Comparative approaches in social network ecology

Authors: Gregory F Albery*[1,2], Shweta Bansal[1], Matthew J Silk*[3,4]

Affiliations

[1] Department of Biology, Georgetown University, Washington, DC, USA

[2] Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

[3] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

[4] Institute of Ecology and Evolution, School of Biological Sciences, University of Edinburgh, Edinburgh, United Kingdom

*Corresponding authors: Department of Biology, Georgetown University, Washington, DC, USA. gfalbery@gmail.com (GFA); Institute of Ecology and Evolution, School of Biological Sciences, University of Edinburgh, Edinburgh, UK. matthewsilk@outlook.com (MJS)

Abstract

Social systems vary enormously across the animal kingdom, with important implications for ecological and evolutionary processes such as infectious disease dynamics, anti-predator defense, and the evolution of cooperation. Comparing social network structures between species offers a promising route to help disentangle the ecological and evolutionary processes that shape this diversity. Comparative analyses of networks like these are challenging and have been used relatively little in ecology, but are becoming increasingly feasible as the number of empirical datasets expands. Here, we provide an overview of multispecies comparative social network studies in ecology and evolution. We identify a range of advancements that these studies have made and key challenges that they face, and we use these to guide methodological and empirical suggestions for future research. Overall, we hope to motivate wider publication and analysis of open social network datasets in animal ecology.

Introduction

The social lives of animals vary immensely and across many axes (Hinde 1976; Whitehead 1997; Hobson *et al.* 2019; Prox & Farine 2020). In some species, individuals live predominantly solitary lives, only interacting with others sporadically, while others form spectacular aggregations of many thousands. Similarly, while some species live in stable groups and form social bonds that last a lifetime (Mitani 2009; Bruck 2013; Dakin & Ryder 2020), in others social preferences may be weaker and the identity of social partners relatively unimportant.

Variation among social systems is closely tied to ecological and evolutionary pressures faced by different populations (Kurvers *et al.* 2014; He *et al.* 2019; Evans *et al.* 2020; Cantor *et al.* 2021b). Variation in well-studied benefits (e.g. access to information, avoidance of predation) and costs (e.g. competition, parasitism) of social interactions across species likely explains why particular social systems are associated with specific environments (Leu *et al.* 2016) or taxonomic groups (Chak *et al.* 2017). However, given the ecological environment can also cause variation in social structure within populations (e.g. (Jordán *et al.* 2021)), it is important to decompose intra- and inter-specific variation in social structure. Because, the social structure of populations alters the direction of evolution (Fisher & McAdam 2017, 2019), determines the outcome of ecological processes like disease spread (Keeling & Eames 2005; White *et al.* 2017), and potentially influences a species' resilience to global change (Fisher *et al.* 2021) identifying explanations for inter-specific variation in social structure has important implications and applications. Consequently, comparative approaches are popular with researchers examining the evolutionary ecology of sociality (Lukas & Clutton-Brock 2013; Lukas & Huchard 2014; Kappeler & Pozzi 2019).

Nevertheless, there are substantial challenges in applying comparative approaches in socioecology, of which a major one is classifying or quantifying variation in animal social systems. Recent work (e.g. (Lang & Farine 2017; Prox & Farine 2020)) has begun to provide higher-dimensional classifications of sociality, but there remain limitations in the power and universality of these approaches, as qualitative classifications only provide coarse approximations. Further, in many contexts, it is the specific pattern of interactions that plays a role rather than the type of social system *per se*. With the popularisation of social network analyses in behavioural ecology, the time is ripe to apply more quantitative comparisons that address diverse questions around interspecific variation in social structure and dynamics.

Social networks have become an integral part of a behavioural ecologist's toolkit (Farine & Whitehead 2015; Webber & Vander Wal 2019). They provide the link from individual behaviour to group- and population-level structure and outcomes (Fig. 1), and so help study various aspects of animal behaviour including dominance (Shizuka & McDonald 2012; Hobson *et al.* 2021a), cultural evolution (Voelkl & Noë 2008; Cantor *et al.* 2021a), and epidemiology (Keeling & Eames 2005; Bansal *et al.* 2007; White *et al.* 2017). Applications of network approaches in socioecology have grown rapidly and now encompass substantial geographic and taxonomic diversity, albeit with remaining biases (Webber & Vander Wal 2019).

Despite the recent growth in animal social network analyses, few studies have undertaken multispecies comparisons of social networks or used meta-analytic approaches to test for broader evolutionary or ecological patterns in animal social structure. This is despite multispecies analyses of social networks having multiple advantages for comparative analysis in social ecology. These benefits emerge from network descriptions of social systems providing: diverse measures to succinctly quantify different aspects of social structure; the ability to quantify fine-scale variation in social systems beyond features such as group size; and a way to unify analyses across social scales, from individual- to group-, and population-level features. Two main issues have limited the use of comparative analyses on social networks: i) it is challenging to compare the structure of networks of different sizes (Faust 2006), especially when they are generated by different behavioural processes

(Hobson *et al.* 2021b); and ii) there has been a shortage of animal social network datasets available to compare.

With the recent development of multi-species repositories of social network data (*Box 1*) and an increasingly advanced statistical toolkit, there is now the potential to overcome these issues and exploit the potential of comparative social network analyses in ecology and evolution. Here, we review the existing studies that have undertaken such analyses. We then identify outstanding challenges to successfully employing comparative and meta-analytic approaches with social network data, suggesting potential solutions and highlighting specific areas in need of further methodological research, as well as identifying promising areas for future empirical research. Overall, our paper provides a roadmap for conducting these analyses in ecology and evolution and aims to inspire the development of new statistical tools to increase their accessibility, as well as motivating the collection and publication of further open social network datasets.

The current state of comparative network analysis

The Data: As of 3rd November 2022 we uncovered 49 studies that compared multiple species' social networks, spanning 16 years (2007-2022; Table S1). Initially, these studies typically compared a small number of species and networks; however, over time, these numbers have increased exponentially (Figure 1). While some studies still compare a few species at a time, there are now many that encompass several hundred networks encompassing dozens of species – three of which also included humans. These larger studies often featured replication of several networks within each species, (potentially) allowing estimation of within- and between-species variation in network structure. On three occasions researchers have developed (or are developing) substantial publicly available databases (*Box 1*). Otherwise, larger studies tended to produce their network datasets through literature searches and independently contacting researchers to request data (Nunn *et al.* 2015; Rocha *et al.* 2021), or by aggregating datasets that the authors themselves collected (Bhadra *et al.* 2009; Pasquaretta *et al.* 2014). Given the few independent datasets, substantial reuse of said datasets, and growing exploitation of the animal social network repository (ASNR; *Box 1*), there has been encouragingly little duplication of effort in producing network meta-datasets. In the near future, researchers carrying out comparative behavioural analyses will be well-placed to use much of the available data, rather than encountering issues with dataset harmonisation and unification – as has been the case with datasets of host-pathogen associations, for example (Gibb *et al.* 2021).

Taxonomic skew: Many studies (19/49; 39%) were focused primarily or entirely on primates, with a particular focus on macaques (*Macaca* sp.; e.g. (Sueur *et al.* 2011; Ciani *et al.* 2012; Balasubramaniam *et al.* 2020)). Otherwise, there was broad coverage of different taxonomic classes, including fish (Roose *et al.* 2022), hymenoptera (Bhadra *et al.* 2009), and elephants (de Silva & Wittemyer 2012), as well as large-scale studies that included diverse vertebrate classes and some invertebrates (Sah *et al.* 2017; Rocha *et al.* 2021). It is unclear how the taxonomic skew of these databases could influence the results of pan-dataset analyses.

Species-level analyses: Many comparative papers (11/49=22%) examined how species' traits correlated with their social network topology with others doing so qualitatively. For example, several analyses linked primates' cognition or behaviour with the structure of their networks (Sueur *et al.* 2011; Pasquaretta *et al.* 2014). Conversely, two studies (Poulin & Filion 2021; Collier *et al.* 2022) used the ASNR to examine how a range of species' contact network structures were associated with their parasite communities, focusing on parasite species richness (Poulin & Filion 2021) or the evolution of parasite species transmitted over the focal host's contact networks (Collier *et al.* 2022). These studies incorporated external databases of host-parasite associations (Stephens *et al.* 2017) and human parasite traits

(Richardson *et al.* 2001; European Centre for Disease Control 2016), as illustrated in Figure 2.

Generative models: Two papers (2/49=4%) developed generative models for the formation of social networks, which they validated using multi-species network datasets. For example, (Ilany & Akcay 2016) developed a model for network formation by social inheritance, validating their predicted networks using data from four species.

Methodological studies: Several studies (6/49=12%) used animal social network meta-datasets to illustrate new methods or confirm trends in network science or related fields. These included identifying novel scaling trends (Rocha *et al.* 2021; Ward 2021; Ojer & Pastor-Satorras 2022), producing new approaches (Shizuka & Farine 2016; McDonald & Hobson 2018; Ward 2021; Ojer & Pastor-Satorras 2022), or deriving new network traits (Péron 2023).

Dynamical simulations: A particularly common approach (13/49 studies; 27%) to comparative social network analysis was the simulation of transmission dynamics (e.g. (Nunn *et al.* 2015; Sah *et al.* 2017, 2018; Romano *et al.* 2018; Collier *et al.* 2022; Fountain-Jones *et al.* 2022)). This approach may be so popular because, so far, networks have been used to test general ideas for a broad set of potential pathogens. This reduces the importance of disparity in data collection methods and timescales, as (to some extent) the networks are providing a substrate to test ideas in network epidemiology rather than to provide broader ecological insights. These approaches have also often used unweighted (binary) versions of networks, mitigating the impact of variable edge weighting across different studies (see below).

Individual-level meta-analyses: Finally, among our identified studies, there was only one (1/49=2%) “true” meta-analysis – i.e., one that did not use raw data, but rather analysed a series of model estimates published in other studies (Briard & Ezenwa 2021). All other papers derived network-level traits and carried out species-level comparative analyses. We capture the distinction between these approaches in *Box 2*.

Biological overview of comparative network studies

In behavioural ecology: Comparative network analyses in behavioural ecology have predominantly been used to provide insights into the structure and dynamics of animal groups. Frequently, it has been applied to quantify population-level social structure for taxonomically similar species (e.g. bats: (August *et al.* 2014); elephants: (de Silva & Wittemyer 2012); equids: (Sundaresan *et al.* 2007; Rubenstein *et al.* 2015)). In these cases, using a comparative approach can reveal fine-scale differences in social structure that were previously undetected (e.g. (Sundaresan *et al.* 2007)). These studies have also often demonstrated the role of ecological differences between closely related species in explaining variation in social network structure. For example, different social network structures between Australian snubfin *Orcaella heinsohni* and Indo-Pacific humpback dolphins *Sousa chinensis* were attributed to differences in diet, prey availability and feeding behaviour (Parra *et al.* 2011). In a similar way, the role of mating systems (Matsuda *et al.* 2012) and variation in individual traits, such as cognitive capabilities (Pasquaretta *et al.* 2014), have also been investigated. One approach that has perhaps been underutilised is to use comparative network analyses to find general rules for animal social structure. For example, (Rocha *et al.* 2021) found a potential power law relationship between group size and social connectivity, with some evidence that it varied depending on social interaction type.

