Animal social networks - an introduction for complex systems scientists

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Many animals live in societies where individuals frequently interact socially with each other. The social structures of these systems have in recent years been studied in many species by means of network analysis. Animal social networks is now a well-established research area that has provided important insights into animal behaviour, ecology, and social evolution. Animal social network research, however, seems to not be well known by scientists outside of the animal behaviour field. Here we provide an introduction to animal social networks for complex systems researchers. We believe that a better integration of animal social networks with the interdisciplinary field of complex systems would be mutually beneficial for various reasons. Increased collaboration with complex systems researchers could be valuable in solving challenges of particular importance to animal social network research. Furthermore, high-resolution datasets of social networks from different animal species can potentially be very useful for investigating general hypotheses about complex systems. In this paper, we describe what animal social networks are and how they are scientifically important; we give an overview of the methods commonly used to study animal social networks; and finally we highlight challenges in the study of animal social networks where interaction between animal social network research and general complex systems research could be particularly valuable. We hope that this will help to facilitate future interdisciplinary collaborations involving animal social networks, and lead to better integration of these networks into the field of complex systems.

I. INTRODUCTION

Animals of many species live in groups, where individuals spend time in close proximity to each other and frequently interact [1]. The patterns of social interactions and spatial proximity across individuals constitute the social structures of the populations. A large number of species have in the last two decades been subject to investigation of their social structures by means of network analysis (reviewed in [2]). This body of research, primarily conducted by biologists, seems to not yet be well known by researchers outside the field of animal behaviour. This is not surprising, since animal social networks is a research area that has only recently established itself (for foundational texts see [3–7]). By now, social network analysis is a well-integrated part of animal behaviour research that continues to provide important new insights [2, 8, 9].

The purpose of this paper is to introduce animal social networks to the wider complex systems research community, in the hope that this can facilitate a better integration of this area of research into the interdisciplinary field of complex systems and networks. We believe that this would benefit both our understanding of animal social systems and the general research in complex systems for various reasons. Firstly, animal social network research is facing specific challenges that computational and theoretical scientists with knowledge about complex systems could potentially help addressing by providing new perspectives and methods that are not yet being applied by animal behaviour researchers. Overcoming these challenges is a relevant scientific endeavour because animal social networks constitute a class of networks that play a central role in evolutionary and ecological processes [2, 8, 9], and they are therefore important to study in their own right to understand the workings of nature, as well as to improve species conservation efforts [10, 11]. Secondly, animal social network quantification has resulted in a large set of time-series of social interactions (or spatial associations) - some in very high resolution - which may be useful for studies that address general questions connected to this type of network data. Furthermore, non-human animals represent a wide range of study systems that can be used to test network theory empirically under both natural and experimental conditions. Animal social networks can thus potentially contribute significantly to our general understanding of complex systems.

In the following we first briefly explain what animal social networks are (Section II). We then provide an overview some topics where studies of animal social networks are playing an important role for gaining new insights (Section III). We thereafter give an introduction to the methods used in studies of animal social networks (Section IV), followed by an outline of current challenges where interdisciplinary collaboration may be particularly valuable (Section V). We finish with a note on the availability of animal social network data (Section VI), and a brief conclusion (Section VII).

II. WHAT ARE ANIMAL SOCIAL NETWORKS?

Here we provide a brief explanation of what animal social networks are - what kind of data they represent and what types of patterns are typically observed in them. For further information about the methods used in the data collection and in the construction and analysis of the

