# An introduction to generative network models and their use in animal sociality research

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## Abstract

Social networks constitute an important approach in the study of animal social behaviour. So far, the main focus has been on statistical analysis of animal social network structures. However, social networks can also be studied by generative network models - procedures that create simulated network structures. These models play a key role in wider network science, but while they have been used in the animal behaviour field, they have not yet been as well integrated as other approaches. We believe that generative network models have considerable unexploited potential as a tool for understanding animal social systems. Here: 1) we provide a general introduction to generative network models, including a description of questions they are used for investigating in wider network science, explanation of key model features, and an overview of common models; 2) we consider generative network models in relation to the study of animal social behaviour, including description of questions about animal systems they can be used to investigate (demonstrated by case studies), an overview of animal behaviour studies that have used generative network modelling, the relevance of the key model features for animal behaviour studies, and consideration of how to choose a suitable generative network model for studies of animal social systems. We hope that this can help to further integrate generative network models into the study of animal sociality.

## Keywords

Generative network models, social networks, social structure, social behaviour, animal sociality, network methods, network modelling

**INTRODUCTION**

Social systems, be they human or non-human, emerge from the pattern of relationships between individuals within populations (Hinde 1976). Social network methodologies, which inherently model individuals and their social connections, are therefore an attractive framework from which to approach studying these systems. Quantitative network analysis has been adopted from the interdisciplinary field of network science (Brask et al. 2021) and is now a central part of the scientific investigation of animal sociality, where it has been used to study in detail the structures of animal social systems, and the wide-ranging ecological and evolutionary consequences that these structures have (Kurvers et al. 2014, Snyder-Mackler et al. 2020, Cantor et al. 2021).

The study of animal social network structures has, up to this point, mainly been based on descriptions and statistical analysis of empirically observed network structures (Webber & Vander Wal, 2019). While data-based studies also play a large part in wider network science, another central vein in this field is the development, study and use of models that can create simulated (artificial) networks – often without any data input. We refer to these models as "generative network models". These models are used in diverse settings, ranging from mathematical studies of networks to studies of specific real-world systems (Newman 2018). They constitute a fundamental theoretical framework with which to approach network structures, including those observed in nature. By providing a concrete approach to investigate networks theoretically, generative network models are highly useful both for gaining fundamental insights into the emergence and consequences of animal social networks, and for making predictions that can be tested with empirical studies (e.g. Franks et al. 2010, Puga-Gonzalez et al. 2015, Silk et al. 2015, Ilany & Akçay 2016a, Firth et al. 2017, Siracusa et al. 2023, Brask et al. 2026). While a theoretical framework can be useful in any research area, the usefulness for animal social systems is emphasized by the fact that data collection for these networks often requires considerable time and resources.

Generative network modelling has been used by researchers working on animal social systems, but has not played as central a role in this research area compared to their importance in network science more generally. This is likely in part because tools for easy use of generative network modelling directed towards the animal behaviour field have not been readily available. This is, however, beginning to change (Ross et al. 2024, Silk & Gimenez 2023, Brask et al. 2026).

We believe that generative network models hold unexploited potential as a means to gain insights into animal social systems. First, they provide a flexible approach to investigate the connection between individual behaviour and network structure in detail - a topic of which we currently lack a good understanding despite its importance. And second, by combining them with transmission simulations, they can be used to study how processes such as cultural and pathogen transmission are linked to social structure. Furthermore, fitting the parameters of generative network models to data can give insight into the processes underlying observed social networks beyond those possible with standard regression-based analyses. Generative network models are thus a highly useful tool for the study of both the emergence and the consequences of animal social structures. Therefore, to facilitate further integration and use of this approach in the animal behaviour field, we here provide an introduction to generative network models and consider how they have been used in the animal behaviour field so far, and how they can be used to increase our understanding of animal sociality.

The paper is structured as follows. In the first half, we provide a general introduction to generative network models, and in the second half, we consider them in relation to animal behaviour research. While the two parts can be read separately, the first part provides information that may be useful for following the second part. In the first half, we consider what generative network models are and what they are typically used for in wider network science,

and we describe general features of the models. In the second half, we consider how generative network models have been used in animal behaviour studies and may be used in this field in the future, we consider the relevance of each of the above-mentioned model features for animal behaviour studies, and we discuss how to choose generative network models for animal behaviour studies. We end with a brief conclusion.


## WHAT ARE GENERATIVE NETWORK MODELS?

Generative network models are algorithms that construct networks according to specific rules. Concretely, a generative network model may be thought of as a recipe that describes how to build a network. This recipe can then be implemented as a piece of computer code to generate a network. The generated network simply consists of numbers indicating the positions and strengths of network links (edges), usually stored in the format of an adjacency matrix or edge list (as with empirical network data). The models contain model parameters set by the user. These vary between models but typically include the number of nodes, some way to tune the density of edges, and parameters concerning how nodes connect to each other. The structure of the generated network depends on the model (i.e. the network construction rules) and the parameter values set. This enables users to create different network structures, by selecting models with different linking rules and using different parameter settings.

The term 'generative network model' is used in various ways. For the purpose of this paper, we here define generative network models as procedures that generate an adjacency matrix (or other network data format), and which do *not* do this by randomising an observed network dataset. This definition includes models that are usually considered generative network models in wider network science, and it excludes permutation procedures, which have been extensively used in the animal behaviour field for statistical inference of observed networks and are not our focus here (these have been treated in depth elsewhere, e.g. Bejder et al. 1998; Croft et al. 2011, Farine 2017, Hobson et al. 2021). A way to distinguish permutation models and generative network models (as defined here) is that the former uses a top-down approach (removing structure from observed network data), whereas the latter uses a bottom-up approach (building simulated networks based on linking rules and algorithmic procedures). These two approaches are therefore useful for different purposes, and permutation models have mainly been used for statistical inference whereas generative network models are widely used for theoretical simulation studies (although, as we will consider later, they can actually additionally be used for statistical inference). Existing generative network models that fall under the definition above mostly do not require any data input, although some of them do take some feature from an existing network as input – such as a degree distribution.

While new generative network models are sometimes developed for the purpose of a specific study, many studies across research fields use generative network models that are already available, and some models have been very extensively used. In Table 1 we provide an overview of some generative network models that are widely used (across different disciplines) and/or are particularly theoretically important, and describe them by means of model features that we consider in later sections.

The procedures (algorithms) that generative network models use for constructing networks can take many forms. Many generative network models used widely in network science are quite simple in terms of their procedures (including most of the models given in Table 1), but they can also be more complex (such as some types of exponential random graph models; Table 1). Many models follow one of the three following procedures. First, some models include two steps, where they first calculate linking probabilities for all pairs of nodes based on specified linking rules, and then draw all the links based on these probabilities. A simple example of this is the Poisson model, where the probability of linking is the same for all pairs

**Table 1. An overview of common generative network models.** For each model, information is given concerning its name(s), the type of network it generates, five model features (which are further considered in later sections), and a main reference. Many other generative network models have been developed - we have selected models that are particularly well-known and have been widely used (or very influential) in network science. These models have each been used for many different purposes. Note that the information given here is for the models in what may be considered their most essential or common form. The models may also be used in other versions (for example with network growth, link weights, or extra parameters added).

| Name(s) of model | Type of network generated | Linking rules | Model parameters | Uses node attributes* | Involves network growth | Produces link weights** | Reference |
|---|---|---|---|---|---|---|---|
| **Poisson model** <br> **Random graph model** <br> **Erdős-Rényi model** <br> **G(n,p) model** <br> **G(n,L) model** | Random network / Poisson network | Random linking | n (number of nodes) <br> p (linking probability) <br> *or:* <br> n (number of nodes) <br> L (number of links) | No | No | No | Erdős & Rényi 1959 |
| **Small-world model** <br> **Watts-Strogatz model** | Small-world network (for some parameter settings) | Random rewiring (of a clustered initial network) | n (number of nodes) <br> k (average degree) <br> β (rewiring probability) | No | No | No | Watts & Strogatz 1998 |
| **Preferential attachment model** <br> **Price model** | Directed scale-free / power law network | Preferential attachment (i.e. linking based on node degree) | t (number of timesteps) | Yes (intrinsic) | Yes | No | Price 1976 |
| **Preferential attachment model** <br> **Barabási-Albert model** | Scale-free / power law network | Preferential attachment (i.e. linking based on node degree) | m0 (initial number of nodes) <br> m (number of edges for each added node) <br> t (number of timesteps) | Yes (intrinsic) | Yes | No | Barabási & Albert 1999 |

| Model | | | | | | | Reference |
|---|---|---|---|---|---|---|---|
| **Configuration model** | Random network with a specified degree sequence | Random linking (with a given degree sequence) | None, but a degree sequence is given as input | No | No | No | Newman et al. 2003 |
| **Hidden variable model Hidden parameter model Fitness model** | Depends on the hidden variable distribution | Linking based on node attributes ('hidden variables') | n (number of nodes) p(x) (hidden variable probability distribution) f (hidden variable function) | Yes (extrinsic) | No | No | Caldarelli et al. 2002 |
| **Stochastic block model** | Modular network with communities / network with assortative mixing | Linking based on node similarity (categories) | n (number of nodes) c (number of communities) P (linking probability matrix) | No / Yes (extrinsic)*** | No | No | Holland et al. 1983 |
| **Exponential random graph model ERGM** | Depends on specifications | Depends on specifications | Depends on specifications | Depends on specifications | No | No/yes | Robins et al. 2007 |

\* For explanation of intrinsic and extrinsic node attributes, see the section 'Features of generative network models'.

\*\*This concerns whether the original model produces link weights; link weights can always be added (see the section 'Features of generative network models').

\*\*\*Linking in this model may be interpreted as being based on community membership (i.e. the model does not use any node attributes as such), or being based on categorical node attributes (i.e. the model uses extrinsic node attributes).

of nodes (Box 1); in other cases, the linking probabilities may depend on aspects such as node attributes (details in the later sections about model features). Second, some models start with an initial standard network structure, which is then rewired according to certain rules and probabilities (for example the small-world model, Table 1). Third, some models add the nodes sequentially and thereby grow the network to the desired size, with the linking of the added node following specific rules and probabilities (for example preferential attachment models, Table 1; network growth is considered further in the later sections about model features). An alternative approach is to simulate the interactions between nodes directly (e.g. by repeated groupings of individuals, or by individuals moving in space; see references in the sections concerning animal behaviour).

Generative network models are usually stochastic, in the sense that networks made with the same model and parameter setting are unlikely to be identical to each other, although they will be similar. This is a useful feature, because it means that the models can be used to create large ensembles of networks with common structural properties and random structural variation among the networks. The networks in an ensemble (i.e. a set of networks generated from the same model and parameter setting) may be thought of as replicates in a simulated experiment, and ensembles based on different models - or on the same model with different parameter settings – may be thought of as different treatment groups. Using large network ensembles instead of single networks allows researchers to study networks with specific structural properties while minimising bias from random structural variation, and studies involving generative network modelling usually use network ensembles.

