An introduction to generative network models and how they may be used to study animal sociality

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Abstract

Social networks constitute an important approach in the study of animal social behaviour. So far, 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 despite occasional use, have not yet been as well integrated in the animal behaviour field. 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.

1. 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 provide a fundamental theoretical framework with which to approach network structures observed in nature. 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. 2022, Silk & Gimenez 2023, Brask et al. 2024).

We believe that generative network models hold much 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 of the paper (Section 2-4), we provide a general introduction to generative network models, and in the second half (Section 5-7), we consider them in relation to animal behaviour research. We use this order because the first part provides information useful for following the second part. In the first half, we consider what generative network models are (Section 2) and what they are typically used for in wider network science (Section 3), and we describe general features of generative network models (Section 4). 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 (Section 5), we consider the relevance of each of the above-mentioned model features for animal behaviour studies (Section 6), and we discuss how to choose generative network models for animal behaviour studies (Section 7). We end the paper with a brief conclusion (Section 8).

2. 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, 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 link to each other. The structure of the generated network depends on the model (i.e. the network construction rules) and the parameter values set.

In a broad sense, any stochastic procedure that produces an adjacency matrix (or other network data format) may be considered a generative network model. In principle, this includes procedures based on the randomisation of existing network data – such as those that have been widely used in the animal behaviour field for statistical inference (permutation models; Bejder et al. 1999; Croft et al. 2011, Farine 2017, Hobson et al. 2021). However, the term 'generative network model' often refers to models that do not require an observed network as input, and we here focus on such models rather than permutation models (see Hobson et al. 2021 for a detailed review of permutation approaches and their relation to generative modelling).

Whereas new generative network models are sometimes developed for the purpose of a specific study, many studies use 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 (Section 4 and 6).

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 is the Poisson model where the probability of linking is the same for all pairs 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; see also the later sections about model features).

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 Section 4 and 6), and a main reference. Many other generative network models have been developed - we have selected models that are particularly well-known and are widely used (or very influential) in network science. Note that the information given here is for the models in what may be considered their most essential 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 **Random graph model** **Erdős-Rényi model** **G(n,p) model** **G(n,L) model**	Random network / Poisson network	Random linking	n (number of nodes) p (linking probability) *or:* n (number of nodes) L (number of links)	No	No	No	Erdős & Rényi 1959
Small-world model **Watts-Strogatz model**	Small-world network (for some parameter settings)	Random rewiring of a clustered initial network	n (number of nodes) k (average degree) β (rewiring probability)	No	No	No	Watts & Strogatz 1998
Preferential attachment model **Price model**	Directed scale-free / power law network	Preferential attachment (linking based on node degree)	t (number of timesteps)	Intrinsic	Yes	No	Price 1976
Preferential attachment model **Barabási-Albert model**	Scale-free / power law network	Preferential attachment (linking based on node degree)	m0 (initial number of nodes) m (number of edges for each added node) t (number of timesteps)	Intrinsic	Yes	No	Barabási & Albert 1999

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)	Extrinsic	No	No	Caldarelli et al. 2002
Stochastic block model	Modular network with communities (i.e. network with assortative mixing)	Linking based on node similarity (categories)	n (number of nodes) c (number of communities) P (linking probability matrix)	No / 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 Section 4.

**This concerns whether the original model produces link weights; links weights can always be added (see Section 4).

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

An important feature of generative network models is that they usually contain stochasticity, which means that networks made with the same model and parameter setting are unlikely to be identical to each other, although they will be similar. The models can therefore be used to create large ensembles of networks, with common structural properties and random structural variation among the networks. The networks in an ensemble may be thought of as replicates in a simulated experiment, where different generative models - or the same model with different parameter settings - may be used to generate different treatment groups (ensembles). Using large network ensembles instead of single networks is highly useful because it 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.

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.

3. 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 Section 5).

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 with the purpose of understanding 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.

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. Barabási & Albert 1999, Price 1976, 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 and debate in network science due its properties and impact on network function (Barabási & Albert 1999, Broido & Clauset 2019, Holme 2019).

