Research questions should drive edge definitions in social network studies

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Recently we published a study (Castles et al., 2014) that compared social network metrics that were created from two methods for defining connections (edges) among wild baboon (*Papio ursinus*) individuals (nodes): proximity and interactions. We found that in many (but not all) cases individuals' positions in the proximity networks were not predictive of their positions in the interaction networks and we cautioned researchers about assuming that one is a proxy for the other, which is frequently done in social network studies (e.g. Carter, Macdonald, Thomson, & Goldizen, 2009). In a recent Forum article, Farine (2015) outlines several assumptions that researchers make about how to define edges among individuals that may affect the results of social network studies, before presenting new empirical findings from wild thornbills (genus *Acanthiza*) that he concludes contrast with ours. We are excited that our research has generated such interest, and this new article adds to a growing body of empirical studies that consider sampling issues in social network studies (Castles et al., 2014; Hobson, Avery, & Wright, 2013; Lehmann & Ross, 2011; Madden, Drewe, Pearce, & Clutton-Brock, 2011; see H. Whitehead, 2008 for a comprehensive summary of sampling considerations). We agree that the 'gold standard' in social network studies should be for researchers to incorporate multiple networks using different methods to determine edges into their analyses. However, while Farine usefully highlights assumptions that are important to consider when choosing how to collect and analyse one's network data, several aspects of his article require further consideration before we extend the discussion to broader issues in social network studies.

In the first case, Farine (2015) presents empirical data from mixed species flocks of thornbills, collected over a 6-week period, in which there are correlations between individuals' network positions in proximity and interaction networks. Farine states that this pattern was in contrast to our general conclusion, and so suggests that our findings are not generalizable across species and that in some cases proximity can be used as a proxy for interactions. We feel the first assertion is misplaced, and we caution against the second. Our results were in agreement with those of the thornbills in some years for some social network metrics, where we also found correlations between some proximity and interaction methods (see Fig. 3 and supplementary material in Castles et al., 2014). However, the correlation between the two methods was not found in other years. Thus, our results from two study groups over three years suggest that findings from one time period may not be generalized to the same group(s) in a different time period, let alone to other groups of a particular study species. Had we measured the social network in one particular year (or group) and found a correlation between the methods, we may have erroneously concluded that we can use proximity as a proxy for interaction in all future studies. To return to Farine's first assertion, we are not seeking to generalise patterns from our study but rather the principle that consistency between groups/years should not be assumed until it has been demonstrated. Thus, with respect to Farine's second assertion, we would reiterate our conclusion from Castles et al. (2014): because of the dynamic nature of social networks, we recommend that researchers take care when assuming that proximity can be a proxy for interactions. This is distinct from the suggestions that (a) proximity can never be a proxy for interactions and (b) proximity cannot be used to create social networks—generalisations that we do not advocate.

In the second case, Farine (2014) explores some methodological considerations that were not addressed in our study. We focussed on one decision a researcher could make at the data collection stage, specifically, the behaviours that could be used to create edges in a social network. Yet, as we mentioned in our study (Castles et al., 2014), there are many considerations after the data collection stage, as highlighted by Farine (2015) and outlined in detail elsewhere (H. Whitehead, 2008). We appreciate that Farine is using our study to illustrate some general points, and agree that had we analysed our data differently (e.g., by using rates, rather than proportions, of dyadic grooming interactions) we may have obtained different results. However, this simply further supports our conclusion that social networks measured (and analysed) using different techniques are not necessarily comparable and care should be taken when generalising research findings. These considerations in data collection and analysis also highlight more general issues of research design which have perhaps been overlooked in the largely descriptive studies of social networks thus far (H. Whitehead, 2008). The definition of an edge connecting nodes in a network should first and foremost depend on the research question, and assumptions about correspondence between networks should be tested. In the case of the former, for example, if the research question relates to the transfer of visual information between individuals in a network, then edges based on shared proximity are likely to be most informative (but see our further considerations below). But if the research question addresses the likelihood of ectoparasitic disease spread between individuals, then instances of physical interaction between individuals may be more appropriate. In the case of the latter, we would encourage descriptive studies to adopt richer analyses that encompass multiple methods of measuring associations, as do others (Lehmann & Ross, 2011; Madden et al., 2011; H. Whitehead, 2008). Furthermore, we would return again to the conclusion of our original study that any researchers using proximity as a proxy for interactions (and we appreciate this is often the only available source of data on dyadic associations) should be wary that proximity does not always equal interaction, and *vice versa*. For example, individuals are able to interact via olfaction, vocalisations, and visual signals when not in close proximity, or may be in proximity but not interacting (we develop this further below).

