A framework to evaluate whether to pool or separate behaviors in a multilayer network

Annemarie van der Marel¹, Sanjay Prasher¹, Chelsea Carminito¹, Claire O'Connell¹, Alexa Phillips¹, Bryan M. Kluever², Elizabeth A. Hobson¹*

¹ Department of Biological Sciences, University of Cincinnati, Ohio USA

² United States Department of Agriculture, Wildlife Services, National Wildlife Research Center, Florida Field Station, Florida USA

*Corresponding author: elizabeth.hobson@uc.edu
A framework to evaluate whether to pool or separate behaviors in a multilayer network

Abstract

A multilayer network approach combines different network layers, which are connected by interlayer edges, to create a single mathematical object. These networks can contain a variety of information types and represent different aspects of a system. However, the process for selecting which information to include is not always straightforward. Using data on two agonistic behaviors in a captive population of monk parakeets (*Myiopsitta monachus*), we developed a framework for investigating how pooling or splitting behaviors at the scale of dyadic relationships (between two individuals) affects group-level social properties. We designed two reference models to test whether randomizing the number of interactions across behavior types results in similar structural patterns as the observed data. Although the behaviors were correlated, the sociality measures derived from observed data fell outside the distribution of those derived from the reference model. However, once we controlled for data sparsity in our second reference model, we found that measures from the observed data then fell within the range of those from the reference model which showed that this result may have been due to the unequal frequencies of each observed behavior. Thus, our findings support pooling the two behaviors. This framework can be used for any type of behavior and question, however, caution should be used when interpreting the results as some measures are sensitive to data properties, such as unequal rates of observed behavior in our case. This framework will help researchers make informed and data-driven decisions about which behaviors to pool or separate, prior to using the data in subsequent multilayer network analyses.

Keywords: Behavioral interactions, monk parakeet, *Myiopsitta monachus*, network analysis, social context, social relationships
Introduction

Animals can interact with each other in many ways, even within a single social group. Traditional social network analysis has provided significant insight into the form and function of social systems, but sociality is often multifaceted. Including multiple types of social interactions provides a richer description of social structure (Whitehead and Dufault 1999) and can allow for better integration of multiple factors, such as spatial, temporal, and genetic relatedness along with social interactions to better explain patterns of sociality. This multilayer network perspective has gained recent attention because it provides a framework for combining social analyses and allows researchers to analyze sociality as one mathematical object (Barrett et al. 2012; De Domenico et al. 2013; Bianconi 2018; Silk et al. 2018; Finn et al. 2019; Beisner et al. 2020; Pereira et al. 2020). Analyzing multiple layers together can provide more comprehensive insight into the factors affecting sociality, the hidden mechanisms of a system, and social structure patterns in animal societies than analyzing any one behavioral or network type in isolation.

However, researchers must carefully evaluate which layers to include in a multilayer network analysis and how to assemble those layers. Generally, social network layers are built from associations or interactions among dyads (pairs of individuals). Determining what the layers should represent, and how to construct them, is a critical step in the formation of any multilayer network, regardless of topic. In some cases, this determination is more obvious, especially when the two network layers are very different from one another (for example, genetic relatedness and social associations, (Evans et al. 2020). In other cases, decisions about what behaviors to include, exclude, or treat as equivalent can be much less straightforward.

Seemingly similar behaviors may be pooled, which can provide benefits such as reducing data sparsity problems for some interaction types. In this case, pooling can lead to more
comprehensive networks, which may be better models of the real social structure, and thus allow better measures of sociality. Pooling can also simplify multilayer network analyses by focusing on fewer network types and reducing the number of layers used in the analysis, the risk of committing Type 1 errors, and nonindependence problems (Silk et al. 2013). Pooling behaviors of similar types could also be useful for understanding the function of networks.

Although pooling behavioral data can provide benefits in multilayer analyses, it can also come with potential costs. Seemingly-similar layers may each convey important information when taken separately (Beisner et al. 2015; Beisner et al. 2020). In this case, the combination of two non-equivalent behaviors into a single network layer could introduce unnecessary noise into a multilayer network analysis and reduce the ability of those analyses to reach clear conclusions. Combining non-equivalent behaviors that differ in how commonly or rarely they are observed could also strongly bias the resulting network layer towards the most common behavior (Silk et al. 2013). These costs of pooling behaviors at the dyadic interaction level are especially important to consider in multilevel analyses where the focus is on detecting structure at different levels of social organization. Pooling seemingly-similar dyadic interactions may differentially impact more macro-scale social properties, even in cases where behaviors appear similar on the dyadic level.

