



Review

Quantitative characterization of animal social organization: Applications for epidemiological modelling

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Abstract: Social organization is a key aspect of animal ecology, closely interlinked with all aspects of animal behaviour. The structure of animal assemblages is highly diverse, both within and between species. The complexity and variety of social systems and the dynamic nature of interactions and dependencies between members of social groups have long been major obstacles for developing operational characterizations of social organization. Here, social network analysis, a set of statistical tools rooted in graph theory, suggests itself as a potential solution for this problem, by offering quantitative measures for various aspects of social relationships. In this review I will first introduce network analysis as a tool to characterize the social organization of animal groups and population and, then, focus on the application of this method for epidemiological modelling, specifically the prediction of spreading patterns of pathogens in livestock and its potential for informing targeted surveillance and planning of intervention measures.

Keywords: social structure; social network; transportation network; epidemics; livestock population; disease transmission

1. Animal sociality

The modes of social organization among animals are highly diverse. While some animal species live predominantly solitary lives, seeking the proximity of conspecifics only for reproduction, others live in small individualized groups or in enormous aggregations, schools, flocks or herds consisting of hundreds of thousands or over a million individuals. Even within a single species we can observe considerable diversity in social organization governed by habitat and seasonal variation [1–3]. Social organization is a key aspect of animal ecology, closely interlinked with anatomical, morphological, physiological, and behavioural traits: from organs and structures developed for intra-specific communication and weapons for fighting competitors to dietary preferences, feeding schedules and habitat choice. Social organization has played and continues to play an important part in animal domestication and has been recognized as an important factor in animal housing and husbandry [4,5].

Yet, while the importance of social organization for ecology, evolution, animal breeding and management is generally acknowledged, social organization itself has turned out to be rather difficult to describe and to operationalize.

Robert Hinde described the social structure of a group “in terms of the properties of the constituent relationships and how those relationships are patterned” [6]. While this generic description found broad consent in the scientific community, its implementation into research programmes was hampered by the complexity of those patterns and the unresolved question of how to analyse them. The most basic approach to define the social organization of a group of animals might be just to determine the number and sex of regularly associated conspecifics. As next steps, one can include life-history traits, activity, and pattern of offspring care, mating system, spatiotemporal cohesiveness, and dominance relationships [1,7]. However, behavioural ecologists soon felt uneasy with most classification schemes for social systems when they did not capture the specific features needed, or when it became evident that certain species fit into more than one of the categories. Here, social network analysis might be more than a straw to clutch at. As it introduces measures, usually on a continuous scale, that describe certain structural characteristics, it allows biologists to get rid of the categorization schemes: instead of squeezing species into one of two categories (e.g., “centralized” or “egalitarian”) one can give a centralization index for each species, drawing a much finer and less controversial picture [8–11].

2. Social networks

The idea to conceptualize the relationship of humans in terms of networks for the purpose of research dates back to the 1930's when Jacob Moreno introduced sociometry as a discipline and the sociogram as a preferred tool to visualize social networks [12]. The two types of elements in sociograms are nodes, representing individuals, and links representing social interactions between individuals. The structure of the sociogram allowed not only a visualization of social relationship, but also a quantitative representation that paved the way for new avenues for statistical analysis. In the following years social network analysis became an active research field within education and community studies (see also [13] for a review). Sociologists soon started using the network approach for describing community structure [14,15] but also work relationships in corporations [16,17]. Networks were soon recognized as playing important roles for the spread of information [18–21]. Over the years, social network analysis has found many new applications, including the study of political networks [22,23], social movements [24], economic networks [25], and scientific collaboration networks [26,27]. Finally, the advent of the internet and the world wide web led to both the availability of large data sets on interpersonal communication and group memberships, opening up a whole range of new economic applications for network analysis [13,28,29]. Modern analytical techniques for social network analysis rely heavily on graph theory. A summary of graph theoretic terms and concepts used in social network analysis is given in Figure 1.

