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ANIMAL SOCIAL NETWORKS

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Constructing and analysing time-aggregated networks: The role of bootstrapping, permutation and simulation

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Abstract

1. Animal social networks are often used to describe dynamic social systems, where individual behaviour generates network-level structures that subsequently influence individual-level behaviour. This interdependence between individual behaviour and group structuring is of central concern for questions concerning the evolution and development of social systems and collective animal behaviour more generally.
2. Various statistical methods exist for estimating network changes through time. One approach, time-aggregated networks, takes repeated snapshots of interactions within windows of time to generate a time series of networks. However, there remain many analytical hurdles when implementing the time-aggregated approach. To ameliorate this, we introduce an R package NETTS that focuses on three analytical steps for analysing time-aggregated networks: choosing appropriate time scale using bootstrapping, comparing patterns to relevant null models using permutation and finally building and interpreting statistical models using simulated data. We use simulated data to first highlight these steps, then use observed grooming data from a group of vervet monkeys as an applied example.
3. Our results suggest that the use of bootstrapping and permutation can accurately extract known patterns from simulated data. Using this approach with vervet data suggests that there is consistent social structuring, differing from what would be expected due to chance, and that some individuals are contributing to this structure more than others (i.e. keystone individuals).
4. We demonstrate that bootstrapping, permutation and simulation can aid in constructing and interpreting time-aggregated networks. We suggest that the use of time-aggregated networks to quantify patterns of network change can be a useful tool alongside process-based approaches that seek mechanistic descriptions. Ultimately, by looking at both patterns and processes, dynamic networks can be used to better understand how individual behaviour generates social structures, and in turn how individual behaviour can be influenced by social structures, ultimately leading to a better understanding of the evolution of social behaviour.

KEYWORDS

animal social networks, dynamic social networks, keystone individuals, longitudinal multilevel models, social organization, social structure, temporal networks, time series

1 | INTRODUCTION

Understanding the dependence between individuals in social groups has been enhanced by the use of network approaches. A network approach deconstructs a social group into nodes and edges, representing respectively, individuals and the relationship between individuals (Newman, 2010). This allows for the description of social dependence between two individuals (dyad scale), around the individual (ego scale) and at the entire group level (network scale). This approach has become a successful and common method in various research fields, with the result that many theoretical and empirical predictions are tied to measurements of networks (Chapman et al., 2016; Duboscq, Romano, Sueur, & MacIntosh, 2016; Griffin & Nunn, 2012). In some cases, these theoretical and empirical concerns are temporal in nature, requiring some measure of how social networks change in time, i.e. viewing networks as dynamic rather than static (Aplin et al., 2015; Bonnell, Vilette, Henzi, & Barrett, 2019; Formica, Wood, Cook, & Brodie III, 2017). For example, the magnitude of repeatability in social network position has direct implications for the selection of social phenotypes within a population (Aplin et al., 2015). Similarly, when populations experience demographic changes such as the birth of new individuals, the magnitude of a juvenile copying their mother's social partners can have important consequences for the long-term stability of a population's social structure (Ilany & Akçay, 2016; Jarrett, Bonnell, Young, Barrett, & Henzi, 2018). Thus, network measurements in time can have important implications (Farine, 2018).

One particularly advantageous outcome of switching from static to dynamic social networks is the ability to address questions of process in collective behaviour. For example, to understand how shifts in one individual's behaviour might cause a cascade of changes throughout a social group requires a dynamic network approach. A particular interest in collective behaviour is the feedback between individual- and group-level dynamics. Namely, how variation in individual-level behaviour creates group level structures, which in turn influences further development of individual behaviour (Sumpter, 2010). By treating networks as dynamic, it becomes possible to identify and quantify the processes driving these individual-group feedbacks to gain a better understanding of how individual-level variation develops and what are the consequences for group-level behaviour. Interestingly, this particular focus on individual variation has some parallels with work in population dynamics that might prove useful in social network contexts (e.g. Benton, Plaistow, & Coulson, 2006).

Methodologically, time-ordered and time-aggregated network constructions have been introduced for analysing dynamic networks (Blonder, Wey, Dornhaus, James, & Sih, 2012). On one hand, time-ordered networks are networks that retain the order of interactions. These network constructions have been shown to be especially valuable when interested in questions about flow on a network (e.g. information, disease), as the timing of individual interactions can have important implications for the transmission between distant individuals (Blonder & Dornhaus, 2011), though see Farine (2018) for a discussion about when accounting for timing of interactions might be more/less justified. On the other hand, time-aggregated networks are constructed by aggregating data within a period of time and can be useful for addressing questions regarding changes in network topology. Depending on the scale of aggregation, these time-aggregated networks lose the ability to directly query when two individuals interact. However, they can provide information about how those interactions change between time-aggregated networks and therefore, can be very useful in measuring structural changes in networks through time. For example, time-aggregated networks have been used to compare how density of social networks changes between mating and birthing seasons (Brent, MacLarnon, Platt, & Semple, 2013).

There are a variety of software packages that enable the analysis of networks in time (e.g. Blonder et al., 2012; Fisher, Ilany, Silk, & Tregenza, 2017). In particular, the time-ordered (Blonder & Dornhaus, 2011) package handles both time-ordered and time-aggregated network construction whereas the networkDynamic (Butts, Leslie-Cook, Krivitsky, & Bender-deMoll, 2016) one can be used to extract time-aggregated networks. Here we introduce a custom R package: NETTS. Its purpose is to ease the construction and analysis of time-aggregated networks by: (a) facilitating window size choices by comparing (i) how time series extracted from time-aggregated networks change with window size, as well as (ii) how uncertainty in network measures change with window size, (b) contrasting the observed time series against null models using network permutations, and finally, (c) simulating network data to test, refine and interpret statistical models used to analyse time-aggregated networks. A critical step when constructing time-aggregated networks is choosing the window size, as it defines the temporal scale at which networks are constructed and measured. Choosing a scale that is both biologically meaningful, and contains enough data to construct a network that is representative of the group, can prove to be difficult. Similarly, comparing networks to a range of null network models is becoming standard practice to help identify and interpret structure in a network (Croft, Madden, Franks, & James, 2011; Farine, 2017; Whitehead, 2008). Finally, simulations are becoming an essential part of good statistical practice and can be used to validate the use of a particular statistical tool (Gelman et al., 2013). The NETTS package incorporates advances in these three areas to allow users to choose appropriate time-scales, identify temporal structural changes and to make informed inferences from statistical models.

