Commentary

Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour

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Mixed-species social aggregations are common across taxa. There are two, nonexclusive, hypotheses typically proposed to explain the formation of social groups: increased predator vigilance and greater foraging efficiency. In mixed-species groups, these hypotheses are typically tested with species-level summary measures such as flocking propensity, the assignment of species-level roles, mean body size, and foraging and habitat characteristics. Literature syntheses make it clear that while these hypotheses are important, much about mixed-species groups remains unexplained. We suggest that we can substantially increase our understanding of the evolution and ecology of mixed-species social groups in terms of both traditional and novel hypotheses by shifting the analytical focus to bottom-up approaches common in intraspecific investigations of sociality. Bottom-up approaches to analyses of social structure treat pairwise interactions as the fundamental unit of analysis and social structure as an emergent property rather than relying on a priori assignments of species as units of association. The construction of social networks from pairwise interaction rates allows us to assess the factors that promote group formation on the basis of individuals, a more appropriate level of selection, rather than species groups. We illustrate this approach with data from mixed-species foraging assemblies in tits (Paridae), finding significant effects of dominance on social behaviour within species. This new focus allows us to address questions about active associations among heterospecifics, the role of individuals within mixed-species societies, and the role of environments, which will collectively provide a richer description of the evolution and function of mixed-species societies.

A society is a cohesive group of individuals with organized relationships that impact both survival and fitness. Social groups are distinguishable from random aggregations, for instance when group formation is due to a locally limiting resource, by the presence of nonrandom preferred and avoided interactions between specific individuals over time (Whitehead 2008). Darwin (1871) noted that the tendency to be social is a trait upon which selection can act. Since then benefits to individuals of being social are often cast, and perhaps often best understood, within the context of inclusive fitness (Grafen 2009). Direct fitness benefits can also play an important role in the evolution of sociality but can be difficult to disentangle from indirect kin-based benefits (Clutton-Brock 2002). However, inclusive fitness can be excluded a priori for mixed-species social relationships making mixed-species sociality particularly important for understanding how direct fitness benefits of social relationships can produce complex social structure in the absence of kinship. Mutualism and manipulation are classical explanations for social behaviour among nonkin individuals of the same, or different, species (Clutton-Brock 2009). Mutualistic interactions entail that interacting individuals gain immediate and shared benefits that exceed any costs associated with interacting (e.g. cooperative hunting, foraging and resource defence; Kokko et al. 2001; Clutton-Brock 2009). Although manipulative social behaviours may be selected largely for the benefits accruing to the manipulating individual, both individuals may benefit, albeit disproportionately. An individual mimicking the call of another species in order to attract it to a resource or to mob a predator is a common example of manipulative behaviour.

Despite a long research tradition, particularly in birds (reviewed in Rand 1954; Harrison & Whitehouse 2011), we suggest that our understanding of the evolution of mixed-species sociality can be considerably expanded by a shift in analytical focus. In particular, we suggest that typical conceptual approaches to the studies of mixed-species groups suffer from drawbacks related to a top—down classification scheme when describing heterospecific social structure. First, the typical unit of analysis in the mixed-species flock (MSF) literature is the species. This implicitly imposes a social

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structure (MSFs are structured by species), rather than describing it using social data. Second, selection occurs at the level of individuals and their genes, so the fitness costs and benefits of being social are also best measured at the level of the individual and not the species. Inferences about selection and fitness benefits, and therefore the evolution of MSFs, drawn from top–down examination are consequently constrained to be cursory.

Here we advocate a bottom–up approach, productive in intra-specific studies of animal social structure, for analyses of MSFs (Hinde 1976; Whitehead 2008). Bottom-up studies of sociality have identified substantial variation in the tendency to be social among individuals that is masked by current species-level classifications in typical MSF studies. For example, wild guppies, *Poecilia reticulata*, exhibit greater association strengths that are temporally more stable in higher predation risk environments (Kelley et al. 2011) and exhibit both behavioural (Croft et al. 2009) and physical (Croft et al. 2005) assortment. Similarly, in bats, *Myotis septentrionalis*, associations vary according to age and reproductive stage, with gestating females having fewer associations (Patriquin et al. 2010). Furthermore, a study of meerkats, *Suricata suricatta*, by Madden et al. (2011) describes several levels of social positions according to intrinsic individual characteristics; for example greater body mass deter-mined dominance and males showed assortment. In particular, social network analysis provides a quantitative framework that can integrate across levels, based upon dyadic interactions, from indi-viduals to species. This makes it useful for testing traditional species-level hypotheses as well as additional hypotheses regarding indi-vidual variation within MSFs (Croft et al. 2008; Whitehead 2008).

THE BOTTOM–UP APPROACH FOR MIXED-SPECIES FLOCKING RESEARCH

Hinde (1976) proposed an elegant conceptual framework that has been adopted for the study of vertebrate social organization (Whitehead 2008). His insight was to consider dyadic interactions as the fundamental unit of social analysis. The patterning of inter-actions between pairs can then be used to describe relationships, and social structure inferred from the pattern and persistence of these relationships within the population. At each level the data reveal properties that may not be apparent at the level below; relationships emerge from interactions, and social structure from relationships. Thirty-six years after its publication, Hinde's frame-work continues to be influential, leading to rich and novel insights into the ecology and evolution of complex and cryptic animal societies (Goodall 1986; Cheney et al. 1987; Dunbar 1988; Whitehead 1997, 2008). The mixed-species flocking literature has largely missed these technical and conceptual advances from individual-based approaches in the social structure literature.