3. Animal social networks

3.1. Development of the idea

One of the first ethologists to embrace the idea of conceptualizing animal social relationships as networks and applying tools of social network analysis was the Swiss primatologist Hans Kummer [30]. In his detailed study of the social organisation of Hamadryas baboons (*Papio hamadryas*),

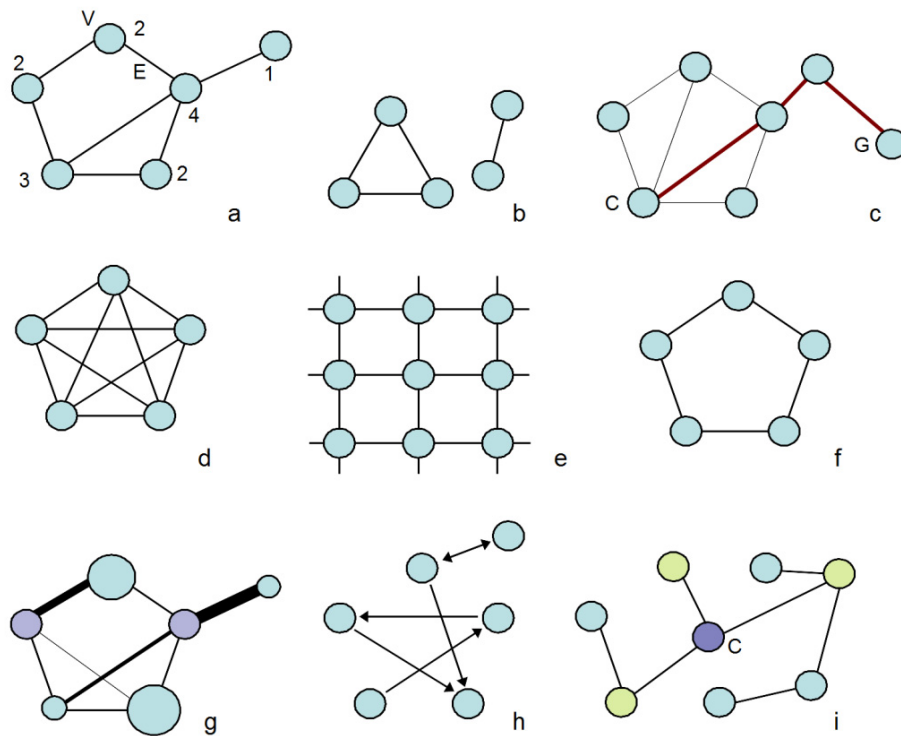


Figure 1. Visual representations of graphs. Graph theory is a branch of discrete mathematics and is concerned with the study of graphs. A graph is a structure consisting of a set of objects that are in some way related to one another. The mathematical abstraction of such an object is called vertex (plural: vertices) and the mathematical abstractions of the relationships between vertices are called edges. In its most simple form a graph is depicted in diagrammatic form as a set of dots for the vertices, joined by lines for the edges. Network analysis is the quantitative description of networks of interacting entities based on the abstraction of the networks as graphs. In the field of network analysis vertices are often referred to as nodes and edges as links. We are speaking of social network analysis if the interacting entities are humans or animals. The diagram representing a social network is called a sociogram. A path is a sequence of edges which connect a sequence of vertices. A graph is connected when there is a path between every pair of vertices. In a connected graph, there are no unreachable vertices. Both vertices and edges can have additional attributes. Quantitative attributes of vertices are called vertex weights, quantitative attributes of edges are called edge weights. Additionally, in a directed graph edges can have a direction. The size of a graph gives the number of vertices it contains. A complete graph is a graph where there exists an edge between all pairs of vertices. A graph where the number of edges is much smaller than the number of edges of a complete graph of the same size is called a sparse graph. Two vertices are adjacent to each other (or linked) if there exists an edge between them. The neighbourhood of a vertex consists of all vertices adjacent to it. The degree of a vertex is the number of incident edges. (a) Vertices (V) are represented by dots, edges (E) by lines. Numbers next to vertices indicate vertex degree. (b) A disconnected graph consisting of two components. (c) A path from vertex C to vertex G is highlighted by the red edges.