In this paper we first give an overview of analysing time-aggregated networks using the NETTS package with simulated data. We then use grooming data from a group of vervet monkeys *Chlorocebus pygerythrus* to provide an example of using time-aggregated data to address questions concerning the temporal dimensions of social structuring in animal populations. Here, comparing the result of simulations to empirical data can be a useful way of inferring candidate mechanisms generating social structure (Farine, Downing, & Downing, 2014; Sumpter, Mann, & Perna, 2012). Given that social structure is generated by individual-level behaviours, we investigated whether some individuals were disproportionately responsible for the maintenance of social structure through time, i.e. are there keystone individuals driving group structuring through their grooming interactions? Here we focus on quantifying the variation in influence of individual grooming behaviour on the social structure of the group through time. This example targets only part of the collective behaviour framework (i.e. individual-level behavior → group-level structuring, not group-level structuring → individual-level behaviour) and provides an example of how the time-aggregated approach can be useful in studying collective animal behaviour more generally.

2 | MATERIALS AND METHODS

To introduce the netTS package, we first present the moving window approach for constructing time-aggregated networks from relational data. We then use simulated datasets to showcase three analytical steps to choose temporal scales and interpret results from the time-aggregated approach: (a) bootstrapping to choose lower limits to window size choices, (b) multiscale time-series analysis to check for natural temporal scales, and finally (c) the use of permutation to interpret network measures extracted from these time-aggregated networks. We perform these steps with two sets of simulated data: one in which there is no structure, and a second one with structure. This allows us to test whether the proposed methods can accurately detect (i) the presence of an underlying network structure and (ii) when there is none. The full package code can be found on github (github.com/tbonne/netTS), along with tutorials (Appendix S1), and the code used in the analyses presented here.

After this introduction to the package using simulated data, we present an example using observed vervet grooming data. We first show how one can use bootstrapping and natural scales to help choose an appropriate temporal scale. We then show how network permutations can be used to identify network structures through time. Finally, we sought to quantify keystone individuals, i.e. individuals whose grooming behaviour has a larger impact on the overall network structure.

2.1 | The moving window approach to aggregation

Generally, when constructing social networks using time-aggregated networks to interrogate relational data, a careful consideration of scale is required, e.g., is it best to group data into daily/monthly/yearly networks (Blonder et al., 2012)? This package aims to help with this process using a moving window approach designed to work with any relational data accumulated through time. The main input to the netTS package is a dataframe with the first two columns defining who is interacting, a third column with a date time stamp and an optional weight column specifying the duration or magnitude of each interaction. Therefore, data collected by ad libitum sampling, focal follows, scan sampling or gambit of the group can be used, though careful consideration of how to control for variation in sampling effort must be considered for each type of sampling methodology (see Section 2.3.1 below).

The moving window approach allows a user to define its size (e.g. windowsize = 1 month) and the amount to shift the window (e.g. windowshift = 1 day). This moving window subsets the relational data within a window and creates a network. It then shifts in time and repeats the process. By altering the size and shift of a moving window, it is possible to generate a time series of networks (Figure 1), which can be thought of as generating a multilayered network in which each network layer encodes the same type of interactions at different time points (Finn, Silk, Porter, & Pinter-Wollman, 2019).

2.2 | Simulated data

To validate our proposed methods, we simulated interaction data following a scan sampling design. In these simulations, an observer will scan a group of individuals a number of times where each individual has the probability of interacting with another individual with probability A. Here we set the probability to 0.10 for all individuals. If during a scan an individual is to interact with another individual, it will choose from its neighbour based on a fixed underlying network. Here we simulate interactions with a fully connected network (i.e. everyone is as likely to groom everyone) and a network with a skewed degree distribution (i.e. everyone has a few grooming partners, and some have a lot). For the simulation with the skewed network we additionally add a seasonal component to interaction probability, where there are seasonal fluctuations in probabilities in which individuals interact. The distances between peak interactions was set to 35 days with an increased interaction probability of 0.2. We provide the function used to simulate these data in the netTS package as the method sim.events.data (see vignette for more information).

2.2.1 | Identifying a lower limit to window size

The ability to alter the window size introduces the possibility of multiple scales being chosen. The lower limit to window size choices can, to some extent, be specified by the fact that as window size gets smaller, less data are aggregated within each network and the network measures become progressively noisier, i.e. more dependent on the specifics of the remaining samples. This lower limit is likely to be a function of the rate of sampling and the biology of the behaviour under study (Farine, 2015).

To identify the lower limit of window size choices, for a particular dataset, we take advantage of a bootstrap approach on the event data used to create the networks. Applying this method, it is possible to take multiple bootstrap samples of the event data within a window, create a network with the bootstrapped sample, calculate a network measure and then estimate the relative similarity between measures from the bootstrapped networks and the observed network

