



Commentary

Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges



Damien R. Farine*

Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford, U.K.

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Grouping is a very common outcome of selection that operates on individual animals. Largely considered to be driven by immediate benefits, such as avoiding predators, animal groups often consist of individuals that are phenotypically more similar than expected from the population distribution. This suggests that the distribution and fitness of phenotypes may be shaped by multiple levels of selection operating along different axes of behaviour. Thus, quantifying assortative mixing, or the measure of association between similar individuals in social networks, should be a key component of the biologist's toolbox. Yet, assortment is rarely tested in animal social networks. This may be driven by a lack of tools for robust estimation of assortment, given the reliance of current methods on binary networks. In this paper, I extend existing approaches that calculate the assortativity coefficient of both nominal classes and continuous traits to incorporate weighted associations. I have made these available through a new R package 'assortnet'. I use simulated networks to show that weighted assortment coefficients are more robust than those calculated on binary networks to added noise that could arise from random interactions or sampling errors. Finally, I demonstrate how these methods differ by applying them to two existing social networks estimated from wild populations, exploring assortment by species, sex and network degree. Given the parallel theoretical developments of the importance of local social structure on population processes, and increasing data on social networks being collected in free-living populations, understanding phenotypic assortment could yield significant insight into social evolution.

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Group living is frequently considered to be an adaptive strategy primarily driven by ecological factors (Krause & Ruxton, 2002). However, the fitness benefits accrued by individual participants may vary not just with group size, but also as a function of its phenotypic composition. For example, the predator confusion effect relies upon individuals being physically identical to other members of their group (Landeau & Terborgh, 1986); that is, they gain fitness benefits through being phenotypically assorted by size, shape and colour. Alternatively, individuals may reduce resource competition by associating with others that are specialized on different niches, which may lead to disassortment by species as seen in mixed-species foraging groups (Buskirk, 1976). In this way, repeated nonrandom interactions between individuals of similar or different phenotypes (or genotypes) can have profound evolutionary implications (West-Eberhard, 1979; Wolf, Brodie, & Moore, 1999).

Social network analysis is a quantitative approach that captures the emergent population-level properties of repeated interactions between individuals (Croft, James, & Krause, 2008; Krause, Croft, & James, 2007; Whitehead, 1997, 2008). Numerous reviews have suggested that this method will provide an accessible way of estimating the evolutionary consequences of social processes (Croft et al., 2008; Farine, Garroway, & Sheldon, 2012; Krause et al., 2007; Wey, Blumstein, Shen, & Jordan, 2008). Yet, one of the simplest and most consequential social network measures, assortative mixing (Newman, 2002a), has been relatively unexplored in animal behaviour, particularly outside of fishes (see Croft et al., 2012; Croft et al., 2009). This is surprising given that it is generally accepted that local social structure within populations can influence individual fitness (for example through indirect fitness, Hamilton, 1964).

Assortment can arise through either active or passive processes. Active assortment typically arises from attraction of individuals to others that are similar. For example fish will often form shoals of similarly sized fish of both single and multiple species (Hoare, Krause, Peuhkuri, & Godin, 2000; Hoare, Ruxton, Godin, & Krause, 2000; Krause, Butlin, Peuhkuri, & Pritchard,

* Correspondence: D. R. Farine, Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

2000), potentially to increase predator confusion (Krause & Ruxton, 2002). Active attraction of behavioural phenotypes, such as degree assortment (strong connections between similarly gregarious individuals), is thought to be critical in mediating processes in networks such as the spread of disease (Ashby & Gupta, 2013) or the evolution of cooperation (Pusch, Weber, & Porto, 2008). Active avoidance may also occur, resulting in disassortment between interacting individuals. This is likely to be common in systems in which different classes, such as males and females, preferentially associate together, as in Tasmanian devils, *Sarcophilus harrisii* (Hamede, Bashford, McCallum, & Jones, 2009). In contrast to active attraction, assortment can arise from passive processes such as differences in habitat use strategies. For example, in some taxa individuals at different life stages commonly occupy different niches, resulting in greater spatial overlap (therefore social association) between similar conspecifics (Holyoak, Casagrandi, Nathan, Revilla, & Spiegel, 2008).

