Inferring networks from multivariate symbolic time series to unravel behavioural interactions among animals

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A traditional way to quantify synchronous interactions between animals has been to use concordance indices, which commonly do not take into account the effects of the length of the sampling time and of behaviour driven by third parties. We overcome these issues by casting the process of investigating behavioural interactions into a network inference methodology. We summarized multivariate time series using a complex network whose construction depends on a surrogate hypothesis testing data analysis of synchronous interactions between animals. The methodology accounts for the effect of third parties on pairwise comparisons, allows one to test the effect of the size of the sampling window on the interactions between animals, and allows one to test behavioural models of increasing complexity. We used a continuous 1-month behavioural data set of the foraging activity of a mixed-sex group of 40 Soay sheep, Ovis aries. We uncovered underlying patterns of behavioural interaction between individual sheep by applying our inferential approach to the symbolic multivariate time series of activity, that is grazing, not grazing. Our findings clearly indicate that animals of the same sex are more synchronized than animals of different sex independent of body size. We advocate that the method proposed is more general and more efficient at detecting patterns of synchronization than traditional concordance indices. We provide the reader with a comprehensive software toolbox to apply the methodology proposed.

Concepts such as evolution, adaptation and resilience are based on the response of living organisms to changing environmental conditions or to behavioural interaction including species competition, predation and cooperation. In many cases, the strength of the response is measured in terms of indices such as synchrony between animals and the surrounding environment. In this paper, we show that the use of a graph or a network is a convenient, clear and capable method of summarizing and unravelling complex behavioural interactions, including synchronicity and social interactions between animals or animal groups (Croft et al. 2004; Krause et al. 2007).

Networks are mathematical structures used to model complex relations between subjects from a certain collection. In this context a network refers to a group of vertices representing the subjects and a number of edges that connect pairs of vertices (Bollobás 2008). The connections between the subjects can, in principle, be calculated using any algorithm that represents the nature of the relationship to be studied, for example two subjects are connected if they have a high value of a pairwise synchrony index.

By using a network to represent the overall structure of interactions among a group of animals we immediately reduce the mass of pairwise synchrony (or concordance or coherence) measures to a single object. The network provides a useful and appropriate alternative mechanism to understand the emergence of structural relations between individuals and subgroups. In large collections of animals this network structure may then be analysed using the statistical machinery of both classical graph theory and the modern field of complex networks. These concepts and tools have matured to the extent that they find widespread application in studies as diverse as power electronics, anthropology, geography, psychology, information science, economics and biology (Strogatz 2001; Costa et al. 2007), although they have had less application in the field of animal behaviour (Krause et al. 2007).

In this paper, we address several technical issues to provide a generic methodology to construct a graph of behavioural interactions from field activity recorded in the form of multivariate time series. We discuss the various competing measures of coherence (or synchrony) between pairs of animals, the construction of network...
interactions from multivariate time series, and propose suitable statistical tests for significance (both pairwise and at a network level). Our methods account for the effect of third parties on pairwise interactions, and allows one to test behavioural models of increasing complexity with the use of surrogate hypothesis, or randomization, testing (Small 2005; Carmeli 2006; Zhang & Small 2006). The algorithms we describe are hence available for practitioners to tease apart interactions, communities and structure from field measurements of complex behavioural interactions.

Behavioural synchronization refers to animal activities that are temporally correlated with external events, such as circadian rhythms, the activity of their peers or predators, or the phenology of plants as a food resource. In the same fashion, asynchrony can be defined as the lack of temporal correlation. The relevance of synchronization to survival is that behaviour is one of the most flexible ways to respond to a changing environment. For example, an animal’s fitness can depend on its ability to synchronize its behaviour to changes in weather conditions (migration, searching for shelter), tidal flows (feeding bouts in fish), presence or abundance of predators (fleeing behaviour, home range shifting, vigilance behaviour), mating opportunities or physiological condition of peers (oestrus). (For examples see Martin & Bateson 1993; Wagner 1998; Cortes et al. 1999; Keren & Olson 2006; Bolliet et al. 2007; Pays et al. 2007a; Visser 2008.)