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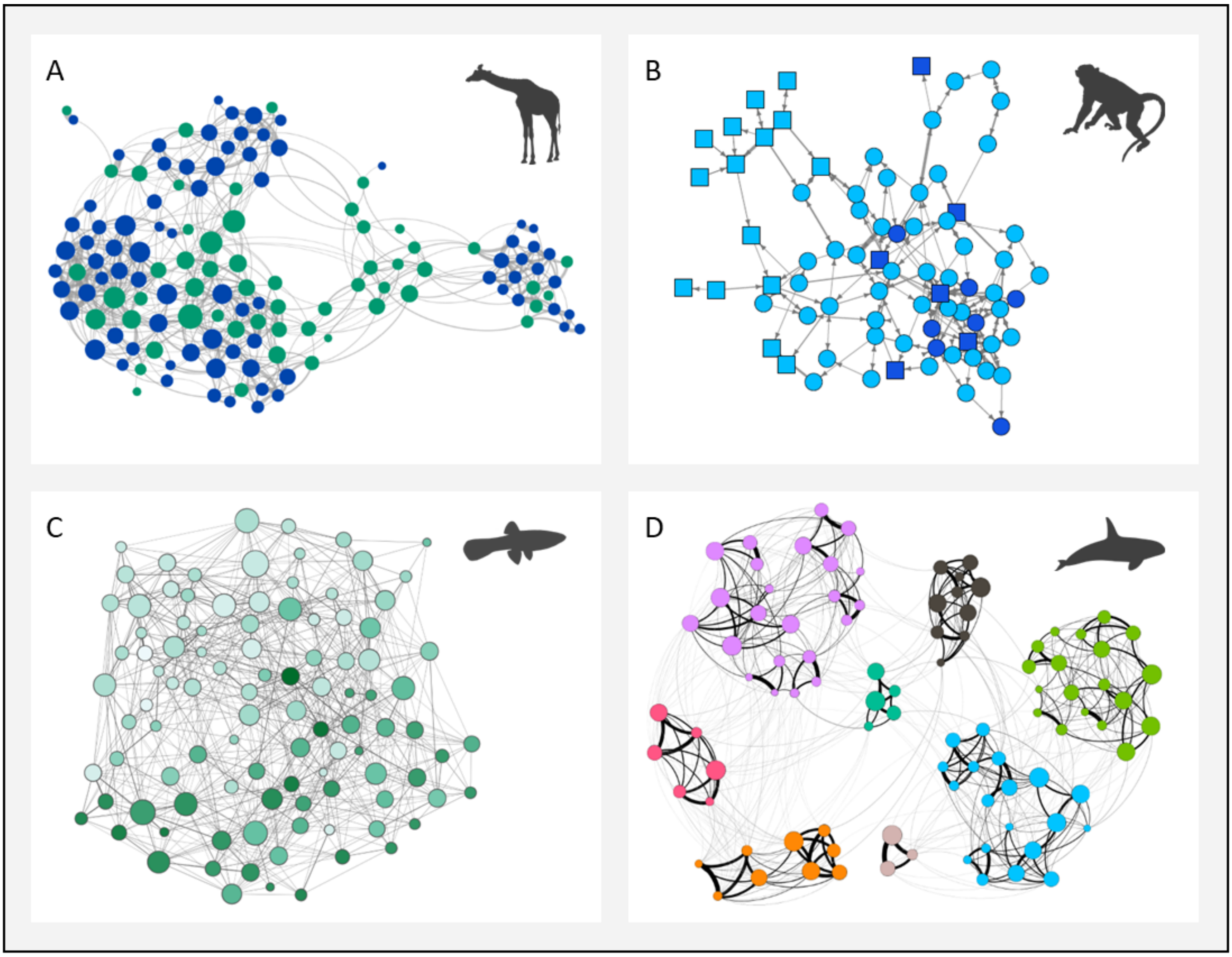

FIG. 1. Examples of animal social network graphs. In all graphs, each node signifies an individual, and thicker edges signify a stronger social relationship (corresponding to a higher rate of social interaction or association). A) A social network of a population of giraffe, based on social associations (individuals observed in the same group). Females are shown in blue and males in green. Larger nodes have higher degree. Very weak edges are not shown for clarity. B) A social network of a group of rhesus macaques, based on grooming interactions. Females are shown as circles and males as squares, and darker node colour indicates high-ranking individuals. C) A social network of a population of Trinidadian guppies, based on social associations (individuals observed shoaling together). Larger nodes have higher degree and darker nodes signify individuals with a larger body size. D) A social network of a killer whale population, based on social associations (individuals observed in the same group). Node colour indicates network communities and larger nodes have higher within-community closeness. Macaque graph reproduced from [12] and killer whale graph modified from [13] with permission from the authors (http://creativecommons.org/licenses/by/4.0/). Killer whale silhouette by Chris Huh (https://creativecommons.org/licenses/by-sa/3.0/).

networks, we refer the reader to Section IV and references therein.