## WHAT ARE GENERATIVE NETWORK MODELS USED FOR IN WIDER NETWORK SCIENCE?

To provide insights into what generative network models can be used to investigate, we here describe some research themes where these models are utilised in wider network science (we consider their use in animal behaviour research in a later section).

Generative network models have been used very widely in network science and across scientific disciplines, with diverse applications. They are used both for studying networks from a general perspective, and for investigating aspects of specific real-world systems. The former is often done with studies largely based on computer simulation, potentially incorporating some empirical network data as examples. The latter is done both by studying ensembles of artificial networks that resemble the structure (or an aspect of interest) of the system in question, or by using generative models as a tool for statistical inference. Diverse types of networks have been studied with generative network modelling, including various human social networks from policy networks (e.g. Metz & Brandenberger 2023), through environmental collective action (e.g. Nohrstedt & Bodin 2020) to school friendships (e.g. Mamas et al. 2020), and non-social networks such as transportation networks (e.g. Natera Orozco 2020), and species interaction networks (e.g. Zhang et al. 2011). The research themes below are relevant both for general and system-specific studies. In Figure 1, we provide an illustration of common procedures used in studies involving generative network modelling.

### Network emergence

Generative network models provide the primary tool to understand how network structure emerges or, more precisely, how rules determining how nodes connect to each other affect network structure (Newman 2018). A famous example is preferential attachment models (e.g. Price 1976, Barabási & Albert 1999, Table 1), which revealed that when nodes (for example individuals) joining a network tend to attach to the most connected nodes, this leads to a network with a scale-free degree distribution, a structural feature which has been of great interest in network science due its properties and impact on network function (Barabási &

**Box 1. Example of a simple generative network model: the Poisson model**

The most fundamental generative network model may be considered to be the Poisson model (also known as the Erdös-Rényi model or the random graph model, see also Table 1). In this model, all pairs of nodes have the same probability of linking. This gives rise to a network where the degrees (number of links for each node) are Poisson distributed. The model is useful for example when Poisson degree distribution is a desired property, or when the study requires purely random network structures (for example for comparison with other structures).

*Model algorithm*
*1.* Set the parameters $n$ (number of nodes) and $p$ (linking probability)
2.  For each pair of nodes $i$ and $j$, draw a random number $q$ between 0 and 1
3.  If $q < p$, place a link between $i$ and $j$
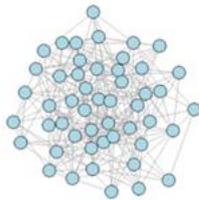
*Using the model*
We can generate networks based on the model by running a computer code that implements the above algorithm (either written by ourselves or from software such as R packages).
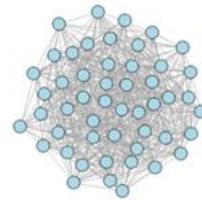
*Example networks generated with the model*
Three Poisson networks with 50 nodes and different linking probabilities:
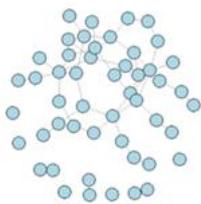


n = 50
p = 0.05

n = 50
p = 0.2

n = 50
p = 0.5

*Alternative form of the model*
An alternative form of the Poisson model is to set the number of links $L$ instead of the linking probability $p$, and then add a link to $L$ randomly drawn dyads. In both cases, the parameter ($p$ or $L$) acts as a density parameter, but in the case of $L$ the density is exactly specified, whereas with $p$ it is stochastic. This exemplifies how a generative network model may be implemented in different ways depending on what is most useful for a specific study. The two forms of the Poisson model are known as the *G(n,p)* and *G(n,L)* model, respectively.

Albert 1999, Broido & Clauset 2019, Holme 2019). Studies on network emergence may often be done by generating a large ensemble of networks based on the process of interest, and a control ensemble which does not include this process (e.g. based on random linking, and then comparing structural features of the ensembles (Fig. 1).

### *Dynamical processes on networks*

Another common use of generative network models in wider network science is for investigations of dynamical processes on networks. For example, they have been used extensively to investigate the spread and maintenance of cooperative strategies in structured populations (reviewed in Szabó & Fath 2007, Roca et al. 2009, Jusup et al. 2022), as well as infectious disease transmission (e.g. Moore & Newman 2000, Gross et al. 2006, Miller 2009, Salathé & Jones 2010). While simulations of such processes can also be done using networks quantified from real-world systems, generative network models can provide large sets of replicated networks with specific properties (as described in the section 'What are generative network models?'), which facilitates studies of how these properties affect the processes of interest (Fig. 1). A classic research theme in this area concerns how clustering (the tendency of your friends to also be friends with each other) and modular structure (social groupings within the network) influence contagions like infectious disease or behaviour spread.
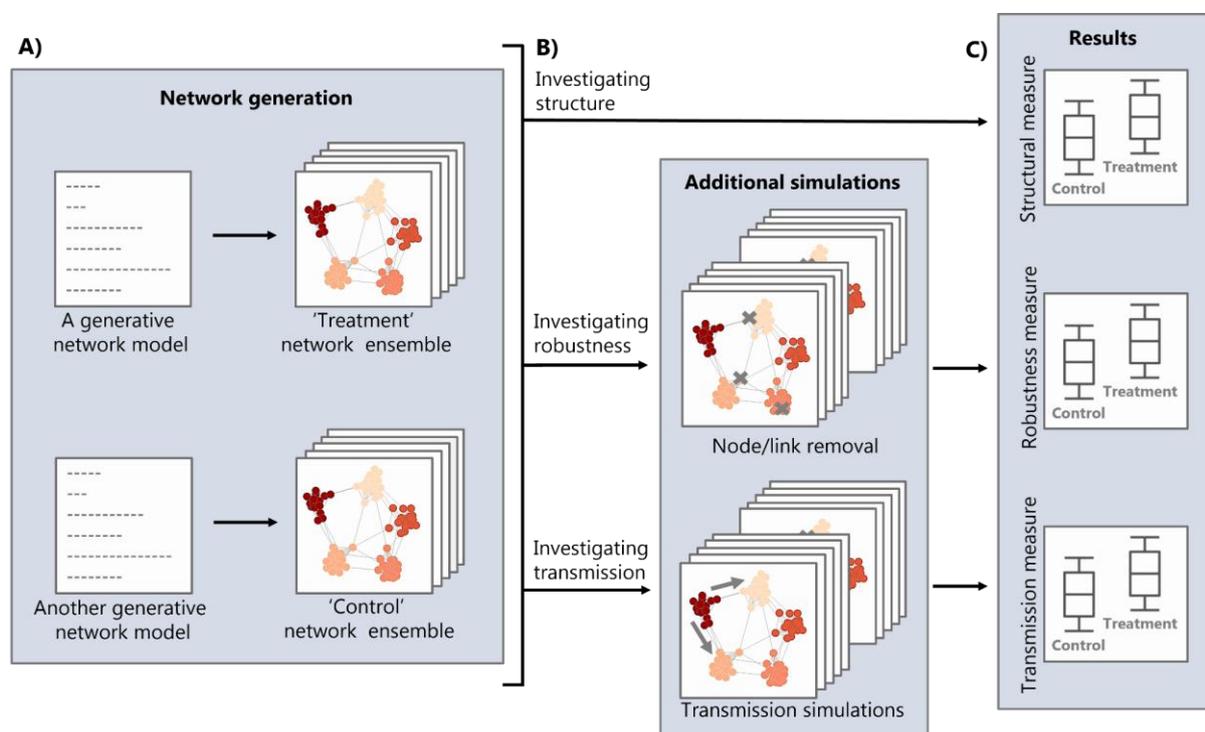


**Figure 1. Examples of common procedures for using generative network models.** Generative network models have been used extensively to study aspects of networks such as transmission properties and robustness, and the relationship between generative processes and structural features. **A)** Usually, two or more large sets (ensembles) of networks are generated; one (or more) treatment ensemble with networks that include a structural feature or generative process of interest, and one (or more) control ensemble to compare with, which does not include this feature or process. The control ensemble may be produced by another generative model than the treatment ensemble (as shown here) or by the same model with different parameter settings. **B)** The ensembles can then be used for investigating network properties of interest for the research question, such as structural features, robustness and transmission properties (the latter two requiring additional simulations). **C)** The results often consist (only) of graphs showing the measurements.

Approaches using generative network models have been central to showing that clustering typically makes it harder for infections to spread (e.g. Miller 2009), and that when networks are highly modular (i.e. contain clear communities that are weakly connected to each other), then infections take longer to spread, and control efforts like vaccination can be targeted at particular individuals (e.g. Salathé & Jones 2010). By studying different contagions across networks generated using the same generative models, we can also learn about how the effect of structural features may vary depending on the type of contagion. For example, informational cascades can be impacted in a different way by modular networks than infection spread if the model for transmission is different (e.g. Nematzadeh et al. 2014).

### Dynamics of networks

While generative network models are often used to produce static network structures, they can also be used for simulating temporal network dynamics, where links change over time. One common use of dynamic network models in wider network science is again to quantify how networks impact infectious disease spread. Moving from static to dynamic generative models for the underlying network structure has revealed that in many cases, the network dynamics can be as important as network structure for how easily infections can spread through a population (e.g. Volz & Meyers 2007). More complex generative models for network dynamics have then been used to develop theory for how the behavioural response of individuals to infection can alter population-level disease dynamics (e.g. Gross et al. 2006) and to look at how informational or behavioural contagions can mitigate the spread of disease (e.g. Silk et al. 2021). Similarly, dynamic generative network models have also been used to study how behavioural strategies such as cooperation spread when individuals can change their social links, for example by severing ties to uncooperative individuals (reviewed in Gross & Blasius 2008, Perc & Szolnoki 2010, Jusup et al. 2022, Berner et al. 2023). Network dynamics can be based on linking rules from models also used for static networks (such as those in Table 1), or can be modelled without an underlying static model. In the latter case, static networks can be extracted from the dynamics and these models are therefore also 'generative' (although this aspect may not always be relevant for a given study).

### Robustness of networks

Another common theme in network science where generative network models have been frequently used is the robustness of different network structures to perturbations or failures of nodes and links (reviewed in Artime et al. 2024, Schwarze et al. 2024). This is relevant in many different real-world circumstances, such as failures of components in physical communication networks (e.g. routers), vaccination schemes (where vaccinated individuals can correspond to removed nodes because disease transmission cannot pass through them), and disappearance of species in ecological networks. A common procedure for investigating network robustness is to sequentially remove nodes (or links) from networks and study the breakdown processes (often referred to as *percolation*; Artime et al. 2024). The focus is often on the connectedness of the remaining network during the removal process, and particularly the timing of the phase transition where the network goes from having a large main ('giant') component to breaking into multiple smaller components (network parts without connection to each other). Using such removal procedures on large ensembles of artificially generated networks (see Fig. 1 and the section 'What are generative network models?') allows for investigating the relationship between specific structural properties and network robustness.