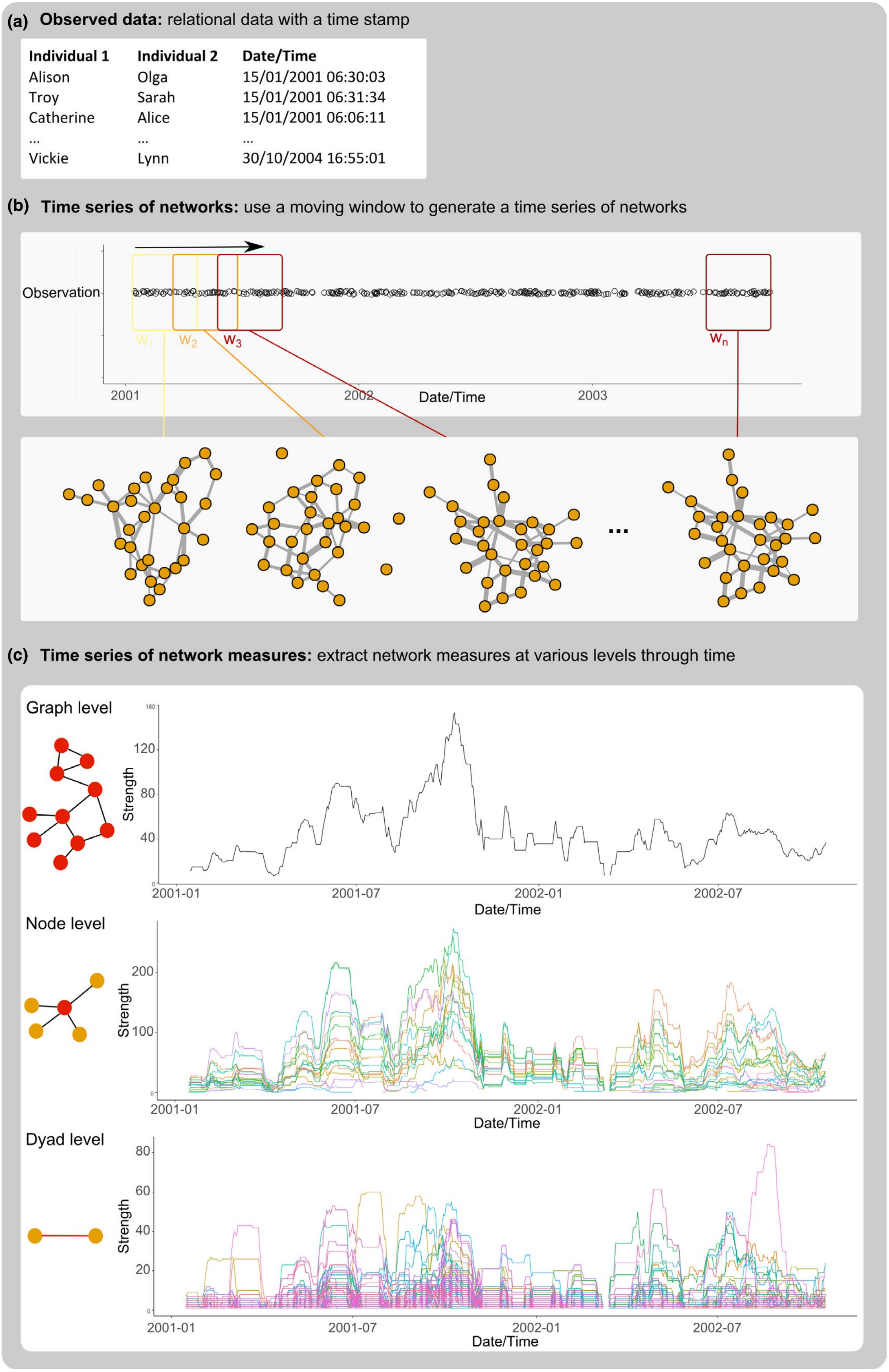

FIGURE 1 Overview of using a moving window approach to extract network measures over time: (a) the relational input data, (b) generate the time series of networks using a moving window approach, and (c) extract network measures at the dyadic, node and network scales

(Costenbader & Valente, 2003; Farine & Strandburg-Peshkin, 2015; Lusseau, Whitehead, & Gero, 2009). Highly similar estimates, and low variation in estimates, indicate that the network measure is robust to bootstrapped sampling, suggesting that the chosen window size is adequate to provide a good measurement. To test the efficacy of the bootstrapping approach, we provide a simulation test that suggests the relationship between bootstrapped networks and observed networks can provide useful information about the relationship between observed networks and a network constructed with all interactions (i.e. a complete network) (Figure S1).

Additionally, given that the bootstrap can only sample from the observed interactions, there is the possibility that missing interactions can drastically alter the network measure. In order to estimate the sensitivity of the network to missing data, we additionally estimate the effect of subsampling. To do so, we perform the bootstrapping procedure but on a subsampled portion of the observed data, and compare the resulting bootstrapped networks to the measures in the observed network (Carter, Schino, & Farine, 2019; Costenbader & Valente, 2003). This combination of bootstrapping and subsampling provides the user with the ability to assess uncertainty in a network measure under different window size choices. We implement this test in the check.windowsize function in netTS allowing users to experiment with potential window size choices. We further caution that there remains much work to be done in estimating network measure uncertainty (Farine & Strandburg-Peshkin, 2015).

This approach of using bootstrapping and subsampling is meant to test if the observed sample used to generate the network is sufficient to reliably capture network structure, i.e. if you had a slightly different observed sample, would the network structure come out roughly the same? Applying this approach to the simulated datasets, we found that, for the unstructured simulated dataset, increasing the window sizes (even at a 60-day window), the similarity did not increase, and the effect of subsampling was comparably high (Figure 2a,c,e). Whereas for the structured dataset, increasing the window sizes led to higher similarity between bootstrapped samples and observed samples (Figure 2b,d,f). It also reduced the effects of subsampling. This suggests that using bootstrapping to estimate uncertainty can help distinguish between unstructured and structured networks, and identify lower limit to possible window size choices.