This path has a length 3. (d) A complete graph of size 5. (e) Lattices are graphs that are well suited for studying spatial problems. (f) A simple cycle is a graph where all vertices have degree 2. Their simple and symmetric structure makes them well suited for analytical treatments. (g) Weighted graphs are graphs where weights are attributed to the vertices or the edges or both. Edge weights are usually visualized by the thickness of the lines, vertex weights by the size of the dots or, for discrete properties, by colour. (h) Edges can be undirected (as in a-g) or directed. Directed edges are visualized as arrows; they can be unidirectional or bidirectional. A vertex that has only outgoing edges is called a source, a vertex with only ingoing edges is called a sink. (i) The neighbourhood of vertex C are highlighted in green.

Kummer made extensive use of sociograms to document the structural development of the baboon units, as well as changes in the interactions between males and females during phases of their reproductive cycle. In 1965 Donald Sade also began to use sociograms, to describe the grooming interactions among a free ranging group of rhesus macaques (*Macaca mulatta*) [31]. He used his diagrams to visualize how the grooming relationships between mother and offspring remained strong even after offspring reached sexual maturity. After these early publications and through the influential work by Wilson [1] and Hinde [32], sociograms became an increasingly popular way to display all kinds of social interaction data. Another visualization tool which was popular among ethologists in the 1980's was cluster analysis. Like sociograms, cluster analysis provided useful visualizations, such as dendrograms, which could be used to display sub-groupings, i.e. clusters within a group of individuals based on a specific behaviour of interest [33–36]. For most ethologists in the 20th century these two methods were the only brushes with what would nowadays be considered as social network analysis. The one major exception to this was Donald Sade [31,7–39] who was not satisfied with a visualization of the structure but who wanted to derive metrics for quantitative analyses. For this purpose, Sade introduced a measure of centrality referred to as “n-path” centrality [38]. Similar to eigenvector centrality (Table 1), n-path centrality gives an individual's centrality based not only on their own direct connections within the network but also their indirect connection, i.e., the connections of the individuals, they are connected to.

At the beginning of the 21st century a new wave of social network analysis arrived, driven both by the invention of new communication techniques (most notably the internet and the world wide web) that resulted in large scale networks and sociologists developed a range of new statistical tools including various random graph models and a plethora of motif, centrality and connectedness measures that allow sophisticated analysis [29,47]. Within animal behaviour research, David Lusseau [48] described the emergent properties of a social network of bottlenose dolphins and soon afterwards that network approach was picked up by many students of animal behaviour [49–51]. In a widely recognized study, Flack and colleagues [52] used four different network measures (degree, reach, assortativity and mean clustering coefficient) to examine the effect of removing the three highest ranking males from a group of captive pigtailed macaques (*Macaca nemestrina*) on social networks of grooming, play, contact-sitting and proximity. From then onwards, social network analysis was used for different purposes. While some used it for describing social relationships/structures and their potential functions in animal groups [8,11,53–57], others went on to make use of the network approach to address a broader range of topics including social learning and information flow [58–63], the influence of social structure on cooperation [64–66] and the welfare of captive groups of primates [67–69].

Table 1. Network measures frequently used in social network analysis.

Density	The density of a graph is the proportion of existing edges to the number of possible edges, i.e. the number of edges of a complete graph of the same size [40].
Degree centrality	The degree centrality of a vertex reflects the number of edges incident to it [40].
Strength centrality	The strength centrality of a vertex is given by the sum of the edge weights of all edges incident to that vertex [11].
Edge weight disparity	The edge weight disparity is a measure for the heterogeneity of the edges incident to a given vertex [41].
Closeness centrality	Closeness centrality is a measure for how close a vertex is to other vertices on the graph. It is based on the geodesic distances (i.e. the shortest paths) of a vertex to all other vertices [40].
Eigenvector centrality	The eigenvector centrality of a vertex is based on the sum of the centrality of its neighbours, given by the eigenvector corresponding to the largest eigenvalue [42]. As a consequence an individual can gain high centrality through having many neighbours or through having neighbours with high centrality.
Betweenness centrality	Betweenness centrality mirrors how often a vertex lies on the shortest path between two other vertices [43].
Community modularity	Community modularity is a structural graph measure which reflects the degree of fragmentation of a group into subgroups based on the fraction of existing edges within and between subgroups [44]. Subgroups can either be determined by vertex characteristics or through algorithms searching for a partitioning that maximizes modularity [45, 46].
Clustering coefficient	The clustering coefficient characterizes the local group cohesiveness by counting how often vertices that are in the neighbourhood of a given vertex are also direct neighbours themselves [28].