The bottom–up framework of interindividual interactions within mixed-species flocking provides an opportunity for measuring the indirect genetic effects of the social environment. An indirect genetic effect is the phenotypic expression of an individual's trait that is affected by their interactions with other individuals (Moore et al. 1997; Wolf & Moore 2010). Furthermore, fitness consequences of interspecific indirect genetic effects have been suggested as being important in community structure and provide evidence for community-level selection (Shuster et al. 2006; Whitham et al. 2006). Harrison & Whitehouse (2011) suggested that by partici-pating in MSFs, species are able to alter the selective pressures they experience through the process of niche construction, an ecoevolu-tionary feedback modifying community-level selection. The pattern of interactions between pairs of individuals provides a measure of social phenotype that can be assessed against morphological traits and reproductive success in order to determine the effects of selec-tion operating within populations, and how selection varies

according to social conditions. Applying a bottom–up approach to MSFs can provide the basis for exploring the interplay between community-level selection and cooperation based on mutualism.

While this framework will not be suitable for all questions (for example landscape variation in species guilds), the shift of mixed-species flocking research towards a bottom–up approach will provide a quantitative interface between the social behaviour of individuals and population-level phenomena (Croft et al. 2008). This will enable our understanding of MSFs to be explored in the context of theoretical advances in sociality, as well as better informing classical evolutionary theories of group living such as predation risk minimization and foraging benefits. One tool that has proved particularly useful for investigating sociality from a bottom–up perspective is social network analysis (Croft et al. 2008; Whitehead 2008; Newman 2010).

SOCIAL NETWORK ANALYSIS

Social network analysis is a tool for studying the social organi-zation of groups based on the associations or interactions between individuals. Its utility for studying animal populations has been to explore the variations in individual sociality, and the consequences of such variation (e.g. Lusseau 2003; Croft et al. 2004). Thus, while social network analysis methods to test differences between indi-viduals in populations are not novel, their application to MSFs have as yet received little attention. One study has so far used social networks in multispecies groups. Beyer et al. (2010) measured association rates between classes of different fish species, using a network approach to show differential social associations between native and invasive fish. This study, however, was at the level of the species (species were nodes in the network) as opposed to the associations between individually identified animals.

Methods for gathering social network data of animal groups are well described and easily applied to mixed-species populations (Whitehead 2008). These involve recording associations or inter-actions between known or marked individuals repeatedly over time in order to describe connections between individuals, and, prefer-ably, the interaction rate and stability of each dyadic pair. In the context of MSFs, each individual would be treated equally, irre-spective of its species category. The collective dyadic links between individuals produces a network on which metrics can be calculated describing various aspects of an individual's tendency to be social. These measures can be statistically assessed along with both intrinsic traits and extrinsic factors. For example we can measure individual gregariousness (the sum of their associations) and test whether associations are related to species or rather to individual traits (see Whitehead 2008; Croft et al. 2011 for further details and caveats on statistical tests for nonindependent network metrics).

In Fig. 1, we show two simple hypothetical interspecific social networks. Mixed-species populations can be made up of very different species, and the participation of individuals in the social network could be based primarily on species (Fig. 1a) or individual-level characteristics (Fig. 1b). Thus, whereas the position of indi-vidual nodes in Fig. 1a is comparable to the results of existing top–down approaches (where all individuals could be replaced by one node representing species), the social structure of Fig. 1b represents a radical departure from anything that could be quantifiably assessed, or even detected, with species-level analyses.

