Science Progress (2016), 99(1), 68–82
Paper 1500146 doi:10.3184/003685016X14495640902331

Animal welfare: a social networks perspective

TANJA K. KLEINHAPPEL, ELIZABETH A. JOHN, THOMAS W. PIKE, ANNA WILKINSON and OLIVER H.P. BURMAN

Tanja Kleinhappel obtained her PhD from the University of Lincoln in 2015, with a thesis looking at the causes and consequences of social network structure within animal groups.
E-mail: tkleinhappel@lincoln.ac.uk

Elizabeth John obtained her PhD from the University of Alberta in 1989. She then held postdoctoral positions at the University of Michigan Biological Station and the University of British Columbia before taking up a lectureship in Ecology at the University of Sussex in 1992, eventually becoming head of the Department of Biology and Environmental Science. She moved on to the University of Lincoln in 2011, where she is currently head of the School of Life Sciences. Her research interests lie within community ecology and include the effects of heterogeneously distributed nutrient supply on plant growth and competition, the effects of herbivores and nutrient availability on plant community structure, the relation between dominance and diversity in plant communities, and patterns in plant and lichen communities. E-mail: ljohn@lincoln.ac.uk

Tom Pike obtained his PhD from the University of Newcastle in 2004. He then went on to postdoctoral positions at the universities of Glasgow, St Andrews and Exeter, before taking up his current position as Senior Lecturer at the University of Lincoln in 2011. His research focuses on animal sensory and behavioural ecology, with an emphasis on the sensory underpinnings of social behaviours.
E-mail: tpike@lincoln.ac.uk

Anna Wilkinson obtained her PhD from the University of York in 2007. She then worked as a postdoctoral research fellow at the University of Vienna before joining the University of Lincoln in 2010, where she is now a Senior Lecturer. Her research focuses on understanding animal cognition as part of a biological framework, and falls into two main areas: perception and categorisation, and 'cold-blooded cognition' (the way reptiles and amphibians perceive the world, how they learn about their environment and how they use and retain this information). E-mail: awilkinson@lincoln.ac.uk

Oliver Burman obtained his PhD from the University of Bristol in 2001, and remained there in a succession of postdoctoral positions before joining the University of Lincoln in 2010. He is currently a Reader in Animal Welfare. His research focuses on utilising fundamental aspects of behaviour and cognition to underpin advances in animal welfare, including the study of animal vocalisations, the development of novel cognitive methods to assess emotional state, and social recognition, memory and 'forgetting' in non-human animals. E-mail: oburman@lincoln.ac.uk

ABSTRACT

Social network theory provides a useful tool to study complex social relationships in animals. The possibility to look beyond dyadic interactions by considering whole networks of social relationships allows researchers the opportunity to study social groups in more natural ways. As such, network-based analyses provide an informative way to investigate the factors influencing the social environment of group-living animals, and so has direct application to animal welfare. For example, animal groups in captivity are frequently disrupted by separations, reintroductions and/or mixing with unfamiliar individuals and this can lead to social stress and associated aggression. Social network analysis of animal groups can help identify the underlying causes of these socially-derived animal welfare concerns. In this review we discuss how this approach can be applied, and how it could be used to identify potential interventions and solutions in the area of animal welfare.

Keywords: *animal groups, animal management, animal welfare, captive animals, social network analysis, social organisation*

1. Introduction

Animals in captivity, such as in zoos, laboratories and on farms, have to live within the constraints of an environment designed for them, and a failure to cope with this environment can lead to suffering and poor welfare[1]. The needs of an animal differ depending on the species, but also on the specific individual itself. Requirements can be very simple, such as the availability of food, water and resting places, however, they can get very complex when looking at mechanisms that have evolved to support survival and reproduction[2].

Studying the behaviour of both single individuals and groups of animals is of great importance when assessing health and welfare[3], and can help to identify both negative and positive welfare states (*e.g.* ref. 4). One aspect of particular importance in determining the welfare of individuals and groups is the social environment in which the animals are housed. Therefore studies of both positive and negative social interactions between animals within groups, and the potential influence of the environment on these interactions, are common[5–7] and are often used to suggest potential interventions and solutions[8,9]. Most studies that look at the behaviour of individuals within a group are based upon dyadic interactions, *i.e*. the interactions between a pair of individuals. Yet results of these studies can be misleading. This is because observations using dyadic interactions assume that animals living in groups of more than two interact as pairs that do not influence others in their social environment. However, the behaviour of one individual can affect directly, and indirectly, the behaviour of all other individuals in their group.

The observation of a group of animals as a single network of multi-individual interactions has the potential to provide significant advantages, as it allows the inclusion of indirect effects of the presence of other individuals within a group. During the last few decades, the use of network analysis has become increasingly common in studies of animal groups[10–12], and, although its use has spread in a variety of biological fields (*e.g.* neurobiology[13], genetics[14], ecology[15] and behaviour[16]), it has rarely been used in assessing animal welfare. Asher *et al.*[17] first mentioned the advantages of this methodology in combination with animal welfare. But since then, surprisingly few studies have used network theory as an approach when considering different welfare issues[18–21]. These studies along with recent reviews[22–24], describing the use of social network analysis in applied ethology, are good examples of the advantages of this approach.

