

Hypothesis testing in animal social networks

Darren P. Croft¹, Joah R. Madden¹, Daniel W. Franks² and Richard James³

¹ Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Exeter, EX4 4QG, UK

² York Centre for Complex Systems Analysis, Departments of Biology & Computer Science, The University of York, YO10 5YW, UK

³ Department of Physics, University of Bath, Bath BA2 7AY, UK

Behavioural ecologists are increasingly using social network analysis to describe the social organisation of animal populations and to test hypotheses. However, the statistical analysis of network data presents a number of challenges. In particular the non-independent nature of the data violates the assumptions of many common statistical approaches. In our opinion there is currently confusion and uncertainty amongst behavioural ecologists concerning the potential pitfalls when hypotheses testing using social network data. Here we review what we consider to be key considerations associated with the analysis of animal social networks and provide a practical guide to the use of null models based on randomisation to control for structure and non-independence in the data.

The potential and challenge of hypothesis testing using social network data

Quantifying the social structure of populations and unravelling the mechanisms and functions underpinning this structure is central to many areas of behavioural ecology, evolutionary biology and conservation [1–3]. An individual's social interactions will affect their access to information and resources, with implications for key behaviours including: finding and choosing a sexual partner, developing and maintaining cooperative relationships, and foraging and avoiding predators [3–6]. Who interacts with whom and the resulting local and global population social structures that these interactions produce [2,3] have implications for population-level patterns and processes, such as population genetic structure, frequency dependent selection, the maintenance of co-operation and the transmission of information and disease [3–6].

An emerging trend in behavioural ecology is the application of social network analysis (SNA) to describe the social structure of animal populations [3–6]. SNA is a powerful framework which provides metrics that quantify social structure at different levels of organisation (individuals, groups, communities and populations). SNA has tremendous potential as an analytical tool to address fundamental questions in behavioural ecology [3–6]. For example, SNA provides metrics that describe how individuals are socially interconnected [3]. These metrics can be used to test hypotheses regarding the relationship between an individual's phenotypic attributes and social network

position [7–9] and/or an individual's social network position and their attributes (e.g. reproductive success or parasite load) [10–12]. Whilst the approaches for visualising social networks and calculating descriptive statistics are well established [3,13] the statistical analysis of social network data is less well developed and needs careful consideration [14,15].

There is a natural and understandable urge for behavioural biologists to construct and test hypotheses (often null hypotheses) using animal social network data [5,6,16,17]. Despite the reservations about the use of null hypothesis significance tests (NHST) [18] and a laudable call for more emphasis on the calculation of effect size and confidence intervals [19] and less on tests of significance, there is still scope for hypothesis testing in social analysis [1], as long as we restrict attention only to null hypotheses that could conceivably be true [20] and that truly help us unravel the biology of our study system. Unfortunately, NHST is not straightforward when applied to networks. Networks represent relational data and metrics that describe the structure of these relationships are non-independent [15,21]. Therefore statistical methods that assume data independence are not appropriate [22].

Currently, we believe that the most robust and flexible approach to cope with the type of non-independence present in network data is to use null models based on randomisations of the data. As work in this area intensifies, it may become apparent that statistical approaches such as mixed-effects models [23] are the best and most general way. As with all randomisation tests [24], there are important decisions to be made about what in the data to randomise and what to constrain, based on the details of the data sampling, the network metrics being used and the hypothesis being tested. Here we outline what in our opinion are current key issues in the testing of hypotheses using animal social network data.

Key considerations

Before discussing the details of randomisation-based null models we first list key factors for consideration when analysing animal social networks. These are introduced in the order they are likely to arise.

Are relations observed directly or inferred?

This is a crucial question. We should expect that our sampling of network edges (relationships or interactions between individuals) is imperfect [25–27], so statistical

Corresponding author: Croft, D.P. (d.p.croft@exeter.ac.uk).