Social network analysis provides a catalogue of quantitative metrics that can be calculated for an observed population (Newman 2010). These span three scales: the individual, the dyadic pair and the population. At each level, comparisons can be made with null models of randomized networks (Bejder et al. 1998; Whitehead 2008; Croft et al. 2011) to test for nonrandom characteristics of the observed social structure. At the dyadic level, variations in link
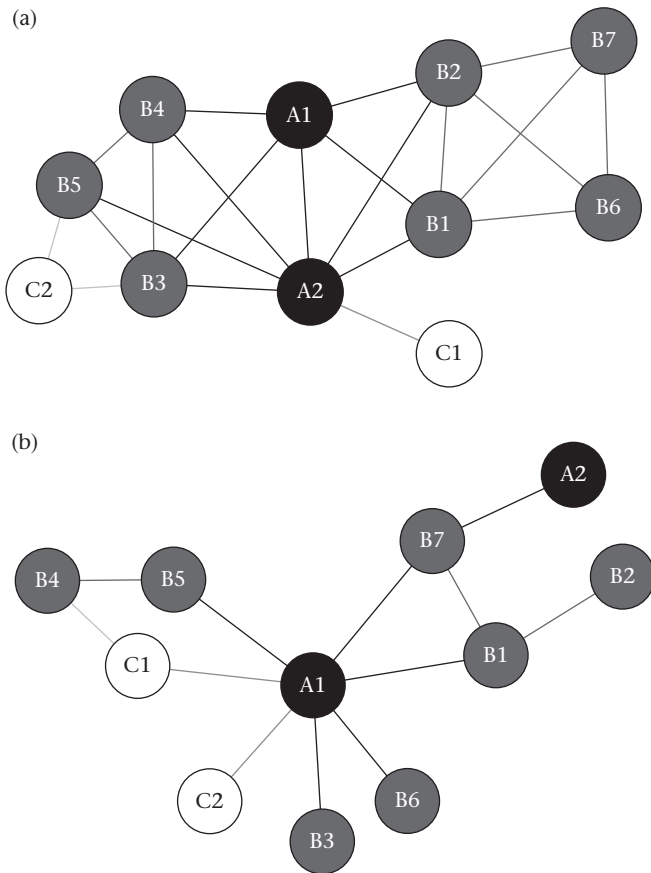
Figure 1. Example interspecific social networks showing different network structures. In (a) the network shows clear species assortment, at least for species A and B. This would indicate stronger attraction with conspecifics, where, for example, species A may be a resident monogamous species, B a cooperative breeder and C perhaps a migratory species. The social participation of individuals in this network is homogeneous within species. In contrast, (b) shows a network with greater individual variation that is not necessarily attributable to species. For example, node A1 has a highly central role, whereas A2 is poorly connected.

strengths (preferred associations) can be tested against morphological, ecological and environmental factors. Individual differences can then be related to biological features, such as personality or genotype, to understand their impacts on social behaviour.

APPLICATIONS TO MIXED-SPECIES FLOCKING

Here we discuss some key questions in mixed-species flocking to which social network analysis could be readily applied, and explore how doing this might in turn advance our understanding of the evolution of social behaviour more generally.

Are There Active Associations Among Heterospecific Individuals?

One outstanding question in mixed-species flocking is whether preferential, or avoided, associations exist between heterospecific pairs of individuals. Nonrandom associations between individuals within species have been shown in a wide range of taxa and specifically tested for in wild populations of, for example, dolphins (Lusseau 2003), ungulates (Sundaresan et al. 2007) and guppies (Morrell et al. 2008). In the case of mixed-species flocking, being familiar with associates may provide benefits over socializing with random individuals. Stable associations can lower uncertainty, thereby increasing payoff of mutualistic interactions through

reduced costs of competition (stable dominance hierarchy) and predation. For example, Blumstein et al. (2004) showed that individuals can discriminate the identity of alarm callers in order to ascertain the level of vigilance that is required. Stable associations can also provide more opportunity for information transfer through social learning or other mechanisms (Krebs 1973). A population containing both resident territorial flocks and transient associates would be ideal for exploring benefits of long-term cooperation over random associations. Permutation tests of pairwise associations can be used to determine preferred or avoided individuals (Whitehead 2008) and lagged association rates to measure their persistence over time, which is important as benefits may be delayed or reciprocal (Clutton-Brock 2002).

What are the Social Roles of Individuals in MSFs?

The mixed-species flocking environment has been suggested as having the potential to modify selection on within-species variation (Harrison & Whitehouse 2011) but the adaptive significance of variation must be analysed at the level of individuals rather than species. Juvenile connectivity in birds has been shown to increase social status in the short term (house finches, *Carpodacus mexicanus*: Oh & Badyaev 2010) and the long term (long-tailed Manakin, *Chiroxiphia linearis*: McDonald 2007), providing subsequent fitness benefits. Individuals may also interact both mutualistically and manipulatively. In non-randomly associating flocks different individuals may therefore gain different direct fitness benefits from their position relative to others as the benefits to cooperation can be asymmetrical (Gibson et al. 2002; Magrath et al. 2009; Nolen & Lucas 2009). This potentially leads to preferences for active, passive and avoided associations in dyadic pairs, and hence enables emergent self-organization and sociality. Social network analysis provides many different measures that can evaluate the social phenotype of individuals. However, empirical studies may require support from simulation results to provide an a priori classification of network measures and roles.

How Does the Physical Environment Affect Mixed-Species Flocking?

Community composition is influenced by habitat characteristics at several scales. Understanding the differing roles that individuals and species play in different habitats can provide insight into mutualistic interactions that may allow their habitat tolerability to be greater than their niche otherwise permits. The best evidence (Harrison & Whitehouse 2011) that flocking can be mediated by community composition comes from Diamond (1975) who found that New Guinean islands lacking key species did not have any mixed-species flocking in those that remained, and Maldonado-Coelho & Marini (2000) who found that the absence of one nuclear species from forest fragments in Brazil led to the loss of mixed-species flocking occurring in those fragments. These examples point to manipulation by the flocking species underlying the evolution of flocking within those communities. Furthermore, variations in the relative proportions of syntopic species may affect not just social structure but also social roles. For example, the fitness benefits of mixed-species flocking to individuals from a scarce species may be much greater where its population density is low than where it is high. In such cases, there might be selection for more interspecifically gregarious phenotypes to colonize or maintain presence in less preferred habitats or at the edge of their range. The social network of populations would be structurally very different in the presence of relative changes in species abundances, and therefore whole network structure can be used to relate these differences to environmental conditions. This has, to our knowledge, remained unexplored.