3.2. Levels of network description

Social network analysis can be split up into three broad levels of analysis; the individual (nodal) level, the sub-group level and the group level. The question of which level of analysis to use, goes usually hand in hand with the research question and the purpose of the study. At the individual or ‘nodal’ level social network analysis is used for ascribing certain ‘nodal properties’ to an individual (usually animal). As such, this is the level of analysis that allows researchers to consider an individual’s social niche within a group or population. This can be done using a single network metric such as a centrality measure or a clustering coefficient, or a list of several different nodal network measures. In the latter case it has been suggested that these measures could even be summarised to form a personality profile for each individual [70]. The purpose of the individual level analysis is usually to correlate nodal network measures with other biological characteristics of the individuals such as sex, age, social rank, ‘personality’ descriptors [37,71], parasite load [72], physiological measurements such as glucocorticoid levels [73], or health status [74].

At the sub-group level social network analysis allows insights into how a given group is structured by identifying clusters or subgroups within it and to identify how these subgroups are connected to each other. This identification process is often referred to as subgroup or community detection [75,76] or motif analysis [77]. A good example of this level of analysis comes from Snyder-Mackler et al. [78] who studied the multilevel societies of Gelada baboons (*Theropithecus gelada*), which consist of two or more nested levels of organization: one male units, teams, bands, and communities. Sueur and colleagues [79] used community modularity to examine how frequently matrilineal units within different species of macaques interact. Measures at the sub-group level deliver insights into the structuring of the entire network; though as the information is not distilled into a single statistic for the entire network, they provide a more nuanced picture of the network structure. As I will discuss in more detail below, it is exactly this property that makes measures like community modularity specifically suited for predicting the propagation of information, parasites, or disease within a group. For example, Voelkl and Noë [59,80] found that the expected average path length of a transmission process can be explained by the community modularity of a group.

The purpose of group or population level analysis is usually to either compare the properties of different groups or populations [8,11,31,56,70,76,81], or to track changes in the overall group structure over time [54,55,67,69,82]. For example, Foster and colleagues [82] found a relationship between the connectivity of the social network of Orca (*Orcinus orca*) and food abundance, with a more interconnected social network in years of high salmon abundance. Physicists have defined a large variety of measurable properties of networks for describing overall characteristics of entire networks [83, 84]. The most frequently used measures for this sort of analysis are usually either graph-wide measures which describe a property of the whole network—e.g., graph density—or moments of the distribution of nodal measures, like the skewness of the degree distribution or edge weight disparity [85]. The degree distribution is the most frequently used way for investigating the heterogeneity of nodes (i.e. individuals) in the network. Apart from those measures, the number and size of strongly connected components and the size of the giant component are characteristics with relevance for epidemiological models [86–88].

4. Social networks and epidemics

Many diseases spread through close contact of susceptible individuals with infected individuals. In those cases, connections between individuals that allow an infection to propagate create a network

of inter-connected individuals [89–91]. Incorporating the network structure of the population allows a detailed characterization of the epidemiological dynamics. For example, the application of network models allowed the discovery of so-called 'super spreaders' during the SARS (Severe Acute Respiratory Syndrome) outbreak in 2003 [92,93]. Models of the spread of infectious diseases acknowledging the contact network of the population were first employed to study the spread of sexually transmitted diseases in humans [94–96]. Since then, network epidemiology has become a rapidly expanding and prospering field of research, because an understanding of the structure of the transmission network allows more detailed predictions about the distribution of infections—specifically during the initial phase of an epidemic outbreak.