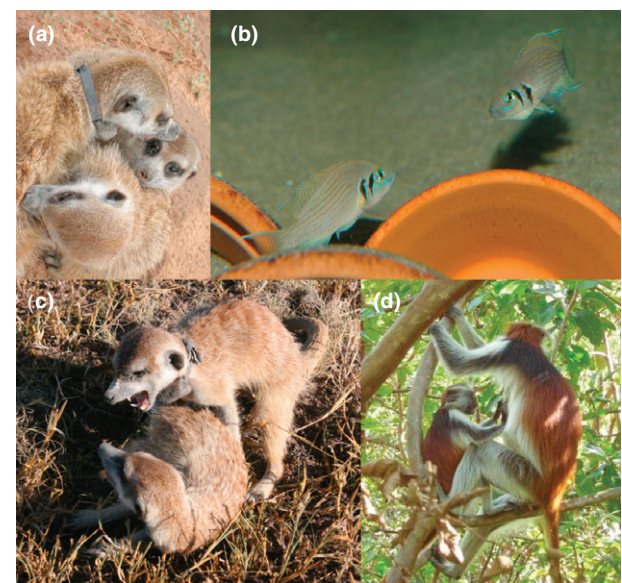
Box 1. Collecting data for social network analysis

Direct observations of social relationships

If we are working with relatively small populations and able to observe and record behavioural interactions that occur between individuals (e.g. aggression and grooming) then we might be able to quantify social relationships directly. This type of data is normally based on dyadic interactions, for example, individual *a* is aggressive to individual *b* (see Figure 1) that can be directional (*c* grooms *d* more frequently than *d* grooms *c*, for example). With these types of data we are essentially observing the presence, strength and direction of the network edges directly. Though this type of data can be harder to collect than information on group composition, the hard work is often rewarded when it comes to the statistical analysis (see Null models for testing network hypotheses).

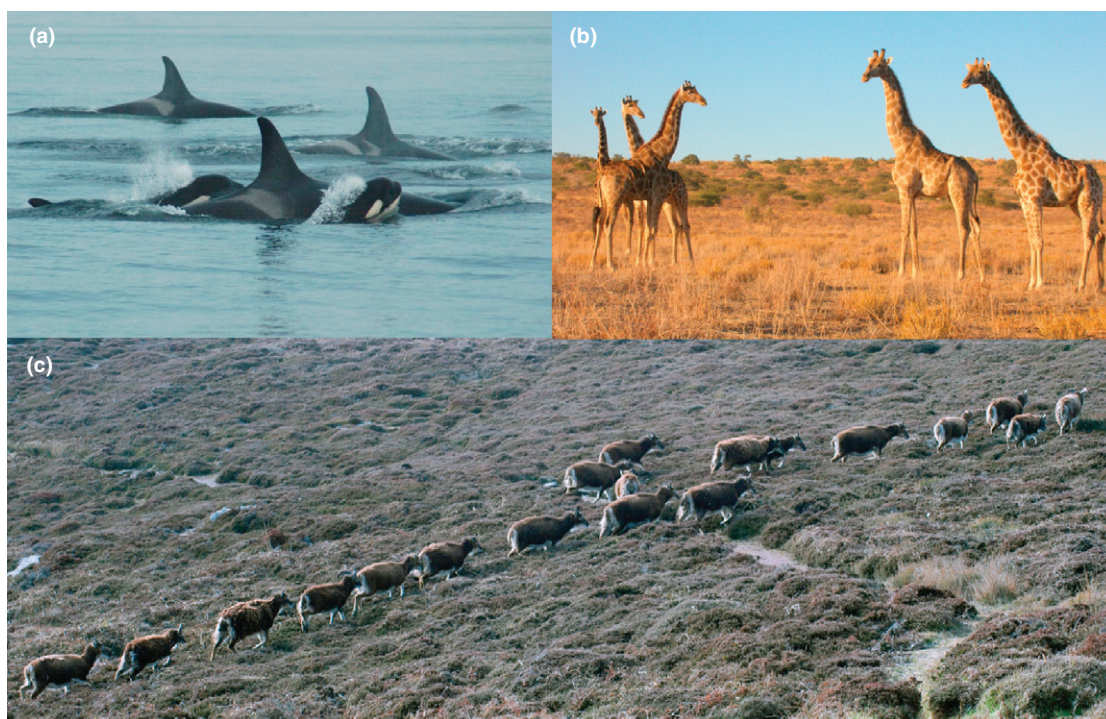
Inferring social relationships from social associations