### FEATURES OF GENERATIVE NETWORK MODELS

Below we describe a set of general features of generative network models that can be useful to be aware of and consider when working with these models. The presence and form of these

features in any given model have consequences for the resulting network structures, and for the usefulness of the model in different studies. We have used the features to describe the models in Table 1. We consider each feature in relation to animal behaviour research in a later section.

### Linking rules

All generative network models necessarily contain rules for how nodes link to each other, and these linking rules may be considered to be the essence of the models, as they play a key role for the structures produced. Linking rules can be very simple, such as in the Poisson model (Box 1, Table 1) where each pair of nodes connect to each other with the same probability (set by the user), or they can be complex, such as in exponential random graph models (Table 1) where multiple factors may influence the linking probability of each pair of nodes. Linking rules for a given model may have been constructed either with the purpose of reflecting a specific linking behaviour of real systems (for example a social strategy), or for the purpose of creating networks with specific structural properties, or both.

### Model parameters

Generative network models contain parameters that are set by the user and affect the structure of the outcome network. The number and types of parameters differ between models (see Table 1 for examples). In most cases, the structural metrics of the network (such as the level of clustering, the average path length, etc.) are not directly set by the parameters. Instead the parameters usually have to do with the nodes and their linking (likely because of the fact that the models work by modelling linking processes). However, the parameters often correlate with structural properties to some extent. The parameters may also affect a range of interlinked structural properties, and this means that when a model is used to produce networks with a given structural feature (e.g. high modularity), this can induce constraints on other structural properties, which can be important to be aware of. In some cases, a structural feature is given directly as an input to the model and is thus fully specified by the user (for example degree distributions in the configuration model, Table 1).

### Node attributes and dyadic attributes

Some generative network models do not involve any node-related attributes – in other words, all nodes are considered identical, and the placing of links does not depend on any features of the nodes (see Table 1 for examples). However, in real-world systems the properties of nodes are often important for the network structure, and they can therefore be relevant to take into account in generative network models. This can be done by including node-related attributes in the models. We distinguish between *node attributes*, which concern each single node, and *dyadic attributes*, which concern each pair of nodes. We further divide node attributes into two categories: *extrinsic* and *intrinsic*. The latter are derived from the network, whereas the former are not.

***Extrinsic node attributes*** are any node characteristics that are not derived from the network. This could be, for example, the size of airports in an air transport network, the species in an ecological network, or traits and characteristics of individuals (such as their age and sex) in a social network. Such node attributes are known to affect the probability and weights of links in many real-world systems. For example, the size of airports is likely to correlate with the number of flights between them, and the age and sex of individuals are likely to affect how they interact socially. Generative network models may include one or more extrinsic node attributes (see Table 1 for examples), which may be simulated or derived from real-world data.

***Intrinsic node attributes*** describe the network positions of nodes, and typically take the form of standard node-based network metrics (e.g. degree, strength, betweenness, etc.). Intrinsic

node attributes can be used in growth models (where the network is constructed by adding nodes sequentially; see 'network growth' below), by letting the network metrics of current nodes affect the linking of the next added node. This introduces a temporal dependency in the network construction, where a nodes' probability of linking to others depends on the links that have already been placed. In a social setting this reflects the assumption that the building of social ties depends directly on the social positions of potential social partners. For example, in preferential attachment models (Table 1), each new node connects to existing nodes with a chance that is proportional to the existing nodes' current degree (i.e. individuals prefer to link to well-connected others). Intrinsic node attributes have also been used in models of temporal network dynamics (see for example Fefferman & Ng 2007a,b).

*Dyadic attributes* are attributes that concern each dyad (pair of nodes) rather than each single node. They typically consist of measures of distance (or closeness) between the two nodes (in terms of node attributes), such as their genetic relatedness or age difference. Given that they are derived from properties of the individual nodes, dyadic attributes may in some models be given to the model as node attributes, whereafter the model calculates the dyadic attributes (for example, the model may require ages as input even if it uses age differences for network construction). To know whether a model uses node or dyadic attributes, it is therefore not enough to know which are given as input.

### Network growth

The process that a generative network model uses to construct the network may or may not involve network growth, where the nodes are added to the network sequentially. Growing the network is often used in models that involve intrinsic node attributes (i.e. where nodes use the network position of others to determine who to connect to, see above), as is for example the case in preferential attachment models (Table 1). Models that calculate all linking probabilities first (see the section 'What are generative network models?') typically do not require growth procedures, but can be used with them. They are typically used without growth because it is faster and usually leads to the same network structures, but using them with growth can be relevant if the growth process itself (rather than the final network) is of interest.

### Edge weights

Edge weights are used to describe the strength, magnitude or load of network links (edges), such as the strength of social relationships. In wider network science, working with unweighted networks (where all present links are considered of equal strength) is common, for simplicity and mathematical tractability. Many common generative network models therefore do not in themselves contain a procedure for assigning weights to the links (Table 1). Weighted networks can, however, still be produced based on any of these models. This may for example be done by using dyadic linking probabilities from a given model as expected link weights and drawing link weights from distributions that have these probabilities as means (for example as in Brask et al. 2026). In terms of modelling procedures, there are at least three options for how link weights can be modelled: 1) the link weights are not dependent on the structure of the unweighted network (although they could depend on the same features, e.g. extrinsic node attributes); 2) the link weights depend intrinsically on features of the unweighted network (e.g., links in closed triads have higher weights); or 3) the generative model is inherently weighted (i.e. there is no step that generates an unweighted network). Which of these will be most relevant depends both on the research question and, in the case where a specific real-world system is being modelled, the extent to which they each fit with relevant properties of that system.

**USES OF GENERATIVE NETWORK MODELS IN ANIMAL SOCIALITY RESEARCH**

While generative network models have not played as central a role in animal behaviour research as in wider network science, they have already been used in diverse animal behaviour studies (see Table 2 for examples of such studies, and Table A1 in the Appendix for a more comprehensive list). Many of these studies use models developed specifically for that study, with some also (or only) using standard models from network science (or variations on them). Here we consider research themes that seem particularly relevant for the existing and future use of generative network models in animal social behaviour research. For each theme, we highlight relevant existing studies, and we provide an example case study that uses generative network modelling to investigate a research question within the theme, with accompanying R code (see Code availability statement).

### *Emergence of animal social network structures*

By providing formal descriptions of the connection between linking rules (individual behaviour) and network structure, generative network modelling constitutes a key methodology for investigating the processes underlying the structure of animal social systems. One approach for such studies is where a model based on a known or assumed key generative process of animal social structures is developed, and its network structures investigated. For example, Ilany & Akcay (2016a) suggested that simple rules around maternal inheritance of social connections can explain apparently complex social structures, and showed this by a generative network model based on such social inheritance. In a recent study, Brask et al. (2026) investigated how different preferences for traits (i.e. preferences for social partners with a certain sex, body size, relatedness etc.) affect social network structure and function, and found that the specific trait preferences used in a population can have effects on the populations' risk of epidemics and robustness against social breakdown when individuals disappear. Other studies have used generative network models in combination with analysis of empirical data to understand the role of different factors in social structuring (for example cooperativeness, Darden et al. 2020; social aging, Siracusa et al. 2023). In Figure 2, we describe a case study where generative network modelling is used to investigate how social preferences for one's own matriline affect network structure (the code is available, see Code availability statement).

### *Dynamical processes on animal social networks*

Generative network models have been used regularly to investigate dynamics happening on animal social networks, especially the spread of pathogens, information and behaviour. In this context, being able to generate ensembles of networks that either: a) share particular structural properties; or b) are similar to an empirically observed network but incorporate additional stochasticity is very valuable for investigating the link between social structure to epidemiological dynamics. For example, generative network models have been used to test how the modular structure of animal social networks influences the spread of pathogens and behaviours (Sah et al. 2017, Romano et al. 2018, Evans et al. 2021), with results suggesting that the modular structure and module size can mitigate the potential trade-off between behaviour spread and infection spread in groups (Evans et al. 2020). Generative models have also been fitted to empirical datasets and then used to simulate network ensembles resembling the empirical data, to study how social behaviour influences wildlife disease dynamics (e.g., Reynolds et al. 2015, Rozins et al. 2018), and this offers great potential as a tool to partially account for the observation process and ensure robustness of epidemiological dynamics to weak or chance interactions, especially as generative models for animal behaviour become more accessible. In our case study in Fig. 3 we provide some simple examples of generative network models being used as the basis for epidemiological modelling in this way (code available, see Code availability statement).

**Table 2. Examples of (non-human) animal behavioural ecology papers that deploy generative network models.** A more comprehensive list of studies is available in Table A1.

| Paper title | Main aim of paper | Model category | Study species | Citation |
|---|---|---|---|---|
| *Sampling animal association networks with the gambit of the group* | Methodological | Mixed (linking probability and group-based) | Theoretical | Franks et al. 2010 |
| *An Individual-Oriented Model on the Emergence of Support in Fights, Its Reciprocation and Exchange* | Dominance hierarchies | Spatial | Theoretical / macaques | Hemelrijk & Puga-Gonzalez 2012 |
| *Friendship, reciprocation, and interchange in an individual-based model* | Behavioural theory | Spatial | Theoretical | Puga-Gonzalez et al. 2015 |
| *The consequences of unidentifiable individuals for the analysis of an animal social network* | Methodological | Group-based | Brent geese | Silk et al. 2015 |
| *Social inheritance can explain the structure of animal social networks* | Social dynamics | Linking probability | Spotted hyena, rock hyrax, bottlenose dolphin, sleepy lizard | Ilany & Akçay 2016a |

