Layers of latency in social networks and their implications for comparative analyses

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Abstract

Animal social systems are remarkably diverse. Linking this diversity to its ecological and evolutionary drivers and consequences has been a major focus of biological research. Initial efforts have been done within groups, populations, and species. Equipped with this information, researchers are now turning to investigations of social structure that are comparative in nature. However, comparing social networks remains a considerable logistical and analytical challenge. Here we present the 'layers of latency framework', a conceptual framework that helps researchers to uncover and study the latent social structures that are of interest to them. We then use this conceptual framework to examine how we can tackle some of the central challenges to comparing animal social networks, focusing on differences between networks in behaviour type, sampling type, sampling effort, sampling scale and network size. For each of these focus points, we describe why and how they create challenges for comparative analyses, and we suggest potential directions for solutions. The layers of latency framework can help researchers to identify networks and features they can (or cannot) compare. In doing so, this framework facilitates advances in cross-species social network studies with the potential to generate new and important insights into the ecological and evolutionary drivers of variation in social structure across the animal kingdom.

Introduction

The animal kingdom features a remarkable diversity of social systems, from solitary individuals to large cooperative groups (Clutton-Brock, 2016; Rubenstein & Abbot, 2017). Yet, our understanding of the ecological and evolutionary causes and consequences of this diversity remains incomplete (Kappeler et al., 2019; Kurvers et al., 2014). Comparing animal populations facing distinct environmental challenges can provide insights into the influence of ecological variables such as predation and food availability on social patterns (Barsbai et al., 2021; Krause & Ruxton, 2002; Lukas & Clutton-Brock, 2018), and reciprocally, how these social patterns impact ecological factors, such as pathogen transmission (Albery et al., 2021; Bansal et al., 2007; White et al., 2017). Comparative analyses can also reveal how social systems evolve alongside life history traits (Silk & Hodgson, 2021) and interact with demographic mechanisms (Clements et al., 2022; Shizuka & Johnson, 2020).

As a result of countless long-term efforts to collect social data (Clutton-Brock, 2021; Sheldon et al., 2022), numerous animal social datasets exist, capturing social structure across diverse species and environments. With the emergence of large databases bringing together these data across taxa (e.g. MacaqueNet, De Moor et al., 2023; Animal Social Network Repository (ASNR), Sah et al., 2019; DomArchive, Strauss et al., 2022), attention has turned to the statistical methods with which such datasets can be compared (Albery et al., 2024; Ellis et al., 2021).

Comparative social network analysis offers a holistic approach to draw inference about the drivers and consequences of animal social structure (Croft et al., 2016; Pinter-Wollman et al., 2013; Webber & Vander Wal, 2019). By explicitly representing social structure as an emergent property of social interactions between individuals (Hinde, 1976), social network analysis can be used to ask questions on the function and evolution of social relationships at the level of individuals, dyads, social groups and populations (Weiss et al., 2020; Whitehead, 2008). Comparative social network analyses across multiple populations or species can thus generate important insights about ecological and evolutionary processes that shape variation in social structure (Albery et al., 2024; Whitehead, 2008).

However, despite the value of comparative social network analysis, only a relatively small body of literature compares social networks across species and taxonomic groups and only few studies so far have examined networks from multiple species collectively to draw conclusions about the evolution and drivers of variation of social systems (Albery et al., 2024). A major reason for the lack of comparative social network studies is the viability of comparing networks that are generated employing different methodologies, and that are potentially widely divergent in key properties such as network size and behaviour types (Faust & Skvoretz, 2002).

Here, we offer an overview of five key challenges that create disparities between social networks and provide guidance on when and how to overcome these challenges in comparative analyses. A common theme to these challenges is that the observed networks we compare are most often different from the underlying, latent (i.e. unobservable) networks we want to make inferences about. We therefore begin by introducing a 'layers of latency' framework that provides a unified view of how different biological and observational processes interact to influence the social structures we observe. A clear understanding of how sampling biases and constraints contribute to variation in observed social networks helps to make principled decisions on how best to account for differences between networks when comparing them. While we introduce this framework in the context of comparing networks, it provides a valuable conceptual framework for all social network analyses, be they comparative or not.

The layers of latency framework

One key issue in network analysis is that observed networks often do not directly, or exclusively, correspond to the biological phenomenon of interest. Firstly, the social relationships we quantify are usually based on only a subset of social interactions – those that have been recorded – and the observed network therefore does not correspond directly to the real pattern of interactions. Secondly, even when all social interactions that happen in a group are recorded, the network links quantified from those are unlikely to correspond directly to individual preferences regarding social partners, because of constraints that hinder individuals in realising their preferred relationships.

To provide a structured way of thinking about this, we present the *layers of latency framework* where social structure is viewed as a hierarchy of networks: the observed social network to which researchers have access, and two layers of latent networks - a real social network and an underlying social preference network (see Fig. 1 & Table 1). The observed social network represents a sample (i.e. observed interactions or associations) from a real network. The real network is the actual pattern of all interactions or associations between individuals, which itself is a partial realisation of the individuals' social preferences for each other. These preferences can also be represented as a network (e.g. a directed network representing the strength of preference that each individual has for the others): the social preferences network.