Animal social networks quantify the social structure within animal populations (see Fig. 1 for examples of animal social network graphs). Each node in the network corresponds to a specific individual, and the (typically weighted) network edges correspond to the social relationships between the individuals, which are quantified as rates of *social interaction* or *social association* between each dyad. Social interactions commonly used for quantifying animal social structure include grooming and fighting, whereas social associations are based on spatial proximity of individuals. The network may thus quantify very different dimensions of the social system, depending on what type of social interaction (affiliative, aggressive) or social association it is based on. The network data (the adjacency matrix) will often be accompanied by *attribute data*, which usually contains information on the individuals (their sex, age, body size, etc.) or the dyads (e.g. their genetic relatedness).

The data are often collected by direct observation of the animals, but new technology has allowed for automatic data collection, which gives highly detailed datasets. The accumulated raw data are transformed into an adjacency matrix by the application of *association indices* [5], and the network is then typically subjected to statistical tests to investigate hypotheses about its structure.

Animal social network data may be obtained both from wild and captive populations. While field data enables the study of social structure under natural conditions, laboratory-based studies allow for experiments where causality can be tested under controlled conditions. In both cases, the quantified networks are most often relatively small (N < 200).

By now, social networks of animal populations have been quantified and analysed in a wide range of species, including mammals, birds, fish, reptiles and insects (reviewed in [2]). It is clear from this large body of research that social networks of many animal species are non-random, in the sense that their structures differ from what would be expected under random interaction or association. Typical patterns observed in the networks include substantial variation in edge weights, pronounced modularity, and assortment by physical and behavioural individual characteristics (see Fig. 1 for examples). Such non-random structure is found across the taxa investigated - not only in species such as primates that have traditionally been considered more complex [2]. Understanding the processes (evolutionary and proximate) underlying these structural patterns, and the implications of these network structures for social evolution, behaviour, and dynamics on the networks, is a central endeavour in the study of animal social networks.

III. WHY ARE ANIMAL SOCIAL NETWORKS STUDIED?

The introduction of network methods into the field of animal behaviour has opened up for a much more comprehensive understanding of the complex social systems found across species. Analyses of animal social networks are now used in investigations of a wide range of questions about social evolution, behaviour and dynamical processes [2, 8, 9]. As we cannot cover all of these questions here, we instead describe some research themes where animal social networks seem to be playing a particularly important role for gaining new insights. While these networks have until now been studied mostly by biologists, it may be noted that the research themes overlap considerably with common themes in general complex systems science, thus providing a natural base for further integration of animal social network research into this field.

Social centrality, evolution and fitness. A major reason why animal social networks are of scientific interest is that the social environment can impose selection pressures on the individuals and thereby act as an important driver of the evolution of traits (including both physical and behavioural characteristics of individuals). This means that in order to understand evolution, the social environment must be taken into account. Network analysis provides the tools to quantify social structure in detail and across different scales, and has therefore opened up new possibilities for studying the role the social environment plays in evolution, across species. One way to investigate the evolutionary importance of the social environment is to statistically test for relationships between the social network positions of individuals and their Darwinian fitness (i.e. the extent to which they contribute to the future gene pool, which is commonly estimated by measures of longevity, reproduction rate, and offspring survival). In recent years, such studies have been carried out in a range of species, and evidence for correlations between fitness and network centrality has been found widely ([13–20]; see also [21]). The study of animal social networks is thus providing extensive new empirical evidence that social network position is linked to survival and reproduction across species.