Current methods for deciding whether to pool or split behaviors within a behavioral context largely fall into three main approaches found across different animal taxa: (1) unspecified decisions made at either the data collection or analysis level, (2) researcher familiarity with the biology of the study system, and (3) the strength of correlation between the behavior types at the dyadic level.
Details about the decision-making process of what behaviors are included in analyses or how they may have been pooled or kept separate are sometimes not explicitly reported in studies (e.g. Herberholz et al. 2003; Viblanc et al. 2016). These decisions may not be reported because weighing decisions about whether to pool or split behaviors occurs at different points during a study. Decisions about network layers can be made at the time of data collection when observation protocols determine how data are coded. In these cases, it is typical for authors to report which behaviors they collected; it is less common for authors to provide a detailed description of all the behaviors that they could have collected, how those could have been subdivided into more specific categories, and why particular behaviors were categorized in certain ways. For example, in a study to identify the patterns of social ties within cichlid cooperative networks, the authors created affiliative and aggression networks and listed specific behaviors that qualified as either aggressive or affiliative; however, they did not further explain their reasoning for combining the behaviors (Schürch et al. 2010). These decisions at the data collection stage can have downstream effects on later analyses, which may be constrained by the ways data were collected. To ensure flexibility in future analytical approaches, researchers often collect a suite of behavioral interaction and association data in several contexts, such as direct affiliative or aggressive interactions, and more passive tolerance, proximity, or group associations. It is important to note that while recording more detailed observations during data collection can allow for different ways of slicing, combining, or subsetting data for future analyses, detailed data like this can also be more difficult to collect reliably, especially in cases where there are only slight differences between two desired behavioral types. In cases where many types of behavioral data are collected and coded uniquely, decisions about which types to use to construct a specific network layer come at the analysis stage.

Researchers often rely on familiarity with the biology of the system to decide which behaviors “qualify” as sufficiently different or similar enough to be coded separately or included in the
same network layer, respectively. This approach is especially common when researchers perceive two interactions as qualitatively different types of interactions that both fall within the same social context. For example, some studies differentiate between low-level aggression and high-level aggression based on assumptions about the energetic costs or potential for injury (Oczak et al. 2014; Pierard et al. 2019; Wey et al. 2019; Beisner et al. 2020). Although the two behaviors may be coded as separate interaction types, they both fall within an agonistic social context. Researchers can also build on previous work with the same or closely related species to use knowledge of the system to make decisions about which behaviors to include or how to pool them (e.g. Munroe and Koprowski 2014; Beisner et al. 2020; Pereira et al. 2020). If the animals themselves perceive two types of behavioral interactions as socially-equivalent, biologically it would make sense to pool these two behaviors, and knowledge of the study system can be used as a rationale for making these decisions. A danger to this approach is that the study system may not be well enough understood to make these decisions in ways that align with the biological relevance of how the animals themselves perceive the behaviors.

Finally, the choice can be made based on a data-driven approach. Here, researchers may use initial data analyses to evaluate whether the frequency of behaviors between individuals are correlated, whether behaviors can be condensed down to fewer types using dimension-reduction methods, or through comparing behaviors to find dissimilar or unique information. For example, in a study on the effects of perturbations in a social group on hierarchy structure in house sparrows, the authors pooled the interaction types that were correlated per behavioral context (Kubitza et al. 2015). Network layers may also be standardized by consensus ranking to identify significant vertices in separate layers (Braun 2019).
A framework to evaluate whether to pool or separate behaviors in a multilayer network