For the majority of species social interactions are difficult to observe directly; they might occur out of sight or infrequently. In this case the usual approach is to infer social relationships between individuals based on accumulated observations of social associations (i.e. based on group composition, nearest neighbours or spatial proximity – see Figure 1). When using group-based data we invoke the ‘gambit of the group’ [60], assuming that behavioural interactions occur within groups and repeated group co-membership is an indicator of the strength or frequency of those interactions. This type of sampling enforces structure in the data which we might need to control for using null models [3]. In particular, the size and number of groups observed and the frequency with which we observe individuals are important factors influencing the resulting social network structure [3]. As a result, network data of this type, while often easier to gather, are less straightforward to analyse (Box 2).



TRENDS in Ecology & Evolution

Figure 1. A selection of animals showing examples of behavioural interactions that can be directly observed: (a) grooming interactions in meerkats (*Suricata suricatta*) (credit Joah Madden), (b) an aggressive interaction in *Neolamprologus pulcher* (credit Roger Schürch), (c) dominance assertion in meerkats (credit Jess Isden), and (d) grooming interaction in red colobus monkeys (*Procolobus badius*) (credit Jess Isden).



TRENDS in Ecology & Evolution

Figure 2. A selection of animals showing examples of grouping behaviour that can be used to infer social interactions: (a) killer whales (*Orcinus orca*) (credit Emma Foster), (b) giraffe (*Giraffa camelopardalis*) (credit Joah Madden), and (c) Soay sheep (*Ovis aries*) (credit Mathew Edenbrow).

methods and inference will be needed whatever the form of the data. But the choice (and validity) of a particular method depends on whether each dyad is observed directly (A grooms B, C feeds D...) or inferred through, for example,

co-membership of groups (E and F are frequently seen together) (Box 1). This question boils down to whether the network data consist of interactions or associations. If the former, there are now many methods available that

can help with robust hypothesis testing, provided any necessary constraints can be implemented. Most of these methods are based on permutation of node labels. An excellent source in this case is the text by Hanneman and Riddle [22], which accompanies the UCINET network analysis package [28].

Many of the animal social networks built and analysed so far do not fall into this category. Instead, the network edges are inferred from group membership or nearest neighbour measures. Then, even if there are few constraints to consider, we have to work harder to generate null models that are biologically and statistically reasonable. Whitehead's recent book [1] and his SOCPROG software [29] are an excellent place to start, and the book by Croft *et al.* [3] also explores the analysis of association-derived networks.

Binary vs weighted data

Many analyses of animal social networks have used structural metrics borrowed from the social sciences, and designed for binary-weight edges – they are either present (1) or absent (0). As highlighted by Whitehead [1], for most non-human animals we are unlikely to have sufficient data to assign a 0 edge weight with any confidence. Binary network measures are particularly sensitive to data errors such as mis-identification [30]. Furthermore, when using binary metrics we will lose important information on the strengths of interactions between individuals. A number of authors [1,31] have therefore strongly stated a preference for the analysis of weighted networks using appropriate metrics. We agree that using weighted network metrics is the gold standard; however, in our opinion there are instances when binary networks can provide useful information. For example, we might be interested in the number of social partners an individual has (its network degree, an unweighted measure) as well as the strength of those interactions (a weighted network measure). However, binary network measures should be interpreted with caution, unless there is confidence that the 0 edges accurately describe no social interaction.

Non-independence of network data

The fundamental problem encountered when testing hypotheses based on social networks is that the relational data do not satisfy the assumption of independence underlying most statistical tests. Consider for example, an individual's network strength (the sum of weights of its social interactions); by definition this is not independent from the network strength of other individuals in the population. There are still relatively few off-the-shelf ways around this problem. If network-level measures are being compared between populations or species, then one solution (more easily said than done) is to observe replicated populations, each producing an independent network-level metric which can be analysed using conventional statistics [32,33].

