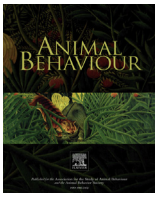
SPECIAL ISSUE: SOCIAL NETWORKS

Animal Behaviour 136 (2018) 239–250

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Special Issue: Social Networks

Edge weight variance: population genetic metrics for social network analysis

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ARTICLE INFO

Article history:
Received 24 October 2016
Initial acceptance 14 August 2017
Final acceptance 23 October 2017
Available online 19 December 2017
MS. number: SI-16-00933

Keywords:
connectivity
cultural transmission
disease network
edge weight variance
effective degree
relationship strength
social complexity
social generalist
social specialist
weighted network

We present novel metrics for analysis of weighted social networks that focus explicitly on the distribution of edge weights at hierarchical scales from node to egonet to community and to the network as a whole. The formulae are adapted from existing measures, originally developed in the context of population genetics to analyse variance in gene frequencies at different levels of organization. Our metrics, including ‘effective degree’ (by analogy to effective number of alleles), ‘concentration’ (by analogy to the inbreeding coefficient), ‘observed’ and ‘expected edge weight diversity’ (by analogy to observed and expected gene diversity) and F statistics allow one to partition the variance in edge weights among hierarchical levels of organization within networks. They provide a quantitative method for addressing issues as diverse as disease transmission, social complexity, the spread of learned behaviours and the evolution of cooperation. We illustrate the utility of these new metrics by applying them to three empirical social networks: long-tailed manakins, *Chiroxiphia linearis*, monk parakeets, *Myiopsitta monachus*, and mountain goats, *Oreamnos americanus*.

Social network analysis has rapidly become a useful quantitative tool for analysis of complex social interactions in animal behaviour and behavioural ecology (Krause, Lusseau, & James, 2009; Lusseau, 2003; McDonald, 2007; Pinter-Wollman et al., 2014). A social network consists of ‘nodes’ (often, in animal behaviour, an individual) and ‘edges’ (ties, associations or interactions among the nodes). Network edges can be directed or undirected (the direction of the interaction may be important). Edges can also be weighted or unweighted (binary 0/1, presence/absence of edge). The edges of a weighted network vary in size numerically; in an animal behaviour context, they might, for example, represent the number, frequency or intensity of interactions, or the size of the ‘pipe’, if information flows along the edges. Weighted social networks often provide a more realistic representation of the complex social interactions among animals than do binary networks (Farine, 2014), and considering the strength of relationships among individuals can be critical for understanding many social phenomena. However, compared to the plethora of metrics for binary (unweighted, undirected) networks, relatively few metrics exist for weighted networks. More metrics are needed for better quantifying the diversity of social relationships and for comparing variability in the strength of relationships across different levels of social organization.

Sometimes, as for example with the application of game theory to animal behaviour (Maynard Smith, 1982), quantitative tools from one discipline can enrich inquiry in a different field. Population genetics has a rich history of metrics for quantifying the variance in gene frequencies in order to understand genetic structure. Here, we adapt existing metrics from population genetics by creating weighted network metrics loosely analogous to several formulae developed for population genetics (Wright, 1978). Our goal is to provide quantitative tools for assessing the diversity and partitioning of variance in relationship strength across social scales.

We focus on population genetic metrics that apply well to network analysis, quantifying the diversity and variance of edge weight proportions and the partitioning of that variance among different hierarchical levels. The metrics provide a framework for considering variability in sociality across social scales. Population

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https://doi.org/10.1016/j.anbehav.2017.11.017

genetics metrics consider variability in genetic structure at the level of individuals, subpopulations and populations. Adapting these methods to social networks allows analysis at the level of 'nodes' (often individuals, and considering only their edges, not any of the adjacent nodes), 'egonets' (all individuals, called 'alters', connected to a focal individual, 'ego', and including all connections among alters), 'communities' (detected by any of a wide range of community-detection algorithms, such as those of Girvan & Newman, 2002, which we use here) and 'whole networks'. Particularly at the level of egonets and communities, few metrics are currently available for comparing among these units.

The effect of variation in edge weights on network function has engaged the attention of network scientists since at least the time of Granovetter's (1973) concept of the importance of weak ties (edges). Nevertheless, network analysis has not often focused on the concept of assessing variance in edge weights, and we are aware of only a few metrics that incorporate both edge weight frequencies and their variance (for consideration of null models for weighted networks, see Barthélemy, Barrat, Pastor-Satorras, & Vespignani, 2005; Boccaletti, Latora, Moreno, Chavez, & Hwang, 2006; Opsahl, 2011; Rankin et al., 2016). In particular, the 'disparity metric' of Barthélemy et al. (2005) and Boccaletti et al. (2006) is similar to our proposed metric, *O*, observed 'edge weight diversity'. Note, however, that their measure is the sum of squared edge weight proportions, whereas ours is 1 minus that quantity. Also, they applied it only at the node level, whereas we generalize to higher hierarchical levels such as the egonet or community. Some existing metrics, such as Kemeny's constant (Levene & Loizou, 2002) assess flow through networks, and in doing so account for edge weights. 'Strength' is a network metric that sums the weights of the edges of a node (Barrat, Barthélemy, Pastor-Satorras, & Vespignani, 2004). Discussions of strength (and strength distributions) in, for example, treatments of betweenness centrality (Barrat et al., 2004) come close to our concept of variance in edge weights, but do not focus explicitly on the skew in the strength distribution across nodes, or at higher levels of network organization.

Wright's (1978) emphasis on the variance offers at least one important advantage. A growing body of evidence suggests that variance is key to any fuller understanding of system dynamics. Long ago, Gillespie (1977) pointed out that when fitness depends on a nonlinear function (for example when fitness is subjected to random effects), the variance will much better predict evolutionary outcomes than will the mean, due to Jensen's inequality (Bradbury & Vehrencamp, 2011, Figure 8.14). More recently, students of climate change have shown decisively that the effects of changes in mean temperature can have far less impact than changes in the variance (Paaijmans et al., 2010; Vasseur et al., 2014; Wang & Dillon, 2014). Many systems in behavioural ecology are underlain by nonlinear functions (Bradbury & Vehrencamp, 2014); network dynamics seem likely also to have nonlinear driving functions. An analogy may also be useful in considering why accounting for variance in edge weights should enhance understanding of network dynamics. Any architect who ignored variance in pipe widths in designing a building would surely court massive plumbing backups. Thus, assessing and understanding the variance in edge weights seems likely to enhance fuller understanding of network dynamics. With the caveat that frequencies will, at some levels (e.g. comparison of nodes with very different total weights), ignore total weights (strength) and instead concentrate on relative weights, frequency-based analysis of network edge weights should be a useful tool for exploring and understanding network structure and function. Examples of population genetic formulae that we argue apply well to social network analysis include measures such as gene diversity (heterozygosity), effective number of alleles and *F* statistics, which are basically a system for partitioning the variances in allele frequencies hierarchically across levels of biological organization from individuals to species.

Here, we adapt some of the ideas for measuring diversity and variance of alleles to measuring diversity and variance of social network edges across social scales. We present several new network metrics: 'edge weight diversity', 'effective degree', 'edge weight concentration' coefficients and *F* statistics for networks. We first provide an overview of, and formulae for, the ways in which specific metrics from population genetics can be adapted for social networks. We then provide concrete examples of the potential utility of these metrics by applying them to empirical weighted network data on long-tailed manakins, *Chiroxiphia linearis* (McDonald, 2007), monk parakeets, *Myiopsitta monachus* (Hobson & DeDeo, 2015; Hobson, Avery, & Wright, 2014) and mountain goats, *Oreamnos americanus* (Côté, 2000). R scripts for the analyses performed here are available at https://github.com/Manakins/popgen-for-networks, along with the input files. Our proposed metrics should be useful for a wide range of network applications, including the study of disease transmission, quantitative comparison of social organization and social complexity, and the flow of learned behaviour or information.

ADAPTING POPULATION GENETICS METRICS FOR SOCIAL SYSTEMS

We used population genetics metrics as inspiration for our new network metrics. Nevertheless, the analogy between alleles in population genetics and edges in social network is by nature an abstract one, and there are important differences between the two. In developing these new network metrics, we focused on incorporating ideas from population genetics about the importance of diversity and variance, and the comparison of these metrics across different scales of organization.