Frequency-dependent selection and social structure. Animal social network studies are also particularly relevant for understanding the evolution of traits for which fitness is frequency dependent (such that the benefit of the trait to the individual depends on the frequency of it in the social environment; [22]). One prominent example of such a trait is cooperative behaviour. The evolution of cooperation in structured populations has been studied extensively across scientific fields via simulations of strategy dynamics in artificial networks [23, 24], and this research suggests that social network structure plays a key role for the persistence of cooperation. An important next step is then to unravel to which extent and under which conditions the various mechanisms predicted from the simulations underlie cooperation in real-world systems. Animal social networks seem very useful for this task, and while only few studies have yet investigated cooperation in connection with real-world animal social structures [25–27], we expect that these networks will have an important role to play for understanding how cooperation, and other frequency-dependent traits, evolve in the real world.

Spread of disease and information in networks. Another area where animal social networks are particularly useful is the investigation of spreading processes in populations, including the propagation of disease and information. Studies in a range of species have investigated empirically to which degree various types of information spread via social links, including knowledge about the location of food [28–31], and innovations such as tool use [32, 33] and other new foraging techniques [34–38]. Regarding disease spread, empirical studies have uncovered relationships between individual network position and infection status or parasite load in multiple species [39–43], and simulation studies involving real-world animal social network data have given insights into the effect of social structure on disease transmission and the vulnerability of populations to epidemics [44–48].

Stability, flexibility and robustness of social systems. Animal social network research is also providing new empirical knowledge about the general stability of social systems across species, and how robust and flexible they are under changing conditions. This is studied by investigations of how social structure correlates with environmental factors such as food availability [49, 50] and general seasonal changes [51–55], to what degree social structure is stable across years [55–59], and how social structure reacts to perturbations such as node loss (see *Network robustness*, Section V).

Wildlife conservation and animal welfare. The fact that social network structure has important implications for health, survival and behaviour across species means that animal social network studies have an important role to play in the conservation of wildlife [10, 11] and in improving the welfare of farm and zoo animals [60, 61], thus providing important drivers for applied animal social network studies. Such studies are for example concerned with estimation of the efficiency of disease control strategies in endangered wildlife [62–64], assessment of social behaviour in connection with relocation or reintroduction of animals into the wild [65, 66], and informing the management of captive populations [67].

New network methodology. Finally, the study of animal social networks requires special techniques for network construction and analysis (described in Section IV), and this means that research in these networks is accompanied by new methodological developments. The topics include constrained permutation models for statistical testing [68–72], network generation models [73, 74], social complexity measures [75], and implications of missing data for the reliability of empirical network structures [73, 76–79].

IV. HOW ARE ANIMAL SOCIAL NETWORKS STUDIED?

The study of animal social networks is complicated by the fact that the data collection often involves inevitable sampling biases and missing observations (especially for wild populations). This must be taken into account in the treatment of the data. Specialised methods for construction and analysis of the networks have therefore been developed, and the field has now somewhat converged on some general standard methodological approaches (although the methodology is continuously evolving). In this section we give an introductory overview of methods that are currently used for data collection, network construction, and network analysis in animal social network research.

A. Collecting animal social network data

The type of data collected for quantification of animal social networks and the method of collection depends both on the research question and on what behaviour is possible to observe. The latter will depend on the species as well as the setting (e.g. whether the study population is wild or captive).

The data fall into two categories: *interaction data* and *association data*. The former concerns direct behavioural interactions between individuals, whereas the latter concerns the spatial proximity of individuals. Association data can furthermore generally be either *group-based* or *individual-based*: Many species live in so-called *fission-fusion societies* where groups are unstable. In this case, social association is inferred from shared group membership (an approach known as *the gambit of the group* [80]), and the network data are collected by recording repeatedly over time which individuals are grouping together in space [81–83]. When groups are either largely stable across the observation period or group boundaries cannot easily be defined, then single individuals may instead be observed one after another in *focal follows* where their nearest neighbour in space, or individuals within a certain distance, is recorded at regular time intervals. Interaction data are also frequently collected via such focal follows, where all interactions with the individual are recorded.