More often we wish to test a hypothesis on a single network, or compare two or more networks from a single population. In our opinion there is currently confusion in the literature on how to proceed with such an analysis and standard statistical approaches are occasionally applied

without consideration of the non-independence of the data. Standard formulas for calculating sample variability have a tendency to underestimate values when applied to social network data [22]. Thus if the non-independence of the relational data is not taken into account in the statistical analysis we run the risk of producing spurious results [22].

Our approach, and that of most authors [1,3], to overcome this issue is to test the data against a null model generated by some form of randomisation of the data [24].

Null models for testing network hypotheses

In essence, all randomisation tests of network hypotheses operate by generating an ensemble of (say 10 000) random networks (RNs). The number of randomisations needed for statistical power will depend on the structure of the data and the alpha value at which we are testing our hypothesis (see [24,34,35] for guidance). A typical null hypothesis might be that structural measure *A* on the real network is no different from random. The hypothesis is accepted or rejected by a comparison of the observed measure *A* with the frequency distribution of *A* calculated for the RNs. From this it is clear that the crucial thing to get right is that the 'null model' used to test the null hypothesis is biologically, as well as statistically sensible. An important assumption of the randomisation approach is that it assumes data points are exchangeable under the null hypothesis.

We have found it useful to consider three distinct families of randomisation, in which we either permute the node labels, rearrange the edges or shuffle observed group membership. Which type of randomisation is appropriate will depend on the nature of the data and the hypothesis. Within each type there will be many variations, reflecting the need to consider carefully the appropriate constraints needed for a given situation. These can include time and/or space constraints (should a fight between two animals be randomised freely, or just between those animals that were in the same place and time?), or on the number of interactions an animal has in a given time period [1], effectively controlling for individual gregariousness [36]. In Box 2 we provide an example of the consequences that the choice of null model can have on inference in social network studies.

Node-label permutation

Node-label permutation can be used when we are confident in the edges in our network; these remain fixed. A null hypothesis is typically that any individual can occupy any network position, so the null model permutes individuals among the nodes in the fixed network. Obvious constraints that might make the null model more robust are that only some individuals (older females, for example) can occupy some network positions.

Social scientists can often measure their relations directly, so it is perhaps not surprising that they have developed many methods for testing network hypotheses using node-label permutation. Hanneman and Riddle [22] give an excellent account of all sorts of statistical tests of network structure, including analysis of variance and multiple regression, though it appears that most of the node-label permutations they discuss are unconstrained (and thus do not control for temporal or spatial structure in the

Box 2. Example of hypothesis testing using group-based data

One of us (DPC) collected group-based association data using ten daily censuses of a population of guppies (*Poecilia reticulata*) occupying two adjacent riverine pools. Each fish was assayed for boldness (see [49] for details). Figure 1 shows the group-derived social network for this population. Edges have a weight w between 0 (two fish never seen together) and 1 (always seen together).

Here we ask whether the guppy associations are assorted by boldness, and whether this depends on w . We consider two networks, one with all edges included (A) and one with only very strong associations (B). We correlate (using Spearman's rank) each individual's boldness score with the mean boldness scores of its neighbours in each network. In A we find $r_s = 0.225$ (with $N = 63$ fish) and in B, $r_s = 0.532$ ($N = 20$).

We need a randomisation test of these correlations. Here we compare three methods: (i) NP: the network structure is held constant and the node labels are permuted, (ii) GR: the membership of each shoal within a daily census is shuffled, and (iii) GRP: as GR, but with the shuffling restricted to shoals within the same pool (see Figure 1).

We use 10 000 randomisations in each analysis to generate a distribution of the Spearman correlation coefficient r_s , yielding p-values for the null hypothesis that r_s is no different from that expected by chance.

For network A (all associations included) we find strong evidence under GRP ($p = 0.022$) that $r_s = 0.225$ represents a non-random correlation, but not under GR ($p = 0.122$) or NP ($p = 0.084$). For network B ($r_s = 0.532$) the pattern changes; a simple node-label permutation test (NP) suggest non-random assortment by boldness ($p = 0.038$) not supported by the group randomisation tests (GR: $p = 0.306$; GRP: $p = 0.206$).