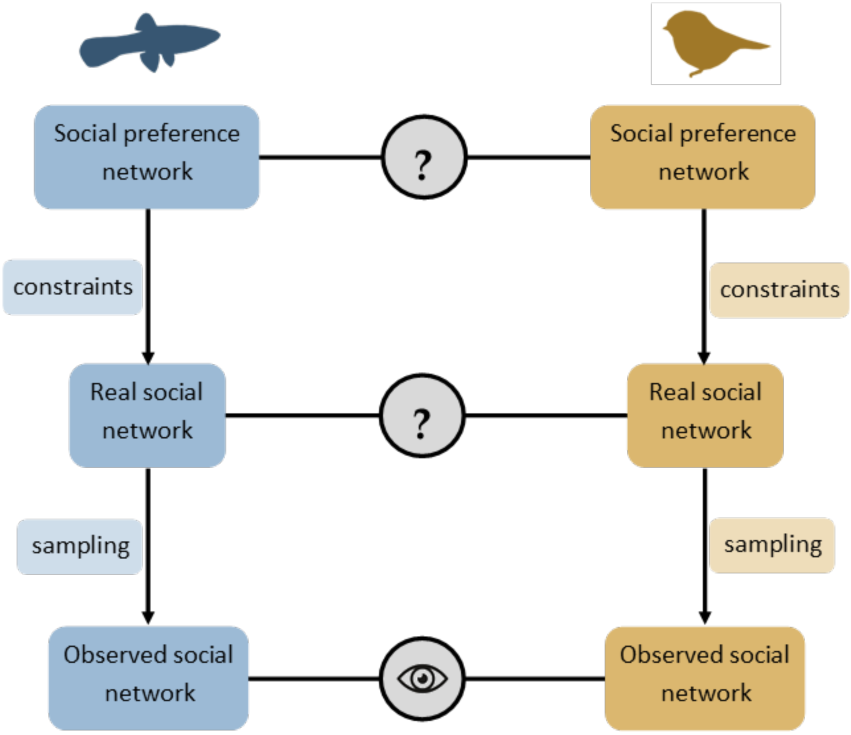


Fig 1. The layers of latency framework. Social structure can be considered as a hierarchy of networks: the observed social network to which researchers have access, and two layers of latent networks - the real social network and an underlying social preference network. The social preference network refers to the patterning of social preferences between individuals, such as the tendency for some individuals to prioritise interactions with relatives (Smith et al 2014)) or with individuals with similar personality traits (McPherson et al 2001). The real social network is the complete patterning of interactions or associations between individuals. The real social network reflects the social preferences impacted by interindividual and/or environmental constraints. The observed social network is the patterning of social interactions or associations as it is recorded by researchers. The observed social network reflects the real social network impacted by sampling biases, and the social preferences network impacted by both constraints and sampling biases. When we compare networks across species (e.g. here a fish and a bird), we typically compare observed social networks (the eye icon), but our research question typically concerns differences between the real networks or between the social preferences networks (the question mark icons). To ensure that analyses of the observed networks accurately reflect the latent networks of interest, it is important to consider any factors along the path from the question mark to the eye that could result in differences between the observed and latent networks. This includes accounting for sampling biases when the focus is on comparing real social networks and accounting for both sampling biases and constraints when comparing social preferences networks.

Mismatches between the observed social network and the two latent networks (or indeed between one latent network and the other) are the result of two main sources of bias: sampling biases and biases caused by constraints (Fig. 1). Sampling biases occur because the observed social network is almost never a perfect sample of the real network, but instead certain individuals or certain interactions are better sampled than others (Altmann, 1974; Bateson & Martin, 2021). For example, a researcher using biologgers to record proximity between pairs of animals may not be able to afford to put a biologger on every individual in the population, or a researcher observing behavioural interactions cannot simultaneously watch all individuals at once. Biases caused by constraints occur because individual social preferences cannot always be realised as social relationships. These constraints may come from different sources, including incompatible preferences between potential interaction partners, and environmental constraints such as spatial distances between individuals and features in the physical environment (Fisher et al., 2021; Webber & Vander Wal, 2018). For example, if all individuals in a group prefer high-ranking individuals, only a subset of those individuals may have those preferences realised, as the time high-ranking individuals have available to socialise is limited (Seyfarth, 1977).

Research questions are almost always about the latent network layers rather than the observed network (Lundberg et al., 2021). For instance, questions about the role of kin and rank in partner choice pertain to the social preferences network (Chakrabarti et al., 2020; De Moor et al., 2020; Smith, 2014; Snyder-Mackler et al., 2016). On the other hand, investigations into the influence of social structure on disease or information transmission (Aplin et al., 2012; Collier et al., 2022; Silk & Fefferman, 2021) pertain to the real social network. However, analyses are typically run on the level of the observed network (Fig 1). Understanding which latent network layer is of interest for a given question, and how the observed network relates to that latent layer is therefore essential for reliable social network analyses.

Challenges of comparative social network analysis

A major challenge for comparative social network analysis is that networks have often been constructed based on different behaviours, data collection methods, sampling effort, and biological scales (Albery et al., 2024; Canteloup et al., 2020; Davis et al., 2018; Faust & Skvoretz, 2002). These differences can impact the extent to which a given observed network corresponds to the latent network of interest. The key challenge in comparing networks is therefore that comparisons are made at the observed network layer, but that the underlying real network or social preferences networks are of interest. Correctly accounting for differences between networks therefore requires understanding how sampling and constraints impact those differences, as these factors can potentially generate spurious and biased differences between the observed network and the real or the social preferences network (Fig. 1). Here, we consider challenges faced when comparing animal social networks, discuss how they fit within our layers of latency framework, and how this framework provides some potential solutions. Specifically, we consider the following challenges: differences in 1) behaviour types, 2) sampling types, 3) sampling effort, 4) size of networks and 5) scale across networks (Table 2). While we treat these challenges independently here for clarity, there are inherently links between them that may be important to take into account when comparing studies with different designs.

Because of the ‘layers of latency’ in social network structure, challenges associated with network comparisons are both methodological and philosophical, and there often is no 'one size fits all' solution. Careful consideration of the question at hand is needed to determine how to deal with the different potential sampling biases and constraints (Fig 1) that might need to be taken into account. In the following sections, we outline some of the main differences between networks, how they can impact sampling biases and constraints, and how best to account for them.