At a finer social scale, comparative network analyses have also been used to study within-group social dynamics, including dominance hierarchies (Balasubramaniam *et al.*

2018; Hobson *et al.* 2021a) , aggression and social stability (Sueur *et al.* 2010, 2011). Here comparing between species can identify general patterns in within-group interactions. For example, (Hobson *et al.* 2021a) compared dominance networks across 172 groups from 85 different species to identify that most species typically distributed aggressive interactions evenly across all lower-ranked individuals rather than on either close competitors or the weakest individuals. This has important implications for quantifying individual variation in the costs and benefits of social strategies. Comparative studies in macaques (*Macaca* sp.) have investigated how social networks influence fission-fusion dynamics and collective behaviour, for example demonstrating how the importance of kinship differs between socially tolerant and intolerant species (Sueur *et al.* 2010). These types of study naturally extend into applications in collective behaviour, including group fission events and departures (Sueur & Petit 2008). Comparative network approaches have also been used to test the applicability of theoretical models of collective behaviour by demonstrating how more differentiated relationships in within-group social networks lead to reduced cohesion and likelihood of consensus when modelling flocking dynamics (Ojer & Pastor-Satorras 2022).

In conservation and applied animal behaviour: By contributing to our understanding of social dynamics and group stability, comparative social network analyses have also occasionally been used in applied ecology and conservation. For example, in the context of human-wildlife interactions, (Balasubramaniam *et al.* 2020) showed differences among macaque species in how within-group social network centrality was associated with the tendency to interact with humans, with implications for pathogen spread. In the context of conservation welfare, comparative network analyses have been applied to captive populations, revealing long-term social bonds that could inform husbandry decisions (Rose & Croft 2017) or evaluating the impact of environmental enrichment (Dufour *et al.* 2011).

In disease ecology: Comparative social network analyses in disease ecology have helped quantify the role of both individuals and emergent group- or population-level social structures in infectious disease transmission. They have also begun to provide a more generalizable understanding of epidemiologically-relevant features of animal social networks that provides insight at both ecological and evolutionary timescales.

Some studies have combined comparative network data with empirical epidemiological data. For example, (Briard & Ezenwa 2021) used a meta-analysis to show consistent positive effects of network centrality on infection probability, with the pattern stronger for local rather than global measures of social centrality. (Poulin & Filion 2021) demonstrated correlations between some aspects of group social network structure and parasite species richness in parasite groups. As more simultaneously collected network and epidemiological data becomes available from wild host-pathogen systems, these types of study are likely to provide ways to test key hypotheses in disease ecology.

Of studies to apply comparative analysis to the outputs of simulated network epidemiological models on multi-species social network datasets, a small number (e.g. (Carne *et al.* 2013)) have focused at an individual level, comparing the role of individual heterogeneity and/or the value of network-targeted vaccination between species. Many more studies have examined how different aspects of network structure impact epidemiological dynamics, for example: providing and testing new methods to quantify the vulnerability of different hosts to outbreaks (Colman *et al.* 2021; Fountain-Jones *et al.* 2022), linking them to key epidemiological concepts such as density-dependence in transmission (Colman *et al.* 2021) and offering insight into how network structure for different interaction types could influence pathogen evolution (Collier *et al.* 2022). An area of particular interest has been the role of modular social structures in shaping epidemiological dynamics (Griffin & Nunn 2012; Nunn *et al.* 2015; Sah *et al.* 2017), providing insight into how group-living shapes disease risk. One study extended these insights to other types of contagion (Romano *et al.* 2018).

Principal challenges for comparative network analysis

Based on our literature review, we identified key challenges facing comparative analyses of social network structure and classified them into three main groups: meta-analytical choices, between-study comparability, and network features. We generated a framework to help researchers with the principal decisions at each stage of a comparative social network analysis (Figure 4), and provide a number of solutions, many of which address several interrelated issues (Figure 5).

Analytical choices for comparison

Sample sizes: In our review, the median number of networks compared was 12 across 4 species. Especially for more powerful comparative approaches (e.g. controlling for phylogeny, machine-learning approaches etc.), this sample size substantially limits the power to deal with confounding variables and reduces how many questions can be answered. A key solution, which the field is well-placed to achieve, is the coordination and centralisation of publicly accessible databases to facilitate sufficient sample sizes. This could generate issues related to managing a large open dataset and ensuring its continuity, but social network researchers could learn from other efforts to maintain open, partially-automated updating datasets (e.g. (Carlson *et al.* 2022)). Increased power could also be achieved through greater replication per species (e.g. see MacaqueNet; *Box 1*), which would allow quantification of within- versus between-species variation in network structure. This could arise through renewed research effort, wider data acquisition, or incorporating networks at a range of temporal resolutions (e.g. weekly, monthly, yearly) where appropriate.

Taxonomic biases: We identified an overpowering focus on non-human primates, especially macaques, across comparative studies. This was present in both the studies themselves and in aggregated datasets; with substantial overrepresentation of primates in the ASNR, for example (Sah *et al.* 2019). A fear of overcoming the challenges of big taxonomic divides may have driven researchers to focus on small subsets and within-subgroup analyses rather than analysing across the animal kingdom. As such, it remains an open question how comparable these systems are, and whether generalisable rules shape social structure across these divides.

There are other subtle biases present in the data: for example, because ant colonies are relatively easy to replicate and observe, the ASNR contains many replicate ant networks, such that ants are overrepresented at the network level rather than a higher taxonomic level (Sah *et al.* 2019). Because sociality is often studied at different intensities across taxonomic groups (Sah *et al.* 2018), other well-studied taxa may be similarly overrepresented. Studies' findings could be swayed by these taxonomic skews. In the short-term, following the lead of previous studies can help mitigate these issues, for example by subsampling networks for over-represented species (Collier *et al.* 2022) or re-analysing without them (Fountain-Jones *et al.* 2022). In the longer term, targeted addition of new datasets can address taxonomic biases, perhaps using innovative approaches to exploit existing social or movement data, such as approximating proximity networks using Movebank data (Kays *et al.* 2022).

Choosing networks relevant to the question: Careful selection of networks from databases is required to ensure they are relevant for the question posed (Figure 4). For example, there may be little value in using networks based on indirect contacts to model the transmission of many contagious pathogens (Albery *et al.* 2021). Similarly, the relevance of wild and captive network datasets will depend on the question asked and the taxa investigated. Importantly, taxonomic biases may interact with these problems: for example, how does the effect of captivity on network structure differ between ants and macaques?

One particularly difficult incarnation of this problem lies in comparing species with qualitatively different social systems: for example, is it meaningful to compare species with well-mixed fission-fusion societies to ones that lives in stable groups? A potential solution is to use existing frameworks (Prox & Farine 2020) to inform decisions about which types of social systems to compare for any given question. These frameworks can be used to summarise networks based on multidimensional traits, employing emergent continuous variables rather than discrete *a priori* "social organisation" categories. Also relevant here are decisions about which behaviours (and so networks) are relevant to a particular research question (see "Between-Study comparability" section below).

Combining network data with external data: Combining comparative network analyses with external data on individual, group or species level traits considerably expands the scope of questions it is possible to answer in diverse research areas. However, only rarely have studies combined their network data with external data sources (Figure 2), with exceptions including cognitive traits (Pasquaretta *et al.* 2014) and parasite richness (Poulin & Filion 2021). These examples collectively illustrate how integrating comparative network data with other traits provides increased power in identifying general factors shaping social structure and testing hypotheses related to the ecological and evolutionary consequences of these structures. Indeed, one reason that simulations are so regularly used is because they allow approximation of epidemiological consequences of social network structures without necessitating additional empirical sources of information.

One limiting factor for some comparative analyses will be the availability of other species-level traits. In general, basic life-history data will likely be available for species that have been sufficiently well-studied to collect social network data, and these types of information have been collated into existing databases such as PanTHERIA (Jones *et al.*

2009). However, other data types may be more limited. For example, a recent integration of the ASNR and global mammal parasite database (Stephens *et al.* 2017; Sah *et al.* 2019) resulted in a sample size of 18 (Poulin & Filion 2021), as limited data availability required the authors to focus on primates. It remains likely that comparative projects will need to compile external, non-network datasets themselves for some traits. Similarly, while existing databases (see *Box 1*) do contain limited individual-level data (e.g. age, sex) for some networks, this may also limit the number of networks that can be included without contacting the authors of original studies. This highlights the importance of authors providing attribute data alongside their networks to improve our ability to answer individual-based questions.

Between-study comparability

Variable methods of data collection: Networks in multi-species datasets are often collected using diverse and potentially incomparable methodologies, and little methodological research has critically considered how this impacts comparative analyses. In some cases, there are clear issues with comparisons. For example, group-based methods of network construction will typically cause much denser social networks than other forms of data collection. However, in others comparability can be much less clear. Additionally, different data collection strategies can be confounded with taxonomy and social system. For example, rodents may be disproportionately trapped, large mammals GPS-tracked, birds ringed or PIT-tagged, and ungulates censused. Similarly, behavioural interactions are easier to observe in species living in stable groups, while network data for less social species may typically be collected using bio-loggers (Smith & Pinter-Wollman 2021). Further challenges will occur if sampling intensities differ across forms of data collection (e.g. more proximity interactions will be missed for data collected using focal sampling than if most individuals in a group are carrying proximity loggers).

Dealing with the difficulties imposed by data collection methods represents a major challenge. Great care is required, especially because interactions with other study or network features are likely and effects may not be linear. The most conservative solution is to be strict with inclusion criteria (Figure 4) and avoid comparing networks collected in different ways. However, the impacts may also be mitigated by solutions highlighted in other sections, especially when data collection method is confounded with the type of behaviour studied or scale of interaction. In these cases, dealing with interactive effects of these confounding variables will be key. Ultimately, the best approach will be not to avoid comparing them, but to compare them explicitly – both with empirical data and simulations – with the aim of discovering such biases. This approach may be particularly powerful where multiple data collection approaches are used in a single system (e.g. (Castles *et al.* 2014)).