4.1. Types of epidemiological models

Network models of population processes are individual-based models, which means that the status and connection of every single entity—in most cases either an individual, a household, or a holding—in the population is explicitly modelled. While analytic approaches have been applied to very simple graph structures (specifically complete graphs, grids, cycles and star graphs), solutions become quickly intractable for more complex graphs. As a consequence, numeric simulations have become the standard approach to modelling the spread of diseases on real-world networks [88]. There are two distinct approaches for modelling disease spread: continuous-time and discrete-time models. In a discrete-time model the disease can be transmitted at each time-step along every link from an infectious node to a susceptible node with a particular probability. At each time step nodes can change their status: recovering, becoming immune or infectious. The probabilities with which nodes change their status can be equal for all nodes in the network or node-specific. Updating can either take place simultaneously—i.e., at each time step the status of all nodes and links is updated once, or sequentially—i.e., at each time step only a single event can occur and only the status of the affected node or link is updated. The choice of the update process has important implications for the resulting dynamics [97]. Simultaneous updating sets natural limits to the speed of the propagation of diseases: within a single time step the disease can only spread from one node to the next but not further. The time steps for simultaneous up-dating are often chosen to be equivalent with the time-frame size during data collection. For example, when animal movements are registered on a daily basis (with the date of the movement but without specified time), then a time step in the model will usually correspond to one day. On the other hand, sequential updating—sometimes also referred to as 'real-time' updating—assumes that time steps are so small that it is unlikely that any two transmission events will take place within the same time interval. If time steps tend towards zero, this assumption is definitely justified. Sequential updating requires, however, a scaling operation in order to translate modelling steps into real-time.

4.2. Types of populations

Pathogen transmission in animal populations has been studied in two rather distinct types of populations: human-managed population of livestock and wild animals. These two population types differ both in the extent of control humans have over movement patterns, interaction and reproduction and in the kind of data available. The contact structure and movements of livestock and poultry are primarily determined by human management actions. However, within herds or flocks individual animal behaviour might also add another level of heterogeneity [98]. Network analysis of livestock and poultry populations has been used for identifying high-risk holdings or suggesting schemes for targeted surveillance [99–104]. As the network indicates potential routes of disease

transmission, knowledge of its structure can be important for disease control policies [88,105]. A recurrent theme of network analysis of farm animals is that a small percentage of holdings contribute to a large percentage of animal movements [102,104,106–109]. These holdings will hold the central positions and are considered hubs for transmission processes. The network structure of natural animal populations, on the other hand, is a result of individual behaviour: migration, dispersal, ranging patterns, mating strategies, territoriality, and agonistic and affiliative social behaviour. As a result, wild animals often have highly heterogeneous contact network structures [9,110,111]. This has direct consequences for disease transmission, which is slowed down in highly modular systems [112–114]. Social network analysis of wild animal groups has been used to identify individuals at high risk of transmitting a disease [72,115,116] and to suggest disease management policies [117,118]. Both, networks for life stock and wildlife can differ drastically in spatial scale: from networks of single groups of animals or local populations [119,120] to networks comprising data for livestock connectivity of entire countries [121–123] or connectivity through migrating species spanning continents [124,125]. In the case that the social network spans large geographic areas, new questions arise and, in addition to individual based networks, one can create spatial networks to identify locations of differential importance for disease transmission [111,126].

4.3. Transmission routes

Infectious diseases can spread through different transmission routes: from environmental contamination to vector-borne, through aerosols, close physical contact or sexual intercourse [112]. Depending on the transmission process different types of networks will be needed for making sensible predictions about spreading patterns. What constitutes a network link relevant for disease transmission will depend on the specific disease in question. In behavioural ecology networks are frequently constructed from observations of physical proximity [3,11,110,127,128]. These proximity measures can either be based on direct observations in the form of nearest-neighbour protocols and mark-recapture records or, as it is becoming more and more common, through telemetry, GNSS (global navigation satellite system) loggers, passive RFID (radio frequency identification) tags or UHF (ultra-high frequency) radio-based proximity detectors [128–132]. These approaches are indiscriminative regarding the underlying causes for the spatio-temporal associations. Based on co-occurrences, a link is drawn between individuals using various indices of associations [3,133,134]. Usually the assumption is made that the likelihood for the transmission of pathogens is proportional to the proximity measure [111,113,128]. This assumption is plausible when diseases are transmitted through vectors like flies or mosquitoes or through aerosols, or when proximity is highly correlated with physical contact of a kind required for disease transmission [135]. For example, Hamede and colleagues [136] used individually fitted proximity loggers, which recorded all instances when one individual came within a 30 cm range of another individual, to study the spread of facial tumour in Tasmanian devils (*Sarcophilus harrisii*). These facial tumours are often fatal and have been identified as a main factor responsible for a drastic population decline. As these tumours are contracted specifically when devils fight with each other and bite their opponents, networks based on direct encounters between individuals seem to be reasonable descriptors for transmission routes.