In population genetics, diploid individuals have two sets of chromosomes, with loci as the places (on a chromosome) where an allele resides (Gillespie, 1998). An allele is a variant of the DNA sequence found at that locus. In social systems, the fundamental units are nodes (usually individuals) and edges connecting nodes (social relationships or associations). One fundamental difference between population genetics and social networks is that network edges, and thus their weights, connect two nodes, whereas alleles are shared only in the sense that alleles in different individuals can be identical by descent. As a result, the weights and edges 'belong', simultaneously, to two nodes, making issues of nonindependence between data points important to consider for certain types of analyses. Unlike the two alleles per gene in diploid organisms, network weights do not exist as obligately paired entities. Thus, the correspondence between allele and individual organism differs importantly from the correspondence between network edge weight and node. Alleles in genetics are 'labelled'. That is, an allele A in one individual can be considered homologous to allele A in another individual. Edge weights have no such labelling. A node with many edges might have several edges of the same weight, and similar weights in different nodes might represent different proportions of the total weight for the different nodes.

Thus, in a network, we assess the distribution of edge weights, without having any labelling that links edges of the same weight in different individuals (where the same number of interactions might represent a different proportion of the node's or egonet's total weight). Furthermore, network nodes can represent entities other than individual organisms. Nodes may, for example, represent organizations, species or even geographical locations. For the purposes of this paper, we will consider only weighted, undirected edges. Extension of the metrics to consider directed edges (with inweights and outweights) should, however, be relatively straightforward.

Edge Weight Proportion

In population genetics, the first summary of genetic structure is to determine, for each locus, the frequency of different alleles that are present in the population of interest. For example, a population of five individuals (10 alleles) may contain three alleles of type A, six of type B, and one of type C, resulting in allele frequencies of $A = 0.3$, $B = 0.6$ and $C = 0.1$. In the network context, one uses the edge weight proportions (p) rather than the allele frequencies. Edge weight proportions (frequencies) are calculated for each individual node, and can be interpreted as the proportion of total edge strength contained in each of the node's edges. For example, an individual (A) that interacts with individual B five times, individual C 10 times and individual D five times would have edge weight proportions AB = 0.25, AC = 0.50 and AD = 0.25. Using proportions of the total weight rather than raw counts is useful, because doing so creates a uniform scale, summing to 1, independent of the units of measurement on which the weights are based. It also facilitates meaningful comparisons among networks whose weights differ, whether in absolute amount or because one has discrete weight units and the other has continuous weight units.

Observed Edge Weight Diversity (O)

In population genetics, allele frequencies are the basis for quantifying ‘observed gene diversity’ (observed heterozygosity) in individuals or populations (Weir, 1996). In a network context, we use edge weight proportions to find the ‘observed edge weight diversity’ (O). As noted earlier, Barthélemy et al. (2005) coined the term ‘disparity’ for a metric, that when applied at the node level, is similar to O. At the node level, O is one minus the disparity. O serves to assess the variance in edge weights at several possible hierarchical levels of network organization, from the edges of a node, to the edges in an egonet, to the edges in a community (subgraph) and finally to the edges in the total network. Note that each of these hierarchical levels of organization has objective (formula-based, and therefore replicable) defining criteria.

The formula for O is:

$$O = 1 - \sum_{i=1}^{k} p_i^2 \qquad (1)$$

where the p_i are the edge weight proportions over the k edges of the unit of interest (node, egonet, community, or network as a whole). Note that, because edge weights do not have ‘labels’, we need not deal with p, q, r, etc., the way we do for $p^2 + 2pq + q^2$ under Hardy–Weinberg. O is at a maximum when the weights are evenly distributed over the edges and decreases as the variance/skew in the weight distribution increases. Thus, an animal with high O has a high diversity of associations. Conversely, one with low O has a lower diversity of associations in terms of how the weight is distributed among its associates. One can also interpret O, at the node level, as a probability of interaction. If one takes two interactions (edge weight increments) at random from a given node, O is the probability that the two interactions are with two different individuals (i.e. that two weight increments to a node's edges will occur along two different edges). For a node with 10 equally weighted edges, the probability that two different interactions (weight increments) will be with different (diverse) nodes is 0.9 (and, of course, $O = 0.9$ also). For a node with 10 edges, but with one edge accounting for 91% of the weight and the other edges each with 1%, the probability of interacting with two different individuals is only 0.17 (low diversity of associations). Note that, for egonets and communities, we ignore edges that extend to the neighbouring unit (egonet or community), including only edges internal to the unit.

For animal social networks, O addresses how biased an animal's associations are towards one or a few social partners at the expense of weak associations with other animals. For example, male long-tailed manakins of high status (10 years old or older) concentrate their associations with their alpha or beta partners, whereas younger males have more evenly weighted associations, even though their number of associates (degree) may be similar (McDonald, 2007, 2014). Later, we provide much more detailed examples of such uses of our proposed metrics. What we argue is that O, and our other proposed metrics, provide quantitative tools for detecting patterns that stimulate testable hypotheses, and provide metrics for testing a priori hypotheses about the structure and function of animal societies.

Expected Edge Weight Diversity (E)

In population genetics, observed heterozygosity (gene diversity) in the population is then compared to expected heterozygosity to determine whether the genetic structure conforms to the null model expectation. A null model, whose most important assumption is random mating, produces the Hardy–Weinberg expectation, which is $p^2 + 2pq + q^2$ in a two-allele system. For application to a network context, we propose the metric ‘expected edge weight diversity’ (E). Instead of the Hardy–Weinberg expectation from population genetics, we propose that E be based on a null expectation of equal edge weights over whatever hierarchical level one is examining (all the edges from a node, within an egonet, community or network). This expectation differs sharply from the Hardy–Weinberg expectation, which is constrained, because of diploid inheritance, to a distribution formulated as a second-order polynomial. For networks, no such architectural constraint exists. The simplest null expectation is that all edge weight proportions be the same. In some cases, other interesting null expectations, such as the negative binomial (Zuur, Ieno, Walker, Saveliev, & Smith, 2009; p. 199), might be plausible. Under other circumstances, other statistical distributions might best cover the null expectation for the distribution of edge weights.

At the level of interest (node, egonet, community or network), we expect the weight to be distributed evenly over the k edges. Interestingly, although we could sum the squared edge weight proportions (which will all be equal to $\overline{p}$), and subtract from 1, the formula reverts to a simple ratio of the number of edges (see a population genetics text, such as Weir, 1996; for the derivation of this simplification). The formula for expected edge weight diversity, E, at the level of a node is therefore:

$$E = 1 - k \times \overline{p}^2 = \frac{k-1}{k} \qquad (2)$$

Effective Degree, D_e

In population genetics, allele frequencies are also used to find the effective number of alleles (A_E) in the population. A_E is the reciprocal of the sum of the squared allele frequencies. A_E can be interpreted as the number of equally frequent alleles it would take to achieve a given level of heterozygosity (gene diversity). A_E reaches a maximum when the allele frequencies are identical and decreases as the skew in the allele frequencies increases. Thus, if a gene has a highly skewed set of allele frequencies, the 'effective' number of alleles will be low. In contrast, if a gene has evenly frequent alleles, it will have an effective number of alleles exactly equal to the observed number of alleles. For a network context, we propose 'effective degree', D_e, using edge weight proportions rather than allele frequencies. In networks, D_e can be interpreted as the number of edges, each of equal weight, that would yield the same total weight as the observed total edge weight (strength) of a node. The formula for D_e is:

$$D_e = \frac{1}{\sum_{i=1}^{k} p_i^2} \tag{3}$$

where we sum the squared edge weight frequencies, p_i, over the k edges (= degree, D) of a node or the higher-level unit of interest. Note that D_e is the reciprocal of the disparity metric of Barthélemy et al. (2005). Nodes (or egonets, etc.) with highly skewed edge weight distributions therefore have low effective degree. For example, a node with 10 edges, but with 91% of the weight on one edge, and 1% on each of the others, has $D_e = 1.02$. That is, effectively, the node has only one 'real' neighbour with whom it interacts frequently or with high intensity. That is, it has a low diversity of interactions in terms of the distribution of edge weights. In the event that a node's edge weights are all identical, D_e is equal to the observed (binary) degree, D, given by a simple count of the edges, disregarding weights. Thus, a node with 10 equally weighted edges has $D_e = D = 10$. As a concrete example, described in greater detail below, an alpha male long-tailed manakin with 15 associates (degree = 15), had $D_e = 1.67$. Compared to a young male with the same binary degree, D, he therefore had a lower diversity of interactions in terms of the distribution of his edge weight among associates. The discrepancy between degree and D_e arises because his total edge weight (strength) was devoted almost exclusively towards his beta partner. Because different nodes will differ in their degree (i.e. have different numbers of edges), it may be useful to consider the quotient of degree/D_e. The quotient tells us how much the effective degree, D_e, is reduced relative to the binary degree, D, the simple count of edges, disregarding weights.