Social/spatial/temporal scale of observation: Studies vary substantially in their scale, whether social (e.g. within-group vs. multigroup), spatial (study area size), or temporal. For example, studies may choose a geographic area and follow (a proportion of) a population there (Firth & Sheldon 2016; Testard *et al.* 2021), or choose certain individuals across a series of groups (Silk *et al.* 2018; Papageorgiou & Farine 2020), or identify a specific group and follow all its members (Kulahci *et al.* 2018). Confusingly, terminology can exacerbate challenges here; some studies use “group” and “network” interchangeably, while others do not. A key challenge is identifying if and when we can compare studies focused on groups with those focused on entire populations/multiple groups. Exacerbating this challenge, other issues such as data collection method and network size are often confounded. Further, the spatial or temporal scale of studies may also be correlated with the proportion of individuals that are tracked or identified, which can also impact topological measures (Gilbertson *et al.* 2021). All these differences could introduce disparities that are difficult to overcome during analysis.

A crucial methodological development would therefore be to identify combinations of sampling approach and types of network measure that can be used more robustly in these contexts, and which should be avoided entirely. Similarly, comparing studies that occur over different timeframes represents a considerable challenge. On the one hand, network data collected over longer durations can lead to greater confidence that the observed network structure is a good representation of reality (Farine & Strandburg-Peshkin 2015; Davis *et al.* 2018; Hart *et al.* 2023). On the other, observing networks for longer will lead to more densely connected networks as more infrequent or random interactions or associations are observed. This will be a greater problem for some data types (e.g. proximity, group-based) than others (e.g. grooming). Networks aggregated over long periods also risk overlooking network dynamics (see subsequent section).

In the short term, careful screening of studies is again important in ensuring the networks used employ a relevant scale. Ensuring that metadata in databases accurately indicates this information (as some already do: (Sah *et al.* 2019)) is therefore vital. Heading towards incorporating data into these databases as dynamic edge lists or at a range of temporal resolutions would allow researchers greater flexibility on whether to include a study or not. It will also be beneficial to apply other previously identified solutions such as (with caution) controlling for the scale of the study within the statistical model (e.g. (Sah *et al.* 2018)), or analysing separately for networks measured at different social scales (e.g. group vs. population) and integrating the results qualitatively or meta-analytically. As with data collection methods, what is most needed is a renewed effort to employ simulations using well-known study systems to more accurately quantify when and how problems will arise when comparing networks across scales.

Disparate edge types: There is substantial variation among networks in how edges are defined (Table 1): some use specific behavioural interactions such as grooming, while others use coarser approaches such as association within a group, or spatial proxies such as home range overlap. Frequently these networks will not be directly comparable (Castles *et al.* 2014). In other cases, it is not necessarily clear the extent to which different observations represent different behaviours *per se*. Some may be nested: for example, sexual contact requires spatiotemporal proximity, and so the former network may represent a subset of the latter. Similarly, it will be challenging to work out what represents comparable behaviour types in taxa with very different ethograms. For example, DomArchive (see *Box 1*) only includes data on dominance networks but includes >150 different "behaviours", some of which are rather distinct. Some network types will also have very different topologies that make them hard to compare directly (Castles *et al.* 2014): for example, fluid exchange networks are generally very sparse and skewed, exhibiting different topologies to direct contact networks (Collier *et al.* 2022). This issue is also confounded with differences in data collection methodologies outlined above, further reducing comparability: for example, GPS tracks might be used to detect grouping, while short-range proximity collars are used to identify direct contacts (Albery *et al.* 2021; Smith & Pinter-Wollman 2021). Because these methods exhibit different sensitivities and sampling frequencies, two networks may have different topologies purely because of this methodology rather than biological differences.

In the short term, careful use of selection criteria can prevent these potential issues (Figures 4 & 5). For example, questions related to within-group social stability may use data on grooming, dominance, social foraging or trophallaxis from the ASNR and combine this with relevant data from DomArchive or MacaqueNet. Researchers can also include data collection methods as fixed or random effects in comparative analyses (e.g. (Albery *et al.* 2022)). However, in many cases, it can be more effective to repeat the analysis for different data collection methodologies and then either qualitatively or quantitatively compare the results. This can even be used as the strength of a study (Collier *et al.* 2022). One could even examine if the results of a comparative analysis are sensitive to inclusion/exclusion of particular behavioural types. In the future, methodological research that uses the comparability of different networks from the same species can help identify interaction types that are more comparable and perhaps use advances in latent network modelling (Young *et al.* 2021; Ross *et al.* 2022) to combine insights from multiple data sources.

Disparate network size: Network size also differs considerably between studies. Historically, differences in network size have been identified as a key problem for comparisons (Faust 2006), by creating several overlapping issues. First and most simply, raw values of many social network measures depend on network size and how best to correct for its effect will differ between measures and is not always intuitive. For example, while degree is best normalised by dividing through by the number of possible *partners* and betweenness is best normalised by dividing by the number of possible *paths*, for other measures this choice is less clear. Second, the value of using size-corrected measures can depend on both the research question and the generative process determining network structure. For example, network size in existing databases could be reflective of either sampling effort or social group size. In the latter case, it can be biologically meaningful that individuals in larger groups have more social connections. Similarly, if the number of connections an individual forms has an upper bound regardless of group size then correcting for group size effects will remove biological signals. However, this will not universally be the case, and in some contexts failing to control for group size could drive misleading conclusions if interpreted incautiously.

Because i) differences in network size may also be driven by variation in sampling (e.g. edge effects or the inability to identify all individuals) and ii) how network measures covary with network size may differ between systems and approaches, great care in interpretation is necessary when network size varies considerably between studies. As such, this is an area in substantial need of methodological research. For example, the advent of Bayesian approaches to impute missing network data (Young *et al.* 2021) and generate uncertainty around edge weights and network measures (Hart *et al.* 2023) can help mitigate issues directly related to sampling differences and allow the focus to be on analytical decisions around the biological effect of group size. One option is to fit network (or group) size as a covariate within comparative models; however, how this is done (e.g. whether it is included as a linear effect) would require careful consideration and cautious interpretation.

Differences in confounding effects of network size and sampling intensity also represent a challenge to comparative analyses assessing the relationship between conditional traits and individual network position (*Box 2*). In these cases, employing Bayesian methods that propagate uncertainty from this initial stage of the analysis through to the cross-system comparative analytic stage would be an ideal solution, especially by enabling studies with better-sampled or larger networks to have greater weight. This is likely to become increasingly feasible as new methods allow uncertainty around social network metric calculations in animal societies (Hart *et al.* 2023).

Network features (and information loss)

Researchers must also decide what level of information loss is acceptable, especially for network dynamics, edge weights and edge sizes (Figures 4 & 5).

Dynamic networks: Social interaction patterns typically change over time and/or between ecological contexts (Silk *et al.* 2017; Smith *et al.* 2018; Shizuka & Johnson 2020) meaning social networks are rarely static, and snapshots or aggregations captured in adjacency matrices are a simplification of reality. Currently very few papers have considered network dynamics within a comparative framework (but see (Rubenstein *et al.* 2015; Chase *et al.* 2022)), in part because dynamic network data is less readily available (e.g. not in the ASNR; (Sah *et al.* 2019)). However, even when conducting comparative analyses using static networks it is important to consider the impact of social dynamics.

Generally, researchers define data collection periods based on their research question (e.g. matching the transmission dynamics of a pathogen (White *et al.* 2017)) and biological knowledge. However, the duration of data collection can also be constrained by convenience factors (e.g. battery performance of bio-loggers, duration of presence in a study location, etc. (Gilbertson *et al.* 2021; Smith & Pinter-Wollman 2021)). Similar considerations and constraints also apply to the frequency of network data collection. This creates a major challenge when conducting comparative analyses because the potential for variation in social dynamics between systems means it is not straightforward to control for study duration. For example, if the rate at which individuals of species A change their interaction partners is much slower than that same rate in species B, then any correction for study duration will introduce bias related to genuine biological differences, rather than achieving what is intended. The potential impact can be limited by focusing a comparative analysis on a subset of social systems (or taxonomic relatives) in which changes in network structure over time are more similar. Alternatively, if using network duration as a control variable, then allowing its effect to vary according to social system, behaviour type, method of data collection, etc. may mitigate this issue to some extent. In the longer run, another effective solution will be storing more data as dynamic edge lists so that researchers have more power to make their own decisions as to whether to use a dynamic or static approach, and the duration over which to aggregate static networks. However, moving towards these higher-resolution datasets may reduce researchers' willingness to share network data, as they contain more information about their study system.

Disparate edge weightings: Considerable variation in edge weight definitions represents another key challenge for comparative analyses, especially when they covary with taxonomy, social system and data collection methods. For example, many studies have used association indices like the simple ratio index (Hoppitt & Farine 2018), and the popularity of alternatives has varied over time and between research communities. In contrast, many contact-based networks use bio-logging devices to measure the duration or frequency of encounters. This creates problems for a comparative analyst because edge weights in different studies can mean very different things. Previous studies have typically used only a subset of networks that use a similar approach (limiting statistical power), extracted only binary networks (losing information on the strength of connections), or fitted a network's weighted/unweighted status as a covariate in the comparative analyses (Collier *et al.* 2022). One potential alternative to this would be to use a simple correction to make edge weights in different networks more comparable (e.g. by dividing all edges by the maximum edge weight to generate a standardised index). However, a potentially more satisfying approach would be to use statistical approaches such as mixture models that can classify edges as belonging to different distributions, e.g. "weak", "intermediate" and "strong" (Weiss *et al.* 2019; Ellis *et al.* 2021). A key advantage would be that any uncertainty in these classifications could be propagated through to subsequent stages of the analysis. Additionally, as is the case with network dynamics, storing network data in raw edge list format would empower those conducting comparative analyses to make their own decisions about how to weight edges to be comparable between studies.

Higher-order interactions: Another source of lost information in all comparative social network studies conducted so far – and in existing data repositories – is that network data is stored as a conventional dyadic network, even in situations where this is a simplification (e.g. group-based networks). This loses information on the size of social interactions that can be captured using higher-order network approaches (Silk *et al.* 2022). While these have only rarely been used in behavioural ecology thus far (Musciotto *et al.* 2022), they are gaining popularity as a tool in broader network science (Battiston *et al.* 2021). It would be valuable to move towards also storing higher-order network data in animal social network databases (e.g. in the form of group-by-individual or incidence matrices) to facilitate approaches that explicitly incorporate this higher-order structure.

Future opportunities for comparative social network analysis

Comparative social network analysis has displayed wide informative power across a range of different topics. Building on and expanding this literature, there remain diverse research areas for comparative social network analysis that are as yet relatively underexplored. Here we focus on disease ecology, behavioural ecology and conservation, as well as the interface between these topics. However, we encourage others to develop additional applications of these approaches, especially as a tool to unify across ecological disciplines.