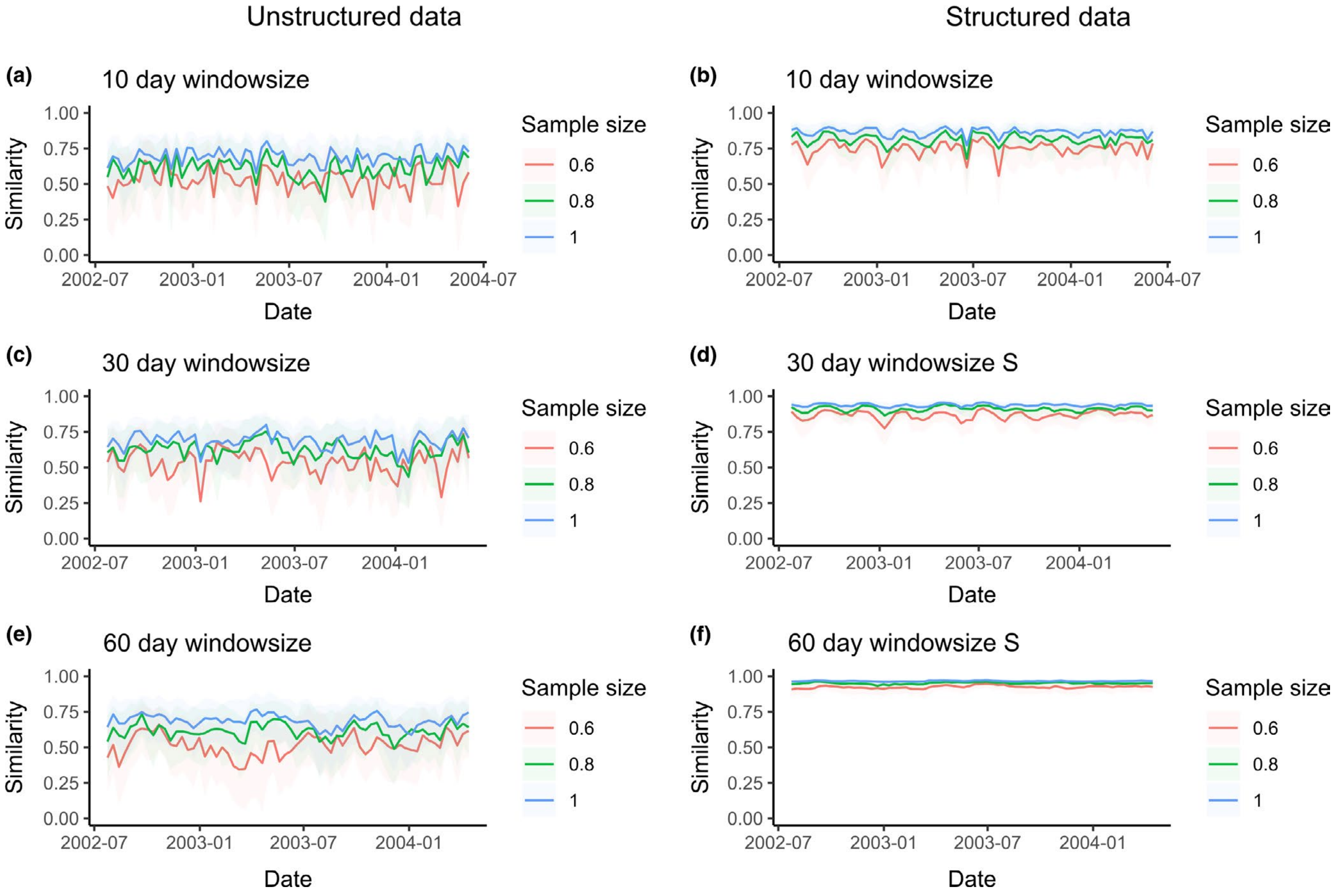

FIGURE 2 Estimating the lower bound of window size choice using bootstrapping and subsampling. Examples are shown for the unstructured (a, c, e) and structured (b, d, f) simulated datasets. Lines represent mean cosine similarity, shaded region the 95% quantiles, from 100 bootstrap comparisons between node degree in the observed and bootstrapped networks. Time series of observed networks were constructed using window size choices of 10, 30 and 60 days. To estimate the sensitivity to missing edges, this procedure was repeated using a random subsample of the original dataset (i.e. 1, 0.8 and 0.6 of the original data)

2.2.2 | Choosing a window size

The choice of the upper limit to potential window sizes, apart from the maximum time-scale of the dataset, has no a priori limit and will increasingly capture longer-term trends. In some cases, depending on the temporal dynamics of the systems of interest, 'natural' scales can potentially exist (Caceres, Berger-Wolf, & Grossman, 2011). To aid in looking for natural scales we introduce the use of sample entropy as an approach that works well with many types of time series data (Richman & Moorman, 2000). This measure is maximized when the time series is either completely random, or completely static and minimized as the time series becomes more structured. Sample entropy is calculated by looking at sequences of values in a time series and comparing how many times each sequence of length n appears in the time series to how many times the sequence $n + 1$ appears. The ratio between the two provides an estimate of predictability, e.g. if the first two values in the time series are 2.5 and 4.6, how many times do you find this sequence of 2, and if it is followed by the value 3.2, how many times do you find this sequence of 3 (i.e. $n + 1$). By looking at how temporal scale alters this ratio, it is possible to identify potential natural scales, and provide a sense of how a particular network measure changes with temporal scale (Costa, Goldberger, & Peng, 2002). The NETTS package provides a function (check.timescale) to plot how sample entropy in a particular network time series measure changes with window size choices (i.e. scale). As the identification of temporal scales is an area of active research, we also provide the ability to input user defined functions to assess how temporal scale alters network time series measures (e.g. how does total coefficient of variation in the time series change with time scale?) (see vignette: choosing window size).

When we apply this approach to the simulated data, we see that in the case where there is no structure (full network) and where interaction probabilities remain constant, we find high sample entropy values (compared to the structured simulated dataset) with a shallow decrease in sample entropy as window size increases (Figure 3a). We also find large divergences between bootstrapped replicates. For the dataset with a structured network (skewed degree distribution and a seasonal change in interaction probabilities), we find lowest sample entropy at the true seasonal time-scale as well as high agreement between bootstrapped replicates (Figure 3b).

Overall, the question of interest and knowledge of the study system are likely to play a large role in choosing the temporal scale to measure network change. In general, apart from attempting to identify one optimal window size, it is likely the case that the way a pattern of interest changes depending on the time-scale chosen will itself be of great interest (Costa et al., 2002; Levin, 1992).

2.3 | Extracting Network measurement through time

Once a window size has been selected and a time series of networks generated, it is possible to use network metrics at the scale of the network, node or dyad (Newman, 2010). Although a few common metrics are built into the NETTS package, the network measure required is a user-specified function. This function takes a network as input and returns a value, or vector of values in the case of node or dyadic measures. By using user-generated functions, the package can take advantage of the wide range of network measures available, without constraining users to a pre-specified list of options (see vignette: Introduction to NETTS).

2.3.1 | Controlling for sampling effort/time

Given the time series nature of the data, as well as the potential for variation in data collection methods through time, it is important to consider how changes in sampling effort might impact a potential measure (Davis, Crofoot, & Farine, 2018; Franks, Ruxton, & James, 2010). In some cases, the ability to use scaled or transformed measures, such as the simple-ratio index (SRI), can facilitate comparisons between networks in time (Farine & Whitehead, 2015). Another option, that keeps the measure on the observed scale, would be to directly control for sampling effort over time. This approach converts

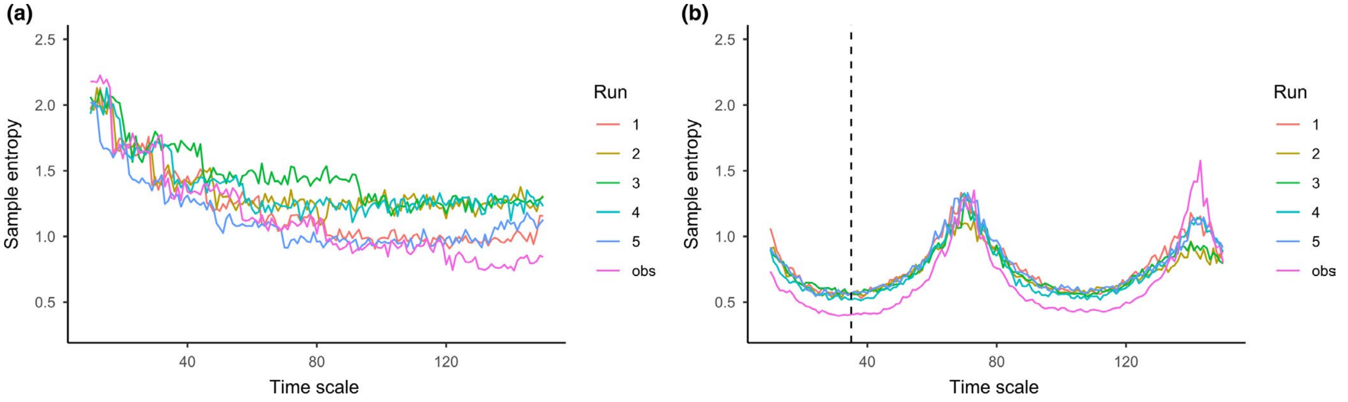

FIGURE 3 Sample entropy by window size for (a) a simulated dataset constructed with no imposed temporal scale, (b) a simulated dataset with a temporal scale imposed. The sample entropy from the observed data, along with five bootstrapped datasets, is calculated for each window size choice. The dashed line in (b) indicates the imposed seasonal component in the simulated data