Synchronization can also play an important role in evolutionary processes. The evolution of the social structure of wild populations is based on the frequency and complexity of the interactions between group members (Mooring & Hart 1995; Croft et al. 2004; Bon et al. 2005; Krause et al. 2007). In many mammalian taxa brain size and cognition seem to be related to social interactions (Dunbar 1988; Pérez-Barbería et al. 2007). Repeated interactions between pairs of peers are the basic requirements for the evolution of reciprocal altruism (Milinski 1987). Furthermore, there is an interesting feedback between activity synchronization and spatial patterns of animal distribution (Bowyer 2004; Pérez-Barbería et al. 2007). Spatial proximity triggers mimetic behaviour between peers, but at the same time animals with synchronized activity bouts might be more likely to form stable groups and therefore segregate from less synchronized peers (Conradt 1998; Ruckstuhl 1998).

A variety of indices and methods have been developed to represent behavioural synchrony between group members with each suited to the particular case studied. They range in order of complexity from traditional concordance indices (Martin & Bateson 1993) to modelling approaches (Gautrais et al. 2007). Concordance indices measure the proportion of occurrences of an event or numbers of events between two or more subjects (Martin & Bateson 1993; Pays et al. 2007b; Caro et al. 2008). Some of these indices attempt to control for the concordance in occurrences that might result by chance from the recording method (Kraemer 1979). Methods have been developed to study the distribution of events across time, for example using the standard deviation as a measure of event clustering when studying allelomimetic vigilance behaviour (Pays et al. 2007a). More sophisticated approaches use Markov chain models to investigate collective oscillations in behavioural synchronization (Gautrais et al. 2007), and fast finite Fourier transformations are used to process data from model simulations to test null hypotheses such as no synchronization between animal groups, or to discover cyclical patterns of synchronization (Pérez-Barbería et al. 2007).

One of the issues when using concordance or similar indices is that the behaviour recorded might last from a fraction of a second to a few seconds (e.g. birds feeding on insects, vigilance scans of antelope groups) to many minutes (e.g. grazing or resting bouts in ruminants). This makes the concordance indices dependent on the size of the sampling window of the observations (Kraemer 1979; Martin & Bateson 1993). Another issue is the effect of third parties in pairwise correlations when representing interactions in networked systems.

We propose here a methodological approach to help the analysis and representation of any of these indices in networked systems. The method combines surrogate hypothesis testing to assess behavioural patterns of interaction and network tools to represent the interactions in these complex systems. The method overcomes some traditional problems when assessing animal interactions, in particular, the effect of third-party interactions (i.e. interactions between elements A and B are driven by interactions between A and C and between B and C, Dahlhaus 2000). We introduce and demonstrate our basic methodology with reference to a multivariate symbolic time series derived from a comprehensive foraging behavioural data set on Soay sheep, Ovis aries (grazing, not grazing) to test for behavioural synchrony among the animals. We provide the reader with a comprehensive software toolbox to apply the methodology proposed (see Supplementary Material).

**METHODS**

**Data Set**

The multivariate symbolic time series data set comes from an experiment by Pérez-Barbería et al. (2007). The experiment consisted of recording the foraging behaviour (summarized in a binomial classification of the activity: grazing, not grazing) of 40 mature Soay sheep classified by gender and body size. Specifically, there were 20 males and 20 females, subdivided into two groups within each sex, namely, five small and five large sheep. The differences in body mass between groups were such that significant differences in behavioural synchronization and consequently in the spatial segregation between groups according to the activity budget hypothesis should be detectable following Ruckstuhl & Neuhaus (2002), although some experimental approaches do not corroborate this (Michelena et al. 2006; Pérez-Barbería et al. 2007).

Each animal was fitted with a data logger that recorded grazing activity through a simple voltage switch every 30 s for a period of a month. Head-down activity (grazing) was noted by the logger and recorded as a 1 and all other activity was regarded as not grazing and recorded as a 0, thus producing a symbolic time series for each animal for each day of the experiment. The accuracy of the loggers was evaluated with three other nonexperimental Soay sheep for 2 weeks before the experiment. A concurrence of 98% between the behaviour recorded by the loggers and the real behaviour as assessed by inspection of CCTV video surveillance was found. The data set comprised a total of 16 days, Tuesday to Friday for each week of the 4-week experiment. A detailed description of the experiment and more explanation on the groupings can be found in Pérez-Barbería et al. (2007). Representative segments of the data over a recording period of 1 h for both a male and a female on a typical day are shown in Fig. 1.