We developed a framework to examine the implications of splitting or pooling behaviors at the dyadic level before deciding on how to construct the layers of networks in a multilayer network analysis. We propose a three-step process for investigating the general implications of pooling versus splitting behaviors: (1) determine whether dyads exclusively use one behavior or multiple types in their interactions, (2) test whether behaviors can be considered “interchangeable”, and (3) test how data sparsity may affect whether behaviors are interchangeable (see Figure 1). Our approach highlights how pooling or splitting behaviors may differentially affect measures of social structure across different levels of social organization (Hobson, Ferdinand, et al. 2019). We focus on how changes in relationships (formed via different types of interactions) may affect group-level social properties like network properties, dominance hierarchy structure, and aggression strategies. We illustrate how this framework can be used by applying it to two types of aggressive behavior recorded in a group of monk parakeets (*Myiopsitta monachus*). Our aim is to provide guidelines for other researchers to better evaluate these implications in their own study systems.
A framework to evaluate whether to pool or separate behaviors in a multilayer network

Figure 1: A 3-step decision tree showing the process of evaluating whether to pool or split behaviors for multilayer network analysis

Methods

Data collection

To illustrate our evaluation methods, we used data collected from monk parakeet social interactions. Monk parakeets are small (100-150g) neotropical parrots that exhibit the potential for cognitive and social complexity (Hobson et al. 2013; Hobson et al. 2014; Hobson and DeDeo 2015).

We collected data on several types of social interactions in a long-term captive population of monk parakeets. The parakeets (n=21 individuals) were housed at the United States Department of Agriculture Wildlife Services National Wildlife Research Center, Florida Field.
A framework to evaluate whether to pool or separate behaviors in a multilayer network

Station, located in Gainesville, FL, USA. Observations occurred during March 2020 (the field season was cut short due to the COVID-19 pandemic). To enable individual identification, we marked each parakeet’s feathers with a unique color combination using nontoxic permanent markers (Hobson et al. 2013). We released these marked birds into a large 45x45m semi-natural outdoor flight pen.

Observers were stationed in blinds in 3 locations around the flight pen to conduct observations; 3-4 observers collected observations between 09:00 and 19:00 daily. We used all-occurrence sampling (Altmann 1974) and recorded dyadic interactions using the Animal Observer v1.0 app, directly inputting the data on iPads. For this analysis, we present data collected on displacements (instances where one bird aggressively approached another bird and supplanted it from its location, sometimes via physical contact) and crowds (where one bird approached another bird which moved away before the aggressor was within striking range) during a 3-day period when the dominance structure was stable in the group. We differentiated these two behaviors because they appeared to differ in the severity of aggression: displacements could result in injuries (Hobson, pers.obs.) while crowds were by definition always non-contact aggression.

Having 3-4 observers recording observations at the same time allowed us to conduct more comprehensive all-occurrence sampling, but often resulted in different observers logging the same interaction. To remove these duplicated observations, we summarized by the number of observations per interaction type that were observed in the same minute across each of the 3-4 observers. We filtered the observations to keep those from whichever observer recorded the highest number of observations of a certain interaction type in each minute, removing all potentially-duplicated observations from other observers. We also filtered the data and only included crowds or displacements where both the aggressor and the subject were identified.
Reference models

To test how pooling two interaction types may affect social properties, we followed our 3-step evaluation framework (Fig.1).

In step 1, we checked the percentage of dyads that performed either one or both behaviors. If there is no overlap in dyads performing both behaviors, then the behaviors may be used to mediate different kinds of relationships. If few to none of the dyads were observed crowding and displacing, then the behaviors should probably not be pooled as the behaviors may reflect different relationships.

In step 2 of our framework, we evaluated whether two behaviors were interchangeable. We constructed reference model 1 to test this. We use the term reference model for random networks where some features are constrained to match those of an observed network (Gauvin et al. 2018; Hobson et al. in prep.). Randomizing some but not all of the structure of interactions is a common tool used in social network research (Farine and Whitehead 2015). For each dyad, we summarized the number of displacement and crowd interactions; the sum of both interactions is the total number of interactions in an agonistic context. We then randomly re-allocated the total number of agonistic interactions back to the two interaction types. This reference model preserved the total number of individuals in the group, which individuals interacted in an agonistic context, and number of total agonistic interactions. The reference model randomized only the number of interactions that were categorized as displacements versus crowds (n=100 runs). If the metrics calculated from the observed data closely match those calculated from this reference model data, then the two interaction types would likely be interchangeable. Such a scenario would support a decision to pool the behaviors for further analyses. In contrast, if observed and reference model data do not lead to similar conclusions
A framework to evaluate whether to pool or separate behaviors in a multilayer network

about sociality, the behaviors may not be interchangeable (and should not be pooled). However, another explanation for differences in summary statistics for the observed data and the reference model runs could be that the behaviors differ in how commonly they were observed, and that data sparsity may be driving the differences rather than something biologically relevant about the behaviors (see step 3).