the observed social behaviour to a rate (e.g. interactions/hours of observation, or interactions/number of scans). For example, to construct an interaction network in Thronbills (genus Acanthiza), Farine (2015) divided the number of observed interactions between individuals by the time observed in the same flock. The NETTS package offers the possibility to include a sampling effort function in order to help the user to control for a certain type of sampling effort. These functions take as input an event's dataframe and return a single value of effort. The NETTS package provides three functions. The first approach sums the total time (effort.time), based on the first and last sample time of each day within a window. This method assumes equal sampling effort throughout the day, i.e. ad libitum data collection. The edges in network are divided by the time spent observing (number of interactions observed/number of hours observed). The second approach (effort.scan) uses a dataframe, supplied by the user, containing the number of scans during sampling periods, e.g. number of scans per day. This approach is useful when observations are captured within set scanning periods and would be suitable for sampling regimes where periodic scans are used to collect data. Here, the edges in networks are divided by the number of scans within a window. Finally, the third effort function is designed to correct for variation in effort with focal data (effort.focal). This method requires a user supplied dataframe with times and durations of focals. Each edge of the constructed network is divided by the amount of time it could have been observed, e.g. an interaction between A and B can only be observed when either A or B is the focal. In other words, if A and B are followed for 10 and 5 min respectively, then 15 min is the total amount of time where A and B could have, potentially, been seen interacting. As sampling effort will vary by dataset and collection method, it is also possible to construct user defined effort functions to correct for sampling effort when estimating network measures (see vignette: controlling for sampling effort). Given that our simulated data do not show variation in sampling effort, we present some examples using these methods below with our field data on vervet monkeys.

Because variation in sampling effort can have a large impact on the network structure, it needs to be considered carefully (Davis et al., 2018; Whitehead, 2008). Here we suggest the use of network indices (e.g. simple-ratio index) tailored in reducing variation in sampling effort, as well as the conversion of dyad weights to ratios by dividing interactions by sampling effort directly. We also propose the use of null network models, that can incorporate variation in sampling effort, to better distinguish what network structures might simply be a result of variation in sampling effort (Croft et al., 2011; Farine, 2017).

2.4 | Interpreting measures through time using null models

Given the ability to compare how a network changes in time, it can also be useful to contrast how this changing network relates to a null model using network permutations. The exact specification of the null model, i.e. how it is constructed, can aid in understanding

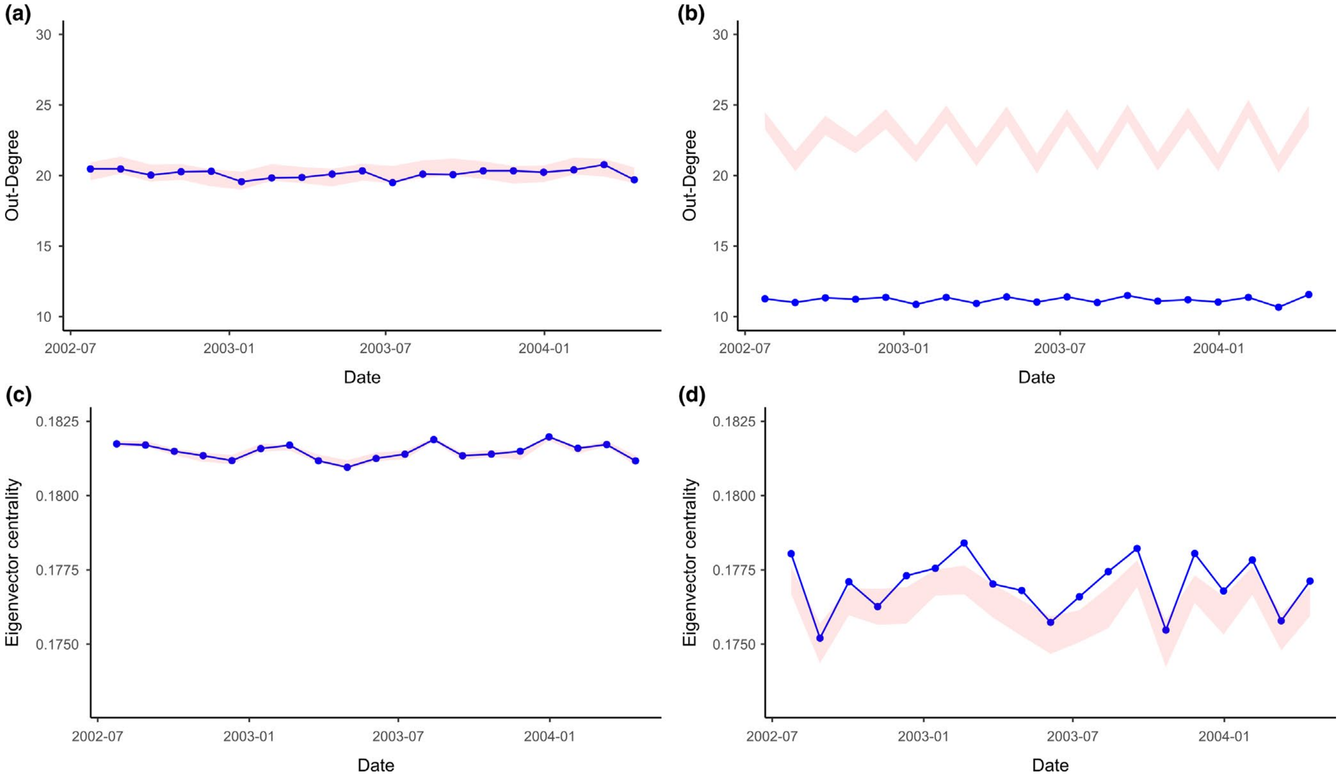

FIGURE 4 Eigenvector centrality extracted from networks generated using (a, c) unstructured and (b, d) structured simulated datasets. Permutations of individuals between simulated interactions were used to generate the range of eigenvector centrality values expected due to random interactions, while retaining individual differences in the amount of interactions

the structure of the observed network. For example, it is possible to construct a time series of centrality measures within a grooming network and look for trends over time. However, if we want to compare centrality measure to what might be expected if grooming partners are chosen at random, we would want to use a null model. The aim of the null model is to create replicated datasets in which the aspect that is of most interest to us, often who is observed with who, is randomized (Farine, 2017). Here, the choices of the null model can help refine how the observed pattern is different (Croft et al., 2011; Farine, 2017; Whitehead, 2008). You could decide to take all grooming events and randomly distribute them between nodes to generate a null model. Similarly, you could retain the fact that some individuals are more present in grooming events than others by permuting individuals between grooming events. You could then compare the observed network to those null models to make inferences about how it differs, or not. The way that the observed networks differ from the permuted networks and the specific choices of how permutations are carried out, can help highlight important structure in the observed networks. In NETTS, by performing permutations for each time-aggregated network, it allows for estimations of how the network diverges from a null model through time (e.g. is it consistently different, or are there only certain times/seasons where there is a difference?). We provide some predefined permutation methods in NETTS, but also allow for user-specified permutation functions that will take an event data frame as input and return a range of network measurement values (see vignette: Using network permutations).