Many studies of animal social networks are based on data that are collected by the researchers directly observing the animals and recording their social interactions or associations. In this case, the researchers must be able to recognise each individual. This can sometimes be done by natural markings such as fur patterns and scars, whereas in other cases the animals are equipped with artificial tags before the data collection. Animal social network data (especially assciation data) can also be collected automatically in various ways (for detailed overviews see [84, 85]), and such methods are becoming increasingly common due to the continuous optimisation of the involved technology. Highly detailed data can be obtained via proximity loggers attached to each animal (Fig. 2), which record when each pair of individuals are close to each other (for example [62, 86–89]); this can give datasets of social associations with a subsecond time resolution. The loggers may also contain other sensors, such as accelerometers, which can provide additional information on the behaviour of the animals. Another possibility is to use RFID tags to record when each animal is present at a specific location (for example [28]). Furthermore, high-resolution social association data can in some circumstances be obtained by simultaneous automatic tracking of multiple individuals from videos with methods based on machine learning (for example [90, 91]), either without tagging the animals or with computer-readable tags such as barcodes. The increase in the development and use of automatic data collection methods means that the future is likely to see high-resolution datasets of animal social networks across many species.

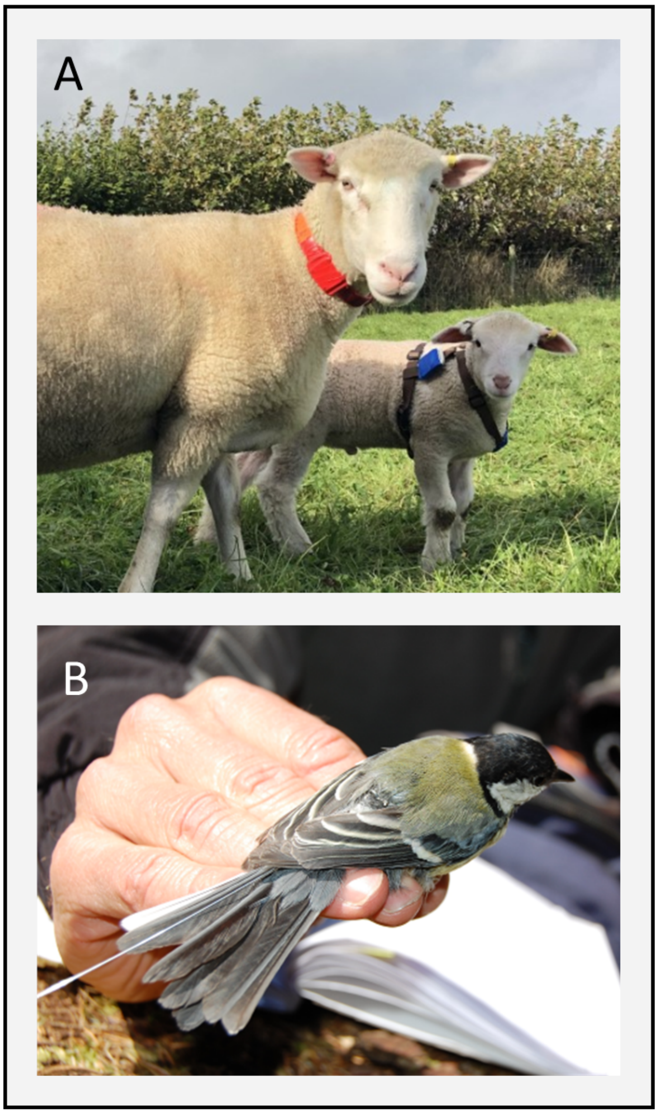

FIG. 2. Examples of animals wearing electronic devices for collection of social network data via proximity sensing. A) Ewe and lamb wearing a collar and harness with devices attached (photo by Emily Price). B) Great tit wearing a miniature device with antenna on its back (photo by Lysanne Snijders).

B. Constructing animal social networks

Most studies of animal social networks do not use the raw counts of social interactions or associations as edge weights. Instead, the edge weights are estimated with calculations that take into account potential sampling biases and pseudo-replication of observations.