Movement or transportation networks differ from encounter networks in that the nodes do not represent individual animals but locations (households, farms, holdings) and edges represent movements of animals from one location to another [88,137,138]. In those models it is either assumed that the movement of infected individuals to a holding will result in pathogen transmission to all individual animals at that holding, or epidemic dynamics within a holding are explicitly

modelled based on mean-field assumptions. In the latter case these models are referred to as meta-population models [122]. Simulations based on transport network data suggested that the early spread of foot and mouth disease in 2001 in Great Britain was primarily due to animal—specifically sheep—movements between farms [139,140]. An insight gained from studies of transport networks (but equally important for other kinds of networks), is the importance that the temporal structure plays for pathogen transmission. If livestock is moved from a holding before the epidemic arrived at that holding, it will not contract the disease. Networks that do not take the temporal order of the movements to and from holdings into account, but that give only monthly summaries of movements, will therefore give different results than so-called dynamic models that account for the precise temporal ordering of movement events [109,141,142]. Consequently, most recent epidemic models for transport networks are dynamic models based on time-stamped data.

4.4. Aims and scope of epidemiological network models

One motivation for incorporating network structure of populations into epidemiological models is the hope that these refined models will improve estimates of the basic reproductive number R_0 , which is the average number of individuals infected by one carrier of a disease. Both simulated outbreak scenarios and empirical data show that population structuring has usually an attenuating effect, leading to a slower spread of pathogens than mean-field models would predict [138,123]. Yet, a simulation study by Sah [143] based on social networks of 43 animal species suggests that subgroup modularity has to be very pronounced in order to have noteworthy effects on the speed of disease spread. While no single network descriptor could be found that fully captures the impact of structuring on the spread of the propagation process [111], several general statements can be made. Pastor-Satorras and Vespignani [144] could demonstrate that epidemic thresholds derived from mean-field models will break down when the degree distribution of a network follows an unbounded power-law. While the degree distribution of real-world animal networks—be it managed populations of livestock or natural populations—hardly ever follow a power-law, their degree distributions are often heavily skewed [96,109] leading to epidemic thresholds lower than expected for evenly mixed populations [88,145]. Several centrality measures have been identified as indicators which individual nodes in a network are more likely to be infected early on during an epidemic outbreak [107,146]. And finally, metrics describing the clustering of the network have also been used as predictors for the propagation dynamics [147–150].

Robinson and colleagues [138] investigated how the introduction of mandatory standstill periods for livestock moving between holdings, introduced in the aftermath of the 2001 outbreak of the foot and mouth disease in Great Britain, affected the structure of the British cattle network. Constructing week-by-week contact networks they could show that the size of the giant strong component of the network (i.e., the number of the largest component of holdings interconnected with each other through movements) was steadily increasing over time, concluding that, despite restrictions of cattle movement, the expected size for the next foot and mouth disease epidemics has in fact increased. Simulations of disease propagation on dynamic networks have been used for suggesting optimal surveillance strategies for livestock [104,106,109,151,152] and identifying the most central individuals in groups of wild animals for targeted vaccination measures [118].

If transmission processes are poorly understood, networks constructed under different assumptions or based on different behavioural data can be compared in their predictive abilities of observed spreading patterns. For example, Drew and colleagues [119] constructed social networks based on three different kinds of interaction (aggression, foraging and grooming) for eight groups of

meerkats (*Suricata suricatta*). Thereafter, they compared dynamic network models for tuberculosis (*Mycobacterium bovis*), infections with observed tuberculosis incidences. Their results indicated that predictions based on grooming behaviour gave the best fit, and that groomers were at higher risk of getting infected than receivers of grooming. In mountain brushtail possums (*Trichosorus cunninghami*), *E. coli* transmission has been shown to be more closely linked to networks of nocturnal interactions rather than to networks based on co-habitation of dens [120], while Godfrey and colleagues [115] found that networks based on refuge sharing in skinks (*Egernia stokesii*) were better predictors for ecto-parasite transmission than networks based on directly observed social associations. García Álvarez and colleagues [153] reported that cattle movements predicted the spread of bovine *Staphylococcus aureus* strains, but other contacts via farm visitors were also correlated with strain distribution, suggesting that contact networks based on transport data alone may not adequately capture the disease dynamics.