This review will build upon these existing examples to examine a variety of welfare concerns, as well as discuss why social network analysis is a suitable method for examining their causes and consequences in groups of living animals. It will give an overview of the advantages that such an approach has above and beyond existing methodologies, and, in addition, it will provide examples of how social network analysis can contribute to our knowledge of how groups cope within their current social environment.

1.1 Animal welfare and the social environment

Captive animals can experience a variety of changes to their social environment during their life. The removal of individuals from social groups (*e.g.* rats[25]) or the reintroduction of previously removed individuals (pigs[26]) is a common husbandry procedure, as is the mixing of unfamiliar individuals (*e.g.* pigs[27]). Due to this frequent modification of group composition, a variety of problems are present in animal groups. One can find high levels of agonistic behaviour between unfamiliar individuals. For example, Simmins[28] showed that the amount of aggressive behaviour differs between static groups and dynamic groups of weaning sows, with a higher level of agonistic behaviour in dynamic groups where individuals were regularly replaced. As well as the potential for injury (*e.g.* skin lesions[29]), the severe fighting after mixing results in a social hierarchy that allows the reduction of social aggression in future disputes between animals, however, the level of severity seems to depend on the group composition (*e.g.*[8,30]). This particular problem of injurious aggression has been of great interest and therefore many studies have been carried out to examine how one can reduce or avoid aggression between individuals in a group.

Erhard *et al.*[8], for example, examined the level of aggressiveness of individual pigs and found that the proportion of high or low level aggressive individuals played an important role in reducing the aggressive behaviour after mixing. Not only individual behavioural characteristics but other factors can have an impact on the level of aggression. For instance, studies have investigated the influence on aggression of castration (*e.g.* ref. 31) early socialisation (*e.g.* ref. 32), addition of straw (*e.g.* ref. 33), mixed sex groups (*e.g.* ref. 34) and mixing related individuals (*e.g.* ref. 35). Group size and space allowance may also have an effect, but, so far, there is little evidence that an optimum group size for good welfare exists[36]. Very little is also known about the influence of space allowance in combination with aggressive behaviour. Existing studies give only some indication that space might have an impact on the amount of long term aggression between members of a group[36].

Injurious aggression between unfamiliar animals is not the only problem for animal welfare. Social stress experienced in the absence of injurious aggression can also lead to changes in the animals' behaviour, like the initial avoidance of unfamiliar individuals in a newly created group. Studies have shown that familiarity affects proximity in cattle, with differences in behaviour and movement patterns between familiar and unfamiliar individuals after mixing[37]. These results emphasise the potentially disruptive effect of introducing new individuals into a group. Social stress can also have an impact on daily activity, for example, a decrease in lying and an increase in standing behaviour (cattle[38]) as well as an influence on feeding behaviour (dairy cows[39]). In rats and mice, thwarted escape behaviour from stressful social environments is thought to result in abnormal behaviours indicative of poor welfare, such as bar-biting, aggressive grooming and urine pooling. It can be stressful for both the dominant and subdominant individuals if the subdominant is not able to escape, and this can be reflected in underlying pathological indices of stress[40].

Besides the instability of group combinations, other environmental factors such as space, lighting regime, suitable foraging opportunities, as well as diet in general, can play an important role in the welfare of group-housed animals. The restricted environment of animals in captivity can prevent individuals from showing adaptive responses to events, and this may result in frustration that can cause various abnormalities of physiology and behaviour[2]. Hens, for example, that are prevented from feeding, can show their frustration by stereotyped pacing and by aggressively pecking at other birds in the flock[41]. The abnormal behaviour of feather pecking in chickens is considered as one of the most widespread and serious problems of today's poultry production, as it can lead to damage of plumage, injuries of skin, and ultimately death (and cannibalism) in extreme cases – a subject of both welfare and economic concern[42]. A large number of studies have tried to identify the causes (*e.g.* refs 6, 42–44) and consequences (*e.g.* refs 9, 45) of this behaviour, as well as how feather pecking spreads through a population of hens[43]. Although advances have been made in the identification of risk factors that may be associated with an increased change of feather pecks[6,42], there is still a need for further investigation of this, and other problem behaviours.

Mason and Mendl[46], and more recently Walker *et al.*[47], proposed fundamental future challenges of animal welfare research, with a particular focus on the refinement of existing methods for investigating positive as well as negative welfare states to enable more valid conclusions about the affective states of captive animals. Methodologies that allow reducing subjective judgements of the researchers itself, as the interpretation of the measures may be influenced by the concern for the animal under consideration. New approaches, such as the analysis of optic flow patterns to investigate welfare concerns such as lameness and/or bacterial infection in large groups of chicken[48–50] already allow continuous and robust monitoring of the welfare of living birds while husbandry changes are still ongoing. However, methodologies that help to understand and improve our insights of socially related behaviours in relation to welfare are still missing and social network analysis could be of great advantage in this area.