The sampling biases arise from the fact that individuals (in most studies) can be out of sight, or visible but unidentifiable, for part of the observation period. Which particular types of sampling bias are relevant, and thus how the edge weights are calculated, depends on whether the data are association data or interaction data (see the preceding section for descriptions of data types). For association data, the edge weights are estimated by *association indices*, the purpose of which is to account for the following two types of sampling bias. Firstly, some individuals can be disproportionately represented in the data when all individuals have, by chance, not been observed for the same amounts of time. Secondly, observations of individuals occurring together - rather than apart - can be overrepresented in the data (e.g. when groups are more likely to be spotted than single individuals) or underrepresented in the data (e.g. if it frequently occurs that some individuals in observed groups are out of sight or unidentifiable). A few different association indices are commonly used, and the choice of which of them to use in a specific study is based on the assumed likelihood and direction of the second of the two types of sampling bias (all the indices account for the first bias. For details see [5, 92, 93]). For interaction data, the second of the above-mentioned types of sampling bias is rarely relevant and edge weights are typically calculated simply as the number of interactions per joint observation time, thus accounting for the first type of sampling bias.

Pseudo-replication in interaction data and association data can arise when repeated observations of individuals are correlated due to temporal closeness. When edge weights are estimated with association indices, pseudo-replication is taken into account by grouping the data into *samples* (samples here being subdivisions of the observation period of equal length, e.g. days), counting the number of samples where the individuals of the dyad were observed together or apart (or not seen), and using these sample-based counts as input to the index (rather than the raw counts of associations and observations). Pseudo-replication in interaction data can be taken into account by applying definitions of when an interaction between a specific dyad is counted as continuing versus starting anew, which can be done either when preparing the data for edge weight calculation or during data collection.

Before the calculation of edge weights, the data is often restricted by applying a threshold for the minimum number of times an individual should be observed in order to be included in the network, to decrease the amount of uncertainty on the edge weight estimates.

With the current increase in the use of automatic data collection methods in animal social network studies, some network construction issues become less relevant (e.g. high uncertainty on null associations [85]), while the new data formats require other considerations and development of suitable data extraction techniques (e.g. inferring spatiotemporal co-occurrences of individuals from data streams [94, 95]).

C. Analysing animal social networks

The properties of animal social network data and the research questions that these networks are used for investigating means that standard analytic approaches are often not relevant or applicable. For example, compared to many other real-world networks studied, animal social networks are relatively small, with the majority of them containing fewer than 200 nodes [96]. This puts certain limits to the characterisation of the network structure, in particular with regard to the degree distributions, which cannot with high certainty be fitted to theoretical distributions [76, 97], thereby hindering the application of hypotheses about for example dynamics and robustness, based on degree distribution. Furthermore, potential sampling biases and data dependencies need to be taken into account. Analyses of animal social networks therefore commonly consist of application of specialised statistical methods developed for the purpose. These methods are continuously evolving and expanding to fit the diverse research questions and data types, but some general approaches are well established. Here we describe key methodological approaches used until now.

A common aim of animal social network analyses is to investigate statistically whether aspects of the observed network structure are reflecting underlying non-random behaviour, rather than resulting from random interaction (or association) and observation biases. Structural aspects typically considered include: 1) global network structure, 2) correlations between network positions and individual attributes, and 3) correlations between edge weights and other dyadic data. The fact that the data points (e.g. node metrics) in network data are inherently non-independent means that they violate the assumptions of most standard statistical tests. The testing of animal social network structure is therefore instead frequently done by comparing the observed network to an ensemble of *null networks* where the hypothesised non-random structural feature or relationship is not present. This approach is used in various forms for investigations of all the three above-mentioned structural aspects. Features of global structure are tested by comparing global network metrics (e.g. assortativity coefficients, edge weight variation) to a distribution of the same metric measured on null networks. Relationships between network position (usually measured by standard centrality metrics) and individual attributes (sex, age, fitness, etc.) are typically tested with linear-model frameworks such as generalized linear mixed models, where significance is determined by re-fitting the model to corresponding metrics measured on null networks. And relationships between edge weights and other dyadic data (e.g. genetic relatedness, space use overlap, and social networks for the same set of individuals measured under other ecological or experimental conditions) are often tested with null-model based matrix correlation tests (e.g. quadratic assignment procedure tests [98]).