In step 3, we investigated whether observed differences between two behaviors could be due to one behavior occurring much more frequently than the other. We constructed reference model 2 to test this. We subsampled all displacement events without replacement, retaining the identity of the aggressors and subjects so that the total number of displacement events in the subsample equaled the number of observed crowds. In our case, crowds were much rarer than displacements. For the reference model, we used the total number of crowd events observed (160 events) to set the number of displacements we randomly subsampled in each run. This reference model preserved the total number of individuals in the group, which individuals interacted in each agonistic context (crowd versus displacements), and the number of crowds observed for each dyad. The reference model randomized only which of the total observed displacements were subsampled in each run (n = 100 runs). We then compared the reference model runs for the subsampled displacement data to all the observed crowd data. We compared these using a suite of summary statistics that reflect group-level social properties (see Analysis section below). If the sociality metrics calculated from the observed crowd data lie within the range of values calculated from the subsampled displacements, there would be support for the idea that any differences between observed and reference model data found in the previous step are due to dissimilar frequencies of each behavior type. Thus, pooling the behaviors may still be warranted. If there are differences in the conclusions reached via the observed crowd data compared to the subsampled displacement data then any prior differences may be the
result of other factors, such as the behaviors having biologically different functions for the individuals studied. In this case, pooling the behaviors should be avoided.

**Analysis**

To evaluate the implications of pooling or separating behaviors, we investigated how these decisions would affect group-level social properties. We first measured the strength of the correlation between crowds and displacements excluding the dyads that did not interact agonistically, using Spearman’s rho. We then measured several more macro-scale group social properties.

We used two network-based measures of the aggression network: density and relationship sparseness. For clarity, we use “directed dyads”, to refer to cases where the actor/subject are important in understanding the relationship or the measure; this definition differentiates between the order of individuals in the dyad (A agonistic to B and B agonistic to A are counted as separate dyads). We use “undirected dyads” to differentiate whether two individuals have a relationship or not (we only counted whether A and B are either agonistic to the other once). We measured network density as the proportion of directed dyads that interacted with crowds, displacements, or both behaviors out of the total number of possible directed dyads (here, n = 420 possible directed dyads). Density ranges from 0 (no interactions) to 1 (all directed dyads interacted). Sparseness is a measure that divides the number of undirected dyads that did not interact by the number of possible undirected dyads (Neumann and Kulik 2020).

We used three measures of dominance hierarchy structure: linearity, steepness, and triangle transitivity. We measured linearity using Landau’s h index with 1000 randomizations using the ‘h.index’ function in the R package EloRating v0.46.11 (Neumann and Kulik 2020). We measured steepness as the slope of the regression line between rank order and the normalized
A framework to evaluate whether to pool or separate behaviors in a multilayer network

David’s scores using the dyadic dominance index using the ‘getStp’ function in the R package steepness v0.2-2 (Leiva & de Vries 2014). Instead of measuring A beats B then B wins of C (linearity), transitivity calculates the orderliness across triads (A wins of B and B beats C, then A also wins of C) (Shizuka and Mcdonald 2012; Shizuka and Mcdonald 2015). We measured triangle transitivity using the function ‘transitivity’ in the R package EloRating v0.46.11 (Neumann and Kulik 2020).

Finally, we assessed the overall strategy type individuals in the group used to direct aggression. Potential rank-structured aggression strategies are the downward heuristic (individuals aggress against any lower-ranked individuals), close competitors (individuals mainly aggress against individuals that are just below them in rank), and bullying (individuals mainly aggress against individuals that are much lower in rank, see Hobson, Mønster, et al. 2019). We assessed strategies using the R package “domstruc” (Mønster, Hobson, & DeDeo, currently available at https://github.com/danm0nster/domstruc).