| | | | | |
|---|---|---|---|---|
| *Indirectly connected: simple social differences can explain the causes and apparent consequences of complex social network positions* | Behavioural theory | Group-based | Theoretical | Firth et al. 2017 |
| *Social style and resilience of macaques' networks, a theoretical investigation* | Behavioural theory | Spatial | Theoretical / macaques | Puga-Gonzalez et al. 2019 |
| *Structural trade-offs can predict rewiring in shrinking social networks* | Behavioural theory | Linking probability | Theoretical | Farine 2021 |
| *Common datastream permutations of animal social network data are not appropriate for hypothesis testing using regression models* | Methodological | Mixed (linking probability and group-based) | Theoretical | Weiss et al. 2021a |
| *Generation and applications of simulated datasets to integrate social network and demographic analyses* | Methodological | Mixed (linking probability and group-based) | Theoretical | Silk and Gimenez 2023 |
| *Ageing in a collective: The impact of ageing individuals on social network structure* | Social ageing | Linking probability | Rhesus macaque | Siracusa et al. 2023 |
| *Far-reaching consequences of trait-based social preferences for the structure and function of animal social networks.* | Behavioural theory and methodological | Linking probability | Theoretical | Brask et al. 2026 |
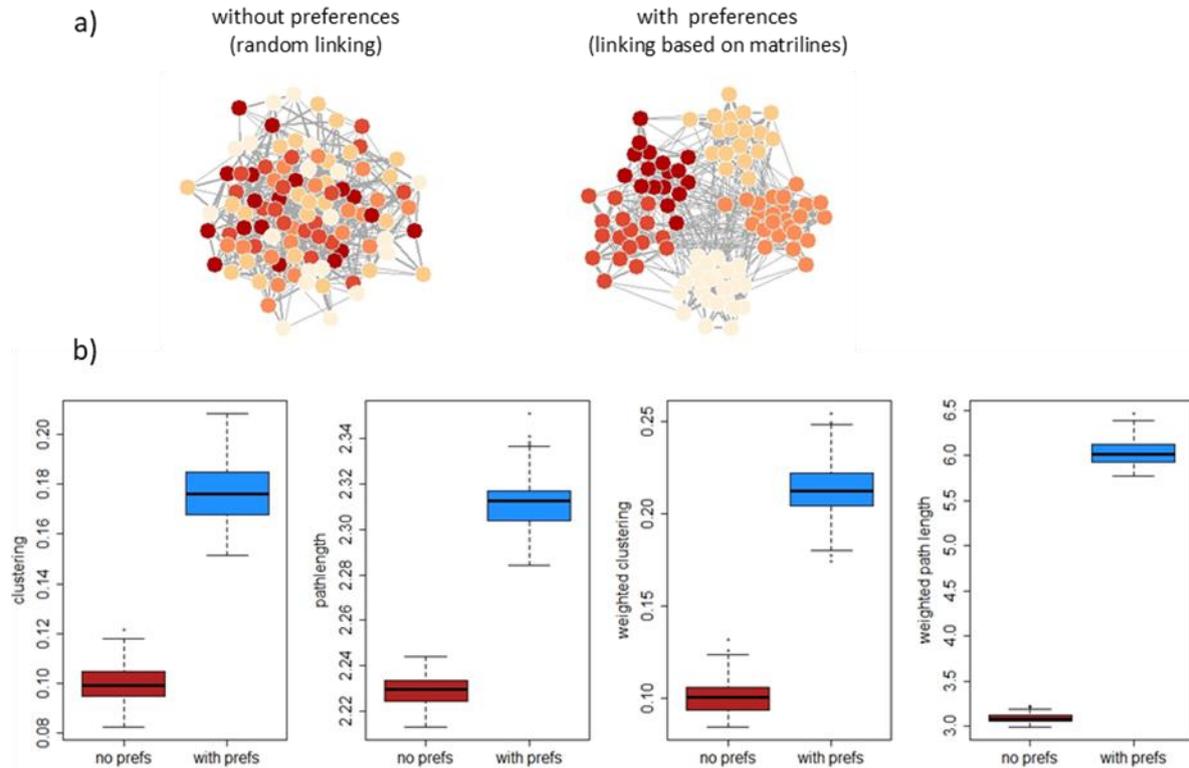
**Figure 2. An example of how generative network modelling may be used to study the emergence of animal social network structures.** We are interested in how social preferences for individuals similar to oneself (homophily) affect social network structure, in a social system where there are five matrilines and individuals prefer to socialise with those of their own matriline. We compare this to a case where individuals do not have such preferences (i.e. they are socializing at random). We use the trait preference model (Brask et al. 2025, Brask et al. 2026) to generate the networks. An example of each type of network is shown in a) (node colours indicate matrilines). For each type, we generate an ensemble of 100 networks and measure four network metrics on each network. The results are shown in b). We see that the matriline preferences lead to increased tendency for individual's friends to be connected to each other (unweighted and weighted clustering) and increased average social distance between individuals (unweighted and weighted pathlength). The results show how preferences for one's own matriline affect structural network properties, and they furthermore imply that such preferences are likely to influence factors that are dependent on these network properties, such as the spread of information and disease.

### Dynamics of animal social networks

While it is convenient to focus on only the (static) structure of animal social systems, social interaction patterns change across time and context (Silk et al. 2017, Smith et al. 2018, Prehn et al. 2019), and these social dynamics can be important for many ecological and evolutionary processes (Farine 2017). Despite this, few studies have used dynamic generative network models in animal behaviour. One exception is in wildlife disease, where generative network models have been used to show how seasonal social dynamics can influence how fast infection spreads (Reynolds et al. 2015). Perhaps even more powerful is to integrate the generative network model with individual states or population-level processes to facilitate the
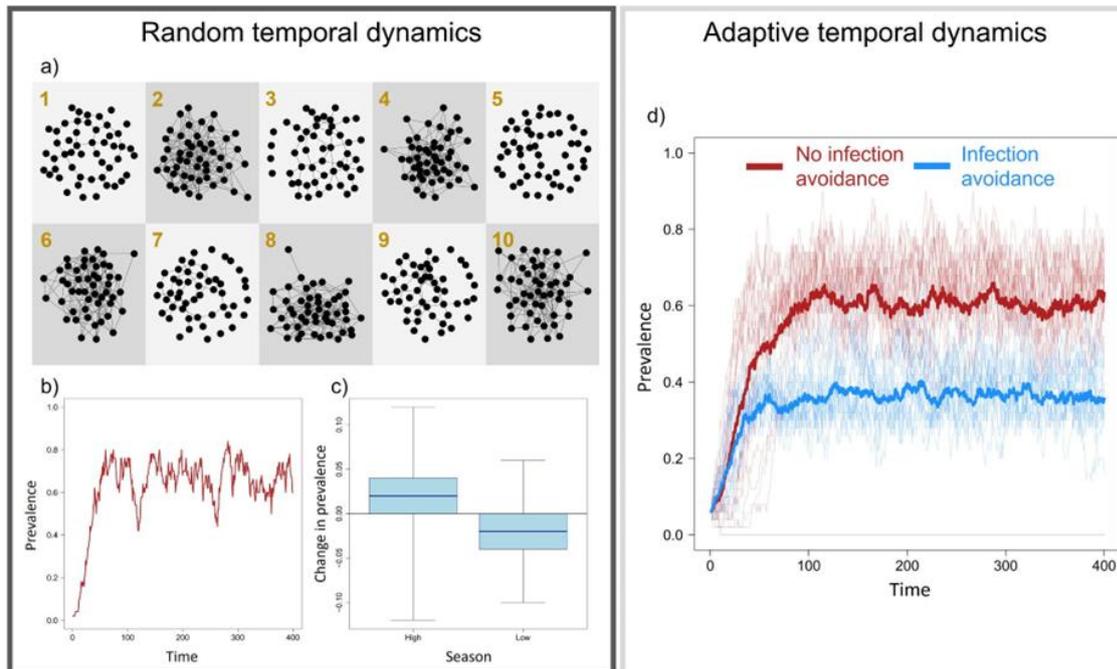
**Figure 3. Examples of how generative network models may be used to study dynamics on and of animal social networks.** We are interested in the spread of diseases in social networks. On the left we use a generative model of random temporal social dynamics unrelated to the disease model. a) the model consists of two seasons (illustrated by dark and light grey boxes) that differ in the extent of connectivity of the social network (the underlying model is the basic Poisson model introduced earlier). b) If we simulate susceptible-infected-susceptible (SIS) disease dynamics over this seasonally dynamic network, we can track the infection prevalence across time. c) We can use this time series to show that prevalence tends to increase during the highly-connected season and reduce during the lowly-connected season, potentially providing valuable information on how the infection persists in the population. On the right we extend our generative model so that the temporal social dynamics of the network are also influenced by the prevalence of disease in the population (social connectivity is reduced when infection prevalence reaches 30%). In d) we show the infection prevalence resulting from this new model (blue lines) and compare this scenario to the original model (red lines). Semi-transparent lines show the prevalence from individual simulation runs, and the thick line shows the mean prevalence calculated across all simulation runs.

modelling of feedback loops. For example, there is growing interest in how social networks respond to demographic change (Shizuka & Johnson 2019) and pathogen spread (Ezenwa et al. 2016, Stockmaier et al. 2021). Similarly, within-group theoretical models of dominance hierarchies (Hemelrijk & Puga-Gonzalez 2012) and collective behaviour (Bode et al. 2012) can benefit from generative network modelling. For example, Gupte et al. (2023) used an agent-based social movement model to study how individual behaviour and population social network structure may evolve in response to pathogen emergence. In our epidemiological case study example (Fig. 3, code available, see Code availability statement), we include dynamics of the networks themselves in two ways. In the first (Fig. 3a-c), the extent of social connectivity differs between two seasons, and in the second (Fig. 3d), the network connections also depend on the current epidemiological state of the group as a whole. This highlights how dynamic generative network models can help answer general questions related to the co-dynamics of social behaviour and infection (Ezenwa et al. 2016).