Using appropriate null networks is essential for avoiding spurious results when analysing animal social networks [72, 99]. The null networks should ideally resemble the observed network in all aspects except the one that is being tested. Therefore, standard network models such as Erdös-Renyi random graphs are usually not appropriate as null networks. Instead, the null networks are commonly created by data permutation procedures, which randomise specific structural features while keeping others constant (for overviews see [5, 72, 83, 99, 100]). These procedures have two objectives: 1) randomise the correct feature for testing the hypothesis of interest; 2) account for sampling biases by keeping any structure resulting from them constant. The first objective is essential for valid testing while the second one may not need to be fulfilled if relevant sampling biases are controlled for elsewhere in the analysis.

Data permutation to generate the null networks may be applied either before the network (adjacency matrix) is constructed (*data stream permutation*, [68] and see below), or afterwards by permuting either features of the observed network such as node labels or edge weights (*network permutation* [99]) or residuals from regression models (*residual permutation* [98]). Furthermore, various rules for restrictions on which data points can be exchanged may be used within the permutation types. Specialised data stream permutation procedures have been developed in the animal behaviour field that use permutation restrictions to simultaneously account for common sampling biases (esp. the number of sightings of each individual, and biases due to demographic changes) and data features usually not of interest for the test (esp. group size distribution), while otherwise randomising the social structure [68–71]. Network permutation and residual permutation may be restricted (e.g. only permute within sexes) or unrestricted, but the restrictions here usually do not control for sampling biases, and these permutation types therefore often need to be combined with sampling bias control elsewhere in the analysis (e.g. in a regression model [72]). Which permutation type and restrictions are used depends on the data and the hypothesis being tested [72].

Another common aim of animal social network analyses - which often requires different methodological approaches than the above described - is to investigate the effect of social structure on the flow of information or disease through animal populations. A frequent methodological approach for studying the spread of information in animal social networks is to use *network-based diffusion analysis*, where observed information acquisition times are compared to models of information flow with social or non-social learning [101]. Methodological approaches used for investigating disease transmission in animal social networks include simulation of disease spread in observed networks with standard epidemic models, and statistical testing for relationships between observed individual network positions, individual attributes, and measured infection states by linear model frameworks [11, 102, 103].

Going forward the field of animal social networks is starting to explore and use additional methodological approaches introduced from other areas of network research, including relational event models [104], exponential random graph models [105], stochastic actor-oriented models [106], time-ordered networks [107], and multilayer networks [108]. Together this points towards increasingly dynamic and multidimensional analyses of animal social networks.

V. CURRENT CHALLENGES FOR ANIMAL SOCIAL NETWORK RESEARCH

While animal social network studies have already made valuable scientific contributions (reviewed in [2]), some potentially fruitful directions of research involving these networks are hindered by the fact that appropriate theory and methods for these directions have not yet been developed or have not been adjusted to this area of network research. In the following, we describe challenges for animal social network studies where we imagine that input from scientists with expertise in other types of empirical networks or in theoretical aspects of complex systems could be particularly valuable for finding good solutions.

Network similarity. An important challenge for animal social network research is how to measure the similarity between real-world networks from different sets of individuals in a meaningful way [97, 109]. Comparison of the social structures of different species, or of populations of the same species living in different environments or containing different compositions of individuals (e.g. with regard to sex or age) could potentially bring new key insights into the evolution of social systems and how they are shaped by internal and external factors. In animal social network research, network similarity is commonly investigated by quadratic assignment procedure matrix correlation methods [98], but these can only be used for networks that contain the same set of individuals (e.g. the same group under different environmental conditions). While network comparison methods that control for different sampling biases (see Section IV for description of common biases) and different network sizes would be very useful, such methods have not yet been well integrated into the field of animal behaviour (although specific approaches have been suggested, e.g. motif analysis [109] and exponential random graph models [105]). Given the fact that graph similarity is a fundamental topic of interest in network science, there should be much scope for interdisciplinary development of network comparison methods specifically designed for animal social networks.