All measures were quantified for crowds only, displacements only, pooled aggression (crowds and displacements), and for each run of the two reference models. We used R v4.0.0 (R Core Team, 2020) for all our analyses and the package ‘Beanplot’ v1.2 to make our figures (Kampstra 2008). All data and code for running the analyses and generating the figures will be made available on GitHub on publication. All animal-related activities were approved by the University of Cincinnati IACUC protocol #AM02-19-11-19-01 and the National Wildlife Research Center.
Results

We observed a total of 1215 agonistic interactions (160 crowds and 1055 displacements) over 23.5 hours (82.2 person-hours). Of the 420 total possible directed dyads, 48.3% dyads interacted agonistically (203 directed dyads). Overall, crowds were much rarer than displacements and accounted for only 13.2% of aggressive interactions. For directed dyads that interacted agonistically in some way, we observed $0.77 \pm 1.63$ crowds per dyad (mean ± SD, range 0-13) and $5.20 \pm 9.31$ displacements per dyad (range 0-86); combined across crowds and displacements we observed $5.99 \pm 10.49$ agonistic events per dyad (range 1-93).

Within directed dyads, crowds and displacements did not occur equally: a small number of directed dyads only crowded (5.9%), a larger proportion of directed dyads both crowded and displaced (35.5%), while the majority of agonistic dyads interacted only with displacements (58.6%).

Correlation between behavior types

The observed number of crowds and displacements in directed dyads that interacted agonistically were weakly correlated ($r_s = 0.33$, $p < 0.001$). This correlation was stronger in the observed data sets than in either reference model 1 or 2 runs (Fig. 2). Reference model 1 shows that randomly re-allocating crowd and displacement events to the two behavioral types reduced the correlation between crowds and displacements compared to the observed data. Reference model 2 shows that this correlation is weakened further when we quantified the relationship between observed crowds and subsampled displacements.
A framework to evaluate whether to pool or separate behaviors in a multilayer network

**Figure 2**: Correlation strength between randomly allocated crowds and displacements in reference model 1 (dark green) and between crowds and subsampled displacements in reference model 2 (light green). Red line shows the correlation between crowds and displacements in the observed dataset.

**Network measures**

Network measures showed that observed agonistic data (pooling all observed crowds and displacements) had higher density and lower sparsity than either behavior alone (Figure 3). Of the two behaviors, observed displacements had a higher density and lower sparsity than crowds. This difference shows that more directed dyads were connected and more undirected relationships were defined for displacements than crowds. Reference model 1 shows that these differences in the observed dataset could be erased by randomly re-allocating behaviors to each behavior type. Both observed crowds and observed displacements had different density and sparseness measures than reference model 1 runs. Reference model 2 shows the effect of the amount of data on each measure; once displacement data were subsampled, both density and sparseness measures overlapped with the observed crowd values.
A framework to evaluate whether to pool or separate behaviors in a multilayer network

**Figure 3**: Two network measures in observed and reference model data for agonistic interactions in monk parakeets: a) density and b) sparseness. Observed values are indicated in red and the distributions show values from reference model runs.

![Figure 3](image)

**Dominance hierarchy structure**

Measures of dominance hierarchy structure mainly demonstrated similar patterns to the network measures. The pooled observed linearity and steepness values were higher than those produced by either crowds or displacements alone, but pooled transitivity values were more similar to each individual behavior’s values (Figure 4). Individually, crowds had lower linearity and steepness values than in reference model 1 while displacements had higher linearity and steepness values in the observed dataset compared to reference model 1. Both observed crowds and observed displacements fell within the distribution of transitivity values both when behaviors were randomly re-allocated (reference model 1) and when displacements were
subsampled (reference model 2). This overlap indicates that transitivity is relatively robust to both random re-allocation of events into different behavioral types as well as random subsampling.

**Figure 4**: Three hierarchy measures in observed and reference model data: a) linearity, b) steepness, and c) transitivity. Observed values are indicated in red and the distributions show values from reference model runs.

**Aggression strategy**

Rank-affected aggression patterns in the observed datasets were all consistently categorized as a bullying strategy (where individuals preferentially aggress against others ranked much lower than themselves, Figure 5). When we randomly re-allocated events as crowds or displacements (reference model 1) we found that almost all runs were also categorized as showing a bullying strategy. When we subsampled displacements (reference model 2), we found a different
pattern: less than 50% of the runs were categorized with bullying strategies and the majority showed evidence of a basic downward heuristic (where individuals aggress indiscriminately towards any individual ranked below itself). These comparisons show that the observed strategies were consistent with strategies in randomly re-allocated events and that strategy type was robust to and preserved despite these randomizations. However, the strategies were less robust to subsampled data. The difference between the observed crowd strategy and the result from reference model 2 show that this difference cannot be explained by data sparsity alone.