Edge Weight Concentration Coefficients, c

In population genetics, the first level of partitioning of genetic variance in Wright's (1978) *F* statistics is *F*, the inbreeding coefficient. For networks, we propose analogues that we will call 'edge weight concentration coefficients', *c*. The concentration coefficient is calculated as

$$c_{x(x=\mathrm{I,E,C,N})} = \begin{cases} 1 \ \text{if} \ E = 0 (\text{pendants, with just one edge}) \\ \dfrac{E-O}{E} \text{otherwise} \end{cases} \tag{4}$$

using Equations (1) and (2) for *O* and *E*. Pendants are nodes with just a single edge linking them to the rest of the network. Note that, for pendants, the *E* in the denominator goes to zero, but the weight is concentrated on that single edge, so they require a special case. The subscripts (I, E, C, N) denote the level of interest: individual node, egonet, community or network as a whole. Thus, c_C assesses the concentration of edge weights within the internal edges of a community (using any of various possible community-detection algorithms), and c_N assesses the concentration of edge weights over the network as a whole. Thus, low *O* tends to correspond to high *c*. Likewise, in population genetics, high inbreeding tends to correspond to low heterozygosity (gene diversity). Whereas, in population genetics, one does not assess *F*, the inbreeding coefficient, beyond the level of the individual, we propose that concentration should be useful at any level of network organization. If individuals have very different edge weight distributions, for whatever interactions we are assessing with our network (for example, young and old males in a lek), then we might be interested either in using patterns of concentration to make inference about roles, or in the consequences of the differences among higher levels of network organization. If egonets or communities have very different concentrations, then one might have quantitative evidence for modularity and subgroup specialization (for example, in social insect societies). For an entirely hypothetical example, foraging workers (perhaps detected as a distinct community in a network analysis) might have low edge weight ties with a large number of fellow foragers, while brood care workers might have much more heavily weighted edges to one or a few fellow brood care workers, while having low-weight edges connecting them to a large number of foragers. Any such modularization could then be detected, quantified and tested with our proposed metrics.

F *Statistics:* F_{IC}, F_{IE}, F_{IC}, F_{IN}, F_{EN}, F_{CN}

In population genetics, Wright's *F* statistics partition the variance in allele frequencies among individuals (I), subpopulations (S) and total populations (T), to yield F_{IS}, F_{IT} and F_{ST} (see http://www.uwyo.edu/dbmcd/molmark/practica/fst.html for a quick primer on *F* statistics). For a network, using weight-based metrics and different subscripts (I, E, C and N), the *F* statistics assess how variance in edge weights is partitioned among hierarchical levels of organization. The multiple hierarchies produce a larger number of statistics than in population genetics, only some of which (F_{IE}, F_{IN}, F_{CN}) we will address in our examples. The generalized formula for network *F* statistics is:

$$F_{LH} = \frac{\sum\limits_{x=1}^{u} E_x \times T_x - \sum\limits_{x=1}^{u} O_x \times T_x}{\sum\limits_{x=1}^{u} E_x \times T_x} \tag{5}$$

where the subscript L denotes the lower-level hierarchy (I, E or C), and H denotes the higher-level hierarchy (E, C or N). The summations are across the $x = 1$ to u lower-level units of interest (individuals, egonets or communities). *E* is the weighted mean of the E_x over the u lower-level (I_x, E_x or C_x) units of interest. *O* is the weighted mean *O* over the u lower-level (I_i, E_i or C_i) units of interest, and *T* is the proportion of the total weight. Note that the 'population' here is a set of edge weights, not individuals (nodes). Thus, the sampling correction (analogue of weighting by population size, *N*, in population genetics) is the proportion of the weight contained in the constituent unit. That is, we are assessing the weighted mean *O* and *E* across the units of interest, where we weight by the proportion of the total weight contained in each of the units (rather than weighting by the number of individuals sampled, as in population genetics). As a specific example of one of the proposed *F* statistics, F_{CN} (analogue to F_{ST}) assesses the partitioning of the edge weight variance in communities (subgraphs), at the lower level, relative to that in the network as a whole, at the higher level.

One interesting possibility emerges when considering F_{IN}, the network analogue to F_{IT}, which, in population genetics, assesses the weighted average individual gene diversity relative to the total expected gene diversity of the population as a whole. F_{IT} is little used in most applications of population genetics to real-world data. In a network context, however, one might uncover interesting patterns in comparing, for example, the edge weight distributions of individuals to those expected over communities (subgraphs), F_{IC}, or against the total network, F_{IN}. As a concrete example, certain types of workers in a social insect colony might have very different edge weight variance compared to that expected in the community or network in which they are embedded. Later, we provide further concrete examples, by applying these *F* statistics to compare the distribution of edge weights at different hierarchical levels within and among our case histories for parakeets, manakins and mountain goats. Another interesting difference arises in the range of possible values for F_{IE}, F_{IC} and F_{IN}. We base expected edge weight diversity, *E*, in Equation (5) on the null expectation of equality of weight across all the edges of the egonet, community or network. *E* is therefore the maximum possible ($(k-1)/k$; Equation (2)), and thus always exceeds or is equal to the observed edge weight diversity, *O*. As a result, none of the network *F* statistics (F_{IE}, F_{IC}, etc.) can be negative. In contrast, F_{IS} in population genetics can be negative, because Hardy–Weinberg expects some homozygotes, whereas, in the extreme case, observed heterozygosity might entail no homozygotes at all. A deficit of homozygotes compared to the Hardy–Weinberg expectation creates a negative F_{IS} ($O > E$, Equation (5)), suggesting disassortative mating (outbreeding), whereas an excess of homozygotes creates a positive value of F_{IS} ($O < E$), indicating inbreeding. As we suggested earlier, a plausible alternative to an expectation of equal edge weights (uniform distribution) might be a negative binomial distribution. If edge weights were more evenly distributed than the (overdispersed, nonuniform) negative binomial expectation, the network *F* statistics could become negative. Such a pattern would be the analogue of a clumped (high variance) as opposed to a random (Poisson) or uniform (low variance) spatial distribution of animals across a landscape.

Networks also differ from genetic populations in having an arguably more objective hierarchical structure, at least from ‘node’ to ‘egonet’ to ‘community’. That is, in the network context, the hierarchical units are explicitly defined by formulae, and therefore replicable across different analyses. The ‘egonet’ is defined as all those nodes (‘alters’) directly linked to the focal node, ‘ego’, along with the edges between the ‘alters’. Above that are ‘communities’, modules of linked nodes, based on many alternative algorithms. The R package, iGraph, for example, implements eight different community-detection algorithms, including ‘edge.betweenness’, ‘fast.greedy’, ‘leading.eigenvector’ and ‘spinglass’. Depending on the choice of algorithm, community assignments and even the number of communities can vary, but these are determined by the algorithm rather than the researcher. Furthermore, the choice of algorithm can be made less subjective by assessing the ‘modularity’ (*Q*; Clauset, Newman, & Moore, 2004) among candidate alternative community-detection algorithms, as we demonstrate in our detailed exemplar analyses. In contrast, the hierarchical delimitation of hierarchical units in population genetics can be somewhat subjective, or at least based on criteria that depend on the choice of the researcher. For example, delimiting a population or subpopulation in genetics is often somewhat subjective (Stegenga, 2010), and several alternative verbal definitions exist (Wells & Richmond, 1995). Note that egonets and communities can have nodes with ‘missing’ edges – those that extend outward to other egonets or communities (called ‘bridges’ when their deletion would break networks into separate ‘components’). While the hierarchical components of social networks have objective boundaries, that may not always be true for the network as a whole. The network may, instead, be a sample of some larger network, with sometimes arbitrary boundaries set by data collection constraints. Regardless, the ability to partition variances in edge weights across many hierarchical levels of organization, and across networks of different types, with differing weight units, should be very useful for comparative analyses of networks of any size.