Table 2: Summary of general challenges faced when comparing animal social networks.

Challenge	Description
Behaviour type	The type of behaviour used as the edges in a social network (e.g. grooming, proximity, aggression) changes the interpretation of network properties. The biological function of the same behaviour may differ between networks, or different behaviours may have similar functions. Whether or not networks based on different types of behaviour (or the same) can be compared therefore depends on the functions of the behaviours in the given populations, and on the research question.
Sampling effort	Sampling effort refers to the amount of data collected. This can vary substantially between networks, leading to levels of uncertainty that vary by network. When conducting comparative network analyses, it is therefore important to use statistical frameworks that take the uncertainty into account in the statistical testing.
Sampling type	Networks to be compared may differ in terms of sampling type. Firstly, they may be based on different sampling protocols, such as focal sampling versus scan sampling. Secondly, network edges can be quantified using different measures, such as probabilities or rates. Network data that come from different sampling protocols and/or different forms of edge weight quantification are not necessarily directly comparable, and sampling type is therefore important to account for when comparing networks.
Network size	Network size is the number of nodes, i.e. individuals, in the network. Network metrics can change with network size, and it can therefore be relevant to control for network size when comparing networks. The relationship between network size and metric value differs between metrics and can also depend on the generative processes underlying the networks. This makes controlling correctly for network size challenging. Whether network size should be controlled for, and how it can be done, depends on the research question as well as the generative processes of the networks and the metrics of interest.
Network scale	The social scale of observation can often differ between studies or between the data available and the research question being asked. For example, one study may look at the full population whereas another may look at a subcommunity. This can be a challenge as it can lead to incorrect inference if ignored, e.g. networks of group-living species can appear cohesive when single groups are studied, whereas networks of that same species may appear highly fragmented if the wider population is included in analyses.

1. Differences in behaviour type across networks

The same social preference network can underlie real social networks corresponding to multiple, different behaviour types. For example, individuals might prefer to associate and affiliate with the same individuals or might rarely fight with their preferred affiliation partners. Therefore, a first issue determining the comparability of networks is the type of behaviour used to construct them. While this may seem straightforward, this issue is anything but trivial. The biological function of the same behaviour may differ between networks, or different types of behaviours may serve similar functions. Both cases could be highly misleading when comparing networks. If the goal of an analysis is to compare networks that represent a similar operational function, it might seem obvious that an affiliation network based on grooming should not be directly compared to an agonism network based on physical aggression (Lehmann & Ross, 2011; Madden et al., 2011). Yet, determining which behaviours can be compared often requires more nuanced considerations that take the research question and in-depth knowledge of the biological function of behaviours into account, especially for between-species comparisons.

For example, various behaviours have been used to quantify social relationships in different studies and species, ranging from direct interactions such as grooming and allopreening (Kenny et al., 2017; Schülke et al., 2022), to spatial associations (Ilany et al., 2015; Mbizah et al., 2020) and co-membership of a group (Franks et al., 2010). Yet, whether these networks can be compared, and considered to represent the same function, will always be contingent on the research question and the biology of the compared study species. Meanwhile, the same type of behaviour can serve different functions in different systems, and might reflect different information depending on the context. For instance, animals sitting in proximity within a 5m range could hold substantial meaning in wild populations, indicating close association, whereas that same distance might not carry the same information in a captive population where individuals have less space over which to spread. Therefore, any comparative study whose question depends on comparing ‘like to like’ will need to carefully evaluate whether the behaviours used represent the same operational function within a given context.

Another crucial consideration with regard to behaviour type in the comparison of networks is the potential impact of sampling bias (Table 1; Bateson & Martin, 2021). Sampling bias can impose divergent impacts on different behaviours, or even the same behaviours in different systems or circumstances. For example, recording interactions can be relatively straightforward in terrestrial species but practically unfeasible in species primarily living in high forest canopies or underwater (Farine & Whitehead, 2015). Consequently, a much smaller fraction of the actual interactions that occur (the real social network in Fig. 1) may be observed for an aquatic species than a terrestrial one. This would result in a much sparser observed network (Fig. 1) assuming the same methodology, even if the true real network was exactly the same on land and in water. Similarly, different constraints (Table 1) might operate on different behaviours. For example, certain behaviours like sex and grooming are often difficult to direct at more than one partner at a time. In contrast, individuals can sit near or vocalise to multiple partners at once and as such these types of behaviours are less constrained by limitations related to partner preference. Hence, behaviours may be less comparable across systems that exhibit disparities in the sampling biases or constraints associated with those behaviours.

In summary, to make meaningful comparisons, researchers should consider the specific biological function(s) of behaviours that matters for their research question, along with inherent differences in sampling biases and constraints across the systems of interest, and tailor their approach accordingly.

2. Differences in sampling effort across networks

In addition to biases in sampling (Fig. 1), another aspect of sampling that can differ between networks and affect their comparison is sampling effort. Sampling effort refers to the intensity with which behaviours have been sampled (such as the length of time for which individuals have been observed), and mainly affects the uncertainty around estimates of edge strengths and network structure (Hart et al., 2023). For instance, in a network constructed based on just one hour of observation, some dyads may appear to spend most of their time in close proximity. Yet, this estimate could be a highly uncertain representation of this dyad's edge in the real network due to the amount of time spent sampling. Extending to a hundred hours of sampling effort may provide a more accurate estimate of the weight of this edge in the real network and may lower the level of uncertainty around that estimate. Because the networks we observe are (typically) only a sample of the real social network (Fig. 1), accounting for sampling effort is crucial to estimating how well the observed network reflects the real network. Incorporating this uncertainty ensures that statistical models can make robust biological inferences that are less influenced by the observation process (Higgins et al., 2008). Uncertainty should therefore not only be quantified, but also carried forward into downstream statistical analysis in empirical research.