### Animal social network robustness

Studying the robustness of animal social networks can provide insights into the resilience of animal social systems to perturbations – both natural and human-induced. As described in a section above ('What are generative network models used for in wider network science?'), network robustness has often been studied by sequentially removing nodes or links from networks and studying their structural breakdown. In relation to animal social networks, node removal can correspond to loss of individuals (e.g. via death or dispersal), and link removal can correspond to loss of social connections or opportunities to interact (e.g. due to habitat fragmentation). In animal behaviour research, robustness studies of generated networks have for example been used in investigations of the effect of poaching on social structures (Wiśniewska et al. 2022), and the robustness of network structures that are based on different types of social partner preferences (Brask et al. 2026). Simulated removal experiments may also be carried out on observed animal social networks (Flack et al. 2006, Williams & Lusseau 2006), and combining robustness simulations on real and simulated networks may be rewarding for future studies. It should be kept in mind that in real populations, individuals may react to the loss of individuals by adjusting their social linking. Removal studies can, however, still be used to give an indication of the inherent robustness of the structures themselves (and thus how much reaction would be necessary to keep a well-connected network), and adjustment of social links can also be incorporated into robustness simulations (i.e. using a dynamic generative network modelling approach, e.g. Farine 2021). In Fig. 4 we show an example case study of how generative network modelling combined with node removal may be used to study the robustness of animal social networks (code available, see Code availability statement). We are interested in the robustness of networks with a modular structure, and we investigate this by measuring the robustness of such networks to different types of loss of individuals (node removal) and comparing the results to the robustness of two types of reference structures made with standard network models.
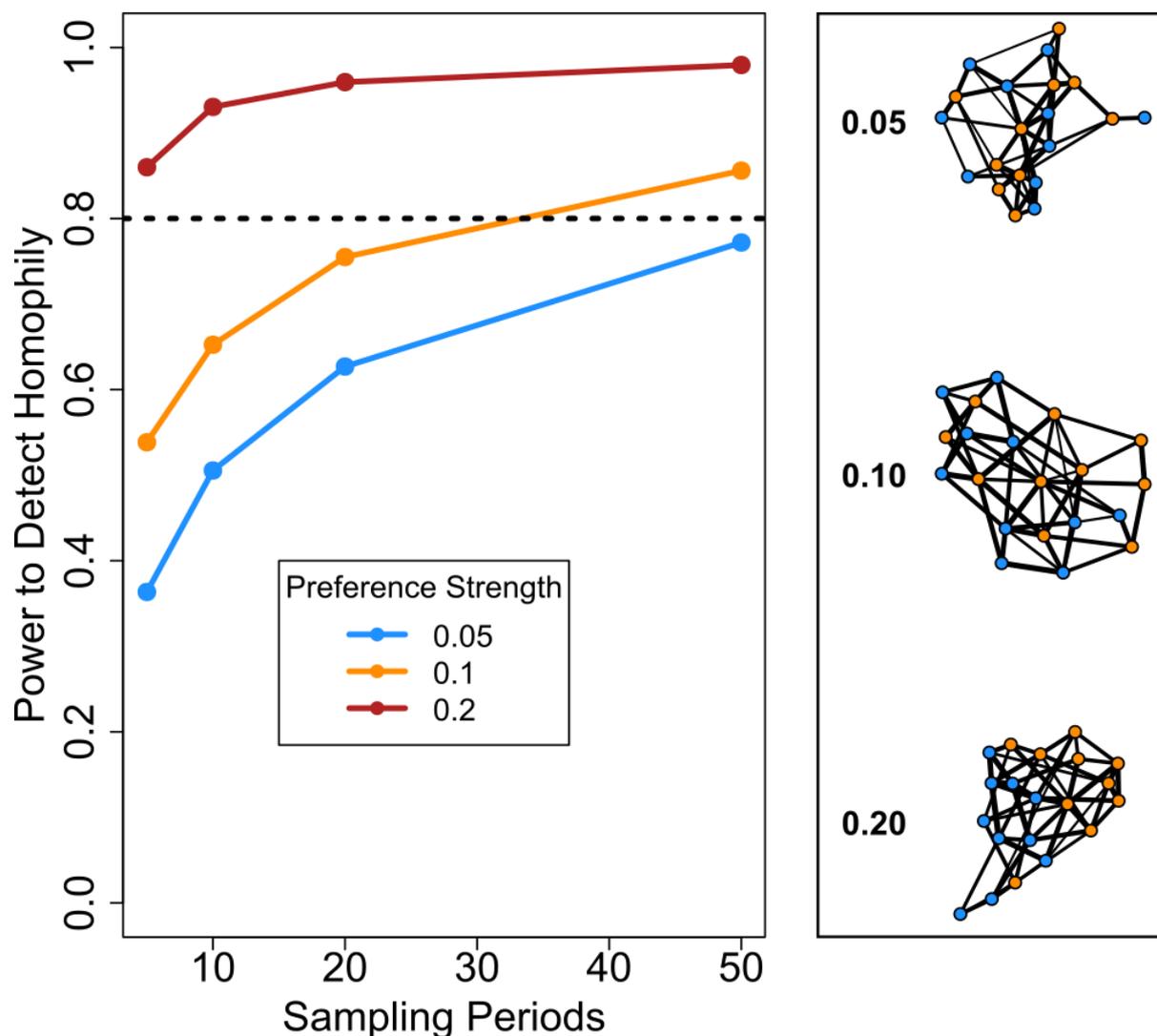
### Animal social network methodology

One area where generative network models have already seen considerable application in animal behaviour is as a tool to evaluate data collection and analysis methodologies for empirical social networks (Table 2, and Table A1 in the Appendix). Here, the purpose of the models is to generate networks that can be used as ground truth in studies investigating, for example, the effect of incomplete sampling and observation biases, or the effectiveness of statistical procedures in detecting known effects. In such studies, the general procedure is to use a generative network model to create "true" social networks, simulate sampling (data collection) from those networks, and then run downstream analyses on the simulated datasets. Such analyses have investigated the impact of unidentifiable or missing individuals on network analysis (Silk et al. 2015), evaluated methods for dealing with uncertainty and bias in data collection (Farine & Strandburg-Peskin 2016; Weiss et al. 2021a), and examined the impact of different sampling schemes on inferred network structures (Franks et al. 2010). The underlying network models in such studies are often quite simple, typically either random linking models or stochastic block models (Table 1). The networks generated with these models are then used as the basis of simulated sampling of interactions, associations, or even grouping events. For example, the genNetDem R package (Silk & Gimenez 2023) allows the simulation of interaction or grouping events (either dyadic or including groups bigger than two) that are based on an underlying network of social preferences. The likelihood of individuals occurring in these events together is a function of their dyadic social preference, as well as their social preferences to other event members. This provides a flexible tool to generate realistic social data for methodological questions rather than simply the network that would be measured. Aside from general examinations of data collection and analysis methods, the above-described procedure can be used to develop power analyses for specific studies prior to data collection from empirical networks. In the case study in Fig. 5 we show an example of this (code available, see Code availability statement). Here, we are interested in determining
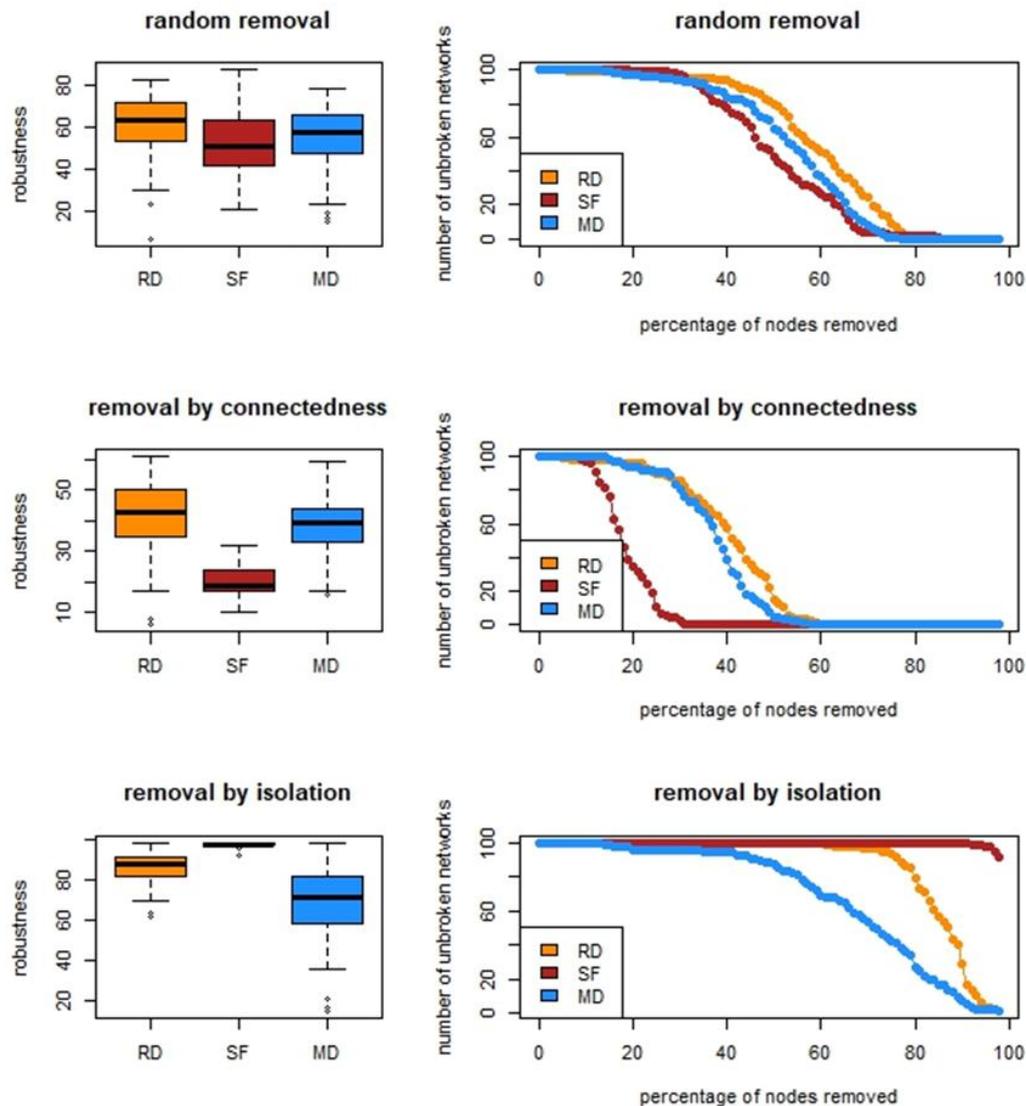
**Figure 4. An example of how generative network modelling may be used to investigate the robustness of animal social networks.** We are interested in the robustness of structures characterised by modularity (network communities), which is frequently observed in animal systems. Using the trait preference model (Brask et al. 2025, Brask et al. 2026), we generate an ensemble of networks where individuals belong to five types (such as different matrilines) and the structure is driven by preference for own type (as in Fig. 2). For comparison, we generate two standard types of networks: random (Poisson) networks (generated with the Erdős-Rényi model, Table 1), and scale-free networks based on preferential attachment (generated with the Barabási-Albert model, Table 1; these networks are characterized by a structure where a few individuals have many links and many have few links). We then measure the networks' robustness to different node removal procedures reflecting different real-world scenarios, where the loss of individuals is either random or correlated with their levels of social connectedness (high degree) or isolation (low degree). We see that the robustness of the modular networks is quite similar to that of the other network types under random loss of individuals. In contrast, they have higher robustness than the scale-free networks when loss correlates with social connectedness, and they have lower robustness than both random and scale-free networks when loss correlates with social isolation. Modularity in animal social networks (such as matriline-based structure) can thus affect their robustness, and the effect depends on whether and how the risk of death or dispersal is linked to individual social connectivity. RD = random, SF = scale-free, MD = modular.

how many sampling periods are needed to detect assortment by a trait in a ('real') network, and we therefore repeatedly simulate sampling on networks generated to have different levels of assortment, and run our statistical analysis on each replicate (Fig. 5).