**Detecting Synchrony**

We investigated the relationship between pairs of animals and groups of animals using three basic synchrony indices. These pairwise indices of synchrony can be used to establish correlation-like matrices, which are further analysed to construct a network summarizing the animals’ synchronization (see $S$ estimators below). Note that we reconstruct a causal (from the recorded data) network and not a physical interaction network.

The first index constructs a correlation-like matrix $C$ whose entry $C_{ij}$ is the causal synchronization score between animal $i$ and animal $j$. Specifically, if the activity of animal $i$ at time $t$ is denoted by $a_i(t)$ then,
the activity time series for animal and (b) male on a typical day. The segments consist of 120 records covering 1 h of activity. Grazing activity is represented by a value of 1 and not grazing or other activity is represented by a 0.

\[
C_{ij} = \frac{1}{N} \sum_{i=1}^{N} \chi \left( a^{(i)}_t = a^{(i)}_j \right)
\]  
(1)

where \(\chi(\cdot)\) is equal to 1 if the condition is true and zero otherwise. The matrix \(C\) will be symmetric with diagonal entries equal to 1. The number of records \(N\) is taken in this instance to be the number of measurements per day, so for each day we construct a new correlation-like matrix. The above index can be readily recognized as the traditional ecological (bivariate) index of concordance (Martin & Bateson 1993).

As animal behaviour is a composite of a number of activities distributed in bouts of different length, we applied two further indices in an attempt to capture the real scale at which the behaviour takes place (Martin & Bateson 1993). A second synchrony index potentially useful in identifying any inherent timescale properties is calculated by considering decimal representations of the activity symbolic time series. For example, consider the activity time series for animal \(i\), \((a^{(i)}_1, a^{(i)}_2, a^{(i)}_3, a^{(i)}_4, a^{(i)}_5, \ldots)\), with a window of length three, the \(t\)th transformed data point is

\[
a^{(i)}_{t+1} a^{(i)}_{t+2} \rightarrow z^{(i)}_t = \sum_{j-t}^{t+2} a^{(i)}_j / 2^{j-t}
\]  
(2)

where \(j\) represents the position of the \(t\)th symbol after the decimal point. The time series \(z^{(i)}\) thus embodies a measurement activity timescale and can be used to construct other correlation score matrices to be further analysed by our network techniques. This index can be thought of as capturing the pattern of activity over a given time span. Similarity of values of this index suggests coherence of patterns of activity between animals. In our study, we constructed the correlation matrices via the Pearson correlation coefficient, which is sensitive to linear relationships among the activity timescale and can be used to construct other correlation matrices to be further analysed by our network techniques.

\[E = - \sum_{i=1}^{p} \lambda_i \log \lambda_i\]
(3)

This is inversely proportional to the strength of interactions between the \(p\) time series. The S estimator scales \(E\) to lie between 0 (for uncorrelated) and 1 (for correlated); specifically, we define \(S\) to be

\[S = 1 - \frac{E}{\log(p)}\]
(4)

The interpretation of the bounds of the S estimator is a consequence of the relationship between the dispersion (entropy) of the eigenvalues of a correlation matrix and the dimension of the underlying dynamics. Synchronization can be thought of as the process of confining the dynamic behaviour of the entire system to a lower dimensional state space. The entropy \(E\) accounts for how many dimensions are significantly visited by the observed trajectory (e.g. the animals’ activity). When all the normalized eigenvalues are within the window is calculated. In this way we construct new activity time series for the animals that summarizes the grazing activity over timescales. These new time series are then analysed using the Pearson correlation scores. In contrast to the previous index, this index attempts to quantify the amount of activity over a specified time window. Similarity of values of this index measures the coherence of activity level between animals across the same time frame.