Consequently, the appropriateness of using proximity as a proxy for interactions will depend on the type of interaction identified as meaningful and important for the research question in the context of the biology of study system.

The biology of a study species is likely to influence the appropriateness of different edge definitions for answering specific research questions. The definition of an edge should not solely be dictated by what is *possible* for a study species, but what is *appropriate* for it with respect to the study question and species biology; one should not use instances of close proximity to infer grooming when the research question is 'does social rank influence grooming equality?', for example, unless this link has been empirically demonstrated (preferably repeatedly) beforehand. Since, for some study systems, building the social network that is most appropriate for a given research question can be prohibited by logistical constraints on data collection, while other methods may be more practical, Farine's question remains: can proximity networks be a proxy for interaction networks? Before we expand on this in more detail, we would mention again that this question is distinct from the value of proximity measures to describe social structure/organisation—we find proximity measures valuable for both this task and for hypothesis testing in networks (but see Macdonald & Voelkl, 2015; Hal Whitehead & Dufault, 1999). As we mention above, we are in agreement with Farine (2015) that the gold standard in network studies requires a multi-network framework. In our original article (Castles et al., 2014), we were largely concerned with issues of comparability between studies which use different methods to define an association, and raised the issue of using proximity as a proxy for interactions in the discussion of our findings. Where we disagree with Farine is in his assertion that proximity edges can sometimes be used to infer interaction edges or *vice versa* without prior testing of this assumption. This does not preclude the use of proximity edges to determine, for example, individuals' preferred associates (for an example, see Carter et al., 2009).

Below, we will consider under which circumstances we might reliably expect a correspondence between proximity and interaction networks in an effort to provide guidelines for researchers wishing to use proximity as a predictive surrogate for interaction (see also Hal Whitehead & Dufault, 1999). This need not be limited to difficult-to-observe species, but could also apply to different methods of collecting data that do not involve direct but remote observation, such as the use of global positioning system collars to assign group membership by some measure of proximity. We also appreciate that understanding how and why different networks may or may not correspond or interrelate is an important research topic in its own right. However, we have not yet imagined any case where one could assume a correspondence between networks without testing for it, though our thought experiment provoked some overlooked considerations in social network studies: (1) some interactions can occur *between* individuals of different subgroups, (2) proximity networks describe only *opportunities* for interaction, and (3) individuals are likely to vary in both their gregariousness—their propensity to be in proximity to others—and their sociability—their propensity to take the opportunity to interact with others when in proximity to them. We will use the baboon system as a worked example of our reasoning by way of explanation where necessary, and we assume for this exercise that the hypothetical proximity network that is putatively predictive of the interaction network is well-sampled and representative of the 'true' proximity network.

Before we address these points in more detail, we should first take a brief digression to define the term 'group' here. To this point, we have used the term to mean a set of behaviourally-connected individuals in which the majority of individuals are connected to most others; this is what H. Whitehead (2008) refers to as a 'community' and is the equivalent of a troop in baboons. From here, however, we will use the term to refer to a 'subgroup'—a subset of a group that is behaviourally connected (either by proximity or interaction) at a particular point in time (Castles et al., 2014)—that is, the level of observation at which social network data are collected. To return to our first consideration then, it is important to address the assumption that researchers make about the proximity needed *for* interactions (Hal Whitehead & Dufault, 1999). As we mention above, individuals are able to interact via olfaction, vocalisations and visual signals when they are not in close proximity, but this is rarely considered as we suspect that it is implied that the interactions are physical. For example, Farine (2015) considered only physical interaction between individuals in his empirical example. In most cases, but not all—consider, for example, olfactory signals provided via latrines or the scent-marking of surfaces—we acknowledge that individuals will have to be within a particular proximity to interact using these other modalities that are of shorter temporal duration. Our point is not that proximity is not important for interaction, but that the range over which visual, auditory and olfactory signals can be transmitted is often beyond the range that is used to define group membership by proximity (and conversely, physical interactions are often well *inside* the range considered for group membership by proximity). This is not a semantic point, but a conceptual one about how we define edges and thus groups by proximity, and how this will limit comparability of networks. To illustrate by an example, baboons can interact via visual signals (using 'come hither' faces and lip-smacking) over tens of meters and via vocalisations over hundreds of meters; often these interaction distances are well beyond what we consider as group membership by our proximity rules. As such, individuals can readily and frequently interact *between* groups: conceptually, individuals could have an association index of zero but a non-zero interaction index. Of course, physical interaction requires group co-membership (however spatially defined) and here again the research question should drive the types of interactions that are reasonable to consider; we mean only to highlight an unconsidered assumption that may lead to a mismatch between edge definitions that may lower comparability between networks and studies.