This example illustrates the importance of choosing the right randomisation test. Both type I (network B) and type II (network A) statistical errors can arise. NP is unsuitable here as it does not control for the group-based data. GR is a step in the right direction, but assumes all individuals within a census are equally likely to associate. As this population is spatially segregated, with little movement between pools (Figure 1) this assumption is biologically

unrealistic, and GRP provides a better null model. As ever, the choice about what to constrain and what to randomise is where the judgement comes in.

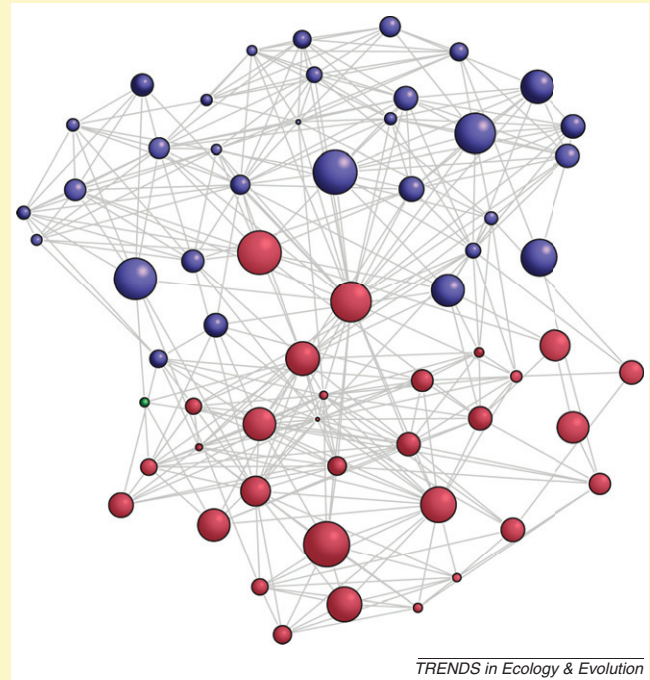


Figure 1. The social network of a wild population of guppies (*Poecilia reticulata*) occupying two pools connected by a shallow riffle. Red nodes were caught predominantly in one pool; blue in the other. One individual was observed in both pools with equal frequency (green). The size of the node represents the boldness score of an individual (see [49] for details).

data). These methods have not yet been widely used by biologists. Wey and Blumstein [37] used the Quadratic Assignment Procedure (a form of node-label permutation) to test whether similarity in age, sex or relatedness was a significant predictor of network structure in yellow-bellied marmots, *Marmota flaviventris*. For multiple attributes the Multiple Regression Quadratic Assignment Procedure [21] can be used.

Node-label permutation is at the heart of most methods that compare two networks (or other matrices) for the same group of individuals. Mantel tests (and variations on the theme) have been used to this end [1,3]. Such tests can prove extremely useful for testing hypotheses relating to reciprocity and interchange [38]. Mantel tests can also be useful for examining the correlation between a social association matrix and a hypothesis matrix [38]. For example, in a study on long-tailed manakins (*Chiroxiphia linearis*) McDonald [39] used a Mantel test to test for a significant relationship between social separation in the social network and geographic distance.

Edge rearrangement

If our edges are again observed rather than inferred, and our biological null model is something like “interactions are equally likely between any pair of nodes”, then an appropriate null model would randomly rearrange the observed interactions among pairs of nodes. An unconstrained choice of the two nodes, but with a maximum

edge weight of 1 yields an Erdős–Rényi random graph [40]. However, for most data sets an unconstrained random graph is unlikely to provide a biologically realistic null model. We might want to constrain the randomisation based on structural properties of the network (e.g. the degree distribution) [41]. We might also want to control for temporal or spatial structure in the data or individual differences in gregariousness [1]. Whitehead's SOCPROG program [29] can be used to permute matrices of association and apply many of these types of constraint. While attractive in many ways, this form of network randomisation test is currently rather rare in the behavioural sciences. As one example, Lusseau [42] compared the clustering coefficient and average shortest path length for a population of bottlenose dolphins (*Tursiops* sp.) to RNs constructed using edge rearrangement.