The correlation-like matrices are further processed to account for third-party interactions. This is achieved by applying a network analysis method (Carmeli 2006). This network method, coined S estimators, uses a recently developed technique for assessing the cooperative behaviour in dynamic networks (Carmeli 2006). The S estimators approach is multivariate; that is, it infers the network structure by endowing the network as a whole and not by considering it purely as an ensemble of independent pairs.
roughly of the same value (maximal dispersion), all the state-space dimensions are almost equally visited; in this case \( E \) is maximal (close to \( \log p \)) and consequently \( S \) is close to 0, meaning no contraction of the embedding dimension, that is, no synchronization.

Alternatively, when nearly all the normalized eigenvalues are roughly 0 and a few of them are appreciably nonzero (minimal dispersion), only a few state-space dimensions are visited; in this case \( E \) is minimal (close to 0) and consequently \( S \) is close to 1, meaning maximal contraction of the embedding dimension, that is, complete synchronization.

The \( S \) estimator can naturally quantify the strength of within-group interactions relative to all other interactions among the remaining subjects. This can be done by block-partitioning \( C \) according to group membership. For example, consider two groups allowing the following partition

\[
C = \begin{bmatrix}
C_{11} & C_{12} \\
C_{12}^T & C_{22}
\end{bmatrix}
\]

where the diagonal element \( C_{11} \) contains the information about the interactions within group 1 which are of interest to us. The element \( C_{22} \) contains information about the interactions among the remaining subjects and \( C_{12} \) the interactions between the two groupings. To extract the true strength of interaction within group 1 it is necessary to marginalize over all other interactions which can be achieved by considering the matrix

\[
H = C_{11} - C_{12} C_{22}^{-1} C_{12}^T
\]

\( H \) is a partial covariance matrix which we transform so that its diagonal elements are all ones thus making it a correlation matrix. This is simply obtained through a similarity transformation with a matrix having the inverse square root of the diagonal element \( s \) of \( H \) along the main diagonal and zeros elsewhere. Finally, the partial \( S \) estimator is computed through the eigenstructure of the partial correlation matrix with the same formula previously described for the \( S \) estimator (equations 3 and 4).

For some network topologies, the partial \( S \) estimator alone may still not allow a satisfactory inference. For example, in a case where \( A \) and \( B \) are uncoupled and commonly driving \( C \), the value of the partial \( S \) estimator between \( A \) and \( B \) will be high because of their common output. In the literature, this case is known as the 'common child' problem (Lauritzen 1996). As such, the combination of both estimators (standard \( S \) and partial \( S \)) may help. For example, it is recommended to take the minimum value of the \( S \) and partial \( S \) estimator to judge the strength of an interaction (Eichler et al. 2003; Carmeli 2006). In our examples we found in all cases the minimum value was that calculated by the partial \( S \) estimator, so henceforth we refer to subsequent quantities as values of the \( S \) estimators. Importantly, in the next step the randomization over group membership can examine whether such groupwise interactions really are significant (see Groupwise interactions below).

It is worth mentioning that the \( S \) estimators have been numerically tested on representative models of dynamic networks with various patterns of connectivity and their performance has been tested under different signal to noise ratio settings. This validation work is shown in Carmeli (2006) which is openly accessible. Moreover, in the Supplementary Material we provide a Matlab (Mathworks, Natick, MA, U.S.A.) toolbox containing an implementation of the \( S \) estimators and the algorithms used in our study.

Kendall’s \( W \)

A more traditional multivariate measure of activity synchrony is Kendall’s coefficient of concordance \( W \) (Martin & Bateson 1993). This can be used to assess the synchrony of particular groups of animals and so is a good candidate measure to compare to the partial \( S \) estimator. As shown in Siegel & Castellan (1988), Kendall’s \( W \) can be computed with the formula

\[
W = \frac{(p - 1)^2 + 1}{p}
\]

where \( p \) is the number of animals in the grouping and \( T \) is the mean of the pairwise Spearman correlations among the \( p \) animals. This quantity ranges from 0 (no concordance among the \( p \) animals) to 1 (full concordance). Despite Kendall’s \( W \) score being multivariate it does not explicitly account for third-party interactions.