Transmission and contagion processes: While transmission has been a major focus of existing comparative network analyses, there remain many unanswered questions. For example, most simulation studies of transmission dynamics examined traits of the networks themselves, rather than using the results to explain between-species differences, despite the potential added by integrating additional data (Fig. 2). A prominent example of this lies in our improved understanding of modularity (Griffin & Nunn 2012; Sah *et al.* 2017), which although highly informative has largely not been related to species traits themselves. Similar studies could also extend beyond concepts such as modularity to further explore what species- and population-level traits explain important network properties revealed by existing comparative analyses (Colman *et al.* 2021; Fountain-Jones *et al.* 2022). Similarly conducting more nuanced comparative analyses that examine differences across multiple types of social association and interaction (Collier *et al.* 2022) could be extended to better quantify the expected dynamics of diverse zoonotic and agricultural diseases in their wild hosts.

Moving beyond pathogen spread, there are relatively few explorations of how other social contagions (e.g. behaviour spread) manifest across systems. Because other contagions often exhibit complex (e.g. non-dyadic) contagion behaviour that can differ from how pathogens spread (Firth 2020), with implications for animal social system evolution

(Evans *et al.* 2020), comparative network analyses represent an opportunity to explore the consequences of different social systems for pathogen *and* behaviour spread, as well as to link this to species traits. For example, (Evans *et al.* 2021) showed that only modular networks with small sub-groups favoured the spread of conformist behavioural contagions over pathogen spread. A nice example of how this could be applied to multi-network comparisons is provided by (Beck *et al.* 2023), who compared different social contagions across multiple great tit *Parus majo*r social networks, providing insight into how individual network position linked to the order of behaviour acquisition. Extending these types of study could generalise their insights across diverse taxa, and link outcomes to species-level traits.

Health and immunity: Applications of comparative network analyses in disease ecology could also include better quantifying cross-species social drivers of health and immunity. While the consequences of network structure for outbreak dynamics are relatively well understood (theoretically at least), an individual's social interactions can also influence their stress physiology (MacLeod *et al.* 2023) and health (Snyder-Mackler *et al.* 2020). Consequently, comparative network analyses can help examine the importance of social network structure for the manifestation of individual and population-level disease (or health) itself. To provide a specific example, because mechanisms of immunity are expected to evolve in response to infection (Graham *et al.* 2011), species- and population-level differences in social network structure should manifest in realised differences in immunity across species via their effects on infection prevalence. Comparative network analyses offer an ideal way to test these predicted relationships that moves beyond coarse measures of sociality like group size (Côté & Poulin 1995; Patterson & Ruckstuhl 2013). Future work could integrate individual-level social network position with group or population-level social network structure and explicitly incorporate physiological markers of health or immunity. It should be noted that comparative studies of immunity are also difficult to perform across species due to issues such as the variable sensitivity of the available eco-immunological tools (Boughton *et al.* 2011), but nevertheless even coarse and generalisable measures like white blood cell count (Cooper *et al.* 2012) may prove informative when integrated with comparative social network analyses.

Socio-spatial ecology and behavioural integration: individuals' spatial and social behaviours are tightly intertwined (Webber *et al.* 2023), with spatial behaviour often being important in explaining social network structure (Mourier *et al.* 2012; Pinter-Wollman 2015; Firth & Sheldon 2016). Comparative network analyses offer an exciting opportunity to look at how the role of the ecological environment and movement behaviour in explaining social structure varies among populations and species, testing to what extent variation in these relationships can be linked to other species level traits such a body mass, mobility and kin structure. Examining how spatial and social network types are linked across and within species could help to inform a wide range of empirical questions, e.g. refining our ability to quantify individual variation in optimal group size and structure (Webber *et al.* 2023), as well as encouraging the integration of spatial data types into social network workflows using spatio-temporally parameterised telemetry tracks (Robitaille *et al.* 2019).

Group structure and dynamics: Existing applications of comparative social network analyses have focused on comparing group- and population-level social structure and patterns of group stability. However, typically this has been between small numbers of closely-related species. Extending these approaches across a diverse set of social systems offers the potential to start teasing apart the importance of the ecological environment, taxonomy/evolutionary history and species-level traits (e.g. body mass, mode of movement, migratoriness, mating system etc.) in explaining broad patterns in animal social structure. Using a comparative network approach provides a more flexible way to capture nuanced variation in social structure and its temporal dynamics than historical approaches. Moving to finer social scales, there is considerable scope to answer novel questions as more social network datasets become available in online repositories. For example, different relationships between the costs of aggression and dominance rank have been documented (Silk *et al.* 2019; Hobson *et al.* 2021a), and comparative network analyses offer promise in finding general patterns for how this relationship varies and depends on other species traits.

The evolution of sociality and cooperation: The evolution of cooperation is a major focus in behavioural ecology, and benefited from previous comparative analyses (Cornwallis *et al.* 2017; Firman *et al.* 2020). Despite studies in this area frequently examining the maintenance of complex sociality (e.g. (Akçay 2018)), they have yet to take full advantage of comparative network approaches, either theoretically or empirically. Moving network models of the evolution of cooperation from theoretical network structures (e.g. (Ohtsuki *et al.* 2006)) to exploit multi-species data from social network repositories could help generalise findings to different real-world network structures. These approaches may also help investigate how the emergence of cooperation in different network structures is linked to species-level traits and how well it aligns with recorded cooperative behaviours. From an empirical perspective, comparative social network analyses can provide further metrics to help construct multidimensional projections of social complexity (Prox & Farine 2020), as well as feeding back to inform the development of social network structures themselves (Akçay 2018). Identifying consistent features of social networks that differ between cooperative and non-cooperative species, for example, could help quantify how the evolution of cooperation shapes wider ecological and evolutionary processes.

Social ageing: Recent interest in social ageing has revealed age-related changes in social behaviours in older individuals become less socially connected (Siracusa *et al.* 2022). Because ageing itself is a complex process that needs to be demonstrated at the individual level (Nussey *et al.* 2008), it will greatly benefit from – if not necessitate – comparative network analyses rather than more classical approaches that look at traits such as group size and composition. Given that age data is regularly monitored in many long-term study systems and already available as a node attribute in some social network repositories, comparative network approaches can play an important role in generalising age-related changes in social interaction patterns across animal species and ecological contexts.

Human-wildlife interactions and conservation: Another opportunity is to test how species' social networks differ in their responses to anthropogenic disturbance and human-induced rapid environmental change (HIREC; (Sih 2013)). For group-living species, social networks may respond in varied ways to these anthropogenic pressures (Fisher *et al.* 2021; Blumstein *et al.* 2023). For example, endangered mountain gorillas' social networks became more cohesive when tourists were too close (Costa *et al.* 2023). Testing to what extent these dynamics vary according to other species traits could help inform which social species are most at risk from anthropogenic pressures and how best to protect them (Snijders *et al.* 2017). In a similar vein, a generalised, cross-species understanding of group social network stability or individual social integration and how it is linked to health could help inform population augmentation or reintroduction attempts if it can be extended to endangered social species. Group stability and social integration are likely to play a key role in the initial success of such projects when social relationships strongly determine fitness.

Concluding Remarks

Comparative social network analyses have huge untapped potential to further our understanding of the evolutionary ecology of animal societies and strengthen the links between different ecological sub-fields. Our review reveals growing interest in comparing network structures and their ecological consequences across taxonomic divides, as well as the increasing power of approaches being used. Especially given the apparent trend of increasing data breadth, depth, and availability over time, we expect that these approaches will only become more powerful for examining socio-ecological trends across species in the near future. Greater use of meta-analyses of within-network trends alongside these approaches will increase the reach and reliability of comparative approaches in social network analysis (Spake *et al.* 2022), and transform the hunt for general patterns shaping the structure of animal social systems.

Acknowledgements

GFA and SB were supported by NSF grant number DEB-2211287. MJS received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No. 101023948 and from Royal Society University Research Fellowship URF\R1\221800.

References

Akçay, E. (2018). Collapse and rescue of cooperation in evolving dynamic networks. *Nat Commun*, 9, 2692.

Albery, G.F., Kirkpatrick, L., Firth, J.A. & Bansal, S. (2021). Unifying spatial and social network analysis in disease ecology. *Journal of Animal Ecology*, 90, 45–61.

Albery, G.F., Sweeny, A.R., Becker, D.J. & Bansal, S. (2022). Fine-scale spatial patterns of wildlife disease are common and understudied. *Functional Ecology*, 36, 214–225.

August, T.A., Nunn, M.A., Fensome, A.G., Linton, D.M. & Mathews, F. (2014). Sympatric Woodland Myotis Bats Form Tight-Knit Social Groups with Exclusive Roost Home Ranges. *PLOS ONE*, 9, e112225.

Balasubramaniam, K.N., Beisner, B.A., Berman, C.M., De Marco, A., Duboscq, J., Koirala, S., *et al.* (2018). The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure. *American Journal of Primatology*, 80, e22727.

Balasubramaniam, K.N., Marty, P.R., Samartino, S., Sobrino, A., Gill, T., Ismail, M., *et al.* (2020). Impact of individual demographic and social factors on human–wildlife interactions: a comparative study of three macaque species. *Sci Rep*, 10, 21991.

Bansal, S., Grenfell, B.T. & Meyers, L.A. (2007). When individual behaviour matters: homogeneous and network models in epidemiology. *Journal of The Royal Society Interface*, 4, 879–891.

Barrett, L., Henzi, P. & Rendall, D. (2007). Social brains, simple minds: does social complexity really require cognitive complexity? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 561–575.

Battiston, F., Amico, E., Barrat, A., Bianconi, G., Ferraz de Arruda, G., Franceschiello, B., *et al.* (2021). The physics of higher-order interactions in complex systems. *Nat. Phys.*, 17, 1093–1098.

Beck, K.B., Sheldon, B.C. & Firth, J.A. (2023). Social learning mechanisms shape transmission pathways through replicate local social networks of wild birds. *eLife*, 12, e85703.

Bhadra, A., Jordán, F., Sumana, A., Deshpande, S.A. & Gadagkar, R. (2009). A comparative social network analysis of wasp colonies and classrooms: Linking network structure to functioning. *Ecological Complexity*, 6, 48–55.

Blumstein, D.T., Hayes, L.D. & Pinter-Wollman, N. (2023). Social consequences of rapid environmental change. *Trends in Ecology & Evolution*, 38, 337–345.

Boughton, R.K., Joop, G. & Armitage, S.A.O. (2011). Outdoor immunology: methodological considerations for ecologists. *Functional Ecology*, 25, 81–100.