Accounting for uncertainty in the estimated network metrics is important for any social network analysis but becomes especially crucial when comparing networks constructed with varying sampling efforts. These networks inherently differ in the uncertainty surrounding their observed edge weights and consequently any estimated network metrics. Failing to account for this uncertainty might lead to wrong conclusions. For example, a comparison between a network constructed from one hour of observation and one built from 100 hours might lead to the erroneous conclusion that individuals in the one-hour sampling network spend more time in proximity. In reality, they may spend the exact same amount of time in proximity, but the conclusion is influenced by divergence in sampling effort between the two networks.

One effective solution to address the challenge of variable sampling effort when comparing networks is to use models that estimate the real network based on the observed network as a latent structure, with an explicit degree of uncertainty. This estimated real network can then be treated as the outcome variable in subsequent analyses (De Bacco et al., 2023; Hart et al., 2023; Redhead et al., 2023). This is in contrast to working with the observed network without uncertainty estimates around the edges, as most commonly done in animal social network analyses. Several Bayesian models have recently been developed to quantifying uncertainty around network edges based on sampling effort across individuals.

For instance, within the BISoN framework (Hart et al., 2023), network metrics are calculated from draws of the Bayesian posterior distribution of the latent real network edge weights. Doing so generates a posterior distribution of network metric values (instead of a single value, or point estimate), therefore explicitly including uncertainty in the metric estimates, where higher observation effort leads to narrower distributions, reflecting higher certainty. Once network metric posteriors have been generated, they can be passed to downstream statistical analyses, such as regressions, thereby carrying uncertainty forward into statistical analyses. As such, BISoN and similar frameworks provide a tool to way reduce the impact of different sampling effort when comparing networks and improves efficiency of analyses.

In summary, when comparing networks, researchers should always account for differences in sampling effort. An effective solution to do so is to consider the real network as a latent structure, which is estimated with a degree of uncertainty, determined by the observation effort. Recent frameworks (De Bacco et al., 2023; Hart et al., 2023; Redhead et al., 2023) provide tools to estimate network metrics as posterior distributions of the estimated latent real network, therefore explicitly estimating uncertainty in network metrics, that can be carried forward in subsequent analyses.

3. Differences in sampling type across networks

Many challenges are associated with comparing networks constructed using different sampling methodologies (Albery et al., 2024). The two we focus on here are differences in sampling protocol and differences in how the collected data are summarised into edge weights in the observed social network.

The first challenge is that networks often differ in the sampling protocols used to build them. Recording the complete set of interactions (the real social network in Fig. 1) among individuals in a network is typically unfeasible, meaning that it is only sampled data (the observed social network in Fig. 1) that is available to researchers. This observed social network, and how it is related to the real social network, will vary depending on how data were collected. For example, recording any interaction that is observed (known as 'ad libitum' sampling) can introduce significant biases to the observed social network, where less conspicuous behaviours or less central individuals are more likely to be missed (Altmann, 1974). To address these biases, sampling methods have been developed to provide systematic samples of interactions (sampling in Fig 1), relying on predefined rules to dictate when and how interactions are recorded and which individuals are observed (Bateson & Martin, 2021). Use of these approaches will result in a more consistent relationship between the real social network and observed social network. Some of the most commonly used sampling protocols include focal continuous sampling (recording all interactions that include a given individual for a set amount of time), group scan sampling (recording the behaviour of each individual in a group instantaneously at regular time intervals), gambit of the group approaches (where individuals observed in the same group are assumed to be associating or interacting) (Altmann, 1974; Whitehead, 2008). More recently, technologies such as camera traps, biologgers, or drones have been used to observe and record animal behaviour remotely (Webber & Vander Wal, 2019).

However, each of these sampling protocols have inherent biases in the behaviours or interactions that are recorded. For instance, focal continuous sampling provides rich detailed data on the focal individual and its social partners for a given time, but overlooks all other social interactions during that time. Similarly, sampling using biologgers is often limited to a subset of individuals in the group because of their higher cost. Sampling the whole group at regular time intervals, on the other hand, captures a greater extent of the overall occurrence of interactions across group members, but may miss rare or short behaviours occurring between sampling intervals (Altmann 1974). The same is true for sampling using camera traps or drones. Networks that researchers may wish to compare have often not been constructed using the same protocols, in particular if the data were not originally collected for the purpose of the comparative study. This creates a challenge, because differences in sampling protocol can generate a discrepancy between the difference of interest (at the real social network level Fig. 1) and the observed difference (at the observed social network level).

A second challenge is that different networks are often built based on different measures of edge weights, which are not always directly comparable and can even sometimes represent different aspects of relationships. For instance, both how often individuals interact with a given partner, and how much of their social time they are willing to spend on a given partner are meaningful components of a relationship, which do not necessarily carry the same information (Dunbar, 1976). Raw data on social interactions typically comes from a count of the number of social interactions and/or the duration of each interaction observed (Martin and Bateson, Altmann 1974). Which of these raw data are used is determined, in part, in part, by the selected sampling protocol, although certain protocols permit the collection of multiple types of raw data. Edge weight may then be represented as the rate of social interactions per unit of time (rates, the count of the number of social interactions over observation time), as the proportion of observation time two individuals spend engaged in a social behaviour (proportions), or as the likelihood of a social behaviour occurring between two individuals within a specific time frame (probabilities, the ratio of samples during which the behaviour is recorded over the total samples). Probabilities and proportions are both unitless measurements bound between 0 and 1. Rates, on the other hand, are the expected number of events per unit time (e.g. associations per hour), with a lower bound of 0 and no upper bound. Because the probability of being in a particular state at a point in time is equal to the proportion of time spent in that state, a unit increase in a probability is equivalent to a unit increase in a proportion, allowing direct comparisons between probabilities and proportions, all else being equal. Comparing probabilities or proportions to rates is, unfortunately, not simple, as there is no natural way to interpret them on the same scale.