2. Social network analysis

Social network analysis is an effective methodology for examining and quantifying the patterns of social structures among interacting individuals, as it offers the possibility of looking beyond dyadic interactions and considering whole networks of social relationships (described in[51–53]). This provides the opportunity to study social groups in a more natural way. A particular strength of social network analysis are the standardised mathematical methods for calculating measures of sociality across different levels of social organisation, on the population, group or individual level[18,54,55]. Quantitative measures of social network structure can be used to describe and compare inter-individual relationships between groups and can also be useful to test factors affecting social structures, such as changes over time or environmental conditions[19,56]. At the individual level, social network metrics allow a quantification of the heterogeneity of sociality within groups[12,18,57–59]. Therefore it is a useful tool to investigate the causes and the consequences of animal social network structure, and with it, the welfare of socially housed animals.

The use of network analysis to study emergent structure is not novel[54]. Rooted in mathematical graph theory, it has found application across disciplines, including fields such as business and economics (*e.g.* ref. 60), the spread of information (*e.g.* ref. 61) and computer science (*e.g.* ref. 62). Moreover, the social network approach for studying social interactions has a long history in social psychology and sociology (*e.g.* ref. 63) and its possible advantages for studying social interactions in animal groups was recognised by Wilson as early as 1975[64]. However, only during recent years has social network analysis become an increasingly common tool for studying animal behaviour and found its application in different fields such as primatology[18,65–67], behavioural ecology[10,11,15,22,68–71] and epidemiology[72–74].

Network analysis regards a social system as a network. This network is built up with a set of nodes (vertices or points), usually individuals but they can also stand for a higher level of social structure (units and communities), connected by edges that indicate their interaction[51–53]. Networks can appear in a variety of formats in the literature. The simplest form is an undirected binary network which contains only one kind of node (can be either connected or unconnected). Weighted networks, in which the thickness of edges indicates a frequency of occurring behaviours or associations between two individuals, provide more detailed information about the social structure of a group. Another common alteration is a directed network. Here the edges represent directed interactions, which can be useful if looking at asymmetric behaviours like affiliative and/or agonistic behaviour in animals. To incorporate even more detail about the individuals of a network one can use networks in which the nodes and/or the edges are divided into distinct classes (depending on age, sex, behaviours *etc*.). Finally, one can combine them. For example, it is common to have weighted directed networks in which nodes belong to different classes (*e.g.* ref. 75).

Common measures to analyse social groups, such as group size, or mating systems, have revealed many consequences of group structure (*e.g.* ref. 76–79). These measures, however, only indirectly reflect the social relationships between individuals and mostly assume homogeneity of environmental or social effect on group members[80]. To further describe and visualise complex interactions, associations or relationships between pairs or groups of animals, researchers may use methods such as sociograms (graphical representations of social interactions) or dendrograms (hierarchical representations of relationships, such as dominance hierarchies), but these only allow a graphical analysis of group structures (described in ref. 81). Network analysis, in comparison, can permit the exploration and analysis of social structure at the level of the individual, dyad, group or population, by incorporating all previously mentioned methods[80,82]. Furthermore, the development of new statistical measurements and software for graphically displaying them is still in progress (*e.g.* ref. 83). This gives the advantage of a steady progress and improvement for future purposes, necessary when new animal welfare concerns requiring investigation are being identified.

Looking at the present literature, one can find a huge amount of different network measurements (*e.g.* refs 52,53,81) and software to calculate and visualise social networks (*e.g.* UCINET[83]; network packages in R[84,85]). This review will therefore not focus on a list of measurements but rather of ideas how to use the methodology in the field of animal welfare. However, some fundamental measurements and examples of network theory will be explained in the next paragraph.

The calculation of animal social networks can start at a basic level, for example when considering properties of edges and/or weights. The presence or absence or the weight can give insight into the value of associations between the individuals. Measurements like the degree (or strength in weighted networks), betweenness or eigenvector centrality give insights about how well individuals are connected within a group (for calculations see refs 51, 53, 75). Depending on the questions researchers want to answer, new and useful computations have been developed. For instance, Flack *et al.*[12] used the measurement reach to assess indirect connectedness between individuals of a group, yet only in a binary network (in which edges are present or not). The indirect connectedness can be important if one is interested in contagion of diseases or transmission of behaviours like feather pecking in chicken flocks. It can also give information about relationships of behaviour, for instance, such an approach might reveal whether only direct interactions are important or also indirect ones in the establishment of dominance hierarchies. Another measurement, the clustering coefficient, is also widely utilised and is useful for measuring the extent to which individuals in a group cluster together and build subgroups[11]. It can be a useful measurement for questions like: do animals with specific problem behaviours interact more with each other than with the rest of the group? Does introducing unfamiliar individuals into a stable group result in the formation of subgroups and if so, how do they change over time? The previously mentioned network measurements are, however, just a small example of commonly used calculations of network metrics[52,53,81].

3. Examples of animal welfare studies applying social network analysis

There are only a few studies present which have applied social network analysis in animal welfare research. Coleing[86] suggested the advantage of social network analysis as a tool to help improve management of captive animal groups, and their specific focus was on captive elephants. Asher *et al.*[17], as mentioned earlier, described network analysis alongside other novel methods like fractal analysis, temporal analysis and agent-based modelling and simulation, as one exciting possibility in assessing animal welfare. More recently Makagon *et al.*[22] extended this brief introduction by describing different social network measurements in detail and mentioning possible applications for applied ethology, like animal welfare. This review will extend and elaborate upon the information presented by these previous papers to discuss how social network analysis can contribute to our knowledge about how groups of animals are influenced and react to their social or non-social environment.