How can mixed-species flocking evolve?

The best supported hypotheses for the evolution of MSFs have been that they lead to increased foraging success and predation risk dilution. However, the presence of preferred and nonrandom associations within these flocks suggests the existence of some higher-level processes. This would support the hypothesis that MSFs are mutualistic, albeit providing a range of benefits that may not be identical for all participants (Clutton-Brock 2002). For example, sentinel species may gain better access to food resources while other species benefit from more rapid detection of predators (Satischandra et al. 2007). By cooperating, organisms can alter their selection pressure (such as through niche construction as suggested by Harrison & Whitehouse 2011). Competition costs may be incurred by both species, and these will be outweighed by the benefits (at least approximately equalled in cases of manipulated species). Maintained associations can enable long-term benefits or potentially enhance them through reciprocity.

EMPIRICAL EXAMPLE: MIXED-SPECIES TIT FLOCKS

The benefits of participating in MSFs are unlikely to be experienced equally by all individuals. Dominant individuals can supplant subdominants from the safest foraging positions, in turn reducing flocking benefits to subordinates (Morse 1978; Ekman 1989). Morse (1978) examined the social dominance hierarchy of tits (*Parus* spp.) in Wytham Woods finding that larger species were dominant over smaller species. Despite significant mixed-species associations, agonistic interactions occurred most often between conspecifics rather than heterospecifics (Morse 1978). Larger more dominant individuals in general can have a larger optimal group size as they incur lower competitive costs and can supplant subdominants from safer and more profitable resources (Krause & Ruxton 2002). This should lead to dominants having a larger number of associates than subdominants regardless of species composition. Mixed-species groups may be more important for subdominants by enabling them to increase their group size either with individuals that are even more subdominant than they are or with those from species that use a different feeding niche. By choosing to flock with heterospecifics of a smaller species, subdominants might thereby increase their relative rank within their flock, increasing their individual benefits of flock participation (Gosler & Carruthers 1999). Subdominants should therefore have a relatively greater number of heterospecific associates than dominants. Finally, dominant individuals have been shown to maintain more central group positions than subdominants in both fish and birds (reviewed in Krause & Ruxton 2002). A central individual is likely to have access to better information on predators or food resources, and be safer from attacks, but incur larger competition costs which may be offset by dominance. As an example of the application of social network analysis to mixed-species flocking, we used social network analysis to test for effects of dominance on associations within and between species. We hypothesized that dominants should have a greater number of associates, that subdominants should flock with more heterospecifics, and that dominants should be found in positions of greater centrality than subdominants.

Methods

We generated four social networks based on the feeding associations of a population of wild birds. Four feeders were placed in a square 300 m apart for the month of January 2012 at Wytham Woods, Oxford, U.K. (51°46′00N, 01°20′00W). Food was available over four consecutive weekends (2 days each, total 8 days) with the feeders closed at other times and not recording visits. Feeders were fitted with RFID antennae in place of the perch for both access holes (Dorset ID, Aalten, Netherlands). These detected visits to each feeder by blue tits, *Cyanistes caeruleus*, coal tits, *Parus ater*, great tits, *Parus major*, marsh tits, *Poecile palustris*, and nuthatches, *Sitta europaea*, fitted with passive integrative transponder (PIT) tags (IB Technology, Aylesbury, U.K.) recording the time, date, location and identity of each individual.

The social network was inferred using a recently developed method utilizing a Gaussian mixture model to detect clusters of visits in time (Psorakis et al. 2012). Mixture models are typically probabilistic models used to represent the presence of subpopulations, but are used here to represent the presence of bursts of arrivals at a feeder within the data stream. Instead of fixing time limits of associations, it allowed us to detect temporally focused bursts in activity, or 'waves', of feeding birds. Observations are then assigned to a group according to the temporal burst in which it occurs. We applied the simple ratio (Whitehead 2008) method for weighting associations to describe the proportion of visits made by individuals within the same group. We used randomization tests, following Bejder et al. (1998), to test for nonrandom associations among individuals. This randomization method controls for important features of the data such as the number of observations, gregariousness and group size. If the standard deviation of the observed association matrix is greater than that of the randomized association matrix then it is likely that there are nonrandom preferred and avoided associations (Whitehead 2008).

Wing length was used as a proxy for expected dominance status. In great tits, wing length is a predictor of dominance within species, with long-winged adults and males being categorically dominant over juveniles and females (Sandell & Smith 1991). The distribution of wing length across species follows the dominance hierarchy described by Morse (1978).

To describe quantitatively the participation of each individual in the network, we calculated the number of associates (unweighted degree) as a measure of gregariousness. We calculated eigenvector centrality which is a measure of an individual's centrality within the entire network. Finally, we split the number of associates into interspecific and intraspecific components, converting the measure into the proportion, or density, of each in order to account for different species population sizes.