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 (described in Section 2), which facilitates studies of how these properties affect the processes concerned. 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. 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 (e.g. 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. 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 (Section 2) allows for investigating the relationship between specific structural properties and network robustness.

4. 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 Section 6.

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 (for example the Poisson model; Box 1, Table 1). 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 are 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. Some general generative network models include a value for each node (e.g. the hidden parameter model, Table 1), and exponential random graph models (Table 1) can include multiple node attributes. Extrinsic node attributes used in generative network modelling 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 and in Section 6), 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 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). 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 (see also Section 2). 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 dyadic linking probabilities (Section 2) typically do not require growth procedures, but can be used with them. They are typically used without growth because it is faster and 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. 2024). 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.

5. Uses of generative network models in animal social behaviour research

Generative network models 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 R code included in the Supplementary Material.

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. Another study (Brask et al. 2024) investigated how different preferences for traits (i.e. preferences for

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	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. 2024

social partners with a certain sex, age, 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 social aging, Siracusa et al. 2023; cooperativeness, Darden et al. 2020). In Figure 1, 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 in the Supplementary Material).

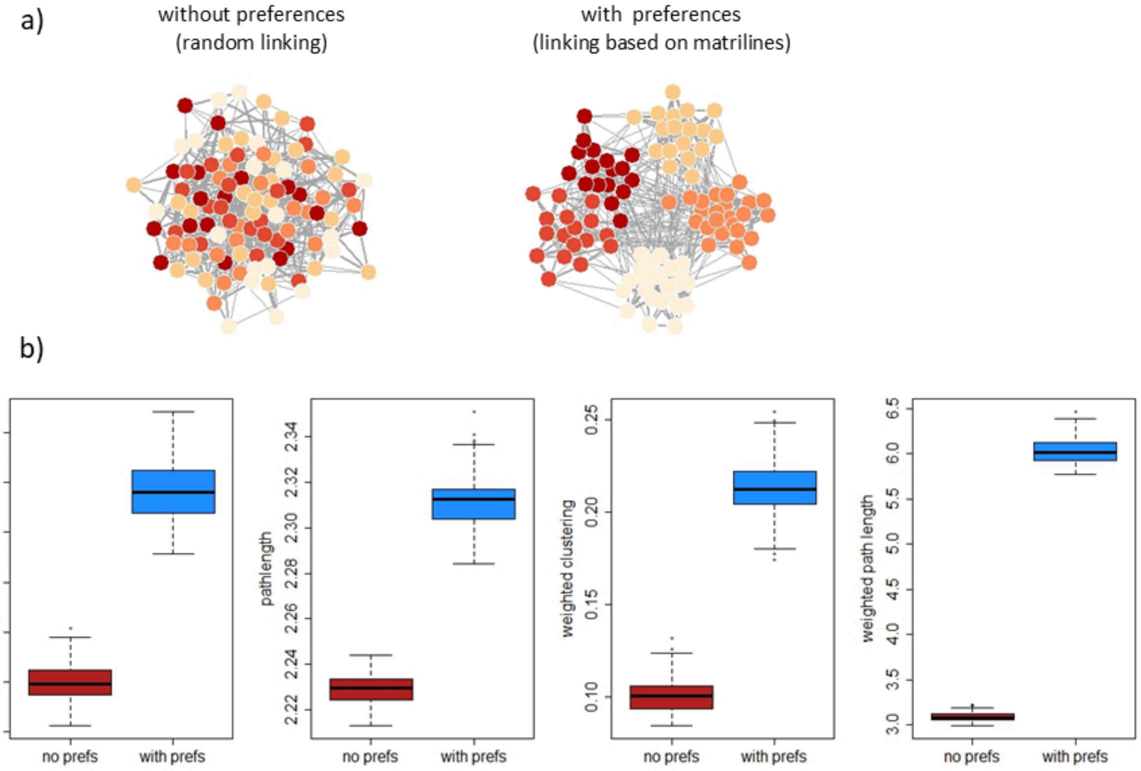

Fig. 1. An example of how generative network modelling may be used to study the emergence of animal social networks. We are interested in how social preferences for individuals similar to oneself (homophily) affect social network structure, in a social system where there are five matrilines and individuals 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 socialising is random). An example of each type of network is shown in a). 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.