**Figure 5. An example of how generative network models may be used for studies of animal social network methodology.** In this example, we use generative network modelling for power analysis. We are interested in testing for social homophily by some categorical trait in a ('real') group of 20 individuals. We intend to measure association networks through a series of complete scan samples of the group, recording which individuals are associated at each time period. To understand how many samples need to be collected to achieve a target power of 0.8, we simulate networks with different levels of trait preferences using the algorithm from Brask et al. 2026 (right), then simulate either 5, 10, 20, or 50 sampling periods (left), and then fit a binomial generalised linear model testing whether association probabilities are higher within vs. between classes (i.e. testing for homophily). When preferences are strong (homophily is pronounced), very few samples are needed (yellow line), however with more subtle preferences even 50 samples would be inadequate to detect homophily with the desired power.

**MODEL FEATURES IN RELATION TO ANIMAL SOCIALITY RESEARCH**

We here revisit the model features described in the section 'Features of generative network models' and consider how and when they are relevant in animal behaviour research. This can be useful for example when planning studies on animal behaviour that involve generative network models.

*Linking rules*

Many generative network models have been developed to investigate the effect of a specific type of linking, or to produce networks with a specific structural property (Table 1). Such models often have simple linking rules where a single factor affects the linking, whereas in real animal social networks, multiple factors are likely to affect the linking. Models with simple linking rules can be relevant for animal behaviour studies if the particular linking rules or structural features of the output networks are of interest for the research question, or as standard reference models (e.g. as in Fig. 4). If the generative process should resemble those of animal social systems more closely, then models where multiple factors can affect the linking may be more relevant (e.g. several simultaneous trait preferences: Brask et al. 2025, Brask et al. 2026, Table 2; or several simultaneous substructure-building processes: exponential random graph models, Table 1, Silk & Fisher 2017). Models that are explicitly based on grouping dynamics may be relevant particularly in cases where the networks should resemble those from gambit-of-the-group data (see for example Silk & Gimenez 2023).

*Model parameters*

In relation to animal behaviour studies, parameters of generative network models can be considered both as a way of setting aspects of the social behaviour of individuals in the simulated population, and as a way of tuning the structure of the networks. Which of these interpretations is relevant depends on the focus of the study (whether the purpose of the modelling is to model specific social behaviour or simply generate networks with specific structural properties). Parameter settings may be chosen by the user or may be set based on measurements from real animal social systems. The former approach can be very useful for example for studies of general questions that do not concern a specific system, and here it may often be relevant to study networks across the parameter range (e.g. as in Brask et al. 2026). The latter approach may be particularly useful if the research question concerns a specific animal social system. For example, Rozins et al. (2018) used a generative model that included group membership and the distance between refuge locations to develop an ensemble of social networks that closely matched an empirically observed network, and Siracusa et al. (2023) studied the effect of individuals' ageing on social networks with a generative model where linking between ages and kin groups was parameterized based on real networks.

*Node attributes and dyadic attributes*

The empirical research on animal social networks implies that node and dyadic attributes play an important role for the structures of these networks, and generative network models that include attributes are therefore relevant for many questions about animal social systems.

***Extrinsic node attributes*** are relevant for animal social systems because the traits of individuals play a key role for the network structures (reviewed in Brask et al. 2026). Extrinsic node attributes can therefore be important if generative network models are to create structures that match real-world animal social structures well, and for understanding the real-world social linking processes and the role that individual heterogeneity plays in them. The trait preference model (Brask et al. 2025, Brask et al. 2026) is an example of a model which is based on empirical knowledge about animal social structures and generates social network

structures from different types of social preferences for one or multiple traits (or equivalent processes related to node attributes). Models based on grouping dynamics can also incorporate node attributes, for example by letting the chance of joining a group depend on a trait.

Effects of *intrinsic node attributes* (i.e. attributes derived from network positions) on social linking could be realistic for some animal social systems. For example, if information access is important for fitness, then individuals could be expected to prefer well-connected individuals as social partners - a behaviour which is epitomised by preferential attachment models (Table 1). A study on lemurs implied that individuals in this system become more central when they are knowledgeable (Kulahci et al. 2018), suggesting that connectivity (i.e. an intrinsic node attribute) in this system could be used as a useful indicator of knowledge. Empirical research on the effect of individual attributes on animal social networks has mostly focused on traits (i.e. extrinsic node attributes), and it is an open question to which extent intrinsic node attributes are important in these systems. In any case, models with intrinsic node attributes could be useful in studies of animal social structures for generating networks with specific structure, or as reference models.

*Dyadic attributes* that derive from the traits of individuals have shown to be widely important in animal social networks (reviewed in Brask et al. 2026). These include genetic relatedness (e.g. De Moor et al. 2020), as well as differences between individuals in traits such as their age and sex (e.g. Weiss et al. 2021b). Models where social linking is dependent on dyadic attributes can therefore be very relevant for studies of animal social systems. To select a model that uses dyadic attributes, it is good to be aware that some models take only node (individual) attributes as input and then change them to dyadic attributes within the model (see also 'Dyadic attributes' in the section 'Features of generative network models').

### Network growth

Models that include a network growth process can be relevant for animal behaviour studies for at least two reasons. Firstly, the network position of others could potentially affect social partner choice in animal species (see *intrinsic node attributes* above). In this case, a growth process (or another dynamic process) can be necessary to simulate the generative process, because individuals use the network position of others to decide who to socialise with. Secondly, the network growth processes in themselves can be relevant to study (whether or not individuals use network positions in partner choice) for understanding various aspects of animal social systems, such as the establishment of social groups.

### Link weights

The types of social connections studied in animal social systems are typically inherently weighted (that is, they can be stronger or weaker, rather than only being present or absent), and the inclusion of link weights in modelled animal social networks is therefore often relevant (see the subsection 'Link weights' in 'Features of generative network models' for how weights may be generated). Unweighted generated networks can also be relevant for some types of investigations of animal social systems - for example theoretical investigations where complexity reduction can be useful, or analyses that do not use weighted network metrics. When using weighted networks, it can be important to use a weight-adding procedure that gives a biologically realistic weight distribution over the network. For example, if the chance of being socially connected is correlated with a node attribute, then it may be more realistic to also let the link weights correlate with this attribute, rather than adding random weights. An example of this is Rozins et al. (2018), who used a zero-inflated negative binomial generalised linear mixed model as a generative model for weighted European badger (*Meles meles*) contact networks, with edge weights related to dyadic attributes (shared group membership and distance between groups), and agent-based model approaches such as GrooFiWorld

(Hemelrijk & Puga-Gonzalez 2012, Table 2) can naturally track the frequency of proximity events or interactions each individual is involved in.


**CHOOSING GENERATIVE NETWORK MODELS FOR ANIMAL BEHAVIOUR STUDIES**

Generative network models can be useful for many different research questions concerning animal behaviour (see the section 'Uses of generative network models in animal social behaviour research'), and which model would be most relevant to use will depend on the research question and approach. Choosing the right model for the right purpose – and being aware of its limitations and the structural properties in its networks – is important for avoiding biases and incorrect conclusions. Key  things to consider when selecting a model include the following:

- **Consider to what extent the linking rules and the network structures, respectively, should resemble those of real-world animal social systems.** If the goal is to model one or more specific generative processes (for example for studying how specific real-world partner choice strategies affect network structure), then it is relevant to select a model where the linking rules resemble the generative process(es) of interest (see the Linking rules' subsection in the 'Model features in relation to animal social behaviour research' section). The model does not have to originally have been developed to resemble the process(es) of interest, as long as the linking rules can be interpreted as those process(es). If the goal is just to create networks with specific structural features (for example for investigating how different structures affect spreading processes), then it may not be important whether the linking rules resemble specific real-world processes, as long as the output networks have the relevant structure. In this case any model that provides the desired structures may be used. If the structures should resemble a specific real-world network, then it can be relevant to parameterize the model based on that network (see the subsection 'Models parameterized by real networks' below).
- **Consider whether the model should include node/dyadic attributes, network growth, and/or link weights.** If one or more of these are important for the study, then it is relevant to consider what form they should take, and if candidate models fit with this. For example, which values the attributes should be able to take and how they should affect linking; or by which rules the network should grow; and how the link weights should be distributed across the network (see the section 'Model features in relation to animal sociality research').
- **Consider in which aspects models used to create 'control' network ensembles should differ from the model used to create the 'treatment' ensemble (Fig. 1).** It can be fine to use models for control networks that are very different from the model for treatment networks, depending on the research question and the purpose of the comparison. It may also often be relevant to use the same model with different parameter settings (or alternatively create networks across the parameter range, instead of having treatment and control ensembles).
- **Get to know your candidate model(s).** After selecting one or more candidate models for your study, explore how the model works. Linking rules can be studied via model descriptions and the model code. The effect of parameters can be investigated by generating network structures across parameter ranges - this can be relevant to do not only for parameters that are of direct interest for the study, but also for others to understand if the results would change if these were set to other values (i.e. conducting sensitivity checks).

Below we consider different kinds of generative network models and when to use them. See Box 2 for where to find tools and code for generating networks with generative network models.

## *Common standard generative network models*

Common standard generative network models, such as those listed in Table 1, have been used relatively little in the animal behaviour field - in particular considering their ubiquity in network science in general. This is maybe because they have been deemed unlikely to generate networks that resemble animal social networks well, and not all of them have been presented in the setting of social systems. There are, however, a number of ways in which these models may be useful in animal behaviour research. For example, if the research question concerns how specific structural properties affect network function (such as disease transmission), it may be relevant to use a model that allows for varying the property of interest while keeping the rest of the structure random. Standard models can also function to create benchmark cases ('control groups') that may be compared to more realistic or real-world networks (as in Fig. 4). For example, Rozins et al. (2018) used both the Poisson model and the configuration model (Table 1) to generate "control" ensembles to illustrate how individual variation in social connectivity and group structure could both influence infectious disease spread in European badgers. It should be noted that while it is perfectly valid to use networks generated from such standard models for comparison, they are rarely suitable as *statistical* null models, as they are unlikely to differ from the real network in the relevant aspects for using them in that way (De Moor et al. 2025); generative network models can, however be used for statistical inference in other ways (see the subsection 'Generative network models for statistical inference' below). Another reason why standard generative network models can be useful in animal behaviour studies is that some standard models can be interpreted as models for specific behavioural strategies, which could potentially be relevant for animal systems. Furthermore, given their widespread use, the standard models can also be useful for comparison of results from other parts of network science, which is relevant because many of the types of questions investigated with generative network models outside animal behaviour are also of interest in this field. Finally, the standard models can be adapted or combined to create new valuable tools in animal behaviour research. For example, the social inheritance model builds on an existing social science model for network growth (Ilany & Akçay 2016a), and the genNetDem R package (Silk & Gimenez 2023) combines features of a simple (two-dimensional) latent space model and stochastic block model (Table 1) in its generation of underlying social networks. Given these considerations, it seems that standard generative network models may be more useful in animal behaviour research than their current use reflects (as long as it is made sure that they are the suitable choice for the research question at hand) and could offer new insights into these systems.