Selecting an appropriate association/interaction index can help mitigate these two sampling issues to a certain extent, and various indices have been devised to address different sampling biases (Franks et al., 2010). In addition, using a standardisation such as Z-scoring makes edge weights (or derived network metrics) interpretable in terms of standard deviations, thereby making rates and proportions/probabilities comparable. The main drawback of this approach is that standard deviations are calculated from point estimates from the data, and won't be accompanied with uncertainty (see previous section *Differences in sampling effort across networks*). Alternatively, the observed network can be used to approximate the real social network. This goal has been the focus of recent methodological developments. For instance, mixture models identify clusters of similar interaction levels in the observed data, creating categories of individuals that share strong, intermediate or weak social relationships (Ellis et al., 2021; Weiss et al., 2019). These categories are robust to variation in sampling type, and can therefore readily be compared. Bayesian models have also been developed to reconstruct the real network (with uncertainty around the estimates) by explicitly incorporating assumptions of how the sampling process impacts how the observed network represents the real network (Young et al., 2020). This approach enables direct comparisons between networks at the network level of interest.

In summary, when comparing networks derived from various sampling methods, it is important to address two key challenges: biases in the recorded social interactions due to differing protocols and variations in how edge weights are measured. Although employing suitable indices and Z-scoring can alleviate some of these concerns, it is essential to recognize how distinct sampling processes may introduce disparities between the observed network and the network of interest. Recent methodological advancements, including mixture models (Ellis et al., 2021; Weiss et al., 2019) and techniques for reconstructing the true network from observed data, (Young et al., 2020) offer promising avenues to navigate these challenges effectively, allowing for more accurate comparisons.

4. Differences in network size

Network size, or the number of nodes in a network, varies substantially in animal societies ranging from only a few individuals (e.g., an immediate family group) to large assemblages of several hundred individuals (Webber & Vander Wal, 2019). This variation is shaped in part by differences in social organisation, dispersal patterns, ranging behaviour and/or territoriality (Kappeler, 2019). Observed networks (Fig. 1) can furthermore include different subsets of the underlying real network, driven by researchers' choices regarding who is observed (for instance focusing only on adults or on habituated individuals). Observed network size therefore depends on features of the social system being investigated (which determine real network size) as well as the decisions made by researchers when designing their study (which determine what subset of the real social network is observed). We use the term *network size* here to refer to the size of real social networks (Fig. 1), that is, the number of individuals within a biologically meaningful social neighbourhood. We explore the effects of sampling different subsets of these networks in the next section (*Differences in network scale across networks*).

Comparing networks of different sizes is a complex challenge, because network size can greatly influence other aspects of network structure in non-trivial ways that depend on the nature of the underlying process generating the network (Boccaletti et al., 2006; Hobson et al., 2021). In addition, this effect can differ from one structural feature to another and thus is often not the same for different network metrics (Anderson et al., 1999; Naug, 2009). Thus, the relationship between network size and network metrics is not simple, but rather is often non-linear, with the shape of the curve depending on the metric and on the underlying generative processes. Therefore, a simple control such as dividing the network metrics with the network size often does not properly remove the size effects, and may even introduce bias. Consequently, finding a suitable approach to comparing networks of different sizes can be difficult and context-dependent.

The first important question to consider is whether and when it is appropriate to control for differences in network size or not. Biological factors may influence key aspects of the network structure, at least in part through their effects on network size. Network size is therefore an important feature of network structure itself. For example, if an individual's risk of being infected by a pathogen depends on its number of social contacts, then being in a larger group helps explain higher exposure risk. In these cases, conditioning network comparisons on network size would mask effects of biological importance (Fig. 2A). However, for other research questions it may be necessary to condition on network size to make a meaningful biological comparison. For example, to test the hypothesis that forest-living species have denser social networks than those in open habitats, conditioning on network size is necessary to demonstrate that habitat influences network structure in a manner that is not solely driven by the relationship between habitat and network size (Fig 2B). Finally, we may consider whether the difference in size between the networks we want to compare represents a general pattern. For example, if we want to investigate whether two species differ in their social structure, then we may want to control for network size if the species do not generally differ in network size (but the networks for which we collect data do), and we may want to not control for network size if the difference in network size reflects a general difference between the species.