**Figure 5:** Aggression strategies in observed data and reference model datasets.

**Discussion**

We developed a framework to examine the implications of splitting or pooling potentially-related behaviors prior to determining how to construct networks in multilayer network analyses. Our approach considers whether dyads interacted using both behavior types, whether there was
A framework to evaluate whether to pool or separate behaviors in a multilayer network

evidence that behaviors could be considered interchangeable, and whether the non-interchangeability of behaviors could be attributed simply to data sparsity.

These approaches also go beyond a simple correlation between behavior types. In our parakeet data, we found that crowds and displacements were correlated in our observed dataset. However, although this correlation was statistically significant, the correlation strength was relatively weak. Our more extensive analysis provides much more detailed evidence that supports pooling behaviors than a correlation alone.

In our monk parakeet dataset, we found that 36% of the dyads performed a mix of the agonistic behaviors, showing that there was no immediate evidence against pooling behaviors. More generally, if there is zero overlap of dyads performing both types of behavior, the behaviors should most likely not be pooled into a single network. However, there is no clear cut-off for when researchers should or should not pool the two behaviors if some, but not a majority, of dyads use both behaviors. A simple test for the correlation strength between behavior types can provide an indication of whether behaviors should be pooled or considered separately but our framework tests for the implications more directly and can help researchers better evaluate these decisions when the correct pooling or splitting is not obvious.

Our measures of parakeet behavior interchangeability showed that for all measures except triangle transitivity and the aggression strategies, the observed data for each behavior separately and pooled did not fall within the range of the reference model. This differentiation can be evidence that each behavior should be considered separately. However, when we investigated further, we found that these results could be due to differences in how commonly or rarely each behavior was observed. When we subsampled our commonly-observed behavior (displacements) to match the frequency of our rarely-observed behavior (crowds), we found that
A framework to evaluate whether to pool or separate behaviors in a multilayer network

the sampled data produced similar results to the observed data. These results provide evidence that the indications against pooling (from reference model 1) could be due simply to data availability rather than biological differences between the two behaviors. Taken together, we concluded that it is likely reasonable to pool the two behaviors into a single agonistic network for future multilayer network analyses.

Overall, researchers can use this kind of framework to investigate the potential implications of pooling or splitting behaviors in their own datasets. We studied the general pattern of dyadic agonistic relationships and group-level social properties, such as dominance hierarchy structure, network-based group measures, and aggression strategies. However, our framework can be used for any behavior (affiliative, agonistic, etc.) and for any type of analyses where you get the choice to pool or keep behaviors separate. For example, you can substitute our group-level for individual-level measures such as an individual’s dominance rank.

Our 3-step process allows researchers to follow a simple series of questions to evaluate whether the combined evidence supports pooling behaviors or keeping them separate. In step 1, if at least some proportion of the total dyads use both behavior types to interact, then it is preliminary evidence that behaviors could be pooled. If none of the dyads use both behavior types, then there is relatively strong evidence that behaviors should not be pooled. In step 2, if observed data for each behavior produces measures that fall within the range of reference model measures (and are thus similar to each other), then the behaviors are clearly interchangeable, and pooling is strongly justifiable. Otherwise, divergence from these distributions suggests that the observed behavior may need to be considered separately. In step 3, if subsampled data for the more common behavior produces similar results to the observed data for the less common behavior this is evidence of two things. First, it provides supporting evidence that behaviors can be pooled because the differences in the summary measures is
likely due to data availability rather than a biological distinction between the behavior types. Second, it illustrates how the particular summary measures chosen may be affected by or susceptible to the availability of data. For example, in studies where datasets are limited and may be sparse, data can either be pooled across behavior types or triangle transitivity can be used as a hierarchy structure measure as it is less susceptible to data sparsity than linearity and steepness (Klass and Cords 2011; Shizuka and Mcdonald 2012; Shizuka and Mcdonald 2015). In cases where separated behaviors produce different summary measures in step 2, overlapping distributions in step 3 provide evidence that differences in results may be due simply to differences in sparsity and it may be reasonable to pool behaviors. However, if the sub-sampled data in step 3 produces different results, this indicates that any earlier differences cannot be attributed to data availability alone and the behaviors should not be pooled.