APPLICATION OF METRICS TO EMPIRICAL DATA

Data Sets and Network Structure

To illustrate the utility of our proposed network metrics, we applied them to published data from male long-tailed manakins (McDonald, 2007), monk parakeets (Hobson & DeDeo, 2015; Hobson et al., 2014) and female mountain goats (Côté, 2000). Long-tailed manakins have a lek mating system, where males partner with other males in cooperative courtship displays to females (McDonald & Potts, 1994; McDonald, 2007). Top-ranking alpha and beta males perform the vast majority of courtship display for females. We used data on 1938 social interactions and cooperative displays among 156 males over the course of 8 years to assemble a male affiliation network. Monk parakeets are a small parrot species, notable for their highly social colonial and communal nesting behaviour (Eberhard, 1998; Hobson et al., 2014) as well as their ability to exhibit strategic aggression based on knowledge of rank in captive groups (Hobson & DeDeo, 2015). We used previously published counts of wins during dyadic aggression from a group of 21 captive parakeets, following rank stabilization (838 aggressive events in ‘Group 1’, study quarters 2–4 in Hobson & DeDeo, 2015, data available at http://datadryad.org/resource/doi:10.5061/dryad.p56q7). Mountain goats are social ungulates that can form stable and linear dominance hierarchies, despite large group sizes (Côté, 2000). We used aggression data from a wild, fully marked population of 45 adult female mountain goats (731 aggressive events, see Table A3 in Côté, 2000). The nature of the interactions differs among the networks, with the manakin data representing affiliative interactions among males at leks, and the parakeet and mountain goat data representing agonistic interactions. The manakin and mountain goat data represent single-sex networks, and were both collected in the wild, whereas the parakeet network represents a mixed-sex network collected in a seminatural captive setting.

For the affiliative manakin data, we weighted network edges by the integer number of affiliative interactions among dyads. For the parakeet and mountain goat aggression data, we focused on total aggressiveness among dyads rather than winners of fights, and therefore transformed data from directed to undirected edges by summing the integer total of wins for each dyadic combination. For example, if individual A wins against individual B 10 times and B wins against A two times, the total aggressive events between A and B is 12. For all three data sets, therefore, the input file was a symmetric, undirected matrix of interactions among all dyads. We used the R package iGraph (Csardi & Nepusz, 2006) for all traditional network statistics and to plot network diagrams.

To illustrate how the new measures work at different social scales, we chose two individuals from each species, where one individual was a social specialist and the other was a social generalist at the smallest social scale. Additional criteria for choosing the comparator individuals were that they have high and equal binary degree, *D*, thereby differing only in the distribution of their edge weights. We first compared these two individuals from the same network (manakin, parakeet, mountain goat), and then compared those pairs with the parallel analysis from the other species. At a higher level of network organization, we compared the community structure of the manakins with that of the mountain goats. We also compared the observed metrics with those obtained from the outputs from 1000 simulations of a random network with the same number of nodes and edges. That is, for each replicate random network, we randomly redistributed the weights (integer units) across the observed edges. The examples are intended to provide concrete examples of the potential utility of the metrics and to inspire new ideas about the very different kinds of questions they allow us to address, rather than to serve as in-depth analyses of the systems themselves.

Variance in Edge Weights Between Exemplar Nodes

Manakins

At the node level, the two exemplar nodes illustrated in Fig. 1 are males with rather different histories. The ‘high-performing’ male M101 (Fig. 1a) was the beta for one of the most successful alpha males in the 18 years of the study. He maintained a strong, steady partnership with the alpha for the 3 years he was banded. In contrast, although the ‘low-performing’ male M104 (Fig. 1d) achieved high rank, he never formed a strong alliance with an alpha above him, nor with a beta below him once he achieved the alpha role. These two males differed sharply in edge weight metrics, despite both having 15 edges (links to other males). Whereas ‘low-

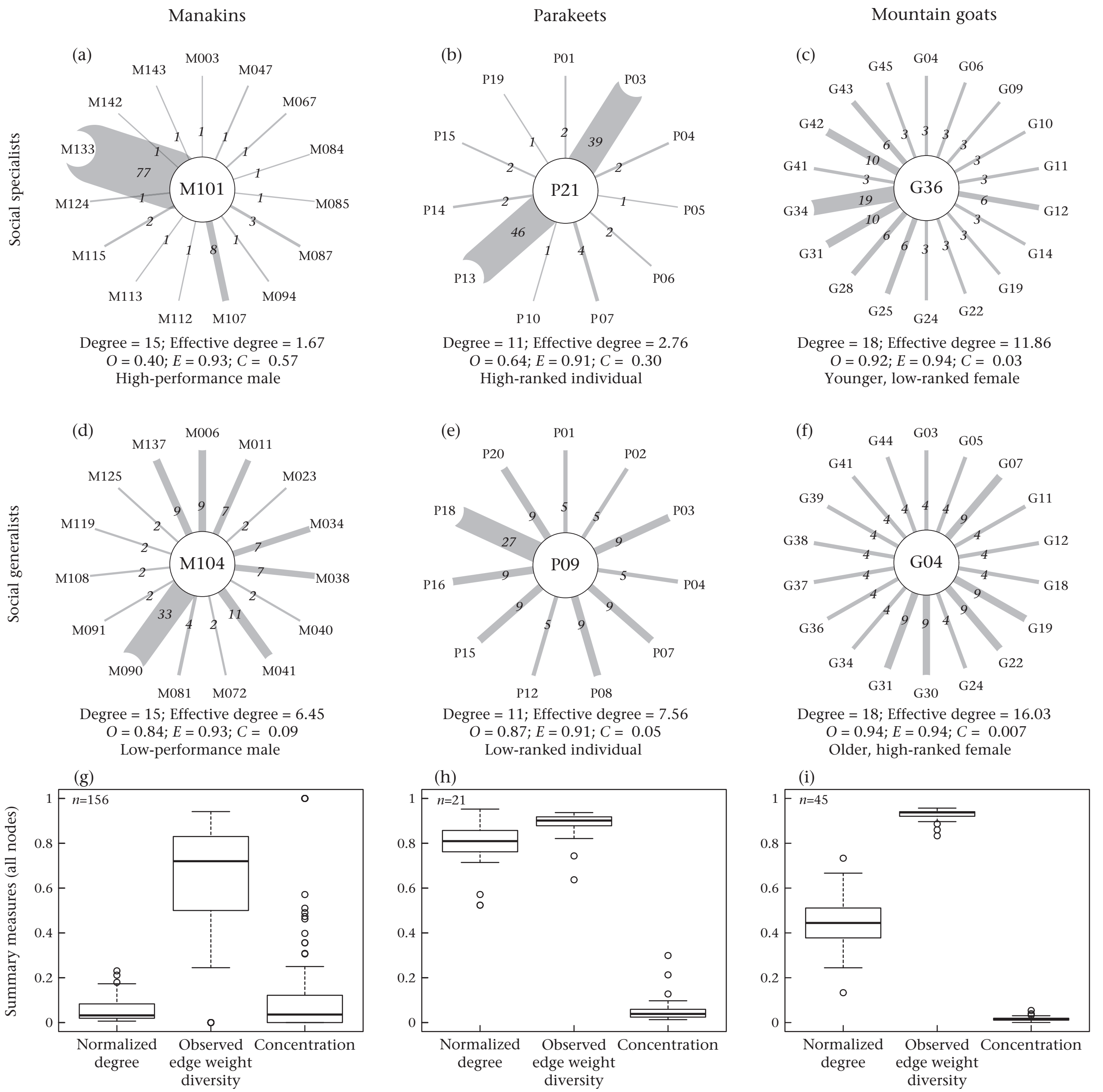

Figure 1. Social interactions at the node level in manakins, parakeets and mountain goats for two exemplar individuals per species (a–f) and summarized across all individuals in the networks (g–i). Network diagrams show only the edges for each focal individual (large node in centre of plots), with the width of edges proportional to the number of interactions, and the overall percentage of total interaction edge weight labelled in italics on each edge (thus, edge weights sum to 100). Panels (a) – (c) show examples of individuals that were social specialists, with lower effective degree, D_e, lower observed edge weight diversity, *O*, and higher concentration values, indicating that most interactions were focused on just a small subset of individuals. Panels (d) – (f) show examples of individuals that were social generalists, with higher D_e, higher *O* and lower concentration values, indicating that these individuals interacted more evenly across their associates. Panels (g) – (i) show the variation across all individuals in the group in the normalized binary degree (proportion of total individuals available that each individual interacted with), observed edge weight diversity, *O*, and concentration metrics for the manakin, parakeet and mountain goat networks. Normalized degree is a node-level metric whose mean is very similar to the network metric ‘density’, with low values indicating a sparse network.