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. 2 we provide some simple examples of generative network models being used as the basis for epidemiological modelling in this way.

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 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. 2, code available in the Supplementary Material), we include dynamics of the networks themselves in two ways. In the first (Fig. 2a-c), the extent of social connectivity differs between two seasons, and in the second (Fig. 2d), 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).

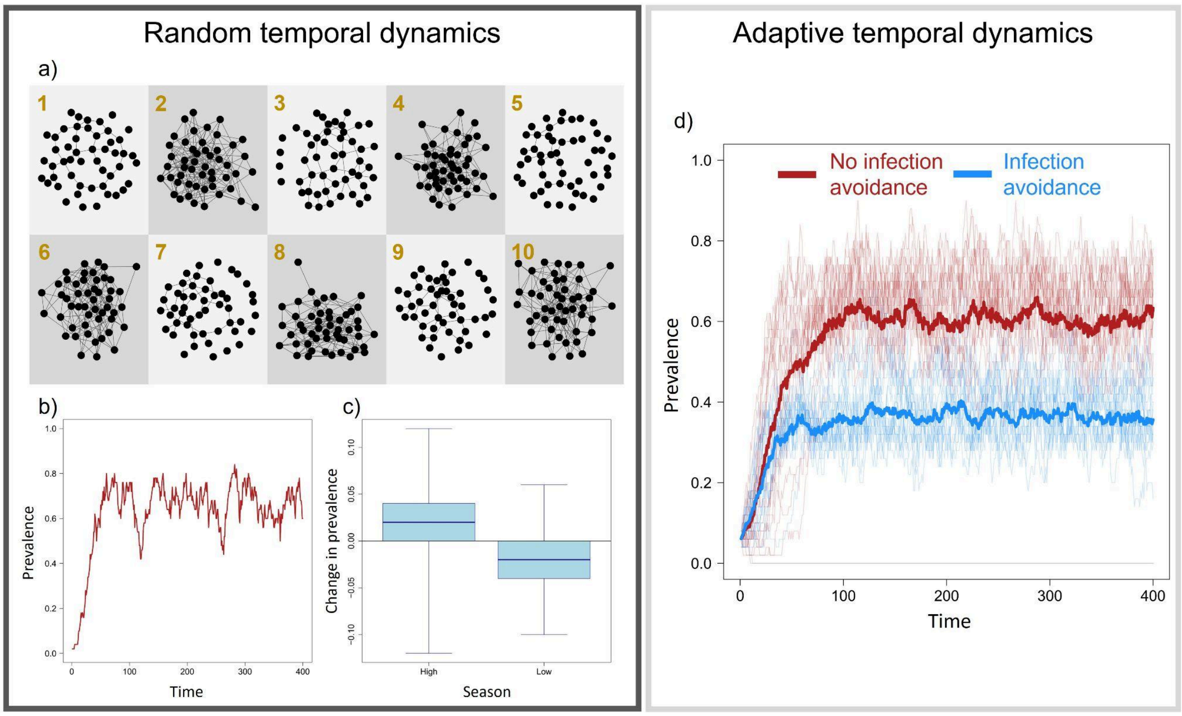

Figure 2. Examples of how generative network models may be used to study dynamics on and of animal social networks. We are interested in the spread of diseases in social networks. On the left we use a generative model of random temporal social dynamics unrelated to the disease model. a) the model consists 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.