**Conclusions**

In this study, we showed how a data-driven approach can be used to decide whether to pool or keep behaviors separate. We illustrated how this framework can be used by applying it to parakeet social interactions. We argue that it is critical to consider how to pool or split data as a first step in many behavioral analyses, particularly multilayer networks. Our proposed analytical approach can provide evidence for or against pooling behaviors and can be used to justify how to treat data in analyses. We expect these approaches to be especially useful in study systems with less-documented social processes, where relying on extensive knowledge of the study system to make decisions about which behavioral types are sufficiently similar or different may be difficult. Other researchers can use our proposed framework as an initial step in their data analysis process, especially those using a multilayer network approach.
Acknowledgements

We thank the staff at the Florida Field Station, especially Eddie Bruce, John Humphrey, Eric Tillman, Danyelle Sherman, and Amber Sutton for their assistance and support.

Author contributions

E. Hobson and A. van der Marel designed the study; B. Kluever provided study support and logistical aid; E. Hobson, A. van der Marel, C. Carminito, C. O’Connell, and A. Phillips collected data, E. Hobson; A. van der Marel, and S. Prasher conducted the analyses; E. Hobson, A. van der Marel, C. Carminito, C. O’Connell, and S. Prasher wrote the paper; all authors provided comments on the drafts.

References

Barrett L, Henzi SP, Lusseau D. 2012. Taking sociality seriously: the structure of multidimensional social networks as a source of information for individuals. Philos Trans R Soc B Biol Sci. 367(1599):2108–2118. doi:10.1098/rstb.2012.0113.

Beisner B, Braun N, Pósfai M, Vandeleest J, D’Souza R, McCowan B. 2020. A multiplex centrality metric for complex social networks: Sex, social status, and family structure predict multiplex centrality in rhesus macaques. PeerJ. 2020(3):e8712. doi:10.7717/peerj.8712.

Beisner BA, Jin J, Fushing H, McCowan B. 2015. Detection of social group instability among captive rhesus macaques using joint network modeling.

Bianconi G. 2018. Multilayer Networks: Structure and Function. Oxford University Press (OUP).

Braun N. 2019. Rank Aggregation Methods For Consensus Ranking in Multilayer Networks.

De Domenico M, Solé-Ribalta A, Cozzo E, Kivelä M, Moreno Y, Porter MA, Gómez S, Arenas A. 2013. Mathematical Formulation of Multilayer Networks. Phys Rev X. 3(4):041022. doi:10.1103/PhysRevX.3.041022.

Evans JC, Lindholm AK, König B. 2020. Long-term overlap of social and genetic structure in free-ranging house mice reveals dynamic seasonal and group size effects. Curr Zool. doi:10.1093/CZ/ZOAA030.

Farine DR, Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. J Anim Ecol. 84(5):1144–1163. doi:10.1111/1365-2656.12418.
A framework to evaluate whether to pool or separate behaviors in a multilayer network

Finn KR, Silk MJ, Porter MA, Pinter-Wollman N. 2019. The use of multilayer network analysis in animal behaviour. Anim Behav. 149(3):7–22. doi:10.1016/j.anbehav.2018.12.016.

Gauvin L, Génois M, Karsai M, Kivelä M, Takaguchi T, Valdano E, Vestergaard CL. 2018 Jun 11. Randomized reference models for temporal networks. arXiv https://arxiv.org/abs/180604032.

Herberholz J, Sen MM, Edwards DH. 2003. Parallel changes in agonistic and non-agonistic behaviors during dominance hierarchy formation in crayfish. J Comp Physiol A Neuroethol Sensory, Neural, Behav Physiol. 189(4):321–325. doi:10.1007/s00359-003-0409-z.

Hobson EA, Avery ML, Wright TF. 2013. An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. Anim Behav. 85(1):83–96. doi:10.1016/j.anbehav.2012.10.010.

Hobson EA, Avery ML, Wright TF. 2014. The socioecology of Monk Parakeets: Insights into parrot social complexity. Auk. 131(4):756–775. doi:10.1642/auk-14-14.1.