Social complexity. Another question of high relevance for research in animal social networks is how social complexity can and should best be defined and measured [110–112]. Social complexity, and its variation between and within species, has long held interest from animal behaviour researchers, both because it provides a framework for understanding the evolution of social systems, and because of its potential links to the evolution of cognitive abilities and communication systems [111, 112]. There is currently no consensus about how to define and measure animal social complexity, and different measures may be relevant for different questions, given that they would catch different aspects of social complexity. Factors that have been considered as indicators of animal social complexity include group size and composition, mating system, social roles, and differentiated social relationships (for details see [110, 111]). The new research area of animal social networks raises the questions of how these networks can be used in the general task of quantifying social complexity in meaningful ways, and how the complexity of social network structures may best be measured and compared across different species and populations. These questions have not yet been much explored (for exceptions, see [75] for a recent suggestion for a complexity measure based on animal social networks, and [5] for a discussion of various potential measures). Collaboration between theoretical researchers with expertise in complexity measures and empirical animal behaviour researchers could potentially advance this area, and a foundation has recently been laid for the integration of complex systems thinking into general animal social complexity research (see [112]).

Network robustness. A topic which has got somewhat more attention and may also particularly benefit from interdisciplinary collaboration is the robustness of animal social networks (i.e. their ability to withstand perturbations, such as the death or removal of individuals). Knowledge about this is important for the conservation of animal populations (e.g. in the face of poaching or habitat destruction, which can lead to network fragmentation and/or reduction in network size), as well as for understanding social evolution. A number of studies have investigated robustness of animal social networks with various approaches, including actual experimental or natural removal of individuals from the population [113–116], simulated removal of nodes from empirical [113, 117] and artificial networks [118], or application of other experimental perturbations [119]. These studies have given indications of the level of resilience of animal social structures in different species and under various perturbation scenarios. Better integration of percolation theory and related topics with animal social network research could potentially further our understanding of the robustness of social systems across species.

Extraction of information from large datasets. Finally, the automated data collection methods that are now in use (see Section IV) means that animal social network datasets are increasingly large and multidimensional, and the extraction of information from the raw data is less direct. Optimisation of the treatment of these data is likely to benefit from interaction with areas of complex systems science where large and complex datasets are routinely dealt with.

VI. WHERE TO FIND ANIMAL SOCIAL NETWORK DATA

Data on animal social networks are to an increasing extent being made publicly available in online repositories, including Dryad Digital Repository (datadryad.org), Network Repository (networkrepository.com/asn), and Animal Social Network Repository (bansallab.github.io/asnr ; [120]), allowing for easy access for complex systems researchers who would like to explore and use such data. Although these data are freely available, we would suggest that the researcher who has provided the data is always contacted before the data are used in scientific projects. This is not only as a courtesy to the researcher, but also to make sure that the data are useful for the intended purpose. Factors that may be relevant to consider in this regard include for example the methods used for data collection, the time frame over which the data were collected, the type of behaviour used to quantify the social relationships, and potential sampling biases that need to be controlled for in the network construction and analysis (see Section IV).

VII. CONCLUSION

It is frequently mentioned in complex systems science that networks can be found on all levels of nature, including the sub-individual level (e.g. gene and protein networks) and the super-individual level (e.g. ecological networks based on species interactions). On the level of the individual (or whole organism), often only human social networks are mentioned, reflecting that animal social networks are not yet well known outside the field of animal behaviour. Nevertheless, to comprehensively understand nature and the complex systems found in it, we must take the many non-human animal species into account.

We believe that the best understanding of animal social networks, and the best use of them for understanding complex systems, is gained by combining intricate knowledge about the specific study systems with innovative and rigorous theory, modelling and analysis. We hope with this introduction to have provided a springboard for future cross-disciplinary collaborations around animal social networks, and that animal social networks will ultimately be integrated as a natural part of complex systems science.

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