  is an animal-specific measure, like a binary variable for cryptic coloration, then the ellipsis may be replaced with:  $\psi_{[1]}S_{[i]}$ , to give the effects of coloration on detectability.

Here, however, we run up against the limits of inference. Since  $\phi_{[i,j]}$  and  $\eta_{[i]}$  multiply, the likelihood cannot distinguish between effects, of  $S_{[i]}$  for example, that increase the odds of a tie and effects that increase the odds of detectability.

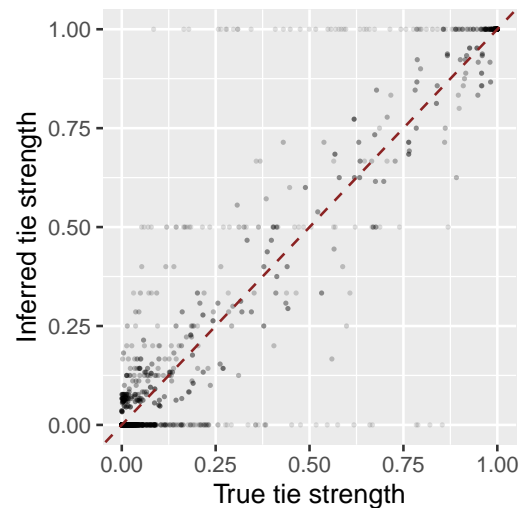
The only way to permit accurate inference, is to use an independent source of data to anchor estimation of  $\eta_{[i]}$ . If,

**Figure 2.** Example data on tie strength generated under a model where a covariate  $Z$  has a strong positive effect on tie probability,  $\phi_{[i,j]}$ , but a negative effect on sampling effort,  $E_{[i,j]}$ . We plot the true dyadic tie strength on the x axis, and the simple ratio index on the y axis. In frame (a), we see that many points lie along the diagonal (as expected), but there are also strips of points along the horizontal lines at  $y = 0.0$ ,  $y = 0.5$ , and  $y = 1.0$ , where the inferred tie strength is not all that reflective of true tie strength. These points correspond to estimates from small samples. Simply plugging in SRI estimates into a downstream regression leads to poor inference, because samples based on few data-points obscure the underlying predictors of tie strength.

(a) Simple ratio index



(b) A Bayesian model would scale the influence of each point in proportion to the sample size of observations, as we show here by scaling the alpha values of each point by  $E_{[i,j]}$ . The fact that most of the weight of evidence lies along the diagonal is now much more apparent.



for example, a researcher conducts  $\bar{Z}_{[i]}$  trials to encounter individual  $i$  in a setting where individual  $i$  is known to be present, and observes individual  $i$  in  $Z_{[i]}$  of those trials, this permits inclusion of a model like:

$$Z_{[i]} \sim \text{Binomial}(\bar{Z}_{[i]}, \eta_{[i]}) \quad (24)$$

allowing estimation of social-network parameters that are robust to censoring, or 'interaction bias'.

### Testing the models using simulations

Describe generative modeling setup and etc.

## Results

Compare STRAND to other methods on Binomial data, no bias

Compare STRAND to other methods on Binomial data, sampling bias

Compare STRAND to other methods on Binomial data, interaction bias

An empirical test case?

## Discussion

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