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 Section 3, 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. 2024). Simulated

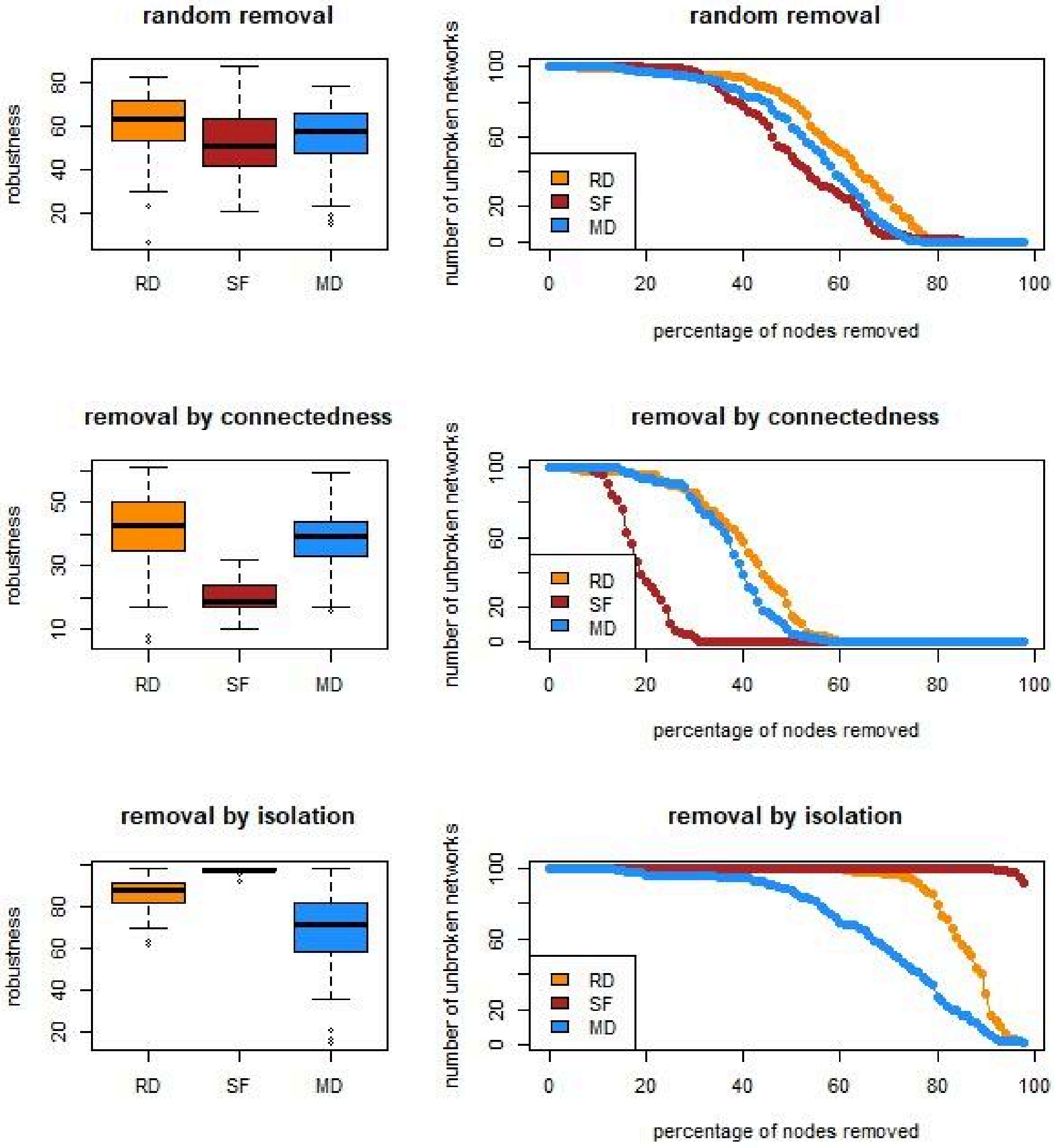

Figure 3. An example of how generative network modelling may be used to investigate the robustness of animal social networks. We are interested in the robustness of structures characterised by modularity (network communities), which is frequently observed in animal systems. Using the trait preference model (Brask et al. 2024), 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. 1). 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). 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.

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). 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. 3 we show an example case study of how generative network models combined with node removal may be used to study the robustness of animal social networks (code available in the Supplementary Material). We are interested in the robustness of networks with a modular structure, and we investigate this by measuring the resilience of such networks to different types of loss of individuals (node removal) and comparing this 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 Fig. 4 we show an example of this (code available in the Supplementary Material). Here, we are interested in determining 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. 4).