Group membership swaps and shuffles

When edges are inferred from repeated censuses of group membership (whether groups are defined through spatial or temporal proximity – see Box 1) a null model that randomises node labels or edges is unlikely to be robust [3]. This is because network structure in this case is very sensitive not just to variations in observation frequency (which can blight any network analysis) but also to variation in group size; variations which should be constrained in the null model. The most frequently invoked null hypothesis is that all animals are equally likely to appear in

any group within some time period; this generates a null model borrowed from island ecology [43] which, although it might not always be biologically ideal [44], is widespread. In the social analysis program SOCPROG [29] the 'MBFM' algorithm [45] swaps pairs of animals between groups. After many swaps the groups become randomised and networks can be constructed from the shuffled group affiliations. Variations of the scheme allow swaps to be constrained by sampling period to control for effects such as individuals entering and leaving the population during sampling, or constrained by individual attributes; for example, swapping females only with other females can test whether males have a preference for a certain type of female [35,46]. For a general discussion of what can be done, we recommend Whitehead's recent book [1]. Croft and co-workers [47–50], analyse data already partitioned into well-defined censuses, in each of which each animal is seen at most once, and between which animals have time to mix freely. In this case, the null model can be implemented by shuffling membership of all groups within a census at once.

Group-level swaps can be used in principle to test hypotheses at the level of the dyad, though as Whitehead has pointed out [35] care is needed to avoid spurious use of 'dyadic p-values'.

Conclusions and Future directions

We have identified a number of key considerations when testing hypotheses using social network data. Null models based on randomisation tests provide a useful solution to the problem of data independence. However, it is important to recognise their limitations and understand that the choice of an appropriate null model is crucial. One of the major considerations when using a null model is what to constrain within the model. This should be informed with as much information on the biology of the study population as possible. Methods of hypothesis testing that are appropriate for one set of network data are not appropriate for all, and it is easy to make mistakes. With the correct application of null models, SNA offers a powerful analysis framework that can scale from the level of the individual to the population and from the population back to the individual.

Model fitting is a potentially different approach to hypothesis testing. In particular, mixed models can account for some forms of data non-independence and have already been applied to the analyses of animal social networks [51,52]. However, it has been long recognised by researchers using generalised linear mixed models (GLMM) to analyse species spatial distributions that it is important to control for autocorrelations in the data [53]; autocorrelations can arise from locations that are close in space exhibiting more similar variable values. Similar structural autocorrelations exist in social networks [21]. Methods exist to account for spatial autocorrelations using GLMMs, such as autocovariate models [53], and such techniques might be adapted for network analyses. When using model fitting we urge researchers to state explicitly how they account for network autocorrelations (and sampling) in their analyses.

Embedding randomisation methods into other approaches for making statistical inference is likely to be a fruitful way ahead. Randomisations can also be modi-

fied to include social biases and model alternative hypotheses (including but not limited to the null hypothesis). This would allow alternative models to be constructed while controlling for the observation biases. Such an approach would allow for advocated alternatives to NHST such as information theory and Bayesian techniques to be used to compare alternative hypotheses [54,55]. We eagerly anticipate developments in this area.

One common theme of the approaches we have outlined is that they all assume that the network data constitute a good sample; more work is clearly needed to consider the effect of missing data [25,30]. An important avenue to explore for future testing of network hypotheses is the generation of useful models of social and/or network structure [56,57]. One approach would be to build convincing (minimal) agent-based models of key behavioural processes, test them against data and use them to generate more robust null models [58] that are not subject to sampling bias and that might help us elucidate the key factors driving the social structure we observe.

With the rapid development of new technologies for automating the collection of association data in animals [59] we envisage that the application of SNA to animal populations will continue to increase. This will generate an increased demand for the development and improvement of models for making inference using social network data. In our opinion the formation of interdisciplinary collaborations could prove very fruitful in advancing this rapidly developing field.

Acknowledgements

We thank Nikolai Bode, Safi Darden, Jens Krause, Stefan Krause and Graeme Ruxton for stimulating discussions, and Dan Blumstein and Hal Whitehead and an anonymous reviewer for their constructive comments on the manuscript.

