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Commentary

The role of weighted and topological network information to understand animal social networks: a null model approach

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Network null models are important to drawing conclusions about individual- and population-(or graph) level metrics. While the null models of binary networks are well studied, recent literature on weighted networks suggests that: (1) many so-called ‘weighted metrics’ do not actually depend on weights, and (2) many metrics that supposedly measure higher-order social structure actually are highly correlated with individual-level attributes. This is important for behavioural ecology studies where weighted network analyses predominate, but there is no consensus on how null models should be specified. Using real social networks, we developed three null models that address two technical challenges in the networks of social animals: (1) how to specify null models that are suitable for ‘proportion-weighted networks’ based on indices such as the half-weight index; and (2) how to condition on the degree- and strength-sequence and both. We compared 11 metrics with each other and against null-model expectations for 10 social networks of bottlenose dolphin, *Tursiops aduncus*, from Shark Bay, Australia. Observed metric values were similar to null-model expectations for some weighted metrics, such as centrality measures, disparity and connectivity, whereas other metrics such as affinity and clustering were informative about dolphin social structure. Because weighted metrics can differ in their sensitivity to the degree-sequence or strength-sequence, conditioning on both is a more reliable and conservative null model than the more common strength-preserving null-model for weighted networks. Other social structure analyses, such as community partitioning by weighted Modularity optimization, were much less sensitive to the underlying null-model. Lastly, in contrast to results in other scientific disciplines, we found that many weighted metrics do not depend trivially on topology; rather, the weight distribution contains important information about dolphin social structure.

The social network paradigm is increasingly being used to study the behavioural ecology of social animals. It holds the promise of expanding the field from investigations about the presence and fitness consequences of associations to understanding the pattern of associations, including how network structures persist over time or serve ecological functions. For example, whereas researchers have plenty of ideas why animals may be social (e.g. for antipredator defence, foraging) and can demonstrate that one's position in the network can lead to higher fitness (Stanton & Mann, 2012), it is more controversial to posit functional importance to structural properties of networks themselves. Consider bottlenose dolphins *Tursiops* spp., where patterns such as triangle-closure, assortativity by sociality, and the presence of ‘social brokers’ between different subgroups are features that are more than just individual-level tendencies to have a certain number of associates. Hypotheses about the ecological function of such ‘social structure’ are few and tentative (Pinter-Wollman et al., 2014), such as facilitating information transmission (Allen, Weinrich, Hoppitt, & Rendell, 2013; Lusseau, 2003). Behavioural ecology remains significantly challenged by the difficulty of defining and measuring social structure. Here, we try to identify which network metrics may be informative about dolphin social structure, and which are redundant to individual-level differences in sociality, such as individual

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differences in 'degree' (number of associates) and 'strength' (sum of weights of associates).

We employ a null-model approach: to calculate expectations of weighted network metrics while conditioning on individual-level properties, and compare such expectations to the observed metrics. For example, if we observe a network and accept its empirical degree-sequence (the number of connections each individual has in the network), then how are we to interpret other network metrics and judge whether they provide evidence of an underlying organizing structure? What metric values are likely even when there are no true underlying structures like 'clusters' or true organizing principles like 'assortativity'? It is by comparing metric values to their null-model expectations that allows us to find potentially meaningful metrics that actually measure aspects of higher-order social structure, or whether metrics are merely redundant to individual-level attributes.

Despite the simplicity of the null-model approach, there is little consensus on how to calculate expectations of network metrics. Two challenges emerge: (1) one must decide what properties to condition upon (e.g. strength-sequence, degree-sequence, both or others); and (2) one needs a way to calculate expectations without biasing results. Behavioural ecologists primarily address these challenges by conditioning on aspects of survey design, observation error and sociality (Whitehead, 2008), and primarily use permutation methods to calculate expectations under random associations (Bejder, Fletcher, & Bräger, 1998). Outside of behavioural ecology, there is a growing suite of 'random-graph' algorithms (Ansmann & Lehnertz, 2011; Leskovec, Chakrabarti, Kleinberg, Faloutsos, & Ghahramani, 2010; Prettejohn, Berryman, & McDonnell, 2011; Serrano, Boguñá, & Pastor-Satorras, 2006; Watts & Strogatz, 1998) which emphasize core properties such as the degree-sequence, strength-sequence, network size and density; they have shown that unless such properties are held constant across random-graphs, then any conclusions about network properties will just reflect variation in the degree-sequence, strength-sequence, network-size, etc. There is a near consensus about the need to condition on the degree-sequence for binary networks, but the matter is more controversial for weighted-networks, and one's conclusions are sensitive to such conditioning (Garlaschelli & Loffredo, 2009; Mastrandrea, Squartini, Fagiolo, & Garlaschelli, 2014).