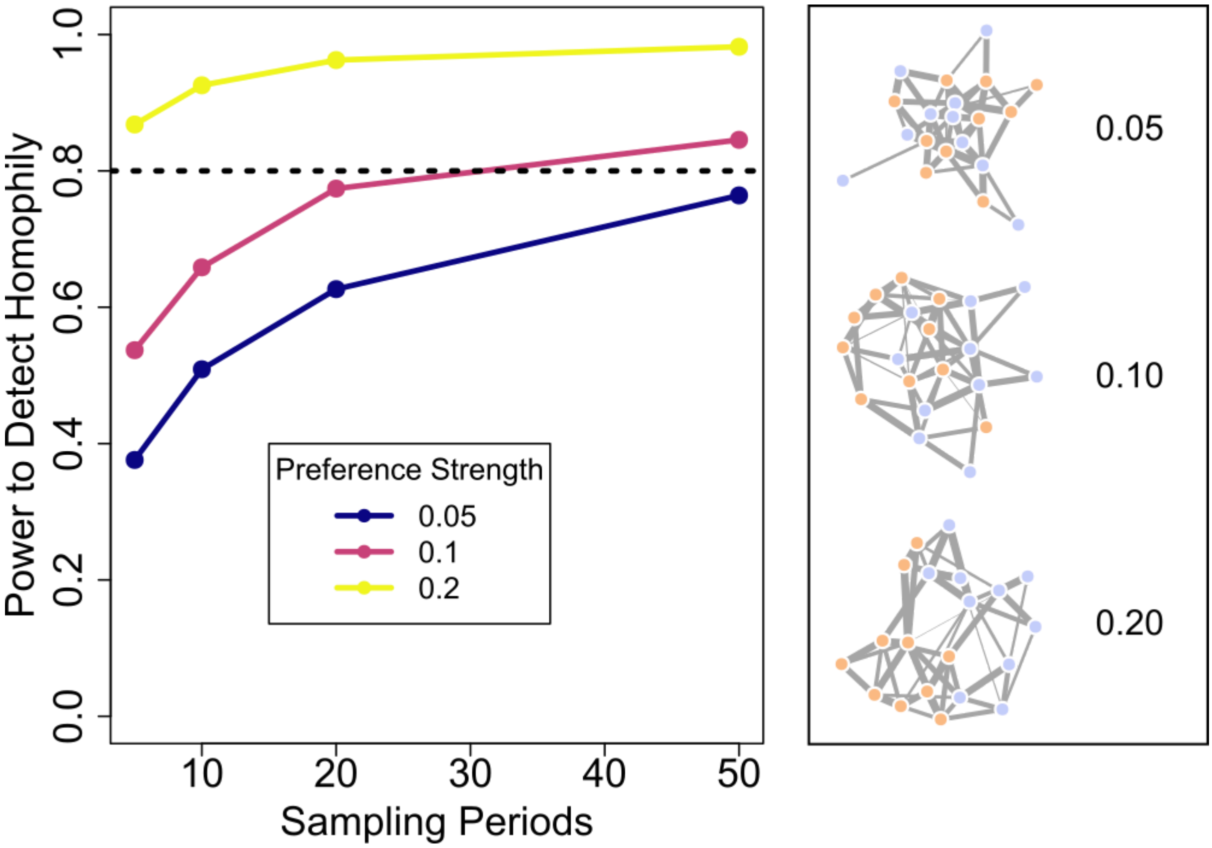

Figure 4. An example of how generative network models may be used for power analysis in animal social networks studies. In this example, we are interested in testing for social homophily by some categorical trait in a ('real') group of 20 individuals. We intend to measure association networks through 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. 2024 (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.

6. Model features in relation to animal social behaviour research

We here revisit the model features described in section 4 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. 3). 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. 2024, Table 2; or several simultaneous substructure-building processes: exponential random graph models, Table 1). 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 are 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 first 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. 2024). The latter approach may be particularly useful if the research question concerns a specific 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 in animal social networks imply 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.