### Generative network models based on animal social systems

A few general generative network models have been developed specifically based on empirical knowledge about animal social systems, such as the social inheritance model (Ilany & Akcay 2016a) and the trait preference model (Brask et al. 2025, Brask et al. 2026). These models may be used when the linking mechanisms and behavioural strategies they simulate are of interest, and/or when the structures they produce are relevant. Similarly to many standard models, these models create networks directly from linking probabilities – meaning that the data from which empirical networks are usually created (e.g. data streams of interactions or group memberships) are not in themselves simulated. In some cases it may be necessary to create artificial data streams of social interactions or associations (for example when studying sampling effects), and there are also tools available for this designed specifically for animal social systems (Silk & Gimenez 2023).

### Generative network models parameterized by real networks

If the purpose of using a generative network model is to generate network structures that closely resemble those of a specific species or population – for example to act as substrate for a theoretical study of transmission processes in that species or population – then it may be relevant to parameterise the model based on observed data. That is, while the model would still build networks by the same procedures, one or more of its parameters would be estimated from a data set instead of being selected by the user (see for example Siracusa et al. 2023). The parameters may for example be estimated while using the model as a statistical inference model (see next subsection), or they may be measured in other ways. Parameterising generative network models with real data makes it possible to generate large ensembles of networks that are similar to the given real network but not identical to it (the networks should ideally catch important aspects of the structure while also reflecting natural stochasticity). It should be kept in mind that there are limitations to how closely the generated networks will resemble those of the input. Firstly, in the case where the networks are generated in connection with statistical inference, then the similarity between the generated networks and the real network depends on how much of the variation in the data the model explains, and the generated networks are likely to only contain structural aspects that have been explained by the model. Therefore, it may often be relevant to check to what extent the model explains the data, and to what extent and in which aspects networks generated from the parameterized model resembles the real network (see e.g. Hunter et al. 2008). Secondly, the generated networks will reflect the real social structure at the time the data were collected, and thus they may not represent the species well if there is high between-population or temporal variation in social structure. However, in cases where the generated networks are not highly similar to the real networks, it can still be relevant to use parameterized models for network generation if these models catch key aspects of interest. It should also be kept in mind that if a model replicates a real structure well, it does not necessarily mean that the modelled generative processes correspond to those that have created the real network, as similar structures can arise from different processes (Hobson et al. 2021).

Alternatively, instead of using a parameterized generative network model, networks that resemble a real network could also be produced by applying randomisation procedures to the real network, where some features are kept as is while others are randomised. Which of these alternatives are most relevant will depend on the way in which the generated networks should resemble the real network. Parameterized generative network models provide a bottom-up approach, where the generative processes of the generated networks are known (because they are defined in the model) and the networks will only contain structure from these processes (which are tuned to the real network by the parameterization). In contrast, randomisation procedures provide a top-down approach, where all structural patterns in the original network are kept (regardless of which processes generated them), except the aspects that are randomised.

### *Generative network models for statistical inference*

While we have here mostly focused on generative network models as a tool for simulation modelling, these models can also be used as tools for statistical inference. This can be done by combining them with inference methods (such as Bayesian inference) and parameterising them based on the observed network of interest. Such statistical inference can in principle be done with any model that estimates linking probabilities; in this context, the linking probabilities of pairs of individuals is the outcome variable, and the statistical model estimates the importance of factors included in the model that can influence this probability (see Brask et al. 2026 for a conceptual example). Note that here no networks need to be generated - the inference is done by assessing the statistical significance of the model parameters. (As mentioned in an earlier section, statistical inference should generally not be done by comparing networks from generative network models to real networks, as the generated networks are usually not suitable as null models for a real network). Vice versa, the fact that generative network models can be used as statistical models also means that some of the generalized linear mixed models that are frequently used for statistical analysis of observed networks can be used as generative network models, as artificial networks can be generated from these models after they have been parameterized with data (see the preceding subsection).

## CONCLUSION

Generative network models are an essential tool for studies of animal social structures, where they can help in investigating a wide range of questions, and can create new fundamental insights as well as predictions for empirical studies. They also provide a promising direction for statistical inference of drivers of animal social network structures. A more extensive use of generative network models in studies of animal social systems could therefore strengthen both the empirical and theoretical side of research in animal sociality. This development is facilitated by increasing accessibility of such models via R packages (Box 2), and by models and code being developed specifically with animal systems in mind (Ilany & Akcay 2016a, Silk & Gimenez 2023, Brask et al. 2026). We hope that the introduction and overview provided above will be useful for researchers taking part in this adventure.

## CODE AVAILABILITY

Code for the example case studies is available at https://github. com/bohrbrask/Generative-network-models-intro.

## ACKNOWLEDGEMENTS

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**APPENDIX**

**Table A1. Non-exhaustive list of (non-human) animal behavioural ecology papers that deploy generative network models.** Studies highlighted in green are also given in Main Text Table 2. The references in this table are listed below the table. ABM = agent-based model, SBM = stochastic block model.

| Paper title | Main aim of paper | Model category | Key model features | Study species | Code available | Citation |
|---|---|---|---|---|---|---|
| *Friendship, reciprocation, and interchange in an individual-based model* | Behavioural theory | Spatial | *FriendsWorld – an extension of GroofiWorld that incorporates stronger social influence of a set of individuals with the strongest social bonds (top 25%)* | Theoretical | No | Puga-Gonzalez et al. 2015 |
| *Indirectly connected: simple social differences can explain the causes and apparent consequences of complex social network positions* | Behavioural theory | Group-based | *Individuals vary in group size preferences and also display some assortativity (by pre-defined 'group' or based on previous associations)* | Theoretical | Yes | Firth et al. 2017 |
| *Social style and resilience of macaques' networks, a theoretical investigation* | Behavioural theory | Spatial | *GrooFiWorld model – a spatial ABM with strong social component to movement and interactions within set radius* | Theoretical / macaques | No | Puga-Gonzalez et al. 2019 |

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|---|---|---|---|---|---|---|
| *Structural trade-offs can predict rewiring in shrinking social networks* | Behavioural theory | Linking probability | *Edge probabilities – Uses both Poisson and Ilany et al. social inheritance model to build initial networks then dynamic model based on second-order connections.* | Theoretical | Yes | Farine 2021 |
| *A complex social structure with fission-fusion properties can emerge from a simple foraging model* | Behavioural theory | Spatial | *ABM of movement between patches* | Theoretical / spider monkeys | No | Ramos-Fernandez et al. 2006 |
| *Personality and social networks: A generative model approach* | Behavioural theory | Linking probability | *Adapts Ilany et al. social inheritance model with a nodal attribute ("boldness")* | Theoretical | No | Ilany & Akçay 2016b |
| *Emergence of complex social networks from spatial structure and rules of thumb: a modelling approach* | Behavioural theory | Spatial | *GrooFiWorld model – a spatial ABM with strong social component to movement and interactions within set radius* | Theoretical / macaques | No | Puga-Gonzalez & Sueur 2017a |
| *Simple foraging rules in competitive environments can generate socially structured populations* | Behavioural theory | Mixed (linking probability and group-based) | *Directed Poisson model with fixed interaction probability. These networks then used to define groups.* | Theoretical | Yes | Cantor & Farine 2018 |
| *The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity* | Behavioural theory | Spatial | *Agent-based model of movement between patches. Co-occurrence at a patch is a network connection.* | Theoretical | Yes | He et al. 2019 |

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|---|---|---|---|---|---|---|
| *Social influence and interaction bias can drive emergent behavioural specialization and modular social networks across systems* | Behavioural theory | Mixed (linking probability and dyadic interactions) | *Edge probabilities using an SBMtype approach to generate homophily and heterophily. Edge probabilities are then used to generate dyadic interactions.* | Theoretical (social insect) | Yes | Tokita & Tarnita 2020 |
| *Social inheritance of avoidances shapes the structure of animal social networks* | Behavioural theory | Linking probability | *Extension of social inheritance model (Ilany et al.)* | Theoretical | Yes | Frère et al. 2023 |
| *Far-reaching consequences of trait-based social preferences for the structure and function of animal social networks* | Behavioural theory and methodological | Linking probability | *Edge probabilities depend on social preferences for traits. Multiple traits and preference types can affect the network simultaneously.* | Theoretical | Yes | Brask et al. 2026 |
| *Sampling animal association networks with the gambit of the group* | Methodological | Mixed (linking probability and group-based) | *Edge probabilities with dyadic random effect and binary trait assortativity. Then formation of groups based on these edge weights.* | Theoretical | No | Franks et al. 2010 |
| *The consequences of unidentifiable individuals for the analysis of an animal social network* | Methodological | Group-based | *Groups generated based on family clusters* | Brent geese | No | Silk et al. 2015 |

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|---|---|---|---|---|---|---|
| *Common datastream permutations of animal social network data are not appropriate for hypothesis testing using regression models* | Methodological | Mixed (linking probability and group-based) | *Various, including: Edge probabilities with a dyadic random effect; Group-based with individual level random effect for group size preference* | Theoretical | Yes | Weiss et al. 2021 |
| *Generation and applications of simulated datasets to integrate social network and demographic analyses* | Methodological | Mixed (linking probability and group-based) | *Edge probabilities based on a simplified SBM (within and between block edge probabilities only) and two dimensional latent space model with individual level variation linked to nodal attributes. Simulation of groups based on these networks* | Theoretical | Yes | Silk and Gimenez 2023 |
| *A note on reconstructing animal social networks from independent small-group observations* | Methodological | Linking probability | *Basic theoretical network models: Poisson, Watts-Strogatz, Barabasi-Albert* | Theoretical | No | Perreault 2010 |
| *Correcting for the impact of gregariousness in social network analyses* | Methodological | Linking probability | *Edge probabilities based on individual traits and modified by dyadic random effects* | Theoretical | No | Godde et al. 2013 |
| *Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges* | Methodological | Linking probability | *Edge probabilities including an assortativity between similar nodes* | Theoretical | No | Farine 2014 |