We used generalized nonlinear mixed models (GLMMs) with random effects to estimate the effect of individual wing length on each network parameter. Binomial and Poisson error distributions were used in models with proportional and count values, respectively. We accounted for the lack of independence in social network measures by analysing four replicates of the social network (Croft et al. 2011), including sampling period (network number) and ring number as random effects. Finally, we tested our models by comparing parameter estimates to randomizations of the dependent variable. If parameter estimates were greater or less than 95% of the randomly generated parameter estimates we considered that variable to have nonrandom effects.

Ethical Note

All work was subject to review by the Department of Zoology (University of Oxford) ethical committee and adhered to U.K. standard requirements. Birds were caught using mist nets and ringed with a uniquely numbered British Trust for Ornithology (BTO) ring on one leg and a PIT tag on the other under BTO licence C5714. PIT tags were fully moulded into an 8 mm plastic ring with no protrusions and supplied by IB Technology. This work was conducted as part of a large ongoing research project at Wytham Woods (for example see Morand-Ferron & Quinn 2011). Previous work found no evidence of and impact of PIT tags on behaviour (Patrick & Browning 2011) or

survival (Nicolaus et al. 2008) in great tits, and no adverse effects on fitness (Schroeder et al. 2011) in passerines.

Results

We detected 234 295 visits to the feeders, and inferred 11 586 gathering events across all four sampling periods. These were used to generate four networks with a total of 272 individuals (185–222 per weekend) across all species (a full network for all periods combined is shown in Fig. 2). Each network was tested for nonrandom associations and in all had significantly greater standard deviation of association weights than the null expectation (one-tailed $P < 0.001$ in all cases). These networks also exhibited significant within-species variation in network measures (Fig. 3). Together, these results indicate that individuals interacted nonrandomly.

We analysed the networks in a GLMM to test the effects of individual wing length on network metrics and account for temporal variation (results in Appendix Table A1). Across species, wing length was significantly related to the number of associates (group size) with larger birds having more associates than small birds (coefficient $\pm$ SE: 0.02 $\pm$ 0.003; $P < 0.001$). Large birds also had a greater proportion of intraspecific associates (coefficient $\pm$ SE: 0.03 $\pm$ 0.01; $P < 0.05$), whereas there was no effect of wing size on the proportion of interspecific associates, indicating that subdominants did not have more heterospecific associates (coefficient $\pm$ SE: 0.008 $\pm$ 0.01; $P = 0.5$). Finally, there was no relationship between eigenvector centrality and wing length (coefficient $\pm$ SE: 0.026 $\pm$ 0.024; $P = 0.2$). Sampling period (random effect) explained very little of the variance in these models, indicating that the patterns were consistent across all four replicates at this timescale.

Discussion

We found that body size was an important determinant of social behaviour in MSFs. As we predicted, large birds had a greater number of associates overall than smaller individuals. Large birds associated
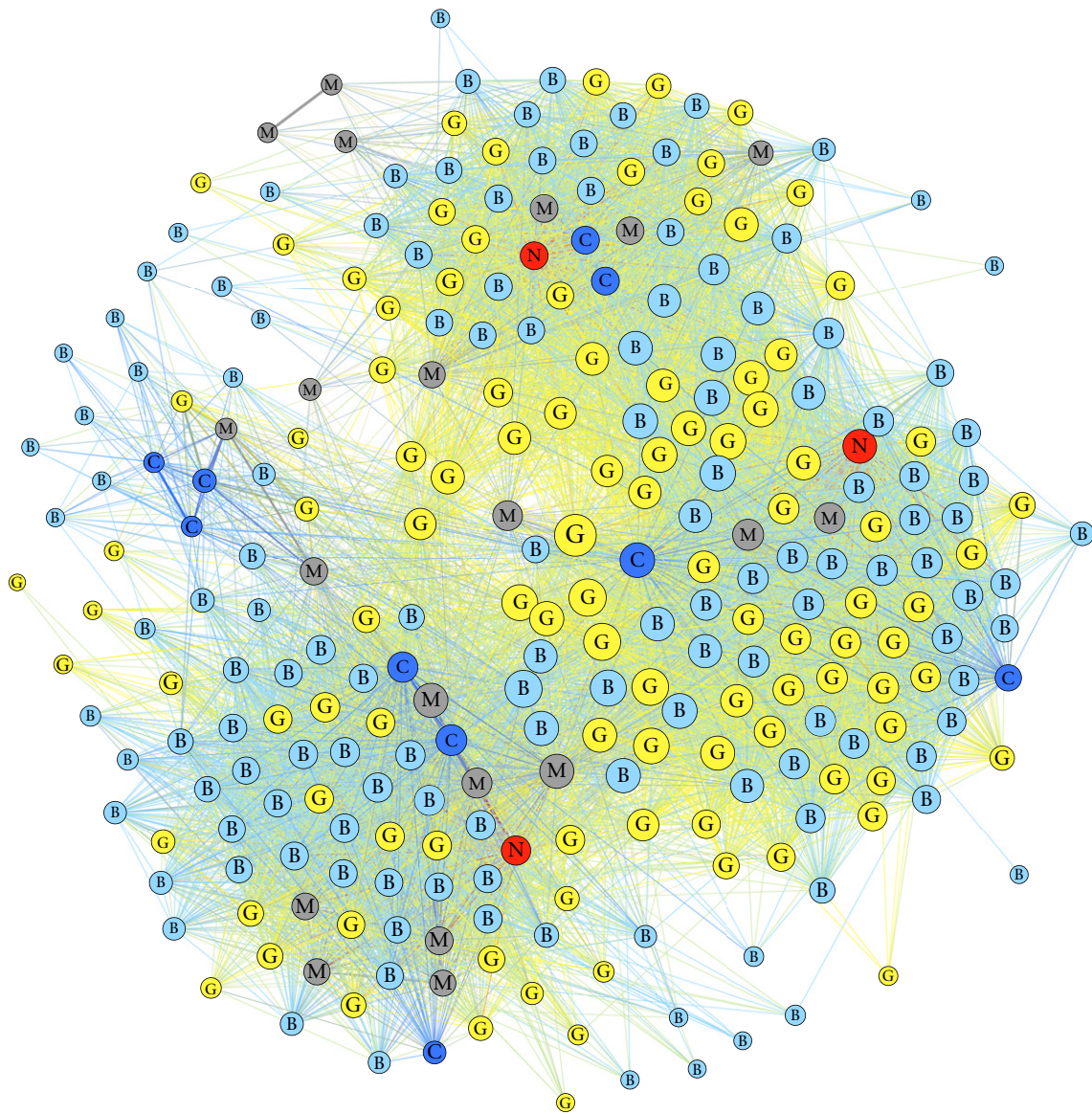