Furthermore, pathogen phylogenetics based on genetic markers or whole-genome sequencing of fast evolving pathogens can be used for reconstructing transmission networks [154–160]. Transmission networks reconstructed from pathogen phylogenetic trees have been used to identify transmission networks in giraffes [159], bobcats [161], cougars [154] and lizards [158]. When the infection process itself defines the network, the network is referred to as a contact tracing network [88]. It is important to note that contact tracing networks based on infections are usually sub-networks of the complete interaction networks, because they only include infected individuals. They contain often only a small fraction of potential routes of infection and are generally tree-like in nature. As such, they can provide insights into the transmission processes, but they cannot be used for predicting potential spreading patterns of future epidemics.

5. Outlook

Many authors attribute the birth of graph theory to Leonard Euler's solution to the Königsberg bridge problem [29]. At the time, graph theory was received as a branch or recreational mathematics and even Euler did not see any important or useful applications for it. This perception has, by now, changed and graph theory has revolutionized many different fields: from economics to cryptology, systems biology and particle physics. For behavioural ecology, graph-based network analysis offers a way to operationalize the description of animal social systems and to express properties of social organization in quantitative ways. This is important if one aims at relating descriptors of the social system to other biological traits, fitness values or genomic data. For epidemiology, a network approach to population structure is particularly valuable, as the network—if based on the right behavioural measures—naturally suggests transmission routes for pathogen transmission [143]. The strength of network models lies in their specificity during early phases of an outbreak, when the prevalence is still very low and heterogeneity in transmission likelihoods plays a larger role [162–164]. As such, social network models are specifically suited for identifying high-risk nodes and for planning surveillance schemes that should detect outbreaks as early as possible. Ready-to-use tools for analysing human social networks are easily available, tempting researchers to directly apply them to animal networks. Yet, if this is done in an unreflective way, this can easily lead to nonsensical outcomes. The choice of network descriptors should not be based on availability, but on how well they capture the underlying biological processes one is apt to study. What these measures are and what kind of data are needed for them, are questions that require further investigations and research. I will, therefore, conclude this review with a short outlook on—what I consider—those methodological aspects of animal social network analysis that will require our specific attention.

While social network analysis has become a popular tool for describing and analysing social organization of animal groups, several authors are warning against 'careless' applications of social network analysis as it is too often observed [3,85,165–167]. For one, network analysis is a 'data-hungry' method, requiring detailed and precise information about all components of the network. If networks are based on poor data, then the GIGO-principle (standing for "garbage in—garbage out") applies and any predictions based on an imprecise network representation are futile. The second major problem is the availability of a vast amount of different network metrics. This variety of measures makes data dredging and p-hacking all too easy, with the result that a considerable proportion of 'significant findings' of exploratory studies might not be reproducible. Finally, for many species we can find high intra-specific variability in social organization and group composition. This is reflected in an equally high variability in network metrics for different groups of the same species, making it difficult to make species level generalisations without data from a large number of groups [11,167]. Care must, therefore, be taken not to jump to premature conclusions from the results of a single study based on a single population or a small homogeneous set of populations.

Epidemiology is a discipline that had picked up network approaches to animal populations more readily and more quickly than most other disciplines [112,135]. Yet, we are still far away from the point where we can say with confidence that our models provide precise and reliable predictors for all aspects of population-level disease dynamics. The most pressing problems are the matching of network and transmission type, multi-modal or uncertain transmission pathways, multi-host pathogens and the empirical validation of predictive network models.