With the simulated data, we show that using permutations can distinguish between the structured and unstructured datasets (Figure 4). The measures of eigenvector centrality and out-degree, for the unstructured simulated dataset, are well within the range expected due to randomized interactions (Figure 4a,c). However, in the case of the structured simulated dataset, we find that out-degree is well outside the range expected due to random, and for eigenvector centrality some values fall inside and outside the range expected due to chance interactions (Figure 4b,d). Given that the permutation used kept the number of times each individual was seen in an interaction, it then also retained the skewed degree distribution in the structured simulated dataset. The difference between the permuted and observed networks are then only driven by the difference in the arrangement of the edges beyond degree distribution. This, therefore, suggests only slightly more centralization than expected, given the skewed degree distribution.

3 | USING NETTS: AN EXAMPLE OF A PRIMATE SOCIAL NETWORK

3.1 | Input data

TABLE 1 Example data used as input for the NETTS package

From <chr>	To <chr>	Date <S3: POSIXct>
Laur	Malc	2015-07-01 12:32:19
Malc	Laur	2015-07-01 12:33:01
Ubun	Wall	2015-07-01 16:08:26

We use grooming data from a fully habituated group of vervet monkey in the Eastern Cape of South Africa (Josephs, Bonnell, Dostie, Barrett, & Henzi, 2016), e.g. Table 1. These gregarious primates occupy a semi-arid environment with large seasonal fluctuations of both temperature and rainfall, and similarly show seasonal breeding patterns (Lubbe et al., 2014; McFarland, Barrett, Boner, Freeman, & Henzi, 2014; McFarland et al., 2015). These data were collected by scan samples taken twice every hour for 10 min, during 10-hr days, approximately 3–5 days per week between July 2015 and July 2016. The group consisted of 9–13 males and 11–16 females over the study period.

3.2 | Correct for changing sampling effort

Given that sampling effort can vary between time periods, it is important to control for it when comparing certain network measures over time, with some measures being more sensitive to sampling effort than others: e.g. node strength versus node degree. Here, we demonstrate how controlling for the number of scans alters average strength of a network over time (Figure 5). All subsequent analyses use these corrected network measures.

3.3 | Assess window size choice

We first use the bootstrap test to identify the lower end of possible window size choice (Figure 6). The results show that, given the temporal resolution of the vervet data network, measurement accuracy is reduced in window sizes below 30 days. By looking at estimates of similarity across the study period, it can also help to identify time periods where sampling effort was not adequate for a particular window size. For this vervet dataset, the consistently high similarity between the bootstrapped and observed networks, using a 60-day window, suggests that the window size results in robust networks.

We then vary the window size from 10 to 150 days to see how sample entropy changes (Figure 7). In this case, sample entropy showed a quick decrease in entropy similar to the shape of the unstructured simulated dataset, though with a lower entropy and higher agreement between bootstrap samples. We also found a smaller scale oscillation of 7 days, picking up that data was not collected during the weekends. Given the bootstrap and sample entropy results, we choose a window size of 63 days, meeting the bootstrap minimum and accounting for the temporal effect of weekend in our data.

It is also important to note that, when looking at how a time series changes with temporal scale (i.e. window size), the results will depend on the particular network measure used to construct the time series, e.g. mean network strength/degree, or eigenvector centrality might show very different responses to changes in temporal scale. In this

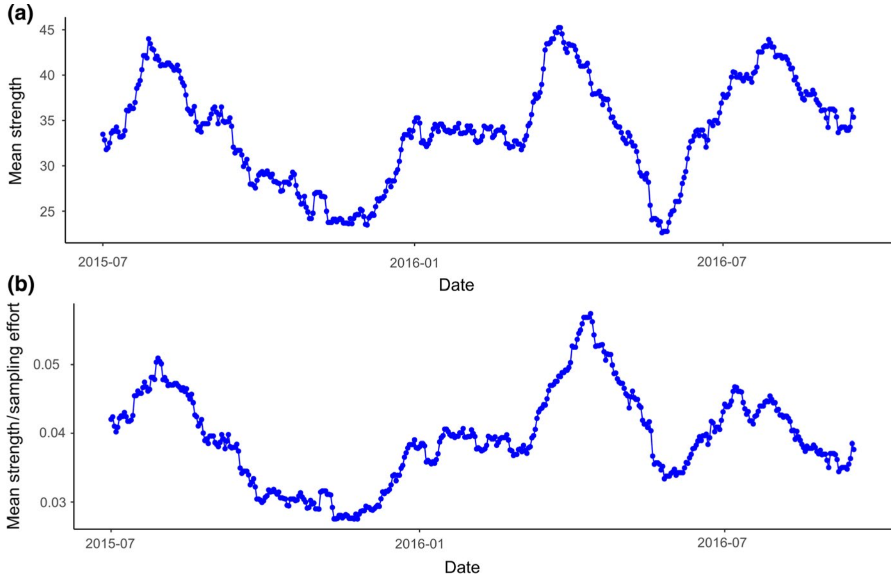

FIGURE 5 Mean network strength over time for a group of vervet monkeys: (a) without correcting for sampling effort in the field, and (b) after correcting for sampling effort