Testing for Synchrony: Surrogate Analysis

The technique of surrogate data analysis is a randomization test method (Theiler et al. 1992; Small 2005). Given time series data, surrogate time series are constructed consistent with the original data and some null hypothesis. For example, if the null hypothesis is that the data are drawn from a source of Gaussian noise, then surrogate time series consistent with this hypothesis can be generated by simply shuffling the time order of the original data in a randomized way. In this way, each surrogate time series will preserve the mean and standard deviation of the original data.

Once surrogate time series have been generated, the next step is to calculate a suitable test statistic to help us reject the null hypothesis with some confidence (Small & Judd 1998). So, in the Gaussian noise case, a pivotal statistic is the autocorrelation at lag 1. We can calculate the autocorrelation of our original data and each of the surrogate time series. If the value of the statistic calculated from the original data lies outside of, or far enough in the tails of, the distribution of the surrogate test statistic values then we can reject the null hypothesis that the data came from a Gaussian noise source with some confidence. In this way one can build up ever more complex null hypotheses with appropriate test statistics to determine what the data are not.

We stress the fact that by using surrogate data we test null hypotheses in a nonparametric way. Consequently, the probability distribution of the synchronization score is derived by the ensemble of scores computed from the surrogate data, which are generated according to the null hypothesis under consideration. By doing so, we can neglect all the assumptions needed when parametric tests for correlation scores are to be applied. For example, we neglect the nonindependence of the time samples generated by time window sampling.

In our present problem, we consider four methods of generating surrogate activity records to be tested with the synchrony scores. The first three methods rely on generating surrogate data according to different modelling assumptions about each individual sheep’s behavioural activity. They allow us to construct activity networks. A study of the resulting network is useful for investigating associations among the animals in relation to their attributes, for example sex and body mass. In contrast, the fourth method attempts to test groupwise interactions straightforwardly. To do so, it does not explicitly take into account the individual sheep’s dynamics, but it relies on the randomization of group membership.

Activity Networks

To infer activity networks, we generate surrogate data for each individual sheep independently from each other, so we destroy any coupling between the surrogate sheep’s activity. In this way, we can test against a null hypothesis that a given pair of animals is not interacting or synchronous. Because a realistic model of sheep
behavioural activity is unknown, we consider three algorithms to generate surrogate activity for each individual animal. The three algorithms refer to behavioural activity models of escalating complexity.

The first surrogate is, as in the Gaussian example above, straightforward shuffling of the activity records. That is, we assume the activity of each animal is random, something very unlikely in continuous patterns of animal activity since they tend to be distributed in bouts, but possible in behaviours of type ‘event’ (Martin & Bateson 1993). For example, in ruminants, grazing bouts are followed by ruminating bouts and their duration depends on gut filling driven by the type and amount of forage available (Penning et al. 1984). Alert displays, however, are more randomly distributed as they can be triggered by external disturbances (Martin & Bateson 1993; Childress & Lung 2003; Mooring et al. 2004).

As a second surrogate generation method we consider the bouts of activity to be random. This could be interpreted as activity bouts being triggered by a combination of multiple effects that result in a random starting time for bouts. In the case of grazing bouts this is still an unlikely hypothesis but we incorporate it as a useful example of how to migrate gradually to more complex explanatory models of the behaviour as each hypothesis is rejected. To illustrate, a typical surrogate obtained by randomizing the bout intervals considers that, say, the activity record of an animal is 1, 1, 1, 0, 0, 1, 1, 1, 0, 0, 0, 1. A surrogate is generated by randomizing the bout periods, preserving the number and length of each bout. An example of such a surrogate would be 1, 1, 0, 0, 0, 1, 1, 0, 1, 1, 1, 0, 0, 0. So, the bout consisting of two grazing activities (1s) occurs first followed by a bout of four not-grazing events (0s), etc. In this way we are randomizing the occurrence of activity but the length of each time series and their total activity are preserved.