Hobson EA, DeDeo S. 2015. Social Feedback and the Emergence of Rank in Animal Society. Salathé M, editor. PLOS Comput Biol. 11(9):e1004411. doi:10.1371/journal.pcbi.1004411.

Hobson EA, Ferdinand V, Kolchinsky A, Garland J. 2019. Rethinking animal social complexity measures with the help of complex systems concepts. Anim Behav. 155:287–296.

Hobson EA, Mønster D, DeDeo S. 2019. Strategic heuristics underlie animal dominance hierarchies and provide evidence of group-level social information. arXiv https://arxiv.org/abs/181007215. doi:10.5061/dryad.f76f2.

Kampstra P. 2008. Beanplot: A Boxplot Alternative for Visual Comparison of Distributions. J Stat Softw. 28:1–9. doi:10.18637/jss.v028.c01.

Klass K, Cords M. 2011. Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: Simulation studies based on data from wild monkeys. Behav Processes. 88(3):168–176. doi:10.1016/j.behpro.2011.09.003.

Kubitza RJ, Suhonen J, Vuorisalo T. 2015. Effects of experimental perturbation of group structure on hierarchy formation and behaviour in House Sparrows. Ornis Fenn. 92(4):157–171.

Munroe KE, Koprowski JL. 2014. Levels of social behaviors and genetic structure in a population of round-tailed ground squirrels (Xerospermophilus tereticaudus). Behav Ecol Sociobiol. 68(4):629–638. doi:10.1007/s00265-013-1677-4.

Neumann C, Kulik L. 2020. EloRating: Animal Dominance Hierarchies by Elo Rating. :R package version 0.46.11. https://CRAN.R-project.

Oczak M, Viazzi S, Ismayilova G, Sonoda LT, Roulston N, Fels M, Bahr C, Hartung J, Guarino M, Berckmans D, et al. 2014. Classification of aggressive behaviour in pigs by activity index and multilayer feed forward neural network. Biosyst Eng. 119:89–97. doi:10.1016/jbiosystemseng.2014.01.005.

Pereira AS, Rebelo ID, Casanova C, Lee PC, Loucaid V. 2020. The multidimensionality of
female mandrill sociality-A dynamic multiplex network approach. PLoS One. 15(4). doi:10.1371/journal.pone.0230942.

Pierard M, McGreevy P, Geers R. 2019. Effect of density and relative aggressiveness on agonistic and affiliative interactions in a newly formed group of horses. J Vet Behav. 29:61–69. doi:10.1016/j.jveb.2018.03.008.

Schürch R, Rothenberger S, Heg D. 2010. The building-up of social relationships: behavioural types, social networks and cooperative breeding in a cichlid. Philos Trans B. 365(1560). doi:10.1098/rstb.2010.0177.

Shizuka D, Mcdonald DB. 2012. A Social Network Perspective on Measurements of Dominance Hierarchies. Anim Behav. 83(4):925–934. doi:10.1016/j.anbehav.2012.01.011.

Shizuka D, Mcdonald DB. 2015. The network motif architecture of dominance hierarchies. J R Soc Interface. 12(105). doi:10.1098/rsif.2015.0080.

Silk J, Cheney D, Seyfarth R. 2013. A practical guide to the study of social relationships. Evol Anthropol. 22(5):213–225. doi:10.1002/evan.21367.

Silk MJ, Finn KR, Porter MA, Pinter-Wollman N. 2018. Can Multilayer Networks Advance Animal Behavior Research? Trends Ecol Evol. 33(6):376–378. doi:10.1016/j.tree.2018.03.008.

Viblanc VA, Pasquaretta C, Sueur C, Boonstra R, Dobson FS. 2016. Behavioral Ecology Aggression in Columbian ground squirrels: relationships with age, kinship, energy allocation, and fitness. Behav Ecol. 27(6):1716–1725. doi:10.1093/beheco/arw098.

Wey TW, Jordán F, Blumstein DT. 2019. Transitivity and structural balance in marmot social networks. Behav Ecol Sociobiol. 73(6):1–13. doi:10.1007/s00265-019-2699-3.

Whitehead H, Dufault S. 1999. Techniques for analyzing vertebrate social structure using identified individuals: Review and recommendations. Adv Study Behav. 28:33–74.