Briard, L. & Ezenwa, V.O. (2021). Parasitism and host social behaviour: a meta-analysis of insights derived from social network analysis. *Animal Behaviour*, 172, 171–182.

Bruck, J.N. (2013). Decades-long social memory in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131726.

Cantor, M., Chimento, M., Smeele, S.Q., He, P., Papageorgiou, D., Aplin, L.M., *et al.* (2021a). Social network architecture and the tempo of cumulative cultural evolution. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20203107.

Cantor, M., Maldonado-Chaparro, A.A., Beck, K.B., Brandl, H.B., Carter, G.G., He, P., *et al.* (2021b). The importance of individual-to-society feedbacks in animal ecology and evolution. *Journal of Animal Ecology*, 90, 27–44.

Carlson, C.J., Gibb, R.J., Albery, G.F., Brierley, L., Connor, R.P., Dallas, T.A., *et al.* (2022). The Global Virome in One Network (VIRION): an Atlas of Vertebrate-Virus Associations. *mBio*, 13, e02985-21.

Carne, C., Semple, S., Morrogh-Bernard, H., Zuberbühler, K. & Lehmann, J. (2013). Predicting the Vulnerability of Great Apes to Disease: The Role of Superspreaders and Their Potential Vaccination. *PLOS ONE*, 8, e84642.

Castles, M., Heinsohn, R., Marshall, H.H., Lee, A.E.G., Cowlishaw, G. & Carter, A.J. (2014). Social networks created with different techniques are not comparable. *Animal Behaviour*, 96, 59–67.

Cattuto, C., Broeck, W.V. den, Barrat, A., Colizza, V., Pinton, J.-F. & Vespignani, A. (2010). Dynamics of Person-to-Person Interactions from Distributed RFID Sensor Networks. *PLOS ONE*, 5, e11596.

Chak, S.T.C., Duffy, J.E., Hultgren, K.M. & Rubenstein, D.R. (2017). Evolutionary transitions towards eusociality in snapping shrimps. *Nat Ecol Evol*, 1, 1–7.

Chase, I.D., Coelho, D., Lee, W., Mueller, K. & Curley, J.P. (2022). Networks never rest: An investigation of network evolution in three species of animals. *Social Networks*, 68, 356–373.

Ciani, F., Dall'Olio, S., Stanyon, R. & Palagi, E. (2012). Social tolerance and adult play in macaque societies: a comparison with different human cultures. *Animal Behaviour*, 84, 1313–1322.

Collier, M., Albery, G.F., McDonald, G.C. & Bansal, S. (2022). Pathogen transmission modes determine contact network structure, altering other pathogen characteristics. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20221389.

Colman, E., Colizza, V., Hanks, E.M., Hughes, D.P. & Bansal, S. (2021). Social fluidity mobilizes contagion in human and animal populations. *eLife*, 10, e62177.

Cooper, N., Kamilar, J.M. & Nunn, C.L. (2012). Host Longevity and Parasite Species Richness in Mammals. *PLOS ONE*, 7, e42190.

Cornwallis, C.K., Botero, C.A., Rubenstein, D.R., Downing, P.A., West, S.A. & Griffin, A.S. (2017). Cooperation facilitates the colonization of harsh environments. *Nat Ecol Evol*, 1, 1–10.

Costa, R.F.P., Romano, V., Pereira, A.S., Hart, J.D.A., MacIntosh, A. & Hayashi, M. (2023). Mountain gorillas benefit from social distancing too: Close proximity from tourists affects gorillas' sociality. *Conservation Science and Practice*, 5, e12859.

Côté, I.M. & Poulin, R. (1995). Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology*, 6, 159–165.

Dakin, R. & Ryder, T.B. (2020). Reciprocity and behavioral heterogeneity govern the stability of social networks. *Proceedings of the National Academy of Sciences*, 117, 2993–2999.

Davis, G.H., Crofoot, M.C. & Farine, D.R. (2018). Estimating the robustness and uncertainty of animal social networks using different observational methods. *Animal Behaviour*, 141, 29–44.

Dufour, V., Sueur, C., Whiten, A. & Buchanan-Smith, H. m. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American Journal of Primatology*, 73, 802–811.

Ellis, S., Franks, D.W., Weiss, M.N., Cant, M.A., Domenici, P., Balcomb, K.C., *et al.* (2021). Mixture models as a method for comparative sociality: social networks and demographic change in resident killer whales. *Behav Ecol Sociobiol*, 75, 75.

European Centre for Disease Control. (2016). Systematic review on the incubation and infectiousness/shedding period of communicable diseases in children.

Evans, J.C., Hodgson, D.J., Boogert, N.J. & Silk, M.J. (2021). Group size and modularity interact to shape the spread of infection and information through animal societies. *Behav Ecol Sociobiol*, 75, 163.

Evans, J.C., Silk, M.J., Boogert, N.J. & Hodgson, D.J. (2020). Infected or informed? Social structure and the simultaneous transmission of information and infectious disease. *Oikos*, 129, 1271–1288.

Farine, D.R. & Strandburg-Peshkin, A. (2015). Estimating uncertainty and reliability of social network data using Bayesian inference. *Royal Society Open Science*, 2, 150367.

Farine, D.R. & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84, 1144–1163.

Faust, K. (2006). Comparing social networks: size, density, and local structure. *Advances in Methodology and Statistics*, 3, 185–216.

Firman, R.C., Rubenstein, D.R., Moran, J.M., Rowe, K.C. & Buzatto, B.A. (2020). Extreme and Variable Climatic Conditions Drive the Evolution of Sociality in Australian Rodents. *Current Biology*, 30, 691-697.e3.

Firth, J.A. (2020). Considering Complexity: Animal Social Networks and Behavioural Contagions. *Trends in Ecology & Evolution*, 35, 100–104.

Firth, J.A. & Sheldon, B.C. (2016). Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. *Ecology letters*, 19, 1324–1332.

Fisher, D.N., Kilgour, R.J., Siracusa, E.R., Foote, J.R., Hobson, E.A., Montiglio, P., *et al.* (2021). Anticipated effects of abiotic environmental change on intraspecific social interactions. *Biological Reviews*, 96, 2661–2693.

Fisher, D.N. & McAdam, A.G. (2017). Social traits, social networks and evolutionary biology. *Journal of Evolutionary Biology*, 30, 2088–2103.

Fisher, D.N. & McAdam, A.G. (2019). Indirect genetic effects clarify how traits can evolve even when fitness does not. *Evolution Letters*, 3, 4–14.

Fountain-Jones, N.M., Silk, M., Appaw, R.C., Hamede, R., Rushmore, J., VanderWaal, K., *et al.* (2022). The spectral underpinnings of pathogen spread on animal networks. *bioRxiv*, 2022–07.

Gibb, R., Albery, G.F., Becker, D.J., Brierley, L., Connor, R., Dallas, T.A., *et al.* (2021). Data proliferation, reconciliation, and synthesis in viral ecology. *BioScience*, 71, 1148–1156.

Gilbertson, M.L., White, L.A. & Craft, M.E. (2021). Trade-offs with telemetry-derived contact networks for infectious disease studies in wildlife. *Methods in Ecology and Evolution*, 12, 76–87.

Graham, A.L., Shuker, D.M., Pollitt, L.C., Auld, S.K.J.R., Wilson, A.J. & Little, T.J. (2011). Fitness consequences of immune responses: strengthening the empirical framework for ecoimmunology. *Functional Ecology*, 25, 5–17.

Griffin, R.H. & Nunn, C.L. (2012). Community structure and the spread of infectious disease in primate social networks. *Evolutionary Ecology*, 26, 779–800.

Hart, J., Weiss, M.N., Franks, D. & Brent, L. (2023). BISoN: A Bayesian framework for inference of social networks. *Methods in Ecology and Evolution*, n/a.

He, P., Maldonado-Chaparro, A.A. & Farine, D.R. (2019). The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behavioral Ecology and Sociobiology*, 73, 1–14.

Hinde, R.A. (1976). Interactions, relationships and social structure. *Man*, 1–17.

Hobson, E.A., Ferdinand, V., Kolchinsky, A. & Garland, J. (2019). Rethinking animal social complexity measures with the help of complex systems concepts. *Animal Behaviour*, 155, 287–296.

Hobson, E.A., Mønster, D. & DeDeo, S. (2021a). Aggression heuristics underlie animal dominance hierarchies and provide evidence of group-level social information. *Proceedings of the National Academy of Sciences*, 118, e2022912118.

Hobson, E.A., Silk, M.J., Fefferman, N.H., Larremore, D.B., Rombach, P., Shai, S., *et al.* (2021b). A guide to choosing and implementing reference models for social network analysis. *Biological Reviews*, 96, 2716–2734.

Hoppitt, W.J. & Farine, D.R. (2018). Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Animal Behaviour*, 136, 227–238.

Ilany, A. & Akcay, E. (2016). Social inheritance can explain the structure of animal social networks. *Nature communications*, 7, 12084.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., *et al.* (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology*, 90, 2648–2648.

Jordán, F., Kovács, B. & Verdolin, J.L. (2021). Resource availability influences global social network properties in Gunnison's prairie dogs (Cynomys gunnisoni). *Behaviour*, 159, 321–338.

Kappeler, P. & Pozzi, L. (2019). Evolutionary transitions toward pair living in nonhuman primates as stepping stones toward more complex societies. *Science Advances*, 5, eaay1276.

Kays, R., Davidson, S.C., Berger, M., Bohrer, G., Fiedler, W., Flack, A., *et al.* (2022). The Movebank system for studying global animal movement and demography. *Methods in Ecology and Evolution*, 13, 419–431.

Keeling, M.J. & Eames, K.T.D. (2005). Networks and epidemic models. *Journal of The Royal Society Interface*, 2, 295–307.

Kiti, M.C., Tizzoni, M., Kinyanjui, T.M., Koech, D.C., Munywoki, P.K., Meriac, M., *et al.* (2016). Quantifying social contacts in a household setting of rural Kenya using wearable proximity sensors. *EPJ Data Sci.*, 5, 21.

Kulahci, I.G., Ghazanfar, A.A. & Rubenstein, D.I. (2018). Knowledgeable Lemurs Become More Central in Social Networks. *Current Biology*, 28, 1306-1310.e2.

Kurvers, R.H.J.M., Krause, J., Croft, D.P., Wilson, A.D.M. & Wolf, M. (2014). The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends in Ecology & Evolution*, 29, 326–335.

Lang, S.D.J. & Farine, D.R. (2017). A multidimensional framework for studying social predation strategies. *Nat Ecol Evol*, 1, 1230–1239.