A common method to measure assortment is the assortativity coefficient (Newman, 2002a, 2003). This provides an index to measure whether associations are typically between phenotypically similar or dissimilar individuals. Although Newman's assortativity coefficient has been used in a number of studies (Aplin et al., 2013; Green, Gregory, & Munro, 2009; Hamede et al., 2009; Leu, Bashford, Kappeler, & Bull, 2010; Lusseau & Newman, 2004; Lusseau et al., 2006; Manno, 2008; Mourier, Vercelloni, & Planes, 2012; Wiszniewski, Lusseau, & Moller, 2010; Wolf, Mawdsley, Trillmich, & James, 2007), its current restriction to binary networks may have hampered wider uptake in animal studies. This is potentially because association data in animal social networks are more frequently inferred (A was seen with B) than known (A directly interacted with B) as is more typical in human networks (Croft, Madden, Franks, & James, 2011; Franks, Ruxton, & James, 2010). As a result, this increases the relative influence of sampling error, or noise, in the data. Thus, binary network-based assortment measures could be underestimating assortment in animal studies. For example, imagine a network in which individuals found in stable groups of six always have the same five associates (they do not have an edge to themselves), and all have the same phenotype. If one sample randomly captures two groups together (through either observer error or otherwise), then each individual in these two groups will have five edges connected to associates of the same phenotype, and six connected to associates with a different phenotype. If both groups are sampled 50 times, then a weighted network will capture the fact that the proportion of edge weights to the nonsimilar phenotypes will be very low. In contrast, a binary network does not make this distinction. Consequently, rare chance events can have significantly greater influence on the perceived social structure in a binary network by being given the same weight as all other observed edges.

One approach that has been suggested for overcoming the limitations of binary networks, such as in the example described above, is to construct these after first thresholding (removing or setting to zero) edges above or below a certain value (James, Croft, & Krause, 2009; Lusseau, Whitehead, & Gero, 2008). In general, biologists typically repeatedly sample populations in order to infer the social network (Franks et al., 2010; Lusseau et al., 2008); hence thresholding is one way of maintaining some of the information contained in the edge weights that would otherwise be thrown away (Croft et al., 2011; Lusseau et al., 2008). The process of then converting networks to binary is generally by directly replacing nonzero edge values with one. For example, Newman's original assortativity coefficient is estimated based on the number of edges that occur between different classes or phenotypes. By counting

edges of each type (where each edge adds 1 to the count), this process is functionally equivalent to having all edge weights converted to equal one.

To assess the biological importance of a network measure, one needs to specify a relevant null model (Gotelli & Graves, 1996). Yet, it remains unclear what constitutes an appropriate method for building null models to assess the significance of the assortativity coefficient in an observed network. In most studies using Newman's assortativity coefficient, authors have reported the standard error calculated from jackknife simulations. However, Croft et al. (2011) highlighted the need for care to be taken when testing significance. They, and other authors (Bejder, Fletcher, & Brager, 1998; Whitehead, 1999; Whitehead, Bejder, & Ottensmeyer, 2005), suggested that null models for social networks should account for potential sampling biases and nonindependence in the data. In the case of assortment, this suggests that it may be inappropriate to assume that the null expectation is a coefficient index of 0 if the sampling method could have introduced some biases. Here there are two generally accepted alternatives that can be used. The first approach for resolving this is a node-based permutation, in which the association matrix is repeatedly randomized by shuffling the rows and columns while keeping the node labels fixed (for example in Aplin et al., 2013). The second method shuffles the data stream in order to control for individual gregariousness and group size distribution. Both these methods have been extensively described in the context of testing hypotheses for social networks (Bejder et al., 1998; Croft et al., 2011; Manly, 1997; Whitehead, 2008; Whitehead et al., 2005). However, they have rarely been compared using empirical data in the context of assortativity.

In this paper, I have the following aims. (1) I first present a method to incorporate weighted network edges into the Newman (2003) assortativity coefficient. Although this approach was derived for continuous measures (Leung & Chau, 2007), I extend it by also deriving the weighted-edge coefficient for nominal node values. To my knowledge, this method has never been used in animal social networks, so I developed an R (*R Development Core Team*, 2013) package 'assortnet' in order to promote its wider use. (2) I then quantify the relative performance of the different approaches of calculating assortativity by assessing the robustness of using weighted, thresholded and binary networks to sampling error. Using simulations, I show that indices incorporating weighted edges are significantly more robust to sampling noise than those using binary edges. (3) Using networks from two recently published studies (Farine et al., 2012; Farine & Milburn, 2013), I then investigate assortment according to different phenotypic traits and demonstrate how weighted and binary measures differ. Given the potential for random interactions to have a strong influence on binary network structure, I predicted that a weighted assortment measure is likely to provide a more robust estimate of assortment when compared to a binary assortment measure applied to the same network. (4) Finally, I compare the three common approaches for testing significance in the assortment measure to determine whether there are incompatibilities between these approaches.

METHODS

Incorporating Edge Weight into Assortment Measures

Newman (2003) defined the assortativity coefficient for nominal classes of individuals as:

$$r_d = \frac{\sum_i e_{ii} - \sum_i a_i b_i}{1 - \sum_i a_i b_i} \quad (1)$$

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