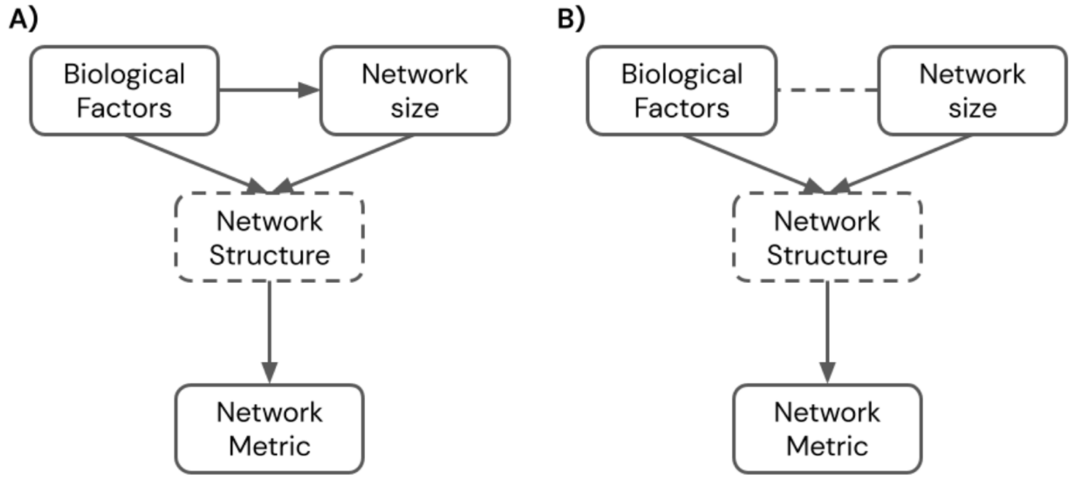


Figure 2: Potential causal mechanisms linking network size to structure. Note that 'network' here refers to the real network (Fig 1). The dashed line between biological factors and network size in panel B indicates a potential non-causal association. The dashed boxes indicate that the structure of the real network is a latent, unobservable variable, which can be quantified, but not entirely captured by a network metric. In A, biological factors affect network structure partially via network size, and controlling for network size would mask some of the influence of biological factors on network size. In B, biological factors do not influence network size, but through exogenous variables, biological factors and network size may be correlated. Unless network size can be effectively controlled for, the overall impact of biological processes on network structure cannot be estimated, as network size is a possible confound. In both cases, potential confounds act on the network structure itself, not on the network metric. As long as the chosen network metric is an accurate quantification of network structure, potential challenges do not lie with the metric, but with underlying causal assumptions.

The next important question to consider is *how* to control for differences in network size. Even when controlling for network size is appropriate for a specific question, doing so in a way that correctly removes size effects not relevant for the research question can be difficult. A main reason for this is that the relationship between size and network metrics depends on the underlying generative processes, and these processes are often unknown. For instance, unweighted network density (the ratio of actual to potential connections in a network) is differently impacted by network size, depending on the process that generates the network (Fig. 3). Similarly, the strength of social relationships can also depend on network size in different ways. For example, relationship strength could decrease with network size if individuals get more partners when the network is larger but are restricted in their socialising time. In contrast, relationship strength can be independent of network size if individuals keep a constant number of partners regardless of network size, or if they get more partners but can also increase their socialising time (so that they can spend as much time with each of their partners even when the number of partners is increased). Each of these scenarios would require different controls, to correctly remove the effect of network size from each of the networks (Hobson et al., 2021).