Social network analysis in relation to animal welfare has found some usage in captive primates. McCowan *et al.*[67] demonstrated its utilisation in assessing the welfare of Rhesus Macaques (*Macaca mulatta*). The results of their study showed that variations in management, like differences in group composition, matriline configuration and kinship patterns, influenced patterns of dominance and affiliative relationships. These are factors that have a great influence on the welfare of captive primates. Beisner *et al.*[65] showed that a lack of close genetic ties, at the matriline level, is associated with increased subgrouping within the matriline grooming network, more fighting between kin, and more frequent wounding. This suggests that genetically fragmented matrilines are less stable than genetically cohesive matrilines. Finally it has been shown that relocation into a new environment can influence the social structure of primate species[19]. In this study, researchers recorded several behaviours, including inter-individual space, to examine how individuals of two different primate species adapt to a new environment. Social network analysis allowed a comparison between, and measurement of, behavioural differences between the old and new enriched enclosures. Results showed, among other things, immediate responses to relocation, which was expressed by spending more time in close proximity. Furthermore, the change of the environment resulted into a network structure containing youngsters in central positions. This might indicate that the relocation was a greater stressor for young individuals of the group. Additionally, the authors described how the strengths of grouping patterns were affected by the relocation. Such studies have implications for how the impact upon welfare of management changes for other species – particularly farm and laboratory animals – could be assessed. Especially, network analysis allows investigation of the welfare of a group as a whole, highlighting changes in social behaviour (*e.g.* increase of aggression between certain animals), as well as changes in space or resource use before, during and after a possible stressor, furthermore it allows comparison of groups.

Non-mammal examples of social network analysis in animal welfare are rare. Jones *et al.*[20] used social network measurements including centrality (measures the quantity of direct connections an individual has with others within the network), density (quantifies the amount of potential connections between individuals that are actually present) and clustering coefficient (measures the extent to which two neighbours of an individual are themselves neighbours) to quantify the effect of high and low stocking densities on the frequency and severity of fin damage in farmed Atlantic Salmon (*Salmo salar*) parr. Although lower density groups had a higher level of total aggression, fin biting was significantly more present in high density groups. Network calculations showed a difference in the group networks according to the different density conditions. In the high density group, specific roles of individuals appeared to be present, like initiators and receivers of aggression (illustrated by in- and out-degree centrality, measured in the amount of aggression received or generated). The authors suggested that initiators are more influential and are likely to gain more resources. This was not present in the low density groups. In another study Jones *et al.*[21] were able to show that feed delivery schedules (predictable *versus* unpredictable) were also able to influence the social network structure of juvenile Atlantic Salmon. These studies are a good example demonstrating the advantage of network analysis, in combination with traditional methods, to gain greater insight into the underlying causes of fin damage. Network analysis can contribute to our knowledge of socially important aggressive individuals, as it can reveal also indirect effects of aggressive behaviour on animals of the group that would not be detected by more conventional approaches. Therefore it might help to find possible solutions for problems occurring during transport and holding conditions as well as determining when interventions are required.

4. Further application of social network analysis in the area of animal welfare

Looking at existing studies in animal social networks (*e.g.* spread of information[10] or disease[72], use of available space[87] and the effect of a changing environment[19]) one can find comparable concerns and questions that also appear in the study of animal welfare. This provides additional advantages that methodologies and measurements have already been developed elsewhere that can be used to gain information about specific behaviours and traits in animal welfare. This part of the review will highlight similarities between present studies and identify potential applications for the future.

4.1 Spread of disease

A topic which is of great interest in studies of human and animal societies is physical health. This includes not only observations about the current health status of one individual, but also the possibility of social transmission of a disease within a group. This again has a clear relevance for animal welfare research, where both physical and psychological health are important considerations[88]. To know how to treat a group of animals during a disease outbreak, and to understand how a disease might spread throughout a group are therefore major questions for animal welfare, as well as being of significant economic concern. Social network analysis can help to measure behavioural patterns and so predict transmission of diseases. For example, measurements like closeness and betweenness can be used as accurate predictors for the risk of transmission of tuberculosis in captive possums[72]. Although a great diversity in the social behaviour between groups was found, consistent trends were present in social network measures. The authors concluded that network specific measurements were more precise, and could be compared across time and between groups, compared to standard analytical approaches to measuring behaviour (like number of partners and frequency of den-sharing events). Another study, conducted by Godfrey *et al.*[89], showed that connectivity of individual lizards in a transmission network predicted parasite infection patterns. The authors concluded that the transmission of ticks was influenced by network structure, with the likelihood of a lizard becoming infected increasing with the number of lizards that it shared crevices with. As this example shows, network analysis could therefore help us to identify which individuals require treatment and, furthermore, if sick animals might need to be removed from the group to prevent transmission. In addition to looking at the spread of disease within a group, changes in individual or group behaviour could be used as predictors for the onset of diseases[90]. Network analysis could help to track changes of behaviours between social group members and with it possibly help to predict and so prevent disease outbreak in a group – a key aim in animal welfare[88].