As a third surrogate method we consider a Poisson model of the activity of each animal. The Poisson model seems suitable to represent the distribution of activity bouts as it is intended to model the probability of a number of events occurring in a fixed period of time (Sokal & Rohlf 1995). We assume the length of activity is drawn from a Poisson distribution with parameter $\lambda = \lambda_0$ for not-grazing behaviour and $\lambda = \lambda_1$ for grazing activity. The $\lambda$s for each animal are obtained by carrying out a maximum likelihood Poisson fit to the daily activity records. A surrogate thus consists of alternating sequences of bouts of grazing activity followed by bouts of not-grazing activity. The length of each activity is randomly drawn from the relevant Poisson distribution.

In all three cases we calculate the test synchrony indices (see Detecting synchrony) to construct correlation-like matrices, which are analysed using S estimators. The S estimator scores are calculated to determine whether the recorded animal activity is consistent with the surrogate scores to conclude whether or not there is evidence of synchrony among animals or animal groupings. This information is usefully encapsulated by the construction of a network where each animal is considered a vertex and an edge between vertices indicates significant evidence for synchronous behaviour.

We note that the combination of our first surrogate test with the index of concordance (equation 1) can be recognized as the traditional bivariate ecological synchrony kappa coefficient (Martin & Bateson 1993). There, an index of concordance is compared to what would be expected by chance, precisely what our first surrogate method does. Indeed, we can consider our proposed interval and Poisson models, together with the index of concordance, to be a generalization of the kappa coefficient to more biologically reasonable models of chance behaviour. Furthermore, within our methodology it is transparent as to what is the measure of synchrony and what are the assumptions of the underlying process.

It is important to reiterate that if a simple process is consistent with the data, then considering more complex processes is unwarranted, because developing behaviourally based models is unjustified if the data cannot be distinguished from noise. Simple models, however unrealistic, must be considered first.

**Groupwise Interactions**

To examine groupwise interaction in a straightforward way, we perform randomization tests across group membership. That is, the surrogates are the observed symbolic time series but we randomize the group membership. In this way we are able to test whether or not the amount of intragroup interactions is comparable to the rest of the interactions among the animals. In other words, we attempt to detect a behaviourally synchronous group of animals by assuming it forms a highly clustered component of the animals’ network.

**Network Statistics**

Our methodology allows us to represent the synchronous behaviour of sheep as a network where each vertex and edge has physically and statistically significant interpretation. These networks can be further analysed using the many statistics available for such structures (Albert & Barabasi 2002; Newman 2003; Costa et al. 2007). In this paper we consider three such quantities. In the first instance we perform a simple count of the within-and between-sex links. In effect, such counts assess the assortativity of our networks and the mixing properties of different types of vertices such as males and females (Newman 2003).

We also calculate the conductance (Bollabás 2008) of the subnetworks associated with females and males. The conductance of a network is a global property that describes how fast a random walk on the network starting within a small subset of vertices will proceed to elsewhere in the network. The value of conductance ranges from 0 to 1. A value of conductance close to 0 means the network contains multiple bottlenecks, while a value of conductance close to 1 means the random walker can spread very fast over the network given the many available paths or links (Bollabás 2008). So, highly connected subnetworks are those with a high value of conductance. This property is closely related to the concept of synchronizability of the network (Boccaletti et al. 2006; Julli et al. 2007; Bollabás 2008). In general, its calculation is computationally costly (NP-hard i.e. nondeterministic polynomial-time hard) but for our female and male subnetworks (less than 20 vertices) it is feasible to obtain exact values of the conductance.

Finally, the clustering coefficient (Watts & Strogatz 1998; Newman 2003) is a measure of the number of triangles (closed cycles of length three) in a network and it ranges from 0 (no link between the vertices) to 1 (a complete graph, in which all vertices are connected to all other vertices). In our case study, a closed cycle of length three would correspond to a group of three animals behaving in a synchronous manner.

**RESULTS**

**Activity Networks from Surrogates**

The first set of surrogates we consider corresponds to the null hypothesis that the daily activity of each animal (grazing, not grazing) is independent and random (Gaussian distribution). We find that for each day the behavioural pattern of activity is significantly different compared with the expected pattern for purely random behaviour. As such, each daily activity network was almost a fully connected graph. There were some missing links on selected
days but overall no conclusion can be drawn other than that, as anticipated, the Gaussian model is not realistic.