performance' M104 was a social generalist, with a low node-level concentration ($c_{\mathrm{I}} = 0.095$, close to the mean $c_{\mathrm{I}} = 0.097$ for nodes in the 1000 replicate random networks) and a higher effective degree ($D_{\mathrm{e}} = 6.45$; $D/D_{\mathrm{e}} = 2.3$), the steadier beta partner, M101, was a social specialist, with a much higher node-level concentration ($c_{\mathrm{I}} = 0.57$) and a lower effective degree ($D_{\mathrm{e}} = 1.67$; $D/D_{\mathrm{e}} = 9.0$). At the egonet level, comparing the percentage of edge weight contained within ego-direct versus inter-alter showed that at a larger social scale, the two exemplar males were embedded in much more similar social environments at the egonet scale than at the node scale (Fig. 2a, d). However, the concentration of their egonets, c_{E}, still differentiated these two exemplar males. Consistent with differences in concentration at the node scale, male M104 had a lower concentration at the egonet scale ($c_{\mathrm{E}} = 0.03$) than did M101 ($c_{\mathrm{E}} = 0.17$), but the values were not as different as those at the node level.

At the community level, we detected eight communities using the fast-greedy algorithm of Girvan and Newman (2002); the communities in which the two exemplar males were embedded differed in the same direction as at the lower levels of organization. Modularity (Q of iGraph; Clauset et al., 2004) assesses how well a community-detection algorithm partitions a network into communities. The fast-greedy algorithm used here had a Q of 0.59, which was greater than or equal to the Q score of any of the community-detection algorithms implemented in iGraph. Social generalist M104 was embedded in a community with 35 males, $D_{\mathrm{e}} = 27.85$ ($D/D_{\mathrm{e}} = 2.9$) and $c_{\mathrm{c}} = 0.02$, at the lower end of c_{c} values. Social specialist M101 was embedded in a community with 11 males, $D_{\mathrm{e}} = 2.43$ ($D/D_{\mathrm{e}} = 8.2$) and $c_{\mathrm{c}} = 0.38$, the community with the highest c_{c} value. At the network level, the manakin network had a high ratio of D to D_{e} (6.7) and a fairly high value of F_{CN} (0.10). When we compared traditional network metrics for the two exemplar nodes, we found that eigenvector centrality was essentially identical for the two manakin males profiled in Fig. 1 (0.34 and 0.35), while their edge weight variance metrics differed dramatically. For the 156 male manakins, we found only very weak correlations between 'standard' network metrics and our concentration metric (correlation between betweenness and concentration = −0.06; correlation between eigenvector centrality and concentration = −0.1).

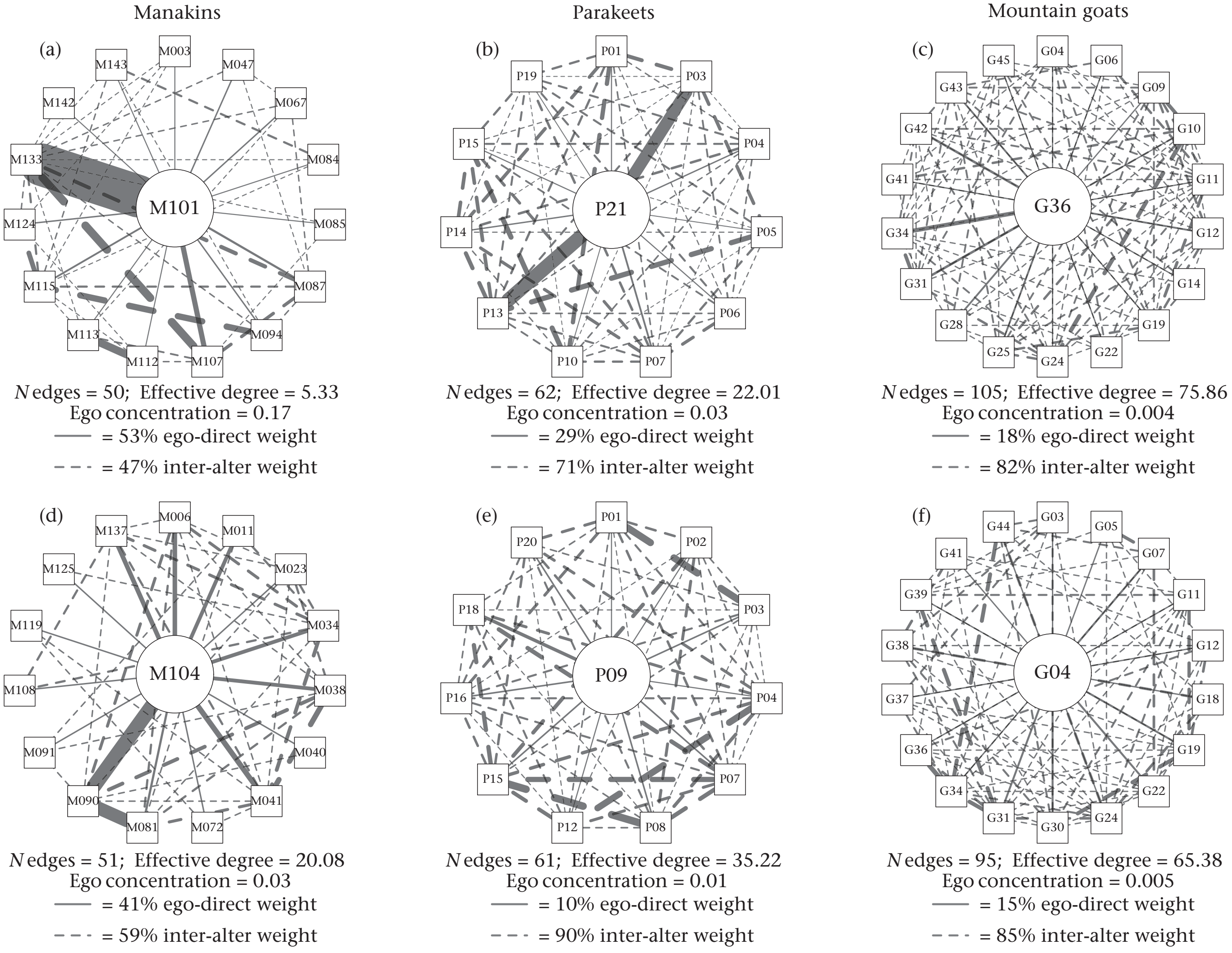

Figure 2. Social interactions at the egonet level in manakins, parakeets and mountain goats for two exemplar individuals per species. Egonets show all edges from ego individual (centre node) to alter individuals (square nodes) and also all edges between those alter individuals. Percentages of total edge weight contained in ego-direct edges (those from ego to alters) compared to inter-alter edges (edges from an alter to another alter) are listed below each network; the width of edges is proportional to the total edge weight contained in each egonet (sum of both ego-direct and inter-alter edge weights). Solid lines indicate ego-direct edges, dashed lines indicate inter-alter edges.