References

- Whitehead, H. (2008) *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*, University of Chicago Press
- Krause, J. and Ruxton, G.D. (2002) *Living in Groups*, Oxford University Press
- Croft, D.P. *et al.* (2008) *Exploring Animal Social Networks*, Princeton University Press
- Krause, J. *et al.* (2007) Social network theory in the behavioural sciences: potential applications. *Behav. Ecol. Sociobiol.* 62, 15–27
- Sih, A. *et al.* (2009) Social network theory: new insights and issues for behavioral ecologists. *Behav. Ecol. Sociobiol.* 63, 975–988
- Wey, T. *et al.* (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* 75, 333–344
- Schürch, R. *et al.* (2010) The building-up of social relationships: behavioural types, social networks and cooperative breeding in a cichlid. *Philos. Trans. R. Soc. B: Biol. Sci.* 365, 4089–4098
- Sundaresan, S.R. *et al.* (2007) Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. *Oecologia* 151, 140–149
- Pike, T.W. *et al.* (2008) Behavioural phenotype affects social interactions in an animal network. *Proc. R. Soc. B: Biol. Sci.* 275, 2515–2520
- Drewe, J.A. (2010) Who infects whom? Social networks and tuberculosis transmission in wild meerkats. *Proc. R. Soc. B: Biol. Sci.* 277, 633–642
- Godfrey, S.S. *et al.* (2009) Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. *Behav. Ecol. Sociobiol.* 63, 1045–1056
- McDonald, D.B. (2007) Predicting fate from early connectivity in a social network. *Proc. Natl. Acad. Sci. U.S.A.* 104, 10910–10914