This paper follows in the spirit of Garlaschelli and Loffredo (2008), to calculate metric expectations based on null models that assume only basic individual-level properties, and to do so by generating an 'ensemble' of random networks based on the Exponential Random Graph formulation. In contrast, our equations are valid for proportion weighted-networks, $w_{ij} \in [0,1]$ used in behavioural ecology (Cairns & Schwager, 1987). An advantage of this method is its principle of 'maximum entropy' to produce an ensemble of networks that makes the fewest assumptions, thereby ensuring that we have randomized all other topological and weight patterns that could be misconstrued as social structure. The method is similar to permutation-based and random-graph algorithms in that they offer null models conditioned on simple assumptions. However, permutation-based and random-graph algorithms do not necessarily guarantee that their ensembles do not have structural correlations or biases that are mere artefacts of the randomization algorithm (Garlaschelli & Loffredo, 2008).

We specified three different null models that are constrained to the degree-sequence (Topology Null Model, TNM), strength-sequence (Weighted Null Model, WNM), and both (Mixed Null Model, MNM) for proportion-weighted networks. We derive the probability distributions for the TNM, WNM and MNM and apply them to 10 years of association data from a well-studied population of bottlenose dolphins, *Tursiops* cf. *aduncus*, in Shark Bay, Western Australia (Mann, Stanton, Patterson, Bienenstock, & Singh, 2012).

Three aims of this study are:

(1) to compare how well observed individual-level network metrics correspond to null-model expectations, for three null models;
(2) to compare averages of whole network metrics to their null-model expectations, especially as a function of network size N (an ongoing controversy in network science; e.g. see Anderson, Butts, & Carley, 1999);
(3) to compare how inferences about network community structure differ according to the null-model used via Modularity optimization (Squartini & Garlaschelli, 2011).

For aims 1 and 2, we focus on 11 popular node-level metrics used in analyses of animal societies, such as clustering, affinity, centrality, dispersion and connectivity.

The method of Garlaschelli and Loffredo (2009) caused considerable upset in other disciplines. For example, Garlaschelli and Loffredo (2009) discovered that some weighted measures 'inherit' trivially from topological features and called for 'a systematic redefinition of weighted network properties', while Mastrandrea et al. (2014) noted that 'the strength sequence is in general uninformative about the higher-order properties of the network'. The implications for behavioural ecologists are that: (1) many weighted-network metrics may not depend on weights per se and actually depend on the underlying binary, topological patterns; and (2) that many metrics of higher-order structure are not significantly different from (and often highly corrected with) the values one would expect from networks with only individual-level constraints (degree and/or strength).

The above claims were supported over a broad range of networks, such as food-webs, online social networks and financial/trading networks. If the conclusions of Garlaschelli and Loffredo (2009) and Mastrandrea et al. (2014) generalize to animal social networks, then it would be a setback to behavioural ecology studies based on network metrics. For example, if clustering and affinity metrics were merely redundant to individual-level attributes, and did not measure higher-order properties as intended, they would produce misleading conclusions about 'social structure', as defined as higher-order structure that is more than the sum of individuals (Holland & Leinhardt, 1979; Faust, 2006). However, the methods and insights from integer-weighted networks cannot be accepted naively for proportion-weighted networks. We show that the eastern gulf Shark Bay dolphins stand as a contrary case to the many and varied networks considered by Garlaschelli and Loffredo (2009) and Mastrandrea et al. (2014).

METHODS

Data

Our data source is a 31-year long-term study of over 1500 individually identified bottlenose dolphins resident in the eastern gulf of Shark Bay, Western Australia (Mann et al., 2012). Associations among individual dolphins were estimated from opportunistically encountered groups during boat-based surveys, using a 10 m chain rule to define in-situ group membership (Smolker, Richards, Connor, & Pepper, 1992). We truncated the data to include noncalf individuals encountered at least five times each year within a constant spatial and temporal domain. The constant space-time domain was evaluated in the following way: (1) we included surveys that occurred between May and November; (2) per year, we calculated a minimum convex hull (MCH) which enveloped all georeferenced encounters; (3) we used the spatial intersection of all 10 per-year MCHs to define a small region of