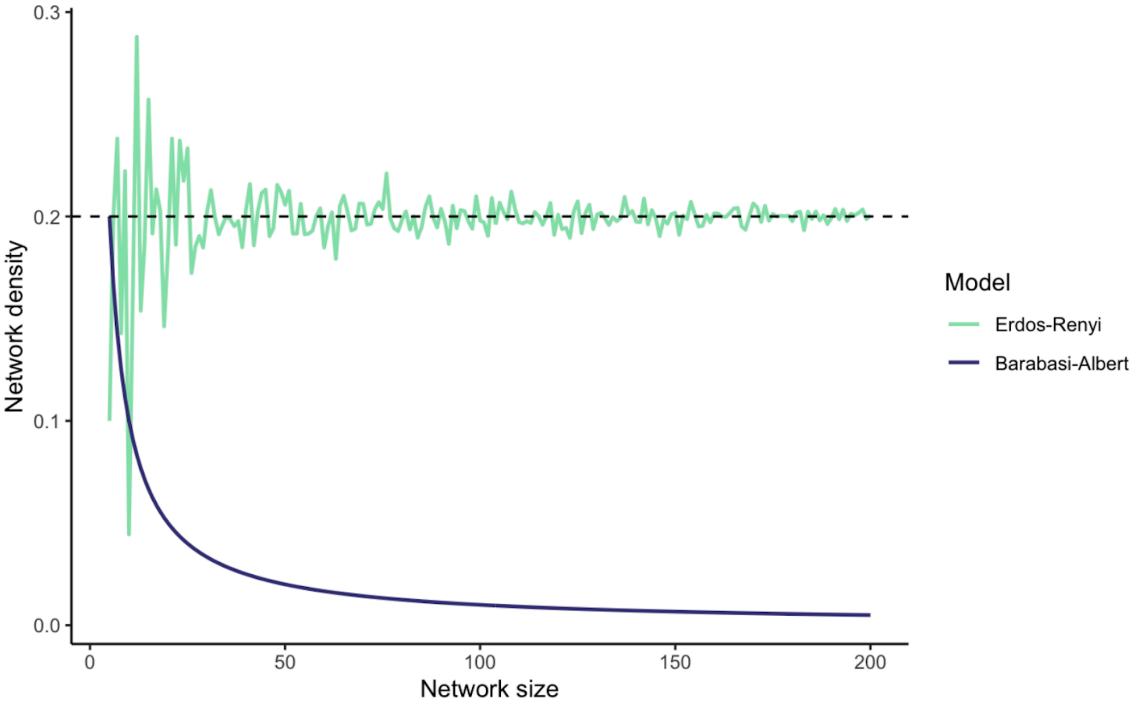


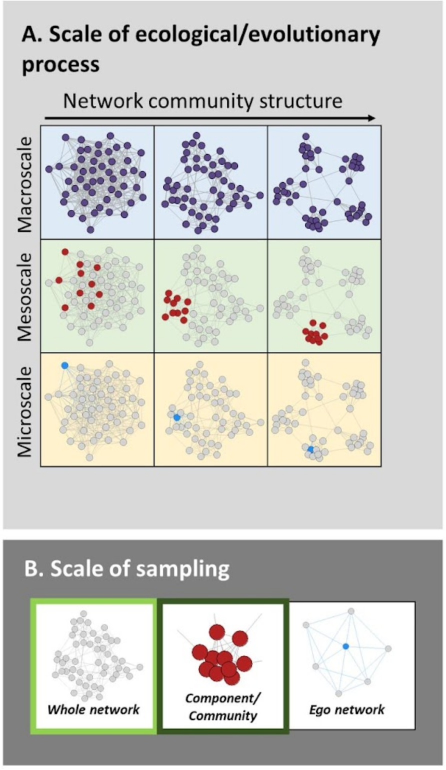
Figure 3: Network metrics can be influenced by network size in different ways, depending on the underlying processes that generate the network. In this example we compare how unweighted network density depends on network size for networks generated from two different processes. If individuals choose their interaction partners at random ('random attachment', captured by the Erdős-Rényi model, Erdős-Rényi 1959) with a fixed probability (e.g. each pair of individuals has a 40% chance of interacting) then the network density stays the same regardless of the size of the network. In contrast, if individuals preferentially interact with their most popular groupmates and each individual contributes with a fixed number of edges ('preferential attachment', captured by the Barabási-Albert model, Barabási & Albert 1999), then the density of the network declines exponentially with its size.

Given the above (and see (Hobson et al., 2021), properly accounting for network size in comparative network analysis is often difficult, if not impossible, unless valid assumptions are established about the individual behavioural rules driving the networks. Gaining information about social preferences underlying the networks to be compared (Fig. 1), as well about as the relationship between network size and relationship strength, can therefore be useful for applying appropriate controls for network size. Understanding the rules of social interactions in a system helps predict how network characteristics change with network size through simulations and informs decisions about whether and how to consider network size in analysis.

To summarise, when comparing networks, differences in network size are almost inevitable. Whether and how to account for these variations in network size is a long-standing challenge in network sciences, and solutions are often context-dependent. When network size is central to how network structure relates to biological variables of interest, conditioning on network size could mask important effects. When biological factors do not directly influence network size, or when the effects of interest arising from biological factors on network structure do not occur through their impact on size, it is advisable to condition on network size. To condition properly, the relationship between network size and network metrics needs to be estimated, which requires knowledge or assumptions about the rules for interactions that are driving the structures, and the relationship between network size and relationship strength (edge weights) Thus, transitioning from the observed network level to the real network level and from the real network level to the social preference level (Fig. 1) can help us in constructing proper controls for network size in comparative analyses.

5. Differences in network scale

A final challenge when comparing networks across studies is dealing with differences in network scales that exist across animal social network studies (Albery et al., 2024). Networks can be studied at different social and spatial scales, depending on the ecological or evolutionary process of interest. For instance, both a single group in a population, and the entire population are (a part of) the real network (Fig 1). As a result, observed networks (Fig. 1) can represent samples of the real network at different scales, which can introduce biases in comparisons if they are not conducted with appropriate caution (Fig. 4). For example, in populations where individuals cluster into groups, network modularity at the group level is likely to be much lower than if measured at the population level. Comparing the networks resulting from a study conducted at the group level with a population-level study of a similar network could therefore lead to the conclusion that the two social systems differ in their modularity. This would be incorrect because the difference comes from sampling on different scales, rather than actual differences in social structure between the systems.



C. Scale of analysis

Response variables	Explanatory variables (*examples*)	
-Network-level measures	-Species traits -Population traits -Demographic traits	Macroscale
-Community-structure -Core-periphery structure -Cliques -Triads	-Species traits -Population traits -Demographic traits -Group traits -Spatial behaviour	Mesoscale
-Dyads	-Individual traits -Relationships (e.g. relatedness, home range overlap)	Microscale
-Node-level measures	-Individual traits -Spatial behaviour	

Figure 4. An illustration of the challenges of scale in social network analyses. A. Social network analyses address diverse questions related to various ecological and evolutionary processes for which different scales of network structure are important. Networks can vary considerably between species across these scales (e.g., in community structure; illustrated). B. Research teams make decisions about the scale at which to sample networks based on biological properties of their study system and their research question as well as any additional constraints (e.g. time, money). C. Research teams make decisions about the scale of analysis, focusing on measures that may capture the structure of their sampled network as a whole down to measurements that quantify the network position of single individuals. Any mismatches in the scales at which networks are sampled can generate challenges for subsequent comparative analyses.

The challenges posed by the spatial or social scale of sampling in comparative network analysis is related to how the observed network is drawn from the real social network (Fig 1). In some cases we sample only a small part of the real social network, while in others we sample much more widely (Fig. 4). This challenge is complicated by the fact that decisions related to the scale of different behavioural studies are often tied to the biology and research questions of the original researchers. This generates a complex causal pathway to explain any differences in observed network structure between studies, especially when comparative analyses are conducted on existing social networks rather than data collected explicitly with the comparison in mind.

The extent to which comparing across network scales poses a challenge depends on the scale of analysis required to answer the question of interest (Fig. 4). If we compare networks using structural measures (network metrics), these can vary from measures of the connectedness of individuals (microscale), to measures of the structure of the whole network (macroscale). Meso- and macroscale (whole) network metrics are likely to be particularly susceptible to differences in the scale of sampling between datasets (Fig. 4). For instance, comparing network density (a macroscale property) from a single social group with network density from an entire population will often be misleading (unless the question is specifically about densities at different network scales), because the scale of the observed network is likely to affect their density, with loosely connected groups at the population-level decreasing the overall density, compared to when only a group is sampled. In contrast to meso- and macro-level metrics, the challenges associated with comparing microscale (node-level) metrics of networks sampled at different scales can be reduced because these are often less affected by scale and will be more reflective of the values in the real networks (including non-sampled individuals). However, this will vary according to the generative processes underlying the real social network structure and the specific choice of node-level metric, meaning caution is still required. For example, individuals from a group-living species that form more between-group connections will have much higher betweenness centrality when a population- rather than group-level network is studied.