Regarding the second consideration, association matrices represent only opportunities for interaction: they describe who *can* interact, but not who *does* interact. While this statement seems obvious, the use of proximity as proxy of interaction is predicated on the implicit assumption that the relationship between proximity strength and interaction rate is probabilistic (and also assumes, as we will do for the rest of this line of argument, that the interaction occurs over a short distance that necessarily places interacting individuals in the same group as defined by proximity; see our point above). This raises a problem with zero edges in the association network. It is logical to assume that individuals who are never in close proximity will never interact: proximity edges valued zero must be coupled with interaction edges valued zero. However, following this logic, the presence of zero-zero proximity and interaction edges will 'tether' any linear model that investigates the correlation between these values to the origin (see Fig. 1 in: Farine, 2015); in fact, these models *must* logically pass through the origin. Combined with the impossibility of negative rates of association, the presence of zero-zero values should increase the probability of at least a weakly positive correlation between proximity and interaction edges as soon as there are *any* non-zero interaction edges, and tells us only that individuals interact with those with whom they have an opportunity to interact (and suggests that proximity edges valued zero should be removed for this kind of analysis as they bias the relationship towards the origin). The only logical argument that holds is that individuals that are never in proximity do not interact. However, the assumption that proximity edge weights will provide (detailed) predictive data on differential rates of interactions between those individuals that are connected cannot be made. Consider, for example, Fig. 1 in Farine (2015): none of the of dyads exhibiting an (above average) proximity edge weight of 0.5 were observed interacting over the six-week study. Thus, proximity networks rather show who is connected and who is not, and therefore who can interact (at some unknown rate, which may include 0) and who cannot.

We feel that it is at this point that disagreements may arise about the usefulness of proximity as a proxy for interaction, and raises our third consideration. We argue that assumptions regarding the patterns of interactions between connected individuals should not be made, since individuals can vary not just in their gregariousness (the propensity to be in proximity to others), but also their sociability (the propensity to interact with others to whom they are in proximity). Furthermore, these propensities need not be positively correlated, and may be influenced by a range of social factors. This may lead to relationships between proximity and interaction that deviate from a neutral probabilistic model (i.e. increasing probability of interaction with increasing time spent in proximity), and—depending on patterns of within- and between-individual variation in these two traits—may result in the correspondence between proximity and interaction differing for different dyads' edges: specifically, individuals exhibiting similar association edge weights, and so similar gregariousness, may have different interaction edge weights if they differ in their sociability. While this is similar to Farine's (2015) fourth point about calculating rates of interaction while controlling for time in proximity as opposed to calculating the proportion of an individual's interactions directed to other individuals, we mean to highlight here the individual variation that may make proximity edge weights a poor predictor of interaction probability.

For example, we consider a hypothetical population (Fig. 1) in which dyads interact on average on half the occasions that they occur in the same group as defined by proximity (we assume that the probability that dyads interact, or P(interact), is 0.5 * P(co-occur)). The dashed line in the graph, therefore, describes the average relationship between shared proximity and interaction rate for this population. This relationship is likely to differ between species and may not necessarily be linear. In this hypothetical example, we have plotted three dyads—A, B and C—which co-occur with a probability 0.5. Dyad B interacts at the average rate for the population (near 0.5) and sits close to the line. However, dyads A and C interact more and less than expected than the average for the population, respectively, and consequently sit in darker parts of the plot. All three dyads are equally gregarious (to be more accurate, the result of the combination of the individuals' gregariousness in the dyads makes them equally gregarious); however, dyads A and C are more and less sociable than expected for their gregariousness, respectively. If researchers are not interested in this variation but are simply interested in determining those individuals who are likely to interact, then using proximity networks as a proxy for interaction *probability* (which requires individuals to be in close proximity) *might* be reasonable. However, if researchers are interested in this variation then information on who can and cannot interact clearly does not provide detailed insight into social interactions between individuals, since *a priori* assumptions cannot be made about the relationship between time in proximity and interaction rates. In this case we feel that researchers should (in order of decreasing preference): (1) collect and use data on individual interactions; (2) test this assumption in their study system, perhaps on a smaller subset of the network with more intensely collected data, before proceeding with the use of proximity data; and (3) use proximity as a proxy for interaction (probability) with caution, understanding that this assumption may not necessarily hold.