4.2 The spread of abnormal behaviour

Potentially comparable with disease transmission is the spread of abnormal behaviour in a group. Abnormal behaviours, such as feather pecking in chickens or tail-biting in pigs, are behaviours that are rarely observed in non-captive populations and are considered to be associated with poor welfare[91]. McAdie and Keeling[43] tried to find out whether feather pecking spreads throughout a flock of chickens by social learning. Their results suggested that animal husbandry had more influence on the spread of the behaviour than the social component. However, it is still unclear exactly how the behaviour is transmitted. Using social network analysis in groups under the same conditions one might be able to find patterns that change over time. The procedure and methods could be similar to those used in studies of disease transmission[72,89]. Comparing measurements like connectivity, closeness or betweenness of individuals between groups and over time might help in gaining more insights in how such behaviours spread, for example, by identifying which individuals are more likely to become 'feather-peckers' and how this is associated with their position in the social network. This could help the development of potential interventions and solutions. Network analysis might help to reveal why problem behaviours like injurious interactions[7] or stereotypies of individuals[40,92] are present in one group and not in another.

4.3 Impact of environmental change

As discussed previously, Dufour *et al.*[19] showed that network analysis is a useful tool for detecting the impact of a changing environment on groups of primates. Captive animals have to cope with numerous changes in their environment throughout their whole life time. Mixing of unfamiliar conspecifics, short removals of individuals due to cage cleaning or health checking before subsequent reintroduction, permanent removal of individuals from a previously stable group, are only a few examples of frequent disturbances of social groups[26,34,37,40,93]. These interruptions can affect the welfare of not only the removed individuals but also those that remain in the group[25]. Observing networks of interactions before and after group changes could therefore help to identify major stressors as well as possible interventions against them. Furthermore it may help to highlight specific triggers of aggression between animals.

4.4 Positive welfare states

Importantly, social network analysis has the potential not only be used to investigate negative affective states of animal welfare but also to be used in the study of methods to induce and to measure positive welfare states – an area of increasing interest (*e.g.* refs 4,94,95). For instance, measuring the effects of environmental enrichment – where modifications are made to a captive environment in order to generate behavioural changes associated with improved welfare – is a major challenge in animal welfare research (*e.g.* ref. 96). For this reason, network measurements might be a valuable tool to assess differences between barren and enriched environments. Differences between, for instance, affiliative behaviour of a network of animals could be compared in different environmental conditions. One could compare the amount of time that animals stay in close proximity to each other before and after enrichment implementation, in addition to revealing more detailed information about resource use. This might help us to understand whether or not the instigated environmental modification is actually 'enriching' or not, as well as indicating how behaviour changes over time and if habituation occurs. The particular advantage of a social network approach that looks at the whole group and their interactions is that it would help us to determine whether all individuals benefit from a specific change or only some. Connectivity between individuals may change in different environmental conditions, with animals interacting more in one condition but less in another[19]. Network analysis might be used to extract causes of behavioural changes by assessing a variety of different parameters.

4.5 Importance of key individuals

Another important topic is the impact of specific individuals on the behaviour of the group. Lusseau[10] mentioned in his study on dolphins that the presence of so called "key individuals" in asocial network, that if not present, groups could for instance break down into subgroups. Identifying such individuals may be of interest in a variety of topics in animal behaviour including the study of animal welfare. For example, Ewbank and Meese[26] removed individual pigs from a group to examine aggressive behaviour and changes in the social hierarchy. They found that removal of individuals on different positions of the hierarchy had a differential impact on the aggressive behaviour during subsequent reintroduction. Additionally, it was shown that the amount of time an animal was removed from a group played an important role. The use of egocentric networks could help animal welfare researchers to gain insight into the impact that one individual has on the group and *vice versa*, allowing the development of a more targeted approach to the removal of individuals from stable social groups to ensure minimal subsequent disruption. All in all, social network analysis may help to detect the impact of removal and adding of particular individuals from, into, or back into a stable group. More importantly, it could be used as a tool to compare between groups and so find consistent patterns and predictors for aggression.

4.6 Hierarchies

Assessing information about these social hierarchies and correlating them with different behavioural traits is a common procedure in the study of animal groups[97,98]. As such, hierarchies of varying types appear to be observed in many different animal species housed in captivity (*e.g.* chickens[99], pigs[26], rabbits[100] and goats[101]) and this also has an impact on animal welfare studies. Researchers measure dominance hierarchies on a variety of social levels (*e.g.* individual, dyadic and group level). Yet, the data on which most calculations are based are dyadic interactions[98]. Using observations of behaviours on a multi-individual level would allow the achievement of more realistic information about the dominance hierarchies of group living animals. Shizuka and McDonald[102] published recently a new method for measuring dominance hierarchies using a social network perspective. Not using indices of linearity but dominance relations among sets of three players has major advantages. In empirical studies incomplete observations between dyads of a group are not unusual, especially with increasing group size. The authors claim that using the approach of triangle transitivity does not require filling in unobserved relations between dyads which then results into a more realistic hierarchy formation. This, and the advantage of managing greater group sizes, are other examples of the benefit of social network perspectives in solving underlying dynamics of social groups as we progress from an initial goal of simply housing social animals in groups to our future goal of housing social animals in effective and beneficial groups; thereby maximising animal welfare.