Network analysis of human communication networks became a major research enterprise with the availability of large amounts of electronic communication data ('big data'). It is therefore likely that, the combination of compulsory registration systems for animal movements that have been implemented in many European countries [123] and individual-fitted data loggers for automated monitoring in precision livestock farming will lead to new opportunities for building more detailed network models [111,168]. Yet, the important question to ask is: what kind of data should we collect? Currently, the predominant approach to network modelling is to take those data that are readily available and try 'to make the most out of them'. In an ideal world, however, we would first identify the precise question to be answered with the network model, then identify the sort of network information required for answering these questions and—based on that—devise a sampling scheme. Apart from the problem of identifying the behavioural measure that depicts transmission pathways most accurately, an issue that is still largely unexplored is the case where animals change their social interaction patterns as a result of an infection. Changes in interaction patterns can either be due to changes in the behaviour of the infected individuals or in the response of healthy individuals encountering ill conspecifics. Both types of changes have been documented [74,169–173] but effects on the network structure are still poorly understood.

One development that could be observed over the past years is the increasing use of dynamic network models [174]. In dynamic network models, the network structure is not assumed to be constant but might be subject to change [29]. The most frequently considered dynamic is a change in the network over time. This is specifically important for movement networks, where vertices denote locations (households, holdings, or geographic regions) and edges represent movements of individuals between those locations. Transport networks of livestock between holdings are the most prominent movement networks that have been studied extensively [86,87,121,122]. In transport networks, transport of livestock from one holding to another is an event that can be located in time precisely. If this information is available, it can be incorporated in epidemiological models of disease spread [106,109,153,175]. Given both the necessity to incorporate the temporal order of events for

improving model predictions and the increasing availability of time-stamped data due to new regulations for livestock transport and trading, it is foreseeable that dynamic models will become increasingly popular and might completely displace static network models in epidemiology.

Many pathogens have multiple transmission pathways or hosts. If pathogens can move from members of one species to another, then all individuals of all potentially affected species constitute one large population which can be represented by a single large network. As pathogeneses and the transmission dynamics will differ between species, nodes of the networks will belong to different classes with different nodal properties reflecting species-specific aetiopathology, and different types of links between nodes can reflect the different transmission dynamics within and between species. Such network models have not been constructed, so far, due to the major challenge of collecting the required information about potential transmission routes and transmission mechanics both within and between all involved species. This will be a challenge for the future and several ideas for analysing multi-level networks have been put forward [126,176]. Multi-host pathogens will require special attention in the future [153,159,177–180]. Networks of multi-host pathogens that also infect humans (zoonoses) have received special attention [181] specifically after recent outbreaks of bird flu [100,108,125], swine influenza virus [182], rift valley fever [183] and, most recently, corona virus [184–186]. Apart from their effects on health of livestock, domestic animals, and humans, multi-host pathogens can have severe consequences for small populations of endangered species, therefore constituting a conservation issue [160,187,188]. Yet, while different sentinel and intervention schemes have been suggested based on network models of pathogen transmission, empirical proofs of their efficiency are currently lacking.

6. Concluding remarks

The study of animal behaviour has come a long way from primarily anecdotal description of haphazard observations of behaviour to a systematic science based on principles of experimental design and statistical reasoning. The methodological revolution, starting in the 1970s, first affected the description and operationalization of individual behaviour. It was, soon, recognized that a similar objective and operationalizable approach will be needed for the characterization of the social organization of animal groups. Yet, how this is to be achieved was a question that tormented many scholars of animal behaviour: the complexity and variety of social systems and the dynamic nature of interactions and dependencies between members of social groups seemed to make an operationalization almost impossible. Here, social network analysis, a set of quantitative tools rooted in graph theory, suggests itself as a potential solution for this problem. Even though, social network analysis is not a magical bullet that will do away with all problems and enable us to answer all questions, it will—without doubt—contribute to the advancement of the field by providing both conceptual insights and direct applications for specific problems.

Acknowledgements

I thank Hanno Würbel, Mike Toscano and Claudia Kasper for comments on an earlier version of this manuscript. This review was written by BV in partial fulfilment of his Habilitation thesis for obtaining the *venia docendi* at the University of Bern.

Conflict of interests

The author declares no conflicts of interest in this paper.

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