The traits of individuals play a key role for the network structures (reviewed in Brask et al. 2024). ***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. 2024) 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 group 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. 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 Section 4).

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 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 ‘link weights’ in Section 4 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. For example, Rozins et al. (2018) use 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), while 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.

7. Choosing the right generative network model for an animal behaviour study

Generative network models can be useful for many different research questions concerning animal behaviour (Section 5), 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. One key thing to consider is to what extent the networks and the linking process (i.e. the modelled social behaviour), respectively, should resemble those of real-world animal social networks (e.g. a specific system/species). It is also important to be aware 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). Below we consider different kinds of models and when to use them. The model features considered in Section 4 and 6 are also relevant to consider when selecting or constructing a model. See Box 2 for where to find tools and code for generating networks with generative network models.

Box 2. Where to find tools for generative network modelling

- **R functions for some common standard models** can be found in network-focused R packages such as igraph (Csardi & Nepusz 2006), sna (Butts 2023), statnet and ergm (Handcock et al. 2018). Many standard models can also be implemented with relatively few lines of code, and programming-experienced researchers may prefer this option for flexibility and control.

- **R packages for general generative network models inspired by animal social networks** have recently started appearing, including the genNetDem package (Silk & Gimenez 2023) and the okaapi package (based on the trait preference model described in Brask et al. 2024).

- **Code for specific generative network models** may be found as supplementary material to the research papers where the model was developed.

Common standard 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. 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 as benchmark cases ('control groups') that are for example compared to more realistic or real-world networks (as in Fig. 3). For example, Rozins et al. (2018) used both the Poisson (Erdős-Rényi) model and the configuration model (Table 1) as "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 such standard models for comparison, they are rarely suitable as *statistical* null models, as constraints on behaviour or imposed by the sampling process will be important to account for (De Moor et al. 2024). 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 (Section 3) are also of interest in this field (Section 5). Additionally, these standard generative models could 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.

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. 2024). These 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 made specifically for animal social systems (Silk & Gimenez 2023).

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 by one or more real network structures (see for example Siracusa et al. 2023). This 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, the similarity between the modelled 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 generative processes of interest.

Generative network models for statistical inference

While we have here 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. 2024 for a conceptual example). Vice versa, this 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 models, as artificial networks can be generated from these models after they have been parameterized with data.

8. 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 2022, Brask et al. 2024). We hope that the introduction and overview given above will be useful for researchers taking part in this adventure.

Acknowledgements

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Supplementary material

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

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.

Paper	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

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

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 a stochastic block model type 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. 2024
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

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

Estimating uncertainty and reliability of social network data using Bayesian inference	Methodological	Linking probability	*Modified stochastic block model 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 stochastic block model 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 stochastic block model 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

Modelling associations between animal social structure and demography	Methodological	Linking probability	*A simplified stochastic block model 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 stochastic block model 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 stochastic block model 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

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 stochastic block model (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.* *Adaptations of Poisson model* *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

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 stochastic block model to generate networks with known modularity.*	Theoretical	Yes*	Evans et al. 2021
When to choose dynamic vs. static social network analysis	Social transmission 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 Disease ecology	Linking probability	*Modified Havel-Hakimi model (in two parts for between and within community edges).* *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 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 Disease ecology	Linking probability	*Simulations from exponential random graph models fitted to empirically-derived contact data*	Raccoon	No	Hirsch et al. 2016

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 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

Mechanisms of reciprocity and diversity in social networks: a modeling and comparative approach	Behavioural ecology	Mixed (spatial and interactions)	*3 models:* *GrooFiWorld* *FriendsWorld* *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

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 of group-level social information	Dominance hierarchies	Interactions	*ABM based on directed interaction rules for each individual*	Theoretical	Yes	Hobson et al. 2021b

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. stochastic block model features). Edge probabilities then used to simulate association events.*	African elephant	No	Wiśniewska et al. 2022

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