5. Conclusions

Network-based analysis provides an exciting method that allows us to look beyond the dyadic interactions of individuals by considering whole networks of social relationships. It has therefore found application in a variety of studies across the animal kingdom (*e.g.* in insects[57], fish[11] and mammals[12]). Furthermore it is used in different fields of biology like behaviour, ecology and evolution (*e.g.* refs 15, 71, 103), game theory (*e.g.* ref. 104), neurobiology (*e.g.* ref. 22) and physiology (*e.g.* ref. 14), but is, as yet, underused in the field of animal welfare. We have identified a variety of areas for future research, including disease spread, spread of abnormal behaviour, the impact of environmental change on the welfare of groups as well as assessing positive welfare states, where this promising approach could be utilised not only to refine and expand upon existing research themes but to develop new areas of investigation that allow us to continue to improve animal welfare.

6. References

1. Dawkins, M.S. (1990) *Behav. Brain Sci.,* **13**, 1 – 61.
2. Broom, D.M. (1991) *J. Anim. Sci.,* **69**, 4167 – 4175.
3. Dawkins, M.S. (2004) *Anim. Welfare,* **13**, 3 – 7.
4. Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I. and Langbein, J. (2007) *Physiol. Behav.,* **92**, 375 – 397.
5. Ruis, M.A.W., te Brake, J.H.A., Engel, B., Buist, W.G., Blokhuis, H.J. and Koolhaas, J.M. (2001) *Physiol. Behav.,* **73**, 541 – 551.
6. Rodenburg, T.B., van Hierden, Y.M., Buitenhuis, A.J., Riedstra, B., Koene, P., Korte, S.M., van der Poel, J.J., Groothuis, T.G.G. and Blokhuis, H. (2004) *Appl. Anim. Behav. Sci.,* **86**, 291 – 298.
7. Schroder-Petersen, D.L. and Simonsen, H.B. (2001) *Vet. J.,* **162**, 196 – 210.
8. Erhard, H.W., Mendl, M. and Ashley, D.D. (1997) *Appl. Anim. Behav. Sci.,* **54**, 137 – 151.
9. McAdie, T.M., Keeling, L.J., Blokhuis, H.J. and Jones, R.B. (2005) *Appl. Anim. Behav. Sci.,* **93**, 67 – 80.
10. Lusseau, D. (2003) *P. Roy. Soc. B,* **270**, S186 – S188.
11. Croft, D.P., Krause, J. and James, R. (2004) *P. Roy. Soc. B,* **271**, 516 – 519.
12. Flack, J.C., Girvan, M., de Waal, F.B.M. and Krakauer, D.C. (2006) *Nature,* **439**, 426 – 429.
13. McIntosh, A.R., Grady, C.L., Ungerleider, L.G., Haxby, J.V., Rapoport, S.I. and Horwitz, B. (1994) *J. Neurosci.,* **14**, 655 – 666.
14. Papp, B., Pál, C. and Hurst, L.D. (2004) *Nature,* **429**, 661 – 664.
15. Proulx, S.R., Promislow, D.E.L. and Phillips, P.C. (2005) *Trends Ecol. Evol.,* **20**, 345 – 353.
16. Pike, T.W., Samanta, M., Lindstrom, J. and Royle, N.J. (2008) *P. Roy. Soc. B,* **275**, 2515 – 2520.
17. Asher, L., Collins, L.M., Ortiz-Pelaez, A., Drewe, J.A., Nicol, C.J. and Pfeiffer, D.U. (2009) *J. R. Soc. Interface,* **6**, 1103 – 1119.
18. McCowan, B., Beisner, B.A., Capitanio, J.P., Jackson, M.E., Cameron, A.N., Seil, S., Atwill, E.R. and Fushing, H. (2011) *Plos One,* **6**, e22350.
19. Dufour, V., Sueur, C., Whiten, A. and Buchanan-Smith, H.M. (2011) *Am. J. Primatol.,* **73**, 802 – 811.
20. Jones, H.A.C., Noble, C., Damsgard, B. and Pearce, G.P. (2011) *Appl. Anim. Behav. Sci.,* **133**, 117 – 126.
21. Jones, H.A.C., Noble, C., Damsgard, B. and Pearce, G.P. (2012) *Appl. Anim. Behav. Sci.,* **138**, 132 – 140.
22. Makagon, M.M., McCowan, B. and Mench, J.A. (2012) *Appl. Anim. Behav. Sci.,* **138**, 152 – 161.
23. Koene, P. and Ipema, B. (2014) *Animals,* **4**, 93 – 118.
24. Rose, P.E. and Croft, D.P. (2015) *Anim. Welfare,* **24**, 123 – 138.
25. Burman, O., Owen, D., Abouismail, U. and Mendl, M. (2008) *Physiol. Behav.,* **93**, 89 – 96.
26. Ewbank, R. and Meese, G.B. (1971) *Anim. Prod.,* **13**, 685 – 693.
27. Holinger, M., Früh, B. and Hillmann, E. (2015) *Appl. Anim. Behav. Sci.,* **165**, 47 – 56.
28. Simmins, P.H. (1993) *Anim. Prod.,* **57**, 293 – 298.
29. Barnett, J.L., Cronin, G.M., McCallum, T.H., Newman, E.A. and Hennessy, D.P. (1996) *Appl. Anim. Behav. Sci.,* **50**, 121 – 133.
30. Meese, G. and Ewbank, R. (1973) *Anim. Behav.,* **21**, 326 – 334.
31. Cronin, G., Dunshea, F., Butler, K., McCauley, I., Barnett, J. and Hemsworth, P. (2003). *Appl. Anim. Behav. Sci.,* **81**, 111 – 126.
32. Rydhmer, L., Hansson, M., Lundström, K., Brunius, C. and Andersson, K. (2013) *Animal,* **7**, 1532 – 1541.
33. Arey, D. and Franklin, M. (1995) *Appl. Anim. Behav. Sci.,* **45**, 23 – 30.
34. Boyle, L. and Björklund, L. (2007) *Anim. Welfare,* **16**, 259 – 262.
35. Fredriksen, B., Lium, B.M., Marka, C.H., Mosveen, B. and Nafstad, O. (2008) *Appl. Anim. Behav. Sci.,* **110**, 258 – 268.