Figure 2. Social network of 136 blue tits (B), 10 coal tits (C), 103 great tits (G), 20 marsh tits (M) and three nuthatches (N) combined over the four periods of data collection. Nodes are coloured according to species and sized according to degree. Edge thickness, or weight, represents association strength between nodes. Node position was determined as the product of the attraction to connected nodes and repulsion from others, using the Fruchterman–Reingold algorithm in GEPHI (Bastian & Heymann 2010). Note that all individuals are connected; however, the edge weight of peripheral individuals is small and may not be visible.
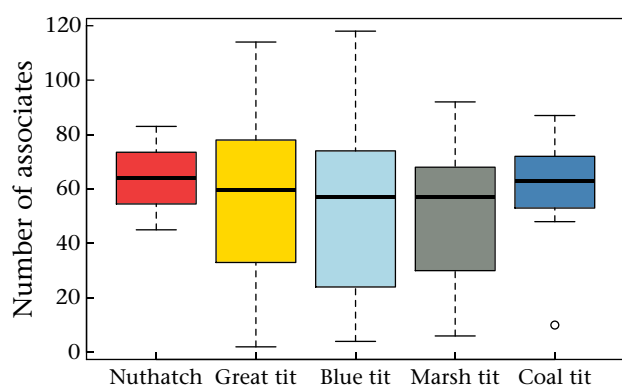
Figure 3. Summary of the number of associates by species for the first period of data collection (7 and 8 January 2012) indicating the presence of overlapping variation in social characteristics within species and overlaps between species. Species are ordered left to right by decreasing wing length and dominance rank as defined by Morse (1978). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circle is an outlier.

with more conspecifics than did smaller birds whereas there was no difference in the number of heterospecific associations between small birds and large birds. This suggests that all individuals aim to achieve a large group size, but that subdominants are limited in their ability to associate with conspecifics, perhaps because of the competitive costs that these associations incur. Thus, unlike our prediction that smaller birds would have more heterospecific associates, there was no effect on the number of heterospecific associates across dominance ranks. This uniform rate of interspecific associations may indicate a benefit in avoiding predation as experimental evidence has shown that information is unlikely to be an important proximal mechanism of mixed-species flocking with regards to feeding (Waite & Grubb 1988). In contrast, larger birds may be attracted to conspecifics in order to gain access to better problem solving (Morand-Ferron & Quinn 2011) or opportunities for scrounging (Giraldeau & Caraco 2000).

However, unlike our prediction that dominant birds should be more central, we found that eigenvector centrality was not linked to wing size. This indicates that dominance had little effect on individuals' positions within the whole network. By associating with heterospecifics, subdominants may be able to maintain central positions in their social groups, whereas in single-species flocks they would become peripheral. Hence, the ability of subdominants to maintain central positions in a population may be a previously undetected benefit of mixed-species flocking. Although we found that dominant individuals had a greater number of conspecific associates, there was no effect of dominance on the number of heterospecific associates. Since there are usually more heterospecific than monospecific links in a network, this can result in subdominants reducing the effect of dominance on their global social position. This may bring significant benefits to subdominants, as while local associations are important, it is likely to be the global network characteristics of individuals that most affect lifetime fitness (McDonald 2007).

This study demonstrates the strength of the bottom–up approach. Morse (1978) could identify the presence of interspecific dominance hierarchies aligned with body size with his observations at the species level. Here, we found that these dominance hierarchies led to social effects at the individual level, and that these were not always aligned with the predictions we made based on studies of sociality in monospecific systems.