When we consider the interval surrogate method, randomized occurrence of bouts of the Poisson model, a clearer picture emerges, indicating female–female or male–male pairing synchrony rather than a pairing of different sexes (Fig. 2a). The information from the networks can be summarized using a simple box plot and hypothesis test (Fig. 2b). We calculated, for each network (one for each day), the ratio of female–female edges to all possible female–female, male–male and female–male edges and confirmed the significance of this statement by carrying out a Wilcoxon two-sample test of the medians. Thus there appears to be a higher level of within-group synchrony for females, and for males, than for mixed-sex groupings.

In Fig. 3a we see that the subnetworks of females typically have higher conductance than those of males. This can be explained by the greater number of edges within the female subnetwork than the male subnetwork, which can be further demonstrated by comparing the clustering coefficient of both subnetworks. As can be seen in Fig. 3b females show more clustering than males. This suggests that females form a more coherent group in terms of activity than males.

**Group Interactions**

In this section we examine group interactions in more detail as well as considering other groupings within the experiment. Rather than perform an exhaustive search over all possible group sizes and memberships to determine whether the within-group interactions show significant evidence for synchrony, we restrict ourselves to the ecologically meaningful groupings relevant to the experiment described in Pérez-Barberia et al. (2007). We emphasize that our purpose is not to compare different groupings with respect to each other; we determine only whether significant evidence exists for within-group synchrony relative to all interactions among the other animals.

**Figure 2.** (a) Activity networks summarizing the synchronous behaviour of the animal’s activity for 2 representative days. □: Female sheep; △: male sheep. The edges (significant synchronous behaviour) are typically between female–female or male–male pairings rather than between females and males suggesting possible segregation by sex. (b) The box plots summarize the within- and between-group (synchronous) interactions of females and males from the networks of the graphs. The Y axis is a ratio of female–female (F–F), male–male (M–M) and F–M (female–male) significant edges to all possible F–F, M–M and F–M edges, respectively. The horizontal line in the box indicates the median, the box edges are the 25th and 75th percentiles and ‘ ’ represents an outlier. The whisker length is set to be 1.5 times the interquartile range.

**Figure 3.** (a) The conductance of the female and male subnetworks for each day using Poisson model surrogates. The female subnetwork is more connected resulting in a higher conductance for all days. (b) The clustering coefficient for the female and male subnetworks. Once again the more connected female subnetwork shows a higher degree of clustering than the male subnetwork. This was confirmed to be a significant difference by using a Wilcoxon two-sample test.

We apply the S estimators to the following six animal groupings: small males, large males, small females, large females, all males, all females. We consider the three synchrony indices described above (Detecting synchrony) and perform randomization tests across group membership.

In Fig. 4 we show the value of the S estimators for the original groupings for each day. The synchrony index used to build the correlation-like matrices for the S estimators is the index of concordance (equation 1). We see that for this index only the groups all males and all females exhibit stronger within-group
interactions than would be expected of a randomly chosen group of animals with the same size membership. When we repeat the above analysis using the two synchrony indices embodying timescale information, we also find that only the all males and all-female groupings persist, suggesting behavioural synchrony for female–female and male–male but not for any other groupings.

We can repeat the above analysis to investigate the significance of female and male groupings using the Kendall’s W score and randomizing over group membership (Fig. 5). We see that the Kendall’s W score is capable of indicating the significance of female and male groupings for most days but not all days (6/16 for females, 10/16 for males). In contrast, the S estimator is capable of demonstrating the importance of female–male segregation for all days (Fig. 4).

Recall that, as described above (Detecting synchrony), for the two synchrony indices that embody timescale information different time scales correspond to different window sizes in which to calculate the decimal representation or activity percentage. Therefore, to explore whether there are any special timescales for synchronization among the groups within the data, we examine the S estimator scores by constructing the correlation-like matrices using different embedding windows for those two synchrony indices.