36. Arey, D.S. and Edwards, S.A. (1998) *Livest. Prod. Sci.,* **56**, 61–70.
37. Patison, K.P., Swain, D.L., Bishop-Hurley, G.J., Robins, G., Pattison, P. and Reid, D.J. (2010) *Appl. Anim. Behav. Sci.,* **128**, 10–17.
38. Gupta, S., Earley, B., Nolan, M., Formentin, E. and Crowe, M.A. (2008) *Appl. Anim. Behav. Sci.,* **110**, 229–243.
39. Grant, R. and Albright, J. (2001). *J. Dairy Sci.,* **84**, 156–163.
40. Hurst, J.L., Barnard, C.J., Hare, R., Wheeldon, E.B. and West, C.D. (1996) *Anim. Behav.,* **52**, 335–360.
41. Duncan, I. and Wood-Gush, D. (1972) Thwarting of feeding behaviour in the domestic fowl. *Anim. Behav.,* **20**, 444–451.
42. Ramadan, S.G.A. and Von Borell, E. (2008) *Brit. Poultry Sci.,* **49**, 250–256.
43. McAdie, T.M. and Keeling, L.J. (2002) *Appl. Anim. Behav. Sci.,* **75**, 147–159.
44. Nicol, C.J. (1995) *Appl. Anim. Behav. Sci.,* **44**, 79–98.
45. Savory, C.J. (1995) *World. Poultry Sci. J.,* **51**, 215–219.
46. Mason, G. and Mendl, M. (1993) *Anim. Welfare,* **2**, 301–319.
47. Walker, M., Diez-Leon, M. and Mason, G. (2014) *Int. J. Comp. Psychol.,* **27**, 80–100.
48. Dawkins, M.S., Cain, R., Merelie, K. and Roberts, S.J. (2013) *Appl. Anim. Behav. Sci.,* **145**, 44–50.
49. Dawkins, M.S., Lee, H.J., Waitt, C.D. and Roberts, S.J. (2009) *Appl. Anim. Behav. Sci.,* **119**, 203–209.
50. Roberts, S.J., Cain, R. and Dawkins, M.S. (2012) *J. R. Soc. Interface,* **9**, 3436–3443.
51. Boccaletti, S., Latora, V., Moreno, Y., Chavez, M. and Hwang, D.U. (2006) *Phys. Rep.,* **424**, 175–308.
52. Croft, D.P., James, R. and Krause, J. (2008) *Exploring animal social networks*. Princeton University Press, Princeton, New Jersey.
53. Newman, M.E.J. (2003) *Siam. Rev.,* **45**, 167–256.
54. Freeman, L.C. (1984) *J. Math. Sociol.,* **10**, 343–360.
55. Sih, A., Hanser, S.F. and McHugh, K.A. (2009). *Behav. Ecol. Sociobiol.,* **63**, 975–988.
56. Hansen, H., McDonald, D.B., Groves, P., Maier, J.A.K. and Ben-David, M. (2009) *Ethology,* **115**, 384–396.
57. Fewell, J.H. (2003) *Science,* **301**, 1867–1870.
58. Lusseau, D. (2007) *Evol. Ecol.,* **21**, 357–366.
59. Williams, R. and Lusseau, D. (2006) *Biol. Lett.,* **2**, 497–500.
60. Levine, J.H. (1972). *Am. Sociol. Rev.,* **37**, 14–27.
61. Liben-Nowell, D. and Kleinberg, J. (2008) *P. Natl. Acad. Sci. USA,* **105**, 4633–4638.
62. Newman, M.E.J. (2002) *Phys. Rev. Lett.,* **89**, 208701.
63. Scott, J. (2011) *Soc. Netw. Anal. Min.,* **1**, 21–26.
64. Wilson, D.S. (1975) *P. Natl. A. Sci.,* **72**, 143–146.
65. Beisner, B.A., Jackson, M.E., Cameron, A. and McCowan, B. (2011) *Am. J. Primatol.,* **73**, 790–801.
66. Flack, J.C., Krakauer, D.C. and de Waal, F.B.M. (2005) *P. Roy. Soc. B,* **272**, 1091–1099.
67. McCowan, B., Anderson, K., Heagarty, A. and Cameron, A. (2008) *Appl. Anim. Behav. Sci.,* **109**, 396–405.
68. Edenbrow, M., Darden, S.K., Ramnarine, I.W., Evans, J.P., James, R. and Croft, D.P. (2011) *Anim. Behav.,* **81**, 551–558.
69. Kleinhappel, T.K., Burman, O.H.P., John, E.A., Wilkinson, A. and Pike, T.W. (2014) *Behav. Ecol.,* **25**, 374–377.
70. Krause, J., Croft, D.P. and James, R. (2007) *Behav. Ecol. Sociobiol.,* **62**, 15–27.
71. Krause, J., James, R. and Croft, D. (2010) *Phil. Trans. R. Soc. B,* **365**, 4099–4106.
72. Corner, L.A.L., Pfeiffer, D.U. and Morris, R.S. (2003) *Prev. Vet. Med.,* **59**, 147–167.