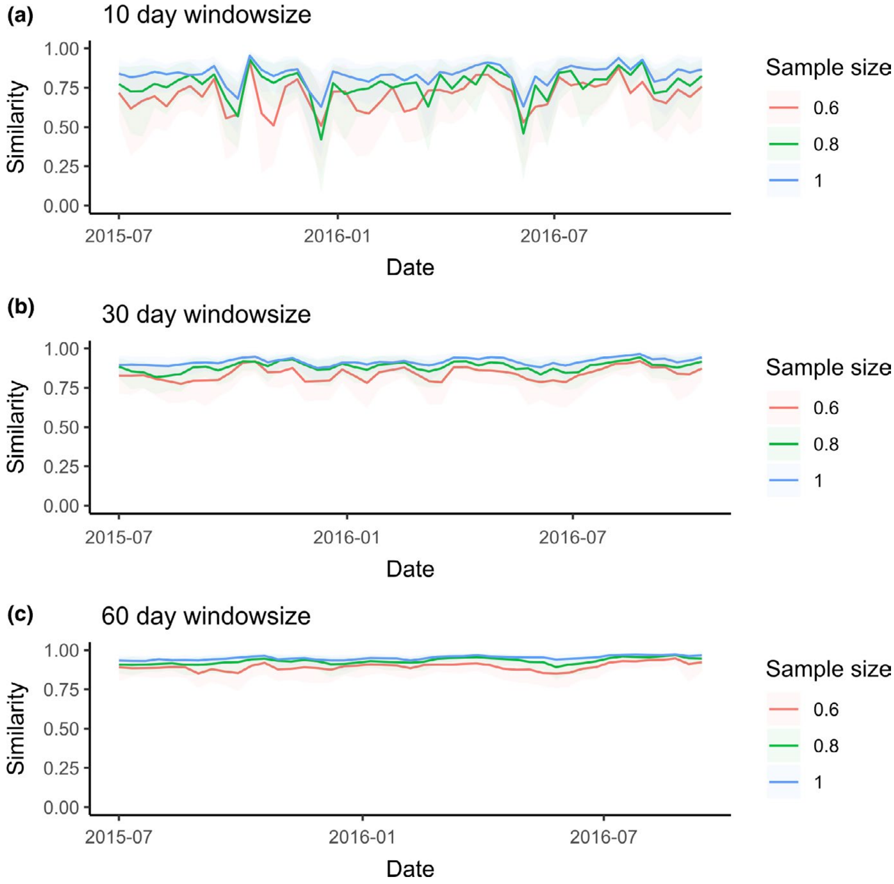

FIGURE 6 Results of the bootstrap test to quantify the uncertainty in networks constructed using (a) 10 day, (b) 30 day, and (c) 60 day window sizes. For each window size, cosine similarity values between observed and bootstrapped estimates of node degree are presented for the full data and subsampled datasets to assess sensitivity of network structure to missing data. Higher similarity estimates and lower variability around these estimates, indicated by the shaded areas (95% CI), suggest more robust network measurements

case, we used mean strength of the network due to our interest in how changes in individual network strength impacts group level structures.

3.4 | Assessing network structure through time

We used a permutation approach to assess the consistency of mean out-degree (the number of partners groomed) and mean eigenvector centrality of the network (magnitude to which the grooming interactions concentrate on a few well-connected individuals) (Figure 8).

We can see from Figure 8 that, within the group, out-degree is consistently lower than expected with random grooming interactions, i.e. individuals are more selective with whom they groom compared to random. Whereas, in the case of mean eigenvector centrality, there is less differentiation between random and observed networks, with only occasional times when mean eigenvector centrality is not lower than expected by chance. In these

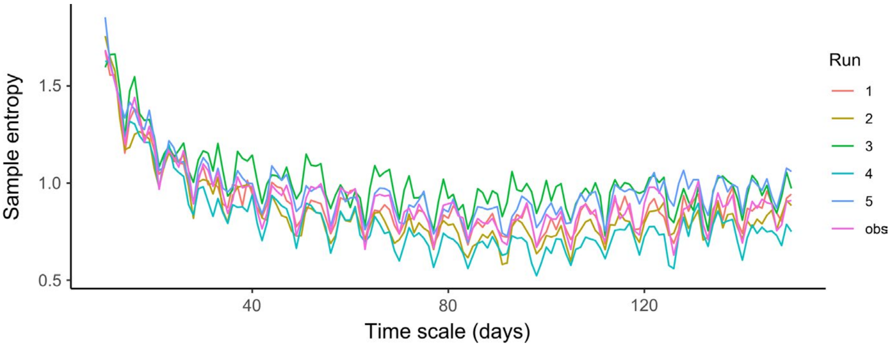

FIGURE 7 The relationship between window sizes used to create networks (i.e. temporal scale), and sample entropy of the resulting time series. Observed sample entropy measures are presented along with measures calculated on five bootstrapped samples from the observed data

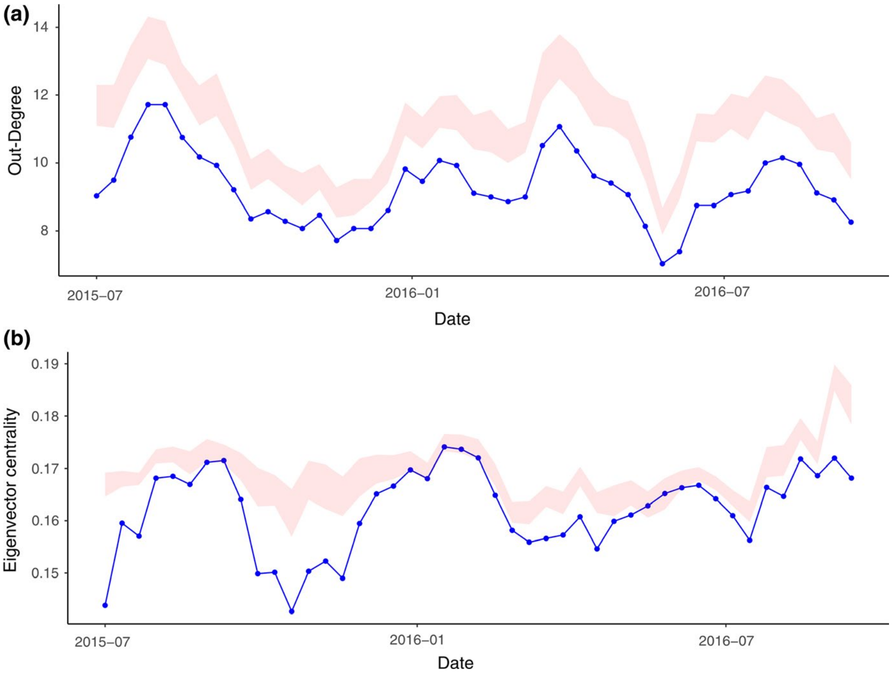

FIGURE 8 Permutation across time: (a) mean out-degree of grooming, and (b) mean eigenvector centrality. The observed values are presented as blue points, and the 95% quantiles generated through permutations are presented as a pink ribbon

examples, the null network had a higher mean out-degree and mean eigenvector centrality compared to the observed. It is also important to note that, in NETTS, it is possible to compare networks to null network models, however there is no function at the moment to compare two networks directly to each other using permutation.

3.5 | Identifying keystone individuals

To identify keystone individuals, we look to see how individual changes in out-grooming behaviour influenced the centrality of the group as a whole. Here, we are interested in answering the question: do some individuals influence the social structure of the group more than other individuals when they groom? If certain network structures have beneficial effects for individual fitness within a social group, are some individuals more responsible for the maintenance of this structure, and how does that relate to who benefits most from a particular social network structure (Alberts, 2019; Brent, 2015; Schülke, Bhagavatula, Vigilant, & Ostner, 2010)? An example of this is that eigenvector centrality has been shown to be a better predictor of offspring survival in female baboons than dyadic-level connections (Cheney, Silk, & Seyfarth, 2016).