Next, we would like to address two other conceptual issues raised by Farine (2015). We will first consider the potential confusion that is introduced in social network analyses by making a distinction between fission-fusion societies and stable social groups. There is an argument that a particular edge definition will be more informative for species of a particular social organisation (Farine, 2015). As we mention above, we made no judgement on the value of proximity and interaction edges as being more or less accurate representations of the 'real' social network in our original paper (Castles et al., 2014). We suggest only that the different methods provide a different aspect of an individual's social environment, both of which we believe are important and both of which should be collected and compared when possible. Furthermore, we are certainly in agreement that species biology should determine the rules used to define edges in networks for a particular method. However, we think it misleading to make assumptions about how *informative* a particular method is for species of particular social organisations for two reasons. First, it is impossible to categorise all species into particular social organisations, let alone categorise unequivocal types of social organisation. Second, there is substantial variation within categories of social organisation such as those suggested by Farine (2015). As this variation is continuous, categorisation is arbitrary and generalisations at the level of social organisation are impractical.

Using the category of fission-fusion species as an example, there is variation among species in the extent of fluidity of individuals among groups, prohibiting the assumption that group co-membership is more informative than interaction in all fission-fusion species. Group membership in fission-fusion species can be highly fluid, where individuals in a local population form one community of connected individuals, such as in guppies (*Poecilia reticulata*) (Darren P. Croft, Krause, & James, 2004). It can also be arranged in a segregated community structure, where association between individuals from the same community is common but association between individuals from different communities is rare, such as in chimpanzees (*Pan troglodytes*) (Symington, 1990) and eastern grey kangaroos (*Macropus giganteus*) (Best, Seddon, Dwyer, & Goldizen, 2013). It can also be based around multilevel societies, where there are tiers of closely-connected individuals nested within 'higher' levels of clustered lower tiers, such as in African elephants (*Loxodonta africana*) (Wittemyer, Douglas-Hamilton, & Getz, 2005) and hamadryas baboons (*Papio hamadryas*)

(Kummer, 1984). We note that these descriptions of the fission-fusion social organisations of these species were all made using proximity (group co-occurrence) methods, demonstrating the usefulness of the proximity method for describing differences in social organisation. However, the assumption that group co-membership in chimpanzees is more informative than grooming equality should, returning to our earlier point, depend on the question that the research is trying inform, not on the fact that they have a fission-fusion social organisation. While this particular example may be hyperbolic, we mean only to highlight that *a priori* assumptions about the *meaningfulness* of one method for all species of a particular social organisation is misguided, based in part on the complications associated with categorising species and variation within categories. We would go so far as to argue that valuing one method above another is equally detrimental to social network studies and should be avoided, not least because we as human researchers are unaware of which distances or timings of co-occurrence, and proportions, counts or durations of interactions that we measure are actually meaningful to the species we study. Furthermore, both proximity and interaction measures are likely to be important and informative for particular biological processes, and we would prefer to see researchers moving towards more holistic frameworks in social network studies that use competing networks to test *a priori* hypotheses about the importance of social networks for animals.

Finally, three inter-related questions resulting from our consideration of these methodological issues remain to be discussed: what makes a network, how should sample sizes be considered in social network studies, and at which level should data be pooled? These questions relate to Farine's (2015) idea of social scale and are generally beyond the scope of this reply to address in detail (being relevant research questions in their own right in many systems). One small consideration of note, however, relates to our point regarding the importance of research questions in determining edge definitions. We defined community above as a set of behaviourally-connected individuals in which the majority of individuals are connected to most others. In baboons, a community (troop) is easy to define because connections between troops are so rare (Cowlishaw, 1995) and connections within troops are common (Castles et al., 2014). For species with higher fission-fusion organisation, where communities are more transient and home ranges can overlap substantially (e.g. eastern grey kangaroos: Best et al., 2013), identifying communities and community membership is less straightforward, and may influence the results of social network analyses. Once community structure has been identified, we must ask which individuals should be included in the 'social network' for a given study. Should all individuals in the local population be included, even if the majority never have a connection to others (see our point above about zero-weighted edges)? Or should the communities be considered separately, even if there are some (sometimes many) between-community connections? While at the node level larger communities will result in larger sample sizes, a limit to the generalisability of network studies' results is not how large the communities are but how many communities are assessed for a particular research question (D. P. Croft, James, & Krause, 2008). For example, if a researcher is interested in the transfer of information among individuals, the relevant unit of analysis is not the number of individuals in the community but the number of communities in which the results can be replicated; the size of the community is irrelevant (unless one is interested in the transfer of information in communities of different sizes, of course). In our baboon system, in most cases we would rarely pool in a common network all of the individuals from both of the communities we study because of the zero-weighted edges that would be generated, but after this stage we may pool individuals (and control statistically for troop membership), as ever, depending on the research question (as we did in Castles et al., 2014). However, we have no prescriptive advice for this problem in other systems with more between-community connections; once again, we merely intend to highlight an issue that is infrequently considered in social network studies which requires the careful attention of researchers.