While ideally, cross-scale comparisons should only compare networks studied at similar scales, this isn't always possible; researchers might not know at which scale networks were sampled (e.g., when it is difficult or impossible to measure the size or scope of a population), or sampling scales of networks for a given analysis can differ (e.g., if one of the networks cannot be sampled at a global scale for practical reasons, or the data were originally collected for another study). In some cases it may be possible to compare networks sampled at different scales by sub-sampling from the network sampled at a larger scale, but this process is untested and fraught with complexity on how best to subsample (e.g., previous section *Differences in network size* for challenges associated with accommodating the correct generative processes).

Another potential solution is to compare models of the real (entire) networks created by network imputation which can be used to "fill in" missing parts of networks sampled at a smaller social or spatial scale (Young et al., 2020). This will typically need a well-specified generative model of each of the social network structures to be compared (which could vary from a well-specified regression model that captures the factors influencing network structure to a complex agent-based model). At times, specifying these generative models may require a quantification of the underlying social preferences (Fig. 1) alongside the incorporation of any physical/ecological constraints. These steps, theoretically at least, facilitate the imputation of unobserved social interactions to align the scales of the networks for comparison. However, in practice there are numerous challenges in doing this successfully. Any comparisons of imputed social networks should include uncertainty around the generative process, whether it be multiple draws from a posterior distribution (Hart et al., 2023) or multiple outputs from a full generative model. Similarly, it may not be possible to get all the necessary information from the empirical data. To provide one example, in many studies focused on within-group social networks, social interactions with members of other groups may not be recorded or may occur so infrequently that they remain unobserved. In these cases it would be impossible to accurately parameterise any model parameters for between-group social interactions. In these cases it is inadvisable to impute the real social network beyond the scale of the original study, and certain comparative analyses may not be possible.

In summary, networks can be samples across various social and spatial scales. This can lead to biases in comparisons if not carefully conducted, as observed networks represent networks of different scales. While there are multiple potential approaches to address the challenges posed by variation in network scale, caution is required when choosing between them, and it may be best to take a conservative approach when comparing social networks collected from very different social systems or across divergent scales.

Discussion

In this paper, we present a conceptual 'layers of latency' framework that captures how observations of animal social networks are related to the social processes that researchers study. In particular, we have focused on how the layers of latency framework applies to comparative analyses of social networks, illustrating how social and environmental constraints together with sampling biases can generate differences between observed networks and the underlying latent networks that are of interest to researchers. Comparative social network analysis offers huge potential for researchers working in ecology and evolution, but this approach comes with a set of big challenges that are yet to be fully resolved (Albery et al., 2023). We use our layers of latency framework to offer broad philosophical and methodological considerations and solutions to five of these challenges. We hope these will help to facilitate the analysis of network datasets, and lead to further developments of methodological tools that enable these types of analysis to be conducted robustly and to fulfil their full potential.

While we have presented the challenges that arise in comparative social network analysis independently here for clarity, a key point is that these challenges are closely linked (Fig. S2). For example, the size of the real network (in combination with the research questions being addressed) may influence the scale at which sampling is undertaken, which can then influence the size of the observed network. In many cases, correctly capturing how these challenges are inter-linked for a given set of datasets or studies will be integral to best identifying how to deploy methodological tools to address them.

Currently, our guidance for comparative network analysis is:

- Identify the network layer to which your research question applies - are you interested in the real network, or the preferences network? This will shape your analytical decisions going forward.
- Be careful when conducting comparative network analyses and be clear about the limitations of any approach used. Networks collected by different researchers on different study populations for different purposes may be particularly challenging to compare, as they are likely to differ in numerous ways.
- Be aware of how sampling can affect the differences between your networks. It may only be possible to compare observed networks if the real network has been sampled in a consistent manner (i.e., sampling type and sampling effort are the same).
- Consider the *generative process* that links the social preference network to the real network, and the *observation process* that links the real social network to the observed network for different sampling methodologies and/or datasets. Understanding these processes can help in making different networks comparable or to (carefully) impute missing information for networks sampled at different scales.
- Maintain uncertainty when moving between network layers - if you estimate the real or social preference network then Bayesian methods can help propagate uncertainty into subsequent comparisons .

Future theoretical and methodological work will be central to facilitating analyses that make use of our layers of latency framework (both for comparative network analyses and more generally). Moving between network layers necessitates detailed knowledge of the key processes that influence the emergent structure of animal social networks. While such knowledge is available for some particularly well studied species, a combination of theoretical modelling and empirical analyses will often be necessary to identify patterns that can be used to pinpoint the generative processes underlying animal social networks. New statistical tools will then be required to efficiently estimate the latent networks, as well as to tailor existing observation models (e.g. from capture-recapture models) to social network contexts. These steps forward will benefit greatly from interdisciplinary collaborations between behavioural ecologists, statisticians and network scientists (Brask et al., 2021).

We hope the challenges and potential solutions presented here will help to move the field towards a more comprehensive suite of tools for comparing social networks. Our proposed framework highlights that appropriately controlling for sampling biases and constraints is an important step in facilitating comparative animal social network analysis. With further development, comparative social network analysis could become an accessible, reliable and powerful approach to answer long-standing questions in ecology and evolution. We hope that this paper provides a better understanding of the key challenges facing researchers applying these approaches, and some potential ways to address them. Good luck!

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