CONCLUSION

We think social network analysis will be a useful tool for refining our knowledge of mixed-species societies. Relative to more

typical top–down approaches this line of questioning is well suited for exploring interspecific interactions among individuals that are likely to be highly complex (Goodale et al. 2010), and may elucidate advances to theories about group living in general. In particular, quantifying interactions between individuals and relating them to direct fitness benefits arising from mutualism or manipulation will open a large number of pertinent and unexplored questions.

The application of social network analysis is valid for a wide range of hypotheses across all contexts, from ecology to evolution to conservation, and entirely compatible with pre-existing paradigms. However, most current work remains focused on exploring patterns of social structure, and the challenge will be to use this approach to understand social processes better (Croft et al. 2008). It may be that mixed-species flocking will be useful for questioning sociality and cooperation theory more generally by simplifying some effects (such as dominance) and eliminating others (such as mate choice), from the measured social affinity. We hope that this paper will stimulate new focus and continued interest in mixed-species flocking.

References

Bastian, M. & Heymann, S. 2010. Gephi: an open source software for exploring and manipulating networks. gephi.org.
Bejder, L., Fletcher, D. & Brager, S. 1998. A method for testing association patterns of social animals. *Animal Behaviour*, **56**, 719–725.
Beyer, K., Gozlan, R. E. & Copp, G. H. 2010. Social network properties within a fish assemblage invaded by non-native sunbleak *Leucaspius delineatus*. *Ecological Modelling*, **221**, 2118–2122.
Blumstein, D. T., Verneyre, L. & Daniel, J. C. 2004. Reliability and the adaptive utility of discrimination among alarm callers. *Proceedings of the Royal Society B*, **271**, 1851–1857.
Cheney, D. L., Seyfarth, R. M., Smuts, B. B. & Wrangham, R. W. 1987. The study of primate societies. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 1–8. Chicago: University of Chicago Press.
Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, **296**, 69–72.
Clutton-Brock, T. 2009. Cooperation between non-kin in animal societies. *Nature*, **462**, 51–57.
Croft, D. P., Krause, J. & James, R. 2004. Social networks in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society B*, **271**, S516–S519.
Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D. & Krause, J. 2005. Assortative interactions and social networks in fish. *Oecologia*, **143**, 211–219.
Croft, D. P., James, R. & Krause, J. 2008. *Exploring Animal Social Networks*. Princeton, New Jersey: Princeton University Press.
Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J. & James, R. 2009. Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, **63**, 1495–1503.
Croft, D. P., Madden, J. R., Franks, D. W. & James, R. 2011. Hypothesis testing in animal social networks. *Trends in Ecology & Evolution*, **26**, 502–507.
Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: J. Murray.
Diamond, J. M. 1975. Assembly of species communities. In: *Ecology and Evolution of Communities* (Ed. by M. L. Cody & J. M. Diamond), pp. 342–444. Cambridge, Massachusetts: Harvard University Press.
Dunbar, R. I. M. 1988. *Primate Social Systems*. Ithaca, New York: Comstock.
Ekman, J. 1989. Ecology of non-breeding social-systems of *Parus*. *Wilson Bulletin*, **101**, 263–288.
Gibson, R. M., Aspbury, A. S. & McDaniel, L. L. 2002. Active formation of mixed-species grouse leks: a role for predation in lek evolution? *Proceedings of the Royal Society B*, **269**, 2503–2507.
Giraldeau, L. A. & Caraco, T. 2000. *Social Foraging Theory*. Princeton, New Jersey: Princeton University Press.
Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C. & Ruxton, G. D. 2010. Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, **25**, 354–361.
Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Harvard University Press.
Gosler, A. & Carruthers, T. 1999. Body reserves and social dominance in the great tit *Parus major* in relation to winter weather in southwest Ireland. *Journal of Avian Biology*, **30**, 447–459.

Grafen, A. 2009. Formalizing Darwinism and inclusive fitness theory. *Philosophical Transactions of the Royal Society B*, **364**, 3135–3141.

Harrison, N. M. & Whitehouse, M. J. 2011. Mixed-species flocks: an example of niche construction? *Animal Behaviour*, **81**, 675–682.

Hinde, R. A. 1976. Interactions, relationships and social-structure. *Man*, **11**, 1–17.

Kelley, J. L., Morrell, L. J., Inskip, C., Krause, J. & Croft, D. P. 2011. Predation risk shapes social networks in fission-fusion populations. *PLoS ONE*, **6**, http://dx.doi.org/10.1371/journal.pone.0024280, e24280.

Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001. The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society B*, **268**, 187–196.

Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.

Krebs, J. R. 1973. Social-learning and significance of mixed-species flocks of chickadees (*Parus* spp). *Canadian Journal of Zoology*, **51**, 1275–1288.

Lusseau, D. 2003. The emergent properties of a dolphin social network. *Proceedings of the Royal Society B*, **270**, S186–S188.

McDonald, D. B. 2007. Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 10910–10914.

Madden, J. R., Drewe, J. A., Pearce, G. P. & Clutton-Brock, T. H. 2011. The social network structure of a wild meerkat population: 3. Position of individuals within networks. *Behavioral Ecology and Sociobiology*, **65**, 1857–1871.