In conclusion, we reiterate that we do not argue that proximity data cannot or should not be used in social network studies, nor that proximity data are not informative, and we appreciate that in many systems proximity is the only readily available measure of association between individuals. We only caution against assuming that proximity is necessarily a proxy for interactions, and encourage that this assumption is tested should it be used. We also advocate that the research question and study species biology should drive the definition of edges (and nodes) in networks as well as the social scales at which these are measured.

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References

Best, E. C., Seddon, J. M., Dwyer, R. G., & Goldizen, A. W. (2013). Social preference influences female community structure in a population of wild eastern grey kangaroos. *Animal Behaviour, 86*(5), 1031-1040. doi: http://dx.doi.org/10.1016/j.anbehav.2013.09.008

Carter, A. J., Macdonald, S. L., Thomson, V. A., & Goldizen, A. W. (2009). Structured association patterns and their energetic benefits in female eastern grey kangaroos, *Macropus giganteus*. *Animal Behaviour, 77*(4), 839-846. doi: DOI 10.1016/j.anbehav.2008.12.007

Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E. G., Cowlishaw, G., & Carter, A. J. (2014). Social networks created with different techniques are not comparable. *Animal Behaviour, 96*(0), 59-67. doi: http://dx.doi.org/10.1016/j.anbehav.2014.07.023

Cowlishaw, G. (1995). Behavioural Patterns in Baboon Group Encounters: The Role of Resource Competition and Male Reproductive Strategies. *Behaviour, 132*(1/2), 75-86. doi: 10.2307/4535250

Croft, D. P., James, R., & Krause, J. (2008). *Exploring Animal Social Networks*. Princeton: Princeton University Press.

Croft, D. P., Krause, J., & James, R. (2004). Social networks in the guppy (Poecilia reticulata). [Journal Article]. *Biology Letters, 271*(Suppl 6), S516-S519. doi: 10.1098/rsbl.2004.0206

Farine, D. R. (2015). Proximity as a proxy for interactions: issues of scale in social network analysis. *Animal Behaviour, in press*.

Hobson, E. A., Avery, M. L., & Wright, T. F. (2013). An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. *Animal Behaviour, 85*(1), 83-96. doi: http://dx.doi.org/10.1016/j.anbehav.2012.10.010

Kummer, H. (1984). From laboratory to desert and back: A social system of hamadryas baboons. *Animal Behaviour, 32*(4), 965-971. doi: http://dx.doi.org/10.1016/S0003-3472(84)80208-0

Lehmann, J., & Ross, C. (2011). Baboon (*Papio anubis*) social complexity - a network approach. *American Journal of Primatology, 73*(8), 775-789. doi: Doi 10.1002/Ajp.20967

Macdonald, S., & Voelkl, B. (2015). Primate social networks. In J. Krause, R. James & D. W. Franks (Eds.), *Animal Social Networks* (pp. 125-138). Oxford: Oxford University Press.

Madden, J., Drewe, J., Pearce, G., & Clutton-Brock, T. (2011). The social network structure of a wild meerkat population: 3. Position of individuals within networks. *Behavioral Ecology and Sociobiology, 65*(10), 1857-1871. doi: 10.1007/s00265-011-1194-2

Symington, M. M. (1990). Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology, 11*(1), 47-61. doi: 10.1007/bf02193695

Whitehead, H. (2008). *Analysing Animal Societies*. Chicago: University of Chicago Press.

Whitehead, H., & Dufault, S. (1999). Techniques for Analyzing Vertebrate Social Structure Using Identified Individuals: Review and Recommendations. *Advances in the Study of Behavior, 28*, 33-74. doi: http://dx.doi.org/10.1016/S0065-3454(08)60215-6

Wittemyer, G., Douglas-Hamilton, I., & Getz, W. M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour, 69*(6), 1357-1371. doi: http://dx.doi.org/10.1016/j.anbehav.2004.08.018

Figure 1

The relationship between the probability of interacting (P(interact)) for a given probability that a dyad will co-occur in the same group (P(co-occur)). The dashed line represents the average interaction rate for the population. The blue shading represents whether individuals are more or less likely to interact than expected for the average of the population, with lighter (white) shading showing that dyads interact at the average rate. Three hypothetical dyads (A, B and C) are shown (see text for details).