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|---|---|---|---|---|---|---|
| ***Estimating uncertainty and reliability of social network data using Bayesian inference*** | Methodological | Linking probability | *Modified SBM with edges weighted by individual variation in nodal attribute* | Theoretical | Yes | Farine & Strandburg-Peshkin 2015 |
| ***Measuring the robustness of network community structure using assortativity*** | Methodological | Linking probability | *Modified SBM with an individual level random effect* | Theoretical | Yes | Shizuka & Farine 2016 |
| ***The next steps in the study of missing individuals in networks: a comment on Smith et al. (2017)*** | Methodological | Linking probability | *Edge probabilities based on a simplified SBM (within and between block edge probabilities only) and two-dimensional latent space model* | Theoretical | Yes | Silk 2018 |
| ***Measuring the complexity of social associations using mixture models*** | Methodological | Linking probability | *Edge probabilities based loosely on a SBM with dyadic random effects* | Theoretical | Yes | Weiss et al. 2019 |
| ***The performance of permutations and exponential random graph models when analyzing animal networks*** | Methodological | Mixed (linking probability and group-based) | *Edge probabilities based on a simplified SBM (within and between block edge probabilities only) and two-dimensional latent space model with individual level variation linked to nodal attributes. Simulation of groups based on these networks.* | Theoretical | No* *broken repository link | Evans et al. 2020 |
| ***Calculating effect sizes in animal social network analysis*** | Methodological | Linking probability | *Edge probabilities as a function of anodal attribute* | Theoretical | Yes | Franks et al. 2021 |

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|---|---|---|---|---|---|---|
| *Modelling associations between animal social structure and demography* | Methodological | Linking probability | *A simplified SBM with within and between block edge probabilities only* | Theoretical | Yes | Clements et al. 2022 |
| *Common permutation methods in animal social network analysis do not control for non-independence* | Methodological | Linking probability | *Edge probabilities based on nodal attributes (and incorporating a modified SBM in the second part). Also a matrix-based simulation based on quadratic assignment procedure* | Theoretical | Yes | Hart et al. 2022 |
| *A new method for characterising shared space use networks using animal trapping data* | Methodological | Spatial | *Movement-based ABM* | Theoretical | Yes | Wanelik & Farine 2022 |
| *A guide to choosing and implementing reference models for social network analysis* | Tutorial | Mixed (linking probability and group-based) | *Various (edge probabilities and group-based) largely specified on a modified SBMI and/or two dimensional latent space model* | Theoretical | Yes | Hobson et al. 2021a |
| *Ageing in a collective: The impact of ageing individuals on social network structure* | Social ageing | Linking probability | *Edge probabilities depend on nodal and dyadic traits* | Rhesus macaque | Yes | Siracusa et al. 2023 |

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|---|---|---|---|---|---|---|
| *Social inheritance can explain the structure of animal social networks* | Social dynamics | Linking probability | *Edge probabilities – network dynamics with inheritance. Interaction probabilities depend on interaction probability with its parent* | Spotted hyena, rock hyrax, bottlenose dolphin, sleepy lizard | Yes | Ilany & Akçay 2016a |
| *Animal social networks as substrate for cultural behavioural diversity* | Social learning theory | Linking probability | *Adaptations of a simplified SBM (within/between block edge probabilities differ only) and two dimensional latent space model* | Theoretical | No | Whitehead & Lusseau 2012 |
| *Social network architecture and the tempo of cumulative cultural evolution* | Cultural evolution | Linking probability | *Range of theoretical network models: Poisson, Watts-Strogatz, Lattice, Basic modular* | Theoretical | Yes | Cantor et al. 2021 |
| *The effect of individual variation on the structure and function of interaction networks in harvester ants* | Social transmission | Linking probability | *Edge probabilities.*<br><br>*Adaptations of Poisson model*<br><br>*So that ants varied in their edge probabilities or increased them over time.* | Harvester ants | No | Pinter-Wollman et al. 2011 |
| *Social transmission in networks: Global efficiency peaks with intermediate levels of modularity* | Social transmission | Linking probability | *Barabasi-Albert preferential attachment model* | Primates | No | Romano et al. 2018 |

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|---|---|---|---|---|---|---|
| *Group size and modularity interact to shape the spread of infection and information through animal societies* | Social transmission | Linking probability | *Modified, iterative implementation of a simplified SBM to generate networks with known modularity.* | Theoretical | Yes* | Evans et al. 2021 |
| *When to choose dynamic vs. static social network analysis* | Social transmission<br><br>Disease ecology | Linking probability | *Dynamic Poisson model with networks at each timestep independent* | Theoretical | Yes | Farine 2018 |
| *Unravelling the disease consequences and mechanisms of modular structure in animal social networks* | Social transmission<br><br>Disease ecology | Linking probability | *Modified Havel-Hakimi model (in two parts for between and within community edges).*<br><br>*See also: https://doi.org/10.1186/1471-2105-15-220* | Theoretical / comparative | Yes | Sah et al. 2017 |
| *Raccoon contact networks predict seasonal susceptibility to rabies outbreaks and limitations of vaccination* | Social transmission<br><br>Disease ecology | Linking probability | *Simulations from exponential random graph models fitted to empirically-derived contact data* | Raccoon | No | Reynolds et al. 2015 |
| *Which mechanisms drive seasonal rabies outbreaks in raccoons? A test using dynamic social network models* | Social transmission<br><br>Disease ecology | Linking probability | *Simulations from exponential random graph models fitted to empirically-derived contact data* | Raccoon | No | Hirsch et al. 2016 |

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|---|---|---|---|---|---|---|
| *Spatial utilization predicts animal social contact networks are not scale-free* | Disease ecology | Spatial | *Spatial ABM with contacts (based on proximity) emerging from individual movement* | Brushtail possums | No | James et al. 2017 |
| *Social structure contains epidemics and regulates individual roles in disease transmission in a group-living mammal* | Social transmission<br><br>Disease ecology | Linking probability | *Simulations from dyadic regressions (zero-inflated negative binomial) fitted to empirically-derived contact data. Also Poisson model.* | European badger | Yes | Rozins et al. 2018 |
| *Novel pathogen introduction triggers rapid evolution in animal social movement strategies* | Disease ecology | Spatial | *ABM of individual movement with social influence* | Theoretical | Yes | Gupte et al. 2023 |
| *Emergent patterns of social organization in captive Cercocebus torquatus: Testing the GrooFiWorld agent-based model* | Behavioural ecology | Spatial | *GrooFiWorld model – a spatial ABM with strong social component to movement and interactions within set radius* | Red-capped mangabey | No | Dolado & Beltran 2012 |
| *Friendships and Social Networks in an Individual-Based Model of Primate Social Behaviour* | Behavioural ecology | Spatial | *FriendsWorld – an extension of GroofiWorld that incorporates stronger social influence of a set of individuals with the strongest social bonds (top 25%)* | Theoretical / macaques | No | Puga-Gonzalez & Sueur 2017b |

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|---|---|---|---|---|---|---|
| *Mechanisms of reciprocity and diversity in social networks: a modeling and comparative approach* | Behavioural ecology | Mixed (spatial and interactions) | *3 models:*<br><br>*GrooFiWorld*<br><br>*FriendsWorld*<br><br>*Reaper – a non-spatially explicit version of the above models which effectively operates as a network growth/change model based on previous interactions* | Macaques | No | Puga-Gonzalez et al. 2018 |
| *The impact of social networks on animal collective motion* | Collective behaviour | Linking probability | *Basic theoretical network models: Poisson, Watts-Strogatz, Barabasi-Albert* | Theoretical | No | Bode et al. 2011 |
| *Leading from the front? Social networks in navigating groups* | Collective behaviour | Linking probability | *Basic edge-based model for a weighted network* | Theoretical | No | Bode et al. 2012 |
| *From social network (centralized vs. decentralized) to collective decision-making (unshared vs. shared consensus)* | Collective Behaviour | Linking probability | *Edge probabilities with one individual having different properties to others (more central) in small networks* | Theoretical | No | Sueur et al. 2012 |
| *Behavioural variation among workers promotes feed-forward loops in a simulated insect colony* | Social insects | Spatial | *Movement-based ABM* | Theoretical | Yes | Easter et al. 2022 |

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|---|---|---|---|---|---|---|
| *Social structure modulates the evolutionary consequences of social plasticity: A social network perspective on interacting phenotypes* | Evolutionary theory | Linking probability | *Edge probabilities based on a two dimensional latent space model with added homophily or heterophily* | Theoretical | Yes | Montiglio et al. 2018 |
| *An Individual-Oriented Model on the Emergence of Support in Fights, Its Reciprocation and Exchange* | Dominance hierarchies | Spatial | *GrooFiWorld model – a spatial ABM with strong social component to movement and interactions within set radius* | Theoretical / macaques | No | Hemelrijk & Puga-Gonzalez 2012 |
| *Emergent Patterns of Social Affiliation in Primates, a Model* | Dominance hierarchies | Spatial | *GrooFiWorld model – a spatial ABM with strong social component to movement and interactions within set radius* | Theoretical | No | Puga-Gonzalez et al. 2009 |
| *Empathy versus Parsimony in Understanding Post-Conflict Affiliation in Monkeys: Model and Empirical Data* | Dominance hierarchies | Spatial | *GrooFiWorld model – a spatial ABM with strong social component to movement and interactions within set radius* | Tonkean macaque | No | Puga-Gonzalez et al. 2014 |
| *Targeting or supporting, what drives patterns of aggressive intervention in fights?* | Dominance hierarchies | Spatial | *GrooFiWorld model – a spatial ABM with strong social component to movement and interactions within set radius* | Bonnet macaques | No | Puga-Gonzalez et al. 2016 |
| *Aggression heuristics underlie animal dominance hierarchies and provide evidence* | Dominance hierarchies | Interactions | *ABM based on directed interaction rules for each individual* | Theoretical | Yes | Hobson et al. 2021b |

| *of group-level social information* | | | | | | |
|---|---|---|---|---|---|---|
| *Trinidadian guppies use a social heuristic that can support cooperation among non-kin* | Cooperative behaviour | Group-based | *Agent-based model of grouping decisions. The network is an emergent property.* | Guppy | No | Darden et al. 2020 |
| *Alarm communication networks as a driver of community structure in African savannah herbivores* | Mixed species groups | Group-based | *ABM of grouping behaviour (model is individual-based but networks are analysed at species level)* | African savannah herbivores (12 species) | No | Meise et al. 2020 |
| *Social information-mediated population dynamics in non-grouping prey* | Predator-prey / Community ecology | Spatial | *Movement-based ABM with interactions based on spatial proximity* | Theoretical | Yes | Tóth & Kőmüves 2022 |
| *Responses of Bat Social Groups to Roost Loss: More Questions Than Answers* | Conservation and applied research | Spatial | *Spatial ABM of roost site choice that also incorporates use of social information* | Northern long-eared bat | No | Silvis et al. 2016 (book chapter) |
| *Simulated poaching affects global connectivity and efficiency in social networks of African savanna elephants—An exemplar of how human disturbance impacts group-living species* | Conservation and applied research | Linking probability | *Edge probabilities depend on age, kinship and group membership (i.e. SBM features). Edge probabilities then used to simulate association events.* | African elephant | No | Wiśniewska et al. 2022 |

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