Magrath, R. D., Pitcher, B. J. & Gardner, J. L. 2009. An avian eavesdropping network: alarm signal reliability and heterospecific response. *Behavioral Ecology*, **20**, 745–752.

Maldonado-Coelho, M. & Marini, M. A. 2000. Effects of forest fragment size and successional stage on mixed-species bird flocks in southeastern Brazil. *Condor*, **102**, 585–594.

Moore, A. J., Brodie, E. D. & Wolf, J. B. 1997. Interacting phenotypes and the evolutionary process. 1. Direct and indirect genetic effects of social interactions. *Evolution*, **51**, 1352–1362.

Morand-Ferron, J. & Quinn, J. L. 2011. Larger groups of passerines are more efficient problem solvers in the wild. *Proceedings of the National Academy of Sciences, U.S.A.*, **108**, 15898–15903.

Morrell, L. J., Croft, D. P., Dyer, J. R. G., Chapman, B. B., Kelley, J. L., Laland, K. N. & Krause, J. 2008. Association patterns and foraging behaviour in natural and artificial guppy shoals. *Animal Behaviour*, **76**, 855–864.

Morse, D. H. 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland during winter. *Ibis*, **120**, 298–312.

Newman, M. E. J. 2010. *Networks: An Introduction*. Oxford: Oxford University Press.

Nicolaus, M., Bouwman, K. M. & Dingemanse, N. J. 2008. Effect of PIT tags on the survival and recruitment of great tits *Parus major*. *Ardea*, **96**, 286–292.

Nolen, M. T. & Lucas, J. R. 2009. Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. *Animal Behaviour*, **77**, 1137–1146.

Oh, K. P. & Badyaev, A. V. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *American Naturalist*, **176**, E80–E89.

Patrick, S. C. & Browning, L. E. 2011. Exploration behaviour is not associated with chick provisioning in great tits. *PLoS ONE*, **6**, http://dx.doi.org/10.1371/journal.pone.0026383, e26383.

Patriquin, K. J., Leonard, M. L., Broders, H. G. & Garroway, C. J. 2010. Do social networks of female northern long-eared bats vary with reproductive period and age? *Behavioral Ecology and Sociobiology*, **64**, 899–913.

Psorakis, I., Roberts, S. J., Rezek, I. & Sheldon, B. C. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. *Journal of the Royal Society Interface*, Published online 13 June 2012.

Rand, A. L. 1954. Social feeding behavior of birds. *Fieldiana, Zoology*, **36**, 1–71.

Sandell, M. & Smith, H. G. 1991. Dominance, prior occupancy, and winter residency in the great tit (*Parus major*). *Behavioral Ecology and Sociobiology*, **29**, 147–152.

Satischandra, S. H. K., Kudavidanage, E. P., Kotagama, S. W. & Goodale, E. 2007. The benefits of joining mixed-species flocks for a sentinel nuclear species, the greater racket-tailed drongo *Dicrurus paradiseus*. *Forktail*, **23**, 145–148.

Schroeder, J., Cleasby, I. R., Nakagawa, S., Ockendon, N. & Burke, T. 2011. No evidence for adverse effects on fitness of fitting passive integrated transponders (PITs) in wild house sparrows *Passer domesticus*. *Journal of Avian Biology*, **42**, 271–275.

Shuster, S. M., Lonsdorf, E. V., Wimp, G. M., Bailey, J. K. & Whitham, T. G. 2006. Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution*, **60**, 991–1003.

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

Waite, T. A. & Grubb, T. C. 1988. Copying of foraging locations in mixed-species flocks of temperate-deciduous woodland birds: an experimental-study. *Condor*, **90**, 132–140.

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

Whitehead, H. 2008. *Analyzing Animal Societies*. Chicago: University of Chicago Press.

Whitham, T. G., Bailey, J. K., Schweitzer, J. A., Shuster, S. M., Bangert, R. K., Leroy, C. J., Lonsdorf, E. V., Allan, G. J., DiFazio, S. P., Potts, B. M., et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics*, **7**, 510–523.

Wolf, J. B. & Moore, A. J. 2010. Interacting phenotypes and indirect genetic effects. In: *Evolutionary Behavioral Ecology* (Ed. by D. F. Westneat & C. W. Fox), pp. 225–245. Oxford: Oxford University Press.

Appendix

Table A1
Output of generalized linear mixed models

Dependent variable	Wing	Ring number	Date
No. of associates	0.0189 (0.005)	0.2585 (0.5085)	0.0123 (0.1108)
No. of conspecific associates	0.0265 (0.0118)	0.0138 (0.1173)	0.0005 (0.0241)
No. of heterospecific associates	0.0077 (0.0119)	0.0100 (0.1002)	0.0001 (0.01044)
Eigenvector centrality	−0.0004 (0.0120)	0.0000 (0.0000)	0.0000 (0.0000)

Wing length was a fixed effect and we give the effect size with SE. Ring number and date were random effects, and the variance is given with SD. We used a Poisson error distribution for the number of associates model, and a binomial error distribution for the other three models.