Leu, S.T., Farine, D.R., Wey, T.W., Sih, A. & Bull, C.M. (2016). Environment modulates population social structure: experimental evidence from replicated social networks of wild lizards. *Animal Behaviour*, 111, 23–31.

Lukas, D. & Clutton-Brock, T.H. (2013). The Evolution of Social Monogamy in Mammals. *Science*, 341, 526–530.

Lukas, D. & Huchard, E. (2014). The evolution of infanticide by males in mammalian societies. *Science*, 346, 841–844.

MacLeod, K.J., English, S., Ruuskanen, S.K. & Taborsky, B. (2023). Stress in the social context: a behavioural and eco-evolutionary perspective. *Journal of Experimental Biology*, 226, jeb245829.

Matsuda, I., Zhang, P., Swedell, L., Mori, U., Tuuga, A., Bernard, H., *et al.* (2012). Comparisons of Intraunit Relationships in Nonhuman Primates Living in Multilevel Social Systems. *Int J Primatol*, 33, 1038–1053.

McDonald, D.B. & Hobson, E.A. (2018). Edge weight variance: population genetic metrics for social network analysis. *Animal Behaviour*, 136, 239–250.

Mitani, J.C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77, 633–640.

Mourier, J., Vercelloni, J. & Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. *Animal Behaviour*, 83, 389–401.

Musciotto, F., Papageorgiou, D., Battiston, F. & Farine, D.R. (2022). Beyond the dyad: uncovering higher-order structure within cohesive animal groups.

Nunn, C.L., Jordán, F., McCabe, C.M., Verdolin, J.L. & Fewell, J.H. (2015). Infectious disease and group size: more than just a numbers game. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20140111.

Nussey, D.H., Coulson, T., Festa-Bianchet, M. & Gaillard, J.-M. (2008). Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology*, 22, 393–406.

Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M.A. (2006). A simple rule for the evolution of cooperation on graphs and social networks. *Nature*, 441, 502–505.

Ojer, J. & Pastor-Satorras, R. (2022). Flocking dynamics mediated by weighted social networks. *Phys. Rev. E*, 106, 044601.

Papageorgiou, D. & Farine, D.R. (2020). Group size and composition influence collective movement in a highly social terrestrial bird. *eLife*, 9, e59902.

Parra, G.J., Corkeron, P.J. & Arnold, P. (2011). Grouping and fission–fusion dynamics in Australian snubfin and Indo-Pacific humpback dolphins. *Animal Behaviour*, 82, 1423–1433.

Pasquaretta, C., Levé, M., Claidière, N., van de Waal, E., Whiten, A., MacIntosh, A.J.J., *et al.* (2014). Social networks in primates: smart and tolerant species have more efficient networks. *Sci Rep*, 4, 7600.

Patterson, J.E.H. & Ruckstuhl, K.E. (2013). Parasite infection and host group size: a meta-analytical review. *Parasitology*, 140, 803–813.

Péron, G. (2023). Weighting the transitivity of undirected weighted social networks with triadic edge dissimilarity scores. *Social Networks*, 73, 1–6.

Pinter-Wollman, N. (2015). Persistent variation in spatial behavior affects the structure and function of interaction networks. *Current Zoology*, 61, 98–106.

Poulin, R. & Filion, A. (2021). Evolution of social behaviour in an infectious world: comparative analysis of social network structure versus parasite richness. *Behav Ecol Sociobiol*, 75, 105.

Prox, L. & Farine, D. (2020). A framework for conceptualizing dimensions of social organization in mammals. *Ecology and Evolution*, 10, 791–807.

Richardson, M., Elliman, D., Maguire, H., Simpson, J. & Nicoll, A. (2001). Evidence base of incubation periods, periods of infectiousness and exclusion policies for the control of communicable diseases in schools and preschools. *The Pediatric Infectious Disease Journal*, 20, 380.

Robitaille, A.L., Webber, Q.M.R. & Vander Wal, E. (2019). Conducting social network analysis with animal telemetry data: Applications and methods using spatsoc. *Methods in Ecology and Evolution*, 10, 1203–1211.

Rocha, L.E.C., Ryckebusch, J., Schoors, K. & Smith, M. (2021). The scaling of social interactions across animal species. *Sci Rep*, 11, 12584.

Romano, V., Shen, M., Pansanel, J., MacIntosh, A.J.J. & Sueur, C. (2018). Social transmission in networks: global efficiency peaks with intermediate levels of modularity. *Behav Ecol Sociobiol*, 72, 154.

Roose, R., Oliver, M., Haulsee, D., Breece, M., Carlisle, A. & Fox, D. (2022). The sociality of Atlantic sturgeon and sand tiger sharks in an estuarine environment. *Animal Behaviour*, 193, 181–191.

Rose, P.E. & Croft, D.P. (2017). Social bonds in a flock bird: Species differences and seasonality in social structure in captive flamingo flocks over a 12-month period. *Applied Animal Behaviour Science*, 193, 87–97.

Ross, C.T., McElreath, R. & Redhead, D. (2022). Modelling human and non-human animal network data in R using STRAND.

Rubenstein, D.I., Sundaresan, S.R., Fischhoff, I.R., Tantipathananandh, C. & Berger-Wolf, T.Y. (2015). Similar but Different: Dynamic Social Network Analysis Highlights Fundamental Differences between the Fission-Fusion Societies of Two Equid Species, the Onager and Grevy's Zebra. *PLOS ONE*, 10, e0138645.

Sah, P., Leu, S.T., Cross, P.C., Hudson, P.J. & Bansal, S. (2017). Unraveling the disease consequences and mechanisms of modular structure in animal social networks. *Proceedings of the National Academy of Sciences*, 114, 4165–4170.

Sah, P., Mann, J. & Bansal, S. (2018). Disease implications of animal social network structure: A synthesis across social systems. *Journal of Animal Ecology*, 87, 546–558.

Sah, P., Méndez, J.D. & Bansal, S. (2019). A multi-species repository of social networks. *Sci Data*, 6, 44.

Shizuka, D. & Farine, D.R. (2016). Measuring the robustness of network community structure using assortativity. *Animal Behaviour*, 112, 237–246.

Shizuka, D. & Johnson, A.E. (2020). How demographic processes shape animal social networks. *Behavioral Ecology*, 31, 1–11.

Shizuka, D. & McDonald, D.B. (2012). A social network perspective on measurements of dominance hierarchies. *Animal Behaviour*, 83, 925–934.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, 85, 1077–1088.

Silk, J.B. (2007). Social Components of Fitness in Primate Groups. *Science*, 317, 1347–1351.

Silk, M.J., Cant, M.A., Cafazzo, S., Natoli, E. & McDonald, R.A. (2019). Elevated aggression is associated with uncertainty in a network of dog dominance interactions. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20190536.

Silk, M.J., Weber, N., Steward, L.C., Delahay, R.J., Croft, D.P., Hodgson, D.J., *et al.* (2017). Seasonal variation in daily patterns of social contacts in the European badger Meles meles. *Ecology and Evolution*, 7, 9006–9015.

Silk, M.J., Weber, N.L., Steward, L.C., Hodgson, D.J., Boots, M., Croft, D.P., *et al.* (2018). Contact networks structured by sex underpin sex-specific epidemiology of infection. *Ecology Letters*, 21, 309–318.

Silk, M.J., Wilber, M.Q. & Fefferman, N.H. (2022). Capturing complex interactions in disease ecology with simplicial sets. *Ecology Letters*, 25, 2217–2231.

de Silva, S. & Wittemyer, G. (2012). A Comparison of Social Organization in Asian Elephants and African Savannah Elephants. *Int J Primatol*, 33, 1125–1141.

Siracusa, E.R., Higham, J.P., Snyder-Mackler, N. & Brent, L.J.N. (2022). Social ageing: exploring the drivers of late-life changes in social behaviour in mammals. *Biology Letters*, 18, 20210643.

Smith, J.E., Gamboa, D.A., Spencer, J.M., Travenick, S.J., Ortiz, C.A., Hunter, R.D., *et al.* (2018). Split between two worlds: automated sensing reveals links between above- and belowground social networks in a free-living mammal. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, 20170249.

Smith, J.E. & Pinter-Wollman, N. (2021). Observing the unwatchable: Integrating automated sensing, naturalistic observations and animal social network analysis in the age of big data. *Journal of Animal Ecology*, 90, 62–75.

Snijders, L., Blumstein, D.T., Stanley, C.R. & Franks, D.W. (2017). Animal Social Network Theory Can Help Wildlife Conservation. *Trends in Ecology & Evolution*, 32, 567–577.

Snyder-Mackler, N., Burger, J.R., Gaydosh, L., Belsky, D.W., Noppert, G.A., Campos, F.A., *et al.* (2020). Social determinants of health and survival in humans and other animals. *Science*, 368, eaax9553.

Spake, R., O'Dea, R.E., Nakagawa, S., Doncaster, C.P., Ryo, M., Callaghan, C.T., *et al.* (2022). Improving quantitative synthesis to achieve generality in ecology. *Nat Ecol Evol*, 6, 1818–1828.

Stehlé, J., Voirin, N., Barrat, A., Cattuto, C., Isella, L., Pinton, J.-F., *et al.* (2011). High-Resolution Measurements of Face-to-Face Contact Patterns in a Primary School. *PLOS ONE*, 6, e23176.

Stephens, P.R., Pappalardo, P., Huang, S., Byers, J.E., Farrell, M.J., Gehman, A., *et al.* (2017). Global Mammal Parasite Database version 2.0. *Ecology*, 98, 1476–1476.

Strauss, E.D., DeCasien, A.R., Galindo, G., Hobson, E.A., Shizuka, D. & Curley, J.P. (2022). DomArchive: a century of published dominance data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377, 20200436.

Sueur, C. & Petit, O. (2008). Organization of Group Members at Departure Is Driven by Social Structure in Macaca. *Int J Primatol*, 29, 1085–1098.

Sueur, C., Petit, O., De Marco, A., Jacobs, A.T., Watanabe, K. & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour*, 82, 845–852.

Sueur, C., Petit, O. & Deneubourg, J.L. (2010). Short-term group fission processes in macaques: a social networking approach. *Journal of Experimental Biology*, 213, 1338–1346.

Sundaresan, S.R., Fischhoff, I.R., Dushoff, J. & Rubenstein, D.I. (2007). Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager. *Oecologia*, 151, 140–149.

Testard, C., Larson, S.M., Watowich, M.M., Kaplinsky, C.H., Bernau, A., Faulder, M., *et al.* (2021). Rhesus macaques build new social connections after a natural disaster. *Current Biology*, 31, 2299-2309.e7.