Parakeets

At the node level, the two exemplar nodes were parakeets that had the same number of edges (social associates, $D = 11$), but P21 had a high dominance rank and P09 had a low dominance rank within the group. At the node level, high-ranked P21 was a social specialist, with a lower effective degree (D_e) and higher concentration, c_I (Fig. 1b) while low-ranked P09 was social generalist, with a higher D_e and lower c_I (Fig. 1e). At the egonet level, almost 30% of the total edge weight for high-ranked P21 was contained in ego-direct edges (Fig. 2b), compared to only 10% for low-ranked P09 (Fig. 2e). As at the node level, P21's egonet had a lower D_e than P09's (Fig. 2b, e). Both birds had similar egonet concentrations (c_E), although c_E was slightly higher for P21 than for P09 (Fig. 2b, e), and this difference between concentrations was much smaller at the egonet level than at the node level.

At the community level, we detected two communities (Fig. 3) using the fast-greedy algorithm of Girvan and Newman (2002). The modularity Q score was 0.20, only slightly lower than the Q score of 0.21 for the optimal community-detection algorithm in iGraph (Csardi & Nepusz, 2006). The optimal algorithm is tractable only for very small networks, so we used the fast-greedy communities for greater comparability with the large 256-node manakin network. The two exemplar nodes were assigned to different communities. Social specialist P21 was part of a small community of four high-ranked individuals, while social generalist P09 was in the larger of the two communities. A greater proportion of the total edge weight (84% versus 64%, Fig. 3) was internal to the social generalist's large community compared to the proportion of internal weight in the social specialist's small community.

Mountain goats

At the node level, the two exemplar nodes illustrated in Fig. 1 were female mountain goats that had different ranks in the dominance hierarchy. Female G36 (Fig. 1c) was a low-ranked individual and female G04 (Fig. 1f) was a high-ranked individual (assessed with R package ‘steepness’, Leiva & de Vries, 2015). Based on the strong positive correlation between a female's age and rank (Côté, 2000), we can infer that high-ranked G04 was an older female while low-ranked G36 was younger. At the node level, we found that high-ranked G04 was a social generalist and had a lower c_I value, while low-ranked G36 was more of a social specialist and had a higher c_I value. In contrast, at the egonet level, the two exemplar mountain goats had almost identical c_E values (Fig. 2c, f) and a similar percentage of total edge weight contained in ego-direct edges (low-ranked G36 = 18%; Fig. 2c; high-ranked G04 = 15%, Fig. 2f) compared to inter-alter edges. At the community level, we detected six communities with the fast-greedy algorithm (Fig. 4b). The two exemplar nodes belonged to different communities: high-ranked G04 belonged to Community 2 (11 members) and low-ranked G36 belonged to Community 4 (10

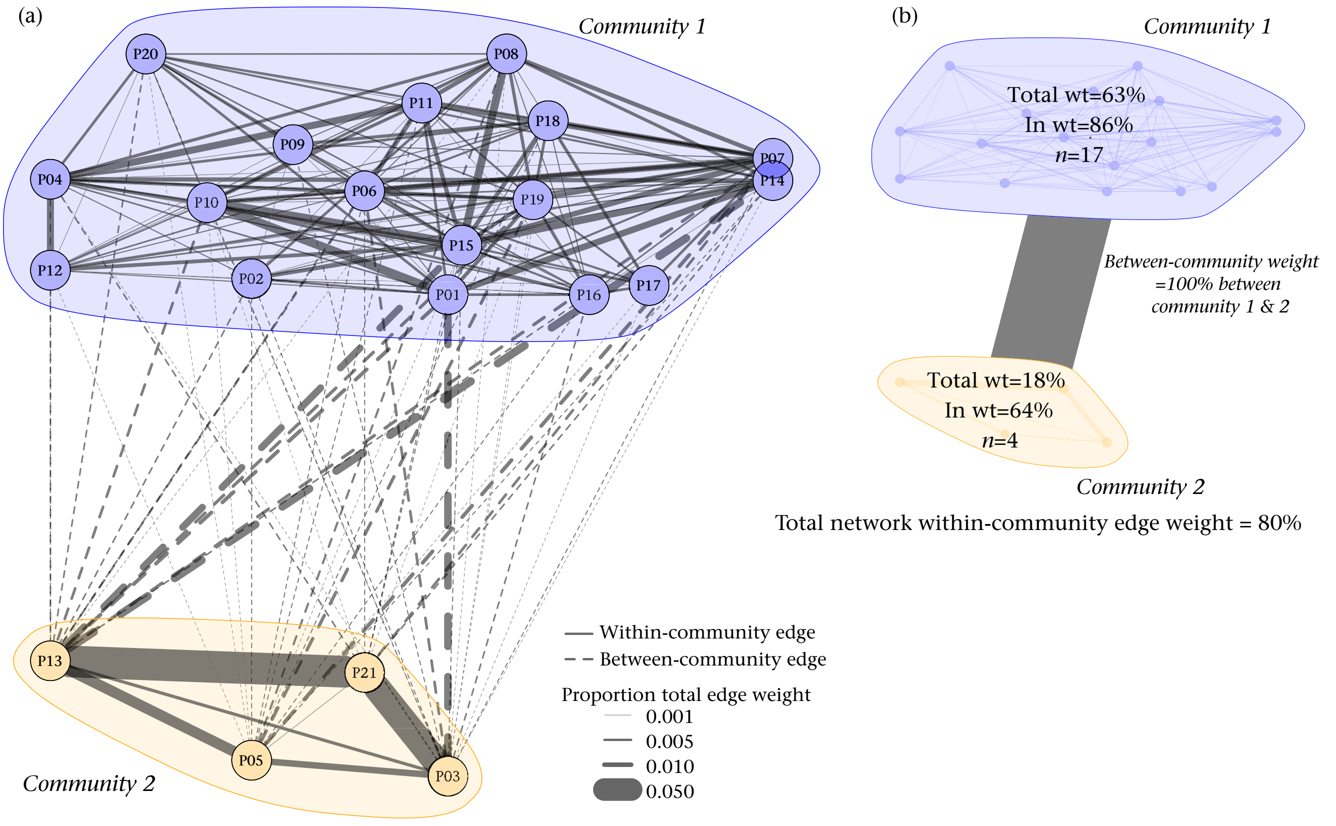

Figure 3. Community structure of parakeet aggression network showing (a) within-community (solid) and between-community (dashed) edges among individuals and (b) within- and between-community edge weights summarized by community. Edge weights in (a) were normalized across the whole network (edge weights sum to 1) to facilitate comparison, although in this case the weight units are all integers and have similar magnitudes. For example, the strongest edge occurred in Community 2 between individuals P13 and P21, and accounted for 7% of the total edge weight in the network. Labels in (b) show interactions summarized at the community level, (1) for the whole network, the total edge weight contained in ties from individuals within communities (Total wt), (2) the percentage of edge weight contained within each community versus directed towards a different community (In wt), and (3) the number of individuals in each community (n). Edge widths among communities are proportional to the percentage of total community outweight directed between communities. For the parakeets, because there were only two communities, 100% of between-community edge weight occurred between Communities 1 and 2.

members). The two communities contained similar percentages of within-community edge weights (Community 2 = 42%; Community 4 = 40%). Of the total between-community edge weights, 15% were between Communities 2 and 4.

Variance in Edge Weights Across Social Groups

In comparing group social patterns across the different species at the node level, we found that the parakeet aggression network was the most connected: individuals had the highest normalized degree (Fig. 1h), indicating that each parakeet interacted with a large proportion of available individuals. In contrast, the manakin network was the least connected (lowest normalized degree, Fig. 1g), indicating that each manakin interacted with only a small subset of potential partners. Observed edge weight diversity, *O*, was lowest and most variable in the manakin network and least variable in the mountain goat network (Fig. 1i). Concentration, c_I, values were highest and most variable in the manakin network, and lowest and least variable in the mountain goat network. The ratio of observed to random network c_I, was highest in manakins (27.6) and lowest in mountain goats (1.6). Taken together, patterns in *O* and c_I indicate that in mountain goats, most individuals interacted at low levels with several other individuals and spread interactions relatively evenly across these individuals, while some manakins interacted at high levels with a few individuals and concentrated their interaction effort on just a small subset of partners (low diversity of associations). Interestingly, we also found a flip in the interaction between dominance rank on the one hand and c_I and specialist versus generalist on the other hand, when we compared the parakeets and the mountain goats at the node level. In the parakeets, the high-ranked exemplar had a higher c_I and was a specialist, whereas the low-ranked exemplar was a generalist. In contrast, in the goats, the high-ranked exemplar had a lower c_I and was a generalist, whereas the low-ranked exemplar was a specialist, suggesting that rank does not necessarily covary with c_I; concentration may, therefore, capture aspects of an individual's social environment in ways independent of its rank.