With the NETTS package, we extracted individual out-grooming strength and eigenvector centrality of the network over time. We then used a generalized additive mixed model to estimate how changes in individual out-grooming influenced the eigenvector centrality of the network. We allowed this effect to vary by individual by using a random slope for the effect of out-grooming. If this random slope turns out to be negligible, it would suggest that changes in out-grooming behaviour for all individuals have the same effect on mean eigenvector centrality. We also control for seasonal effects via a circular basis spline on day-of-year, and model dependence in the residuals using an AR1 process. We fit the model with the BRMS package following a Bayesian approach (Bürkner, 2017).

The model suggests that there are some differences between individuals in the effect of their grooming on centrality of the group (standard deviation in the effect of grooming: *SD* (grooming) = 0.16, 95% CI: 0.10, 0.24) (Table S1). Running the model with and without a random slope (ΔWAIC = −24.38, *SE* = 15.26) suggests that there

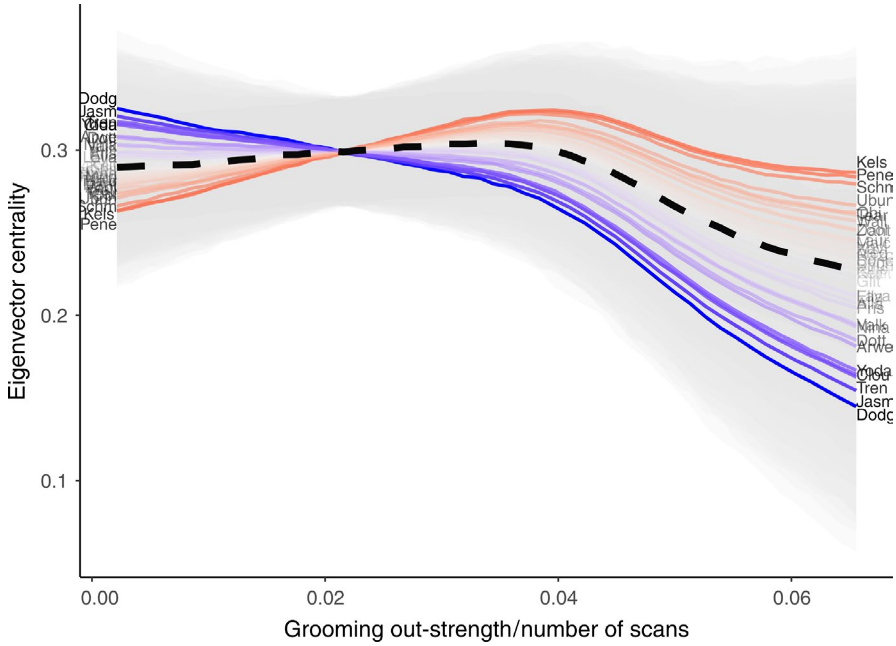

FIGURE 9 Model estimating how changes in out-strength by nodes influence the centrality of the network as a whole: (a) overall mean effect of out-grooming on network eigenvector centrality, and (b) individual level effect of out-grooming on network eigenvector centrality. Individual lines represent the effects of particular nodes (individuals) and are coloured based on their deviation away from the mean effect: i.e. blue is lower than the mean, and red is above the mean effect. Shading indicates the 95% credible intervals for each line. Each line is also given labels based on the name of the individual to aid in identifying those individuals having either a more positive or negative effect on eigenvector centrality

is some evidence for individuals that are associated with increases/decreases in centrality when their out-grooming increases, and points to potential keystone individuals (Figure 9).

To better interpret and make inferences from these results, we use the unstructured and structured simulated datasets. Running the same regression model on simulated data, with a fully connected grooming network, suggests that when individual grooming is not constrained, i.e. all individuals have equal probability of receiving grooming, the model showed little difference in individual influence on group eigenvector centrality (*SD* (grooming) = 0.04, 95% CI: 0.00, 0.08) (Table S2). However, in the case where individuals show constraints in their grooming behaviour (i.e. there was a skewed distribution), the model found differences in the effect of node out-strength on centrality of the group (*SD* (grooming) = 0.09, 95% CI: 0.05, 0.14) (Table S3). Given these simulated data were constructed with a fixed network structure, and no between individual differences in grooming probability, the results suggest that certain positions within the network can have more of an impact on eigenvector centrality. In the case of the observed data, where the network structure is dynamic and there are individual differences in grooming, we see larger estimates of individual differences in their impacts on eigenvector centrality. This suggests that variation in individual contribution to group structuring is more prominent in the observed dataset, though more work would be needed to tease apart the role of individual differences in network position and interaction rates on group level structure. This example, however, does highlight that the use of simulated data can be used effectively to better interpret results from observed data.

4 | CONCLUSIONS

Time-aggregated networks are a promising approach for quantifying patterns of structural change in animal social networks. Taking a dynamic view of social structure can address recent questions in the animal social network literature. For example, if certain network positions or characteristics provide fitness benefits (Alberts, 2019), a dynamic approach to networks can be used to quantify the consistency to which individuals maintain these positions/characteristics and, potentially, could reveal the mechanisms behind these processes (Ostner & Schülke, 2018). Similarly, in a more applied context, given social structuring has the potential to influence population dynamics (Alberts, 2019; Benton et al., 2006; Cantor et al., 2019), a dynamic approach might be used to better understand how environmental changes influence social structuring, providing further insights into population dynamics of social species in response to climate or landscape changes. The construction of time-aggregated networks, however, requires careful consideration of measurement and temporal scale. Similarly, the choice, parameterization and interpretation of statistical models employed to analyse the resulting time series of networks require careful inspection. We advocate for the use of bootstrap, permutation and simulation to facilitate decision-making regarding these choices, and have introduced the NETTS package for this purpose. We suggest that the patterns of change in social networks can be used in combination with process-based approaches, e.g. stochastic actor oriented networks, or relational event models, which seek mechanistic descriptions (Butts, 2008; Snijders, Van de Bunt, & Steglich, 2010). This combination of pattern and process is vital for understanding both the drivers behind social structuring and the subsequent consequences of these structures in social groups, leading to a better understanding of the dynamics of social structuring in animal populations.

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AUTHORS' CONTRIBUTIONS

T.R.B. and C.V. conceived the ideas and designed methodology; C.V. collected the data; T.R.B. analysed the data; T.R.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data used in the paper have been uploaded to github and are available from the package netTS (https://github.com/tbonne/netTS) and (https://doi.org/10.5281/zenodo.3597749) (Bonnell & Vilette, 2020).

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SUPPORTING INFORMATION

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