Vanhems, P., Barrat, A., Cattuto, C., Pinton, J.-F., Khanafer, N., Régis, C., *et al.* (2013). Estimating Potential Infection Transmission Routes in Hospital Wards Using Wearable Proximity Sensors. *PLOS ONE*, 8, e73970.

Voelkl, B. & Noë, R. (2008). The influence of social structure on the propagation of social information in artificial primate groups: A graph-based simulation approach. *Journal of Theoretical Biology*, 252, 77–86.

Ward, J.A. (2021). Dimension-reduction of dynamics on real-world networks with symmetry. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 477, 20210026.

Webber, Q.M.R., Albery, G.F., Farine, D.R., Pinter-Wollman, N., Sharma, N., Spiegel, O., *et al.* (2023). Behavioural ecology at the spatial–social interface. *Biological Reviews*, 98, 868–886.

Webber, Q.M.R. & Vander Wal, E. (2019). Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. *Animal Behaviour*, 149, 77–87.

Weiss, M.N., Franks, D.W., Croft, D.P. & Whitehead, H. (2019). Measuring the complexity of social associations using mixture models. *Behav Ecol Sociobiol*, 73, 8.

White, L.A., Forester, J.D. & Craft, M.E. (2017). Using contact networks to explore mechanisms of parasite transmission in wildlife. *Biological Reviews*, 92, 389–409.

Whitehead, H. (1997). Analysing animal social structure. *Animal Behaviour*, 53, 1053–1067.

Young, J.-G., Cantwell, G.T. & Newman, M.E.J. (2021). Bayesian inference of network structure from unreliable data. *Journal of Complex Networks*, 8, cnaa046.

Box 1: Social network repositories

A recent development is the creation of large-scale, publicly available databases of social network data (Table 1). We introduce three databases for non-human animal social networks here and draw attention to similar efforts for human networks too.

Animal Social Network Repository (ASNR)

The animal social network repository (ASNR; (Sah *et al.* 2019)) was first published online in 2016, although has been regularly updated since then. It has subsequently been used by 7 of the studies in our review. Of all the current social network datasets, the ASNR captures the greatest taxonomic diversity, including insects, fish, birds, reptiles and mammals. Data is currently stored as adjacency matrices. It also incorporates substantial variation in network size and the types of behaviour monitored. However, care is needed when exploiting the ASNR as it also includes networks measured in different ways and over varied social and temporal scales, as well as incorporating both free-living and captive populations

DomArchive

DomArchive is a newly-available database of dominance interactions (Strauss *et al.* 2022), exploiting the long-term focus on social dominance in the animal behaviour literature. The majority of data is available as adjacency matrices (sociomatrices), with a subset stored instead as edge lists. The types of interaction incorporate a wide range of aggressive, formal dominance or submissive behaviours as well as related behaviours such as threats, avoidance and social displacement. The data available will be directly relevant to questions related to social stability and group function.

MacaqueNet

MacaqueNet (Box 1; Table 1) is an in-development social network database focused on macaques (*Macaca* sp.) curated for the purpose of comparative analyses in primatology and behavioural ecology. By concentrating on a well-studied genus that share similar social behaviours, MacaqueNet will offer an exciting opportunity for tackling research questions related to group-living with fewer of the pitfalls of larger datasets. As is the case for the ASNR, all data stored in MacaqueNet is formatted consistently so fully ready for comparative analyses (although note that data collection methods and edge weights can still differ between studies).

Human contact network databases

The SocioPatterns team have collected a range of proximity network datasets using Bluetooth loggers (e.g. primary school (Stehlé *et al.* 2011); scientific conference (Cattuto *et al.* 2010); Kenyan village (Kiti *et al.* 2016); hospital (Vanhems *et al.* 2013)) in addition to one similar dataset from wild baboons. Data are provided as edge lists, and if aggregated as adjacency matrices would be directly comparable with networks connected using similar methods from the ASNR.

Box 2: Classifying comparative network analyses

A diverse set of comparative approaches are possible using social network datasets. Here we provide a framework to distinguish between different approaches (Figure 3)

1. **Comparisons of network properties**

   A first approach involves comparing the topology of different networks as an outcome of other network properties (e.g. network size). This is common in network science where understanding the generative processes underlying network formation is a major focus (e.g. (Rocha *et al.* 2021; Ward 2021; Ojer & Pastor-Satorras 2022)). However, it is also of interest to ecologists, such as with studies that test the relationship between network size and modularity (Griffin & Nunn 2012).

2. **Species-level comparative approaches**

   A second type is a conventional species-level comparative approach, in which a network property of interest is fitted as a response variable with a series of species-level traits as explanatory variables, and potentially alongside a phylogeny to control for non-independence among closely-related species. The appropriate use of random effects can allow multiple observations to be used for a given species. We subdivide species-level approaches by the outcome variable of interest.

   2a) Using network topology

   Often the outcome of interest is a property of the network itself (e.g. degree heterogeneity, modularity). For example, a researcher might want to ask: How does the modularity of affiliative networks in animal groups vary with environmental harshness? These types of question will be common in behavioural ecology, for example in contributing discussions around the role of social complexity in cognitive evolution (Barrett *et al.* 2007) or linking network structure to demographic factors (Shizuka & Johnson 2020).

2b) Using the outcome of dynamical processes

The outcome of interest could also be the ecological consequences of network structure, necessitating additional steps prior to the comparative analysis. For example, studies in disease ecology often conduct simulations of pathogen spread and then use features of the resulting outbreaks as variables in comparative analyses (e.g. (Nunn *et al.* 2015; Sah *et al.* 2017; Collier *et al.* 2022; Fountain-Jones *et al.* 2022)). Similar approaches are useful in understanding the consequences of social structure for information spread and behaviour change (Evans *et al.* 2020).

3. Individual-level meta-analyses

The final category is a meta-analytic approach looking at how relationships between social interaction patterns and conditional traits vary among species. For example, Briard and Ezenwa (Briard & Ezenwa 2021) showed an overall positive association between social centrality and parasite burden across 210 effect sizes covering 16 host species, but they could not explain variation in this relationship using other host traits. While this study was in the context of disease ecology, there is no reason similar methodologies could not be applied to other questions of interest such as the relationship between social network position and fitness (Silk 2007; Snyder-Mackler *et al.* 2020).

We provide a schematic (Figure 3) to display model construction for these three main types of comparative network analyses: 1) analyses examining the relationship between *different* network traits across a range of studies (e.g. How does modularity depend on network or group size? How does network efficiency depend on degree heterogeneity?); 2) analyses of network properties (either topological or the outcome of dynamical processes operating on the network) as an outcome of both network traits and species traits (e.g. How does modularity depend on group size and longevity? How does mean outbreak size depend on fragmentation and body size?); 3) a full meta-analysis to test how relationships between network traits and individual traits vary across species and networks (e.g. Does the relationship weighted degree and fitness depend on species life-history and network modularity?)

Tables

Table 1. Summary of existing social network databases.

Database	**Number of networks**	**Number of species**	**Behaviours**	**Access**
ASNR	790	76	Dominance; Foraging; Grooming; Group membership; Non-physical social interaction; Physical contact; Social projection bipartite; Spatial proximity; Trophallaxis; Mixed	https://bansallab.github.io/asnr/
MacaqueNet	761	14	Spatial proximity Body contact; Grooming; Contact aggression; Non-contact aggression	https://macaquenet.github.io/database/
DomArchive	436	135	Dominance interactions; Submissive interactions; Aggression (*151 subtypes identified*)	https://github.com/DomArchive/DomArchive
SocioPatterns	14*	2	Proximity	http://www.sociopatterns.org/datasets/

Figures

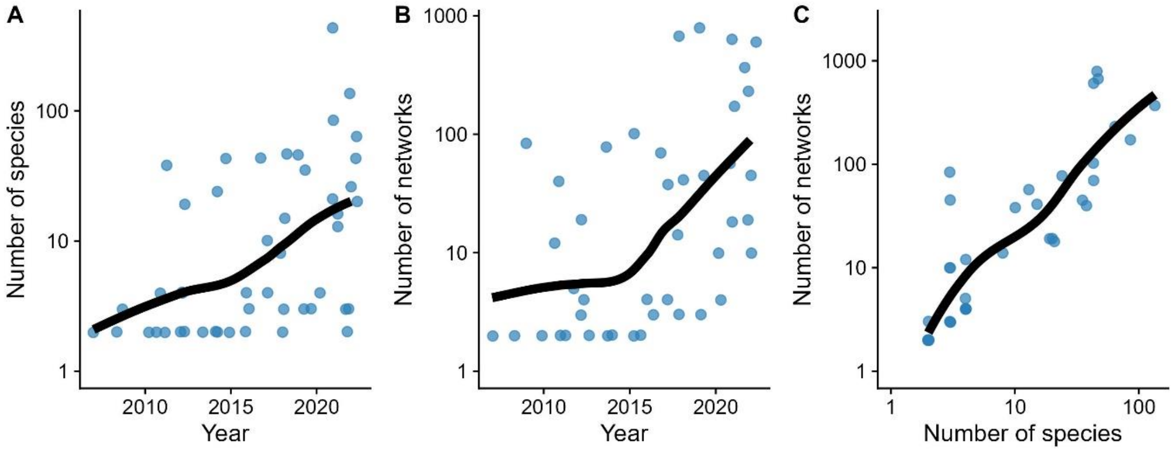

Figure 1. Coverage of our identified comparative social network studies. A) increase in number of species over time; B) increase in number of compared networks over time; C) positive correlation between the number of species investigated and the number of compared networks. Each point represents one of 49 studies; the line represents a Loess smooth fitted to the data. The rug on either axis displays the distribution of the data.