- 13 Wasserman, S. and Faust, K. (1994) *Social Network Analysis: Methods and Applications*, Cambridge University Press
- 14 James, R. *et al.* (2009) Potential banana skins in animal social network analysis. *Behav. Ecol. Sociobiol.* 63, 989–997
- 15 Krackhardt, D. (1988) Predicting with networks: Nonparametric multiple regression analysis of dyadic data. *Soc. Netw.* 10, 359–381
- 16 Krause, J. *et al.* (2009) Animal social networks: an introduction. *Behav. Ecol. Sociobiol.* 63, 967–973
- 17 Sueur, C. *et al.* (2011) How can social network analysis improve the study of primate behavior? *Am. J. Primatol.* 73, 703–719
- 18 Stephens, P.A. *et al.* (2007) Inference in ecology and evolution. *Trends Ecol. Evol.* 22, 192–197
- 19 Nakagawa, S. and Cuthill, I.C. (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* 82, 591–605
- 20 Schusterman, R.J. *et al.* (2000) How animals classify friends and foes. *Curr. Dir. Psychol. Sci.* 9, 1–6
- 21 Dekker, D. *et al.* (2007) Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika* 72, 563–581
- 22 Hanneman, R.A. and Riddle, M. (2005) *Introduction to Social Network Methods*, University of California
- 23 Zuur, A.F. *et al.* (2009) *Mixed Effects Models and Extensions in Ecology with R*, Springer
- 24 Manly, B.F.J. (2006) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, Taylor & Francis Inc.
- 25 Furht, B. *et al.* (2010) Perspectives on social network analysis for observational scientific data, In *Handbook of Social Network Technologies and Applications*, Springer, pp. 147–168
- 26 Franks, D.W. *et al.* (2009) A foundation for developing a methodology for social network sampling. *Behav. Ecol. Sociobiol.* 63, 1079–1088
- 27 Perreault, C. (2010) A note on reconstructing animal social networks from independent small-group observations. *Anim. Behav.* 80, 551–562
- 28 Borgatti, S.P. *et al.* (2002) *Ucinet for Windows: Software for Social Network Analysis*, Analytic Technologies, (Harvard)
- 29 Whitehead, H. (2009) SOCPROG programs: analysing animal social structures. *Behav. Ecol. Sociobiol.* 63, 765–778
- 30 Voelkl, B. *et al.* (2011) Network measures for dyadic interactions: stability and reliability. *Am. J. Primatol.* 73, 731–740
- 31 Lusseau, D. *et al.* (2008) Incorporating uncertainty into the study of animal social networks. *Anim. Behav.* 75, 1809–1815
- 32 Bhadra, A. *et al.* (2009) A comparative social network analysis of wasp colonies and classrooms: linking network structure to functioning. *Ecol. Complex* 6, 48–55
- 33 Darden, S.K. *et al.* (2009) Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. *Proc. R. Soc. B: Biol. Sci.* 276, 2651–2656
- 34 Miklós, I. and Podani, J. (2004) Randomization of presence-absence matrices: comments and new algorithms. *Ecology* 85, 86–92
- 35 Whitehead, H. *et al.* (2005) Testing association patterns: issues arising and extensions. *Anim. Behav.* 69, e1–e6
- 36 Pepper, J.W. *et al.* (1999) General gregariousness and specific social preferences among wild chimpanzees. *Int. J. Primatol.* 20, 613–632
- 37 Wey, T.W. and Blumstein, D.T. (2010) Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Anim. Behav.* 79, 1343–1352
- 38 Hemelrijk, C.K. (1990) Models of, and tests for, reciprocity, unidirectionality and other social-interaction patterns at a group level. *Anim. Behav.* 39, 1013–1029
- 39 McDonald, D.B. (2009) Young-boy networks without kin clusters in a lek-mating manakin. *Behav. Ecol. Sociobiol.* 63, 1029–1034
- 40 Bollobás, B. (2001) *Random Graphs*, Cambridge University Press
- 41 Newman, M.E.J. *et al.* (2001) Random graphs with arbitrary degree distributions and their applications. *Phys. Rev. E* 64, 026118
- 42 Lusseau, D. *et al.* (2006) Quantifying the influence of sociality on population structure in bottlenose dolphins. *J. Anim. Ecol.* 75, 14–24
- 43 Manly, B.F.J. (1995) A note on the analysis of species co-occurrences. *Ecology* 76, 1109–1115
- 44 Krause, S. *et al.* (2009) Social network analysis and valid Markov chain Monte Carlo tests of null models. *Behav. Ecol. Sociobiol.* 63, 1089–1096
- 45 Beijer, L. *et al.* (1998) A method for testing association patterns of social animals. *Anim. Behav.* 56, 719–725
- 46 Sundaresan, S.R. *et al.* (2009) Avoiding spurious findings of nonrandom social structure in association data. *Anim. Behav.* 77, 1381–1385
- 47 Croft, D.P. *et al.* (2006) Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* 59, 644–650
- 48 Krause, S. *et al.* (2005) Assortative interactions and social networks in fish. *Oecologia* 143, 211–219
- 49 Croft, D.P. *et al.* (2009) Behavioural trait assortment in a social network: patterns and implications. *Behav. Ecol. Sociobiol.* 63, 1495–1503
- 50 Croft, D.P. *et al.* (2004) Social networks in the guppy (*Poecilia reticulata*). *Proc. R. Soc. B: Biol. Sci.* 271, S516–S519
- 51 Grear, D.A. *et al.* (2009) Does elevated testosterone result in increased exposure and transmission of parasites? *Ecol. Lett.* 12, 528–537
- 52 Otterstatter, M.C. and Thomson, J.D. (2007) Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies. *Oecologia* 154, 411–421
- 53 Dormann, C.F. *et al.* (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628
- 54 Johnson, J.B. and Omland, K.S. (2004) Model selection in ecology and evolution. *Trends Ecol. Evol.* 19, 101–108
- 55 Csilléry, K. *et al.* (2010) Approximate Bayesian Computation (ABC) in practice. *Trends Ecol. Evol.* 25, 410–418
- 56 Bode, N.W.F. *et al.* (2011) Social networks and models for collective motion in animals. *Behav. Ecol. Sociobiol.* 65, 117–130
- 57 Bode, N.W.F. *et al.* (2011) The impact of social networks on animal collective motion. *Anim. Behav.* 82, 29–38
- 58 White, D.J. and Smith, A.V. (2007) Testing measures of animal social association by computer simulation. *Behaviour* 144, 1447–1468
- 59 Krause, J. *et al.* (2010) New technology facilitates the study of social networks. *Trends Ecol. Evol.* 26, 5–6
- 60 Whitehead, H. and Dufault, S. (1999) Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations, In *Advances in the Study of Behavior* (Vol. 28), Academic Press, pp. 33–74