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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 overcame 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 method 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

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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) 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 $a_t^{(i)}$ then,