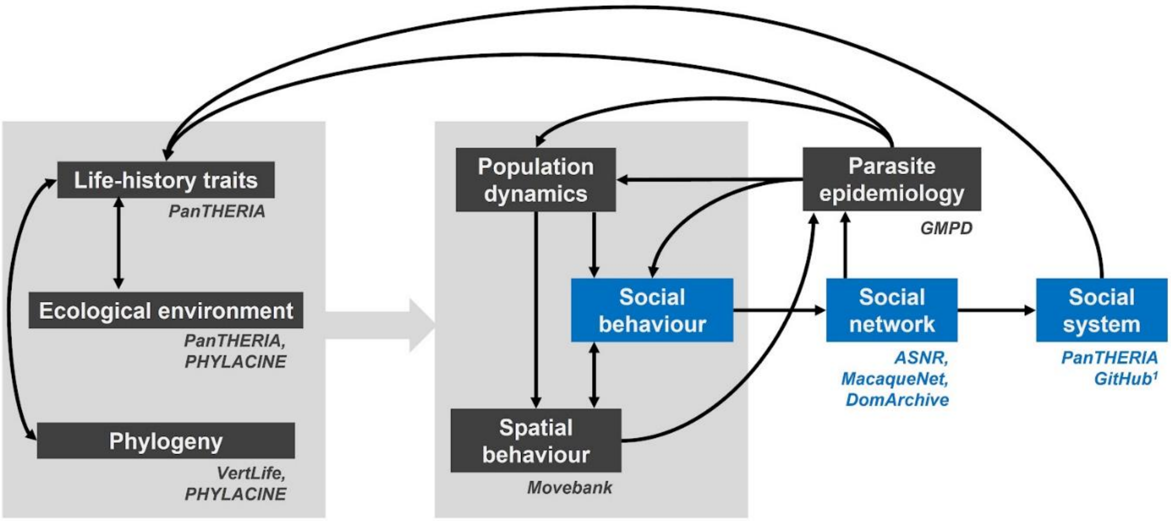

Figure 2. A conceptual overview of the value of how comparative social network analyses fit within a broader framework for social ecology and evolution. We illustrate selected relationships between species- and individual-level traits and social network structure and draw attention to key comparative databases for the main traits illustrated. Github[1] refers to https://github.com/CharlotteAnaisOLIVIER/Social-organization-of-primates.

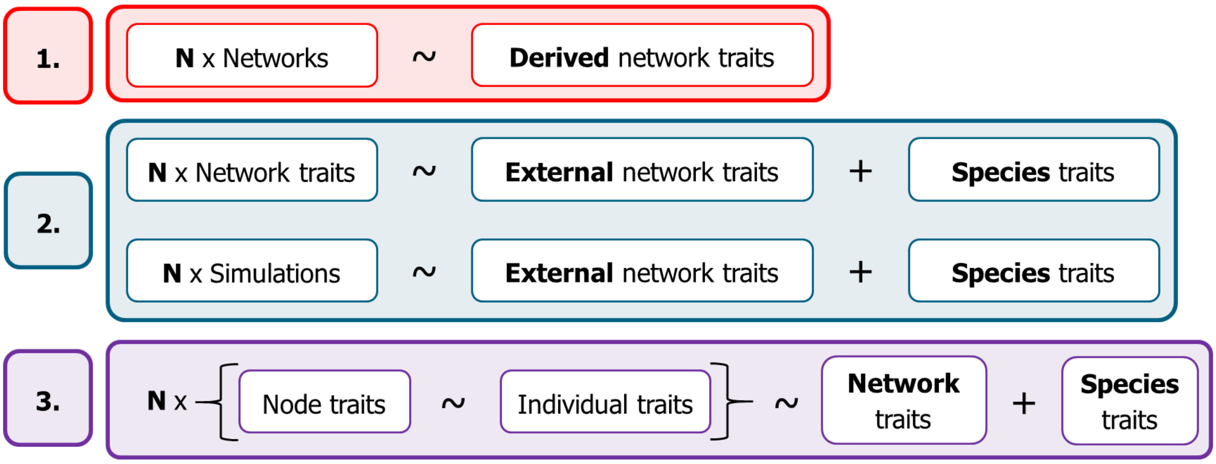

Figure 3. An overview of different types of comparative analyses that can be applied to social network datasets. 1) Network-level analyses that connect network-derived traits with the structure of the network themselves. 2) Network-level analyses that connect network-derived traits or simulation outputs with other traits of the networks and the species that comprise them. 3) Node-level analyses across N networks that involve connecting node and individual-level traits within each system (inside brackets) and then connecting these estimates with species- and network-level traits in a meta-analytical context.

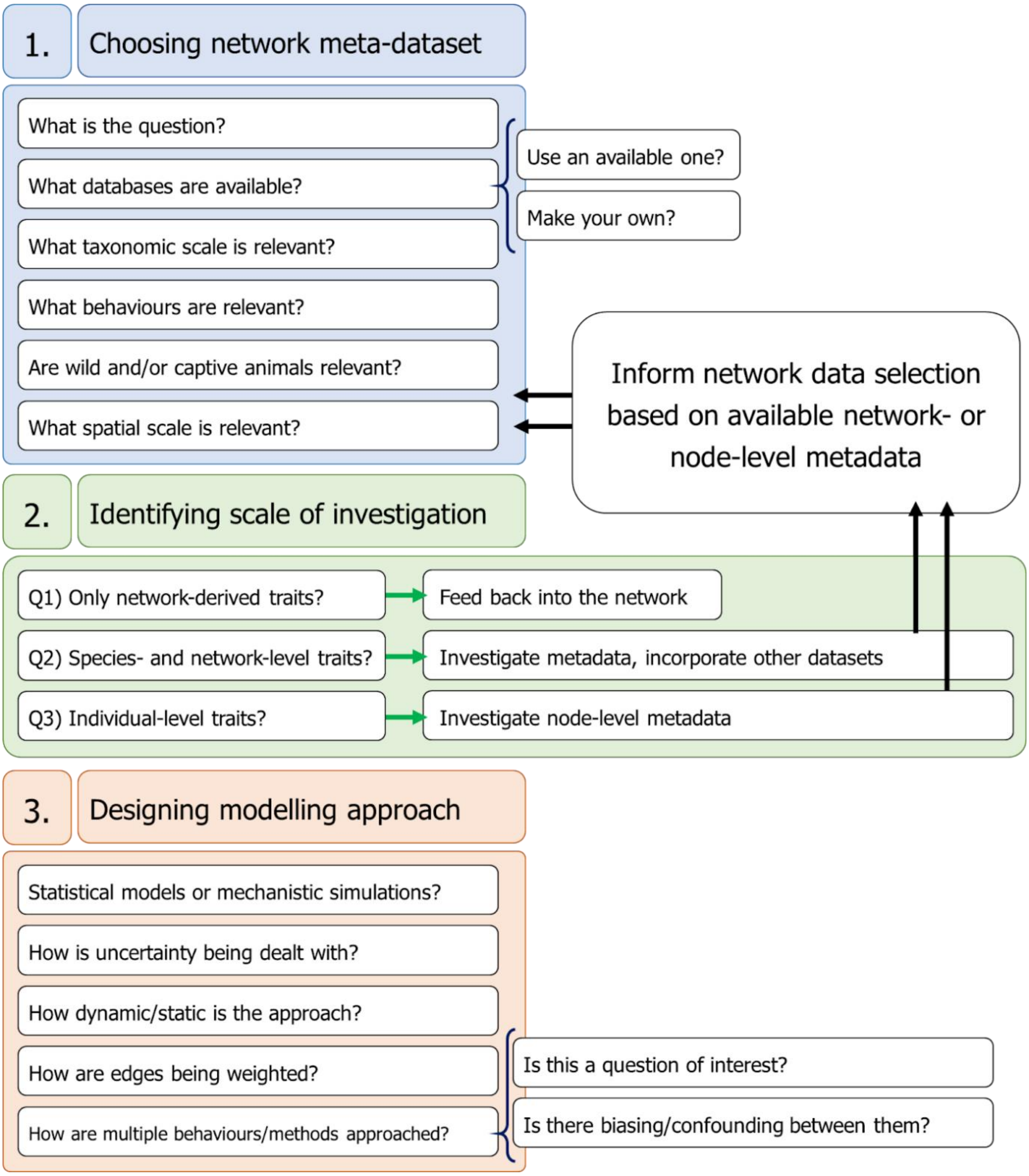

Figure 4. An illustration of our recommended workflow for comparative network analyses, identifying key questions for researchers to consider at each of the three stages of the process: data selection, scale of investigation and model design.

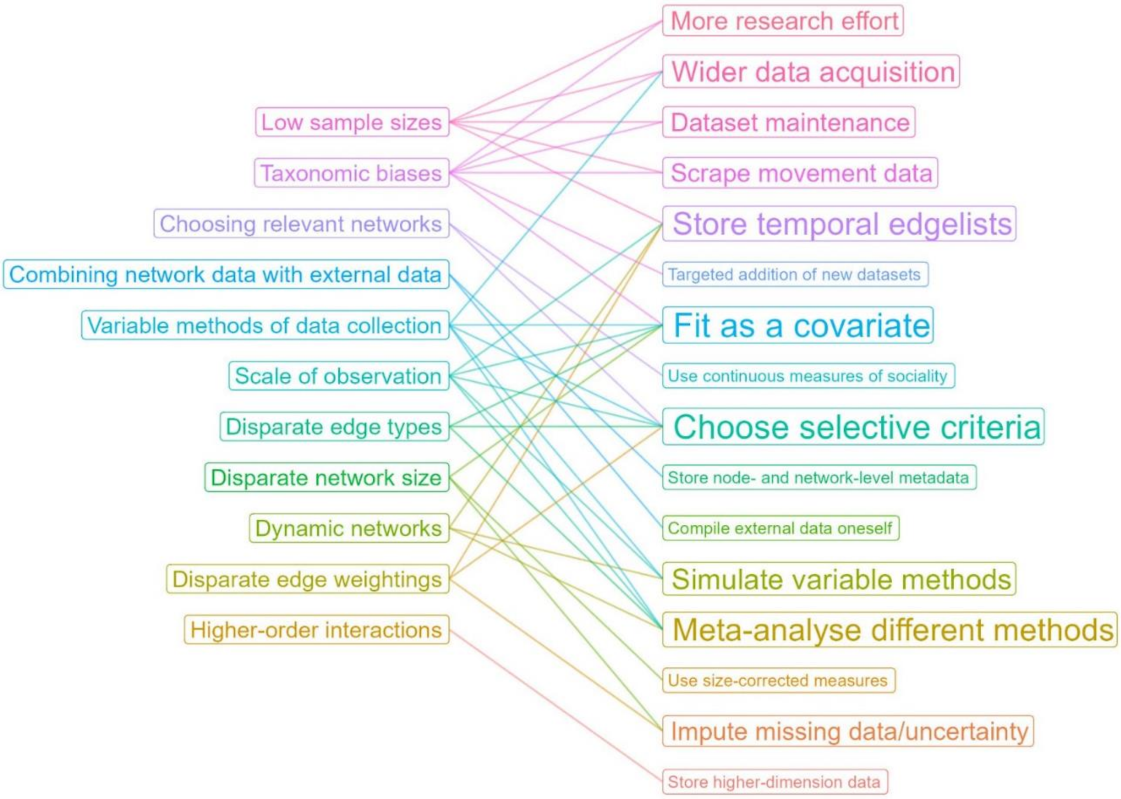

Figure 5. Common problems in comparative social network analyses (left) and solutions that may help to address them (right). Links between problems and solutions are those identified in the *Principal challenges for comparative network analysis* section of the main text as an outcome of the literature review and judgement of the authors. Solutions are sized according to the number of links they have – i.e., the number of problems they are likely to help solve.