73. Martinez-Lopez, B., Perez, A.M. and Sanchez-Vizcaino, J.M. (2009) *Transbound. Emerg. Dis.,* **56**, 109 – 120.
74. Otterstatter, M.C. and Thomson, J.D. (2007) *Oecologia,* **154**, 411 – 421.
75. Newman, M.E.J. (2004) *Phys. Rev. E,* **70**, 056131.
76. Brown, R.E., Schellinck, H.M. and West, A.M. (1996) *Physiol. Behav.,* **60**, 365 – 372.
77. Cote, I.M. and Poulin, R. (1995) *Behav. Ecol.,* **6**, 159 – 165.
78. Dunbar, R.I.M. (1998) *Evol. Anthropol.,* **6**, 178 – 190.
79. Hoogland, J.L. (1995) *The black-tailed prairie dog: Social life of a burrowing mammal*. University of Chicago Press, Chicago.
80. Wey, T., Blumstein, D.T., Shen, W. and Jordan, F. (2008) *Anim. Behav.,* **75**, 333 – 344.
81. Whitehead, H. (2008) *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. University of Chicago Press, Chicago.
82. Krause, J., Lusseau, D. and James, R. (2009) *Behav. Ecol. Sociobiol.,* **63**, 967 – 973.
83. Borgatti, S.P., Everett, M.G. and Freeman, L.C., *Ucinet for windows: Software for social network analysis*. Analytic Technologies, Harvard.
84. Butts, C. (2008) *J. Stat. Softw.,* **24**, 1 – 36.
85. Csardi, G. and Nepusz, T. (2006) *InterJournal, Complex Systems,* 1695.
86. Coleing, A. (2009) *Biosci. Horizons,* **2**, 32 – 43.
87. Bode, N.W.F., Wood, A.J. and Franks, D.W. (2011) *Behav. Ecol. Sociobiol.,* **65**, 117 – 130.
88. Fraser, D., Weary, D.M., Pajor, E.A. and Milligan, B.N. (1997) *Anim. Welfare,* **6**, 187 – 205.
89. Godfrey, S.S., Bull, C.M., James, R. and Murray, K. (2009) *Behav. Ecol. Sociobiol.,* **63**, 1045 – 1056.
90. Littin, K., Acevedo, A., Browne, W., Edgar, J., Mendl, M., Owen, D., Sherwin, C., Wurbel, H. and Nicol, C. (2008) *P. Roy. Soc. B,* **275**, 1865 – 1874.
91. Mench, J.A. and Mason, G.J. (1997) In: Appleby, M.C. and Hughes, B.O. (eds), *Animal Welfare*, pp. 127 – 141. CAB International, Wallingford, CT.
92. Jeppesen, L.L., Heller, K.E. and Dalsgaard, T. (2000) *Appl. Anim. Behav. Sci.,* **68**, 85 – 92.
93. Stookey, J.M. and Gonyou, H.W. (1994) *J. Anim. Sci.,* **72**, 2804 – 2811.
94. Burman, O., McGowan, R., Mendl, M., Norling, Y., Paul, E., Rehn, T. and Keeling, L. (2011) *Appl. Anim. Behav. Sci.,* **132**, 160 – 168.
95. Mendl, M., Burman, O.H.P. and Paul, E.S. (2010) *P. Roy. Soc. B,* **277**, 2895 – 2904.
96. Sherwin, C., Lewis, P. and Perry, G. (1999) *Brit. Poultry Sci.,* **40**, 592 – 598.
97. Drews, C. (1993) *Behaviour,* **125**, 283 – 313.
98. Hemelrijk, C.K., Wantia, J. and Gygax, L. (2005) *Behaviour,* **142**, 1037 – 1058.
99. Murchison, C. (1935) *Pedagog. Semin. J. Gen.,* **46**, 76 – 102.
100. Vervaecke, H., De Bonte, L., Maertens, L., Tuyttens, F., Stevens, J.M.G. and Lips, D. (2010) *World Rabbit Sci.,* **18**, 139 – 149.
101. Langbein, J. and Puppe, B. (2004) *Appl. Anim. Behav. Sci.,* **87**, 293 – 315.
102. Shizuka, D. and McDonald, D.B. (2012) *Anim. Behav.,* **83**, 925 – 934.
103. Curry, O. and Dunbar, R.I.M. (2011) *Biol. Lett.,* **7**, 651 – 653.
104. Abramson, G. and Kuperman, M. (2001) *Phys. Rev. E,* **63**, 030901.