At the scale of communities and of networks as a whole, we also found structural differences between the social groups. Using the full network of interactions among all individuals, and a fast-greedy community-detection algorithm (Girvan & Newman, 2002), we detected eight communities in manakins, two communities in parakeets and six communities in mountain goats. The goat network had the lowest D/D_e quotient and the manakins had the highest (1.4 versus 6.7). The species also differed in the proportion of edge weights contained within communities (directed from one community member to another in the same community) and among communities (directed from a member of one community to a member of a different community). The majority of edge weight in the manakin and parakeet networks was within communities (80% of total edge weight within communities for both species), while the majority of edge weight in mountain goats lay among communities (64% among-community edge weights).

The *F* statistics varied between the three networks at some hierarchical levels but not at others (Table 1). The most notable differences were in F_{IN} and F_{CN}. For F_{IN}, comparing edge weight variance at the individual (node) level to that of the network as a whole, the goat network had lower F_{IN} than did the manakin network (0.06 versus 0.23), as it did at the level of communities compared to the overall network expectation ($F_{CN} = 0.06$ versus

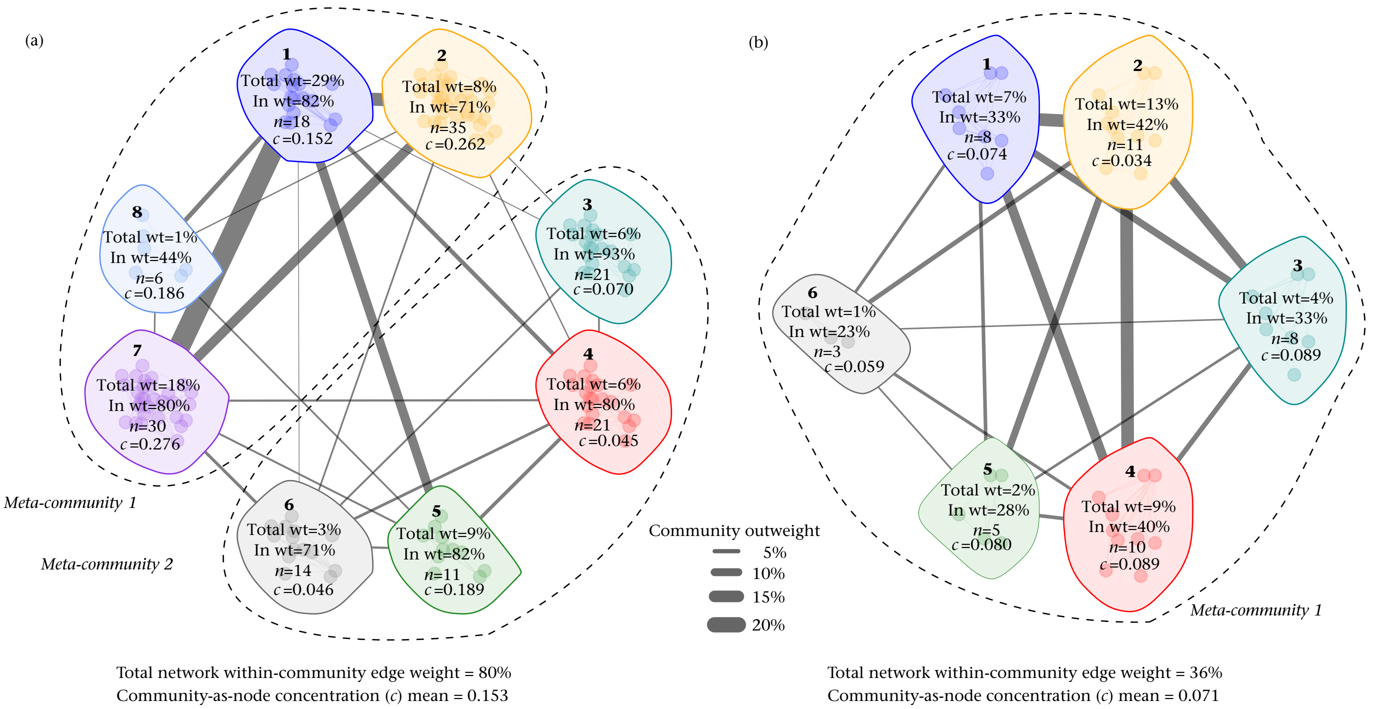

Figure 4. Comparison of edge weights within and between communities for (a) the manakin network and (b) the mountain goat network. Note that the 'nodes' are entire communities collapsed for visual simplicity (coloured polygons); one can then analyse the communities as though they were nodes, using the metrics presented in this paper. Labels indicate (1) community ID (bold numeral), (2) the percentage of the entire network's total edge weight contained in edges internal to each community (Total wt), (3) the percentage of edge weight internal to each community (In wt) versus directed to another community, (4) the number of individuals in each community (*n*) and (5) the concentration (*c*) of each community considering communities as individuals (nodes). Edge widths between communities are proportional to the percentage of total community outweight. For example, in the manakins (a), 26% of the total outweight in the network occurred in edges between individuals in Community 1 and Community 7; in the mountain goats (b), 15% of the total outweight in the whole network occurred in edges between individuals in Community 1 and Community 2. Meta-communities, comprising communities of communities, are outlined by dashed lines.

0.10). The greater modularity of the manakin network is consistent with their social organization in spatially distinct leks, with considerable flow of younger individuals among leks but little movement of high-ranking alpha and beta males (McDonald, 2010). In contrast, the female mountain goats were organized in a single herd, with a strongly linear hierarchy (Côté, 2000). That is, despite a partitioning into six communities, many intercommunity associations occurred in the goat network compared to the manakin and parakeet networks, as further evidenced by a lower modularity ($Q = 0.16$) than the manakins ($Q = 0.59$) or the parakeets ($Q = 0.20$). The parakeets differed from both other networks. In terms of D/D_e quotient (2.8), they were intermediate, but their c_N (0.01) was comparable to that of the manakins, suggesting that differences in edge weight distributions are not simply a product of a comparison between edge types that were affiliative (the manakins) versus agonistic (the parakeets and goats).

Meta-community Analysis: Communities Treated as Nodes

At the community scale, we also quantified relationships among communities by considering the communities themselves as nodes. We used the fast-greedy community-detection algorithm on the full network of interactions among individuals, then pruned those interactions to consider just the edges occurring between communities and pooled those edges by community. These summary edges form a community-by-community interaction network where edge weight indicates the proportion of all between-community edge weights that occurred between specific communities (Figs 3b and 4). For the manakins and goats, both of which had more than two communities overall, we then analysed the communities as though they were nodes, to quantify concentration (c, where the 'individual' nodes are communities) and other edge weight variance metrics. The eight manakin communities had higher network-level communities-as-nodes concentration ($c = 0.08$) than did the six mountain goat communities ($c = 0.03$; Fig. 4). Manakin Communities 2 and 7 had the highest c values and were the most socially specialized, while Communities 4 and 6 had the lowest values and were the most socially generalized (Fig. 4a). In the mountain goats, there was a smaller range and less overall variability of c values than in the manakins (Fig. 4b). Manakin communities (viewed as nodes) had an overall higher mean c than mountain goats, indicating that at the community level, manakins focused between-community edges on particular other communities while the mountain goats were more generalized in how they directed between-community interactions. To assess higher-level meta-community structure, we used the fast-greedy community-detection algorithm on the communities-as-nodes. The eight manakin communities then grouped into two different meta-communities, while the six mountain goat communities formed a single network-encompassing meta-community (Fig. 4).