We consider window sizes encompassing the individual measurements (30 s) up to 2 h, which should capture the length of the feeding bouts of most ruminants of this size. In both cases and across the experiment only the all-male and all-female groupings show any evidence of synchrony, and such synchrony appears to persist over the timescales considered. As an example, we depict this pattern in Fig. 6 for day 16. There does not appear to be any evident window size dependence. The amount of activity within both female and male groupings increases to a maximum for a period of 1 h. The oscillations apparent after 1 h perhaps hint of the circadian rhythm.

**DISCUSSION**

We used a network methodology that allows one to use multivariate time series to assess the level of behavioural synchronization between individual, or groups of, animals. We first proposed the use of three different synchrony indices (two of them can address variability in the size of the sampling window) which can be used to create partial correlation matrices. We then suggested that the pattern of behaviour shown by each subject should be described by an appropriate distribution function, chosen by testing different plausible distributions in escalating order of generality. Once the pattern of the behaviour is characterized by a distribution function, we test for significance in synchronization between animals or within groups, depending on the hypotheses of interest. The significant pairwise comparisons were plotted as edges in a network to reveal networks of synchronization. Finally, we have demonstrated the usefulness of the S estimators to assess synchronization within groups of animals that can be distinguished from interactions with members of third-party groups. We stress that the advantage of the S estimators is that they analyse the network as a whole, in contrast to the limitations imposed by a dyadic approach. We therefore advocate the use of the S estimators over Kendall’s W, as the latter is not capable of resolving third-party interactions.

In our example, we analysed a binomial representation of activity patterns, in which two exclusive activity classes (grazing, not grazing) summarized the behaviour of the animals. However, the synchrony indices used here can be applied to any number of behavioural classes. Some analysis of time allocation to different activities can present problems because they are compositional (i.e. the sum of the proportions of all activities must be 1; Elston et al. (1996)). The proposed surrogate analysis for testing different null hypotheses of activity patterns does not have this setback.

In field conditions the recording of behaviour as time series data can suffer from the problem of missing records. This can create spurious results when analysing synchronization using concordance indices (Martin & Bateson (1993)). This is easily circumvented when automatic behaviour recorders are used, since this provides almost continuous time series of behaviour, as in the example used here. The effect of missing records can also be assessed by using timescale analysis as we have described in our example. However, the most common scenario is that behavioural records are taken by direct observation of the animals in the field at certain intervals, which requires the researcher to make assumptions or use expert knowledge to decide what is a meaningful recording interval of that particular behaviour (Altmann (1974)). An intensive, short, dry run
trial would help to gather a comprehensive data set so that different window sizes could be applied using the methodology proposed here, to investigate the minimum window size required to obtain a meaningful time series in which to calculate synchronization. Analogously, when a number of behaviours of different nature are used, events versus states (Martin & Bateson 1993), it is important to ensure that the recording intervals applied to each behaviour are appropriate, so that the rendered quality of each behaviour is comparable (Kraemer 1979).

Another use of the timescale analysis (sampling window size) is when assessing seasonal differences in activity patterns within species, between populations, between areas that differ in the spatial distribution of food or when comparing activities of different species, as bout length can reflect the relationship between animal energy requirements and environmental conditions (Green & Bear 1990; Cote et al. 1997).

The use of networks with vertices and edges to represent the subjects and their significant synchronization is a powerful way to depict complex relationships between subjects. For large networks, statistics such as clustering coefficients and path lengths can be calculated to extract quantitative measures that extend the utility of patterns detected by visual inspection. Correlation-like matrices have been the common tool to represent this type of information (Ludwig & Reynolds 1988), but the clarity and simplicity of networks excel for these purposes. Networks can also include more complex information on synchronization. For example, if a certain behaviour is initiated by one of the units of a dyad, this can be represented in the graph with symbols and arrows depicting the nature and the direction of the interaction (cooperative, agonistic, neutral). Furthermore, and importantly, our approach and network framework to unravel animal behaviour grasps fully the interplay between individual behaviour and the animal's interaction architecture.

Although we have focused on mammal behavioural synchronisation, the techniques described here can be applied to any behaviour that represents interactions between plants and between animals and also to coevolutionary plant–animal responses to environmental stimuli. Our study attempts to stimulate the use of these techniques and to develop the potential of our ideas further.

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Supplementary Material

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References