DISCUSSION

Our adaptation of metrics from population genetics provides new ways to quantify the diversity and partitioning of variance in relationship strength across social scales in social systems. Even when individuals have very similar network metrics using traditional approaches, our metrics uncover functionally important differences among nodes and across higher levels of network organization (egonets, communities, meta-communities and entire networks). These new metrics provide a method for quantifying sociality in ways that can complement, but be orthogonal to, traditional approaches. Major features of the adaptation of the metrics from population genetics to network systems include that allele frequency becomes edge weight proportion, observed gene diversity becomes observed edge weight diversity (O), expected gene diversity becomes expected edge weight diversity (E), effective number of alleles becomes effective degree (D_e) and Wright's F statistics become edge weight concentration coefficients ($c_{x\ (x\,=\,\mathrm{I,\ E,\ C,\ N})}$) and network F statistics (F_{LH}). We have highlighted areas where analogies to population genetics must be rethought for application to networks, such as sample size correction by edge weight rather than population size (N), the nonindependence of edge weights (because they are shared by two nodes) and network-specific levels of hierarchical organization (egonets, communities, meta-communities).

Applying the Edge Weight Proportions/Variance Approach to Bond Models

Although most applications of social network analysis implicitly or explicitly model the flow of information (sensu latu, to include resources, signals, etc.), the metrics proposed here also apply when the emphasis is on the structure of, not just the flow across, the network — what Borgatti and Halgin (2011) termed 'bond' models, as opposed to 'flow' models. In bond models, position matters, because of the differing partner options available to actors (nodes) purely because of their positions within the network. For nice examples of how position and structure can matter, even when nothing 'flows' through the network, see Figure 6 in Borgatti and Halgin (2011) or Figure 1 in Bonacich (2007), which discusses aspects of the power centrality metric (implemented in the iGraph social network analysis package in R).

Table 1

Comparison of network-level metrics for the three exemplar species and the mean for 1000 corresponding random comparators, where weights were randomly redistributed over the observed edges

	Long-tailed manakin		Monk parakeet		Mountain goat	
	Observed	Random	Observed	Random	Observed	Random
Nodes	156	156	21	21	45	45
Total interactions	1938	1938	838	838	721	721
Density	0.05	0.05	0.83	0.83	0.45	0.45
Communities	8		2		6	
Weight skew	8.5	0.7	5.5	0.4	2	1.3
D/D_e	6.7	1.2	2.8	1.2	1.4	1.2
Concentration	0.009	0.0003	0.011	0.001	0.0008	0.0005
F_{IE}	0.34	0.16	0.13	0.07	0.1	0.1
F_{IN}	0.23	0.14	0.13	0.06	0.06	0.06
F_{CN}	0.1		0.07		0.06	

D = degree; D_e = effective degree; F subscripts I, E, C, N = level of interest: individual node, egonet, community or network as a whole.

Disease transmission

As one example of how our proposed metrics could provide novel insight, consider a disease spreading through a network of individuals. Two individuals in this network have equal degree, D, and both could potentially serve as spreaders of the disease. Imagine that Node 1 has a very skewed weight distribution (high concentration, c_I, low effective degree, D_e). It will likely spread mostly to the individual with whom it associates most (edge with highest weight). In contrast, imagine a Node 2, with even weight distribution (low c_I, high D_e); it could be a 'super-spreader' because it could infect several different nodes (especially if the distributed weight were above some threshold for transmission). Note, however, that depending on the transmission threshold, a node with higher c_I (but whose few heavy edges exceed the transmission threshold) might be a better spreader than a node with lower c_I, none of whose diffuse weights exceeds the transmission threshold. Thus, degree, per se, may be uninformative for predicting the spread potential of a node. The interplay between effective degree and transmission thresholds seems likely to provide a fruitful avenue for exploring and quantifying disease dynamics. Simultaneous assessment of concentration, c, effective degree, D_e, and the transmission threshold should synergistically enhance assessment of the probability and speed of disease transmission over networks.

Learning and cultural transmission of information

Like disease transmission, information transfer and learning are flow processes, and variance in edge weights ('pipe widths') seems likely to be critical to a deeper understanding of the spread of information. Many of the metrics proposed here are easily implemented quantitative tools that should enable comparisons within and among networks. From contact or association patterns, one could make inferences about information spread, not just from the perspective of individuals spreading information or actively learning, but also from the perspective of bystanders or observers (Chase, 1980; Oliveira, McGregor, & Latruffe, 1998). When observation of others is important in spread through a flow network, the metrics we propose here should be useful in predicting how bystanders invest their observational effort, and to which individuals they pay attention.

Social complexity

Many biologists are interested in the presence (and extent) of social complexity in animal societies. Social complexity in animals has been defined in many different ways, and no single generalized approach to quantifying social complexity has yet emerged. Most definitions focus on either the number of differentiated relationships (e.g. Bergman & Beehner, 2015; Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017; Freeberg, Dunbar, & Ord, 2012; Seyfarth & Cheney, 2008) or the hierarchical organization of the society (e.g. Bergman & Beehner, 2015; Couzin, 2006; Richerson & Boyd, 1999; Turchin & Gavrilets, 2009).

The new metrics we present here can be used to quantify aspects of both diversity and hierarchical structuring. First, our diversity metrics can be used to quantify the differentiation of relationships within a particular social context (e.g. aggression or affiliation). Next, these diversity metrics can be compared across social scales to quantify the extent to which diversity of edges changes at different levels of social organization. Our network F statistics can be used to assess and compare hierarchical structuring among different types of animal societies, independent of cognitive ability. Just as in Wright's (1978) population genetics F statistics, F_{IS} looks at individual heterozygosity compared to subpopulation heterozygosity, and F_{ST} looks at subpopulation heterozygosity compared to that of the total population, so one could look at weight and degree differentiation among nodes within a community (subgraph) and among communities and meta-communities. Note, however, that although diversity and relationship differentiation and hierarchical organization are widely thought to be indicative of some aspects of social complexity, there is no general consensus on how to measure social complexity.

Evolution of cooperation

Recent theoretical work (Allen et al., 2017; Ohtsuki, Hauert, Lieberman, & Nowak, 2006) suggests that strong pairwise ties may be key to the evolution of cooperation. Ohtsuki et al. (2006) modelled the evolution of cooperation among unrelated individuals by reconfiguring Hamilton's result for cooperation through kin selection, $b/c > r$ (that is, if the benefits, discounted by the costs, are greater than the relatedness). Their conclusion was that $b/c > k$ favours cooperation among unrelated individuals on a network, where k is the degree (D, number of edges). Low degree (fewer interactor partners) favours cooperation. Furthermore, Allen et al. (2017), in an explicitly network framework, showed that strong pairwise ties favour the evolution of cooperation on any population structure. Male long-tailed manakins exhibit features of both models for the evolution of cooperation. We have shown that skewed edge weight distributions mean low effective degree, D_e, for some individuals, even if their binary degree is high. Alpha–beta cooperators in long-tailed manakins have high degree but low effective degree, D_e, because the huge majority of their interactions are with their partner, and very few with other males (McDonald & Potts, 1994). Even more importantly, the key feature of the social structure of male long-tailed manakins is the lifelong buildup (McDonald, 2010, 2014) of strong ties between alpha and beta males.

Conclusions

Our proposed approach, which explicitly considers the diversity and variance of edge weights, provides novel methods for analysing aspects of sociality in groups. These metrics expand the existing toolbox for quantifying and comparing sociality at the node, egonet, community, meta-community and global network scales. One challenge for future work is to expand these methods to directed networks, because many social networks will be directed as well as weighted. For example, dominance and agonistic interactions are usually inherently directed (McDonald & Shizuka, 2013). Incorporating both directedness and weighting of edges can be analytically challenging and relatively few metrics exist that take full advantage of both features. We hope that the utility of our proposed metrics, combined with the current high level of interest in analysing and comparing aspects of sociality and social network topology, will stimulate further quantification of structural features of social relationships in ways that explicitly consider edge weights, variability in relationship strengths and a comparative perspective across social scales.

Acknowledgments

D.B.M. acknowledges the useful feedback from the University of Wyoming Social Network Working group over the years, particularly Dai Shizuka and Shannon Albeke. E.A.H. was supported by a postdoctoral fellowship from the Arizona State University–Sante Fe Institute (ASU–SFI) Center for Biosocial Complex Systems, with additional funding from the Santa Fe Institute. We thank two anonymous referees for thorough and detailed suggestions that produced a stronger manuscript. D.B.M. also thanks Daniel Rubenstein for organizing the symposium from which this paper took stronger shape.

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