Using the relational event model (REM) to investigate the temporal dynamics of animal social networks

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A R T I C L E I N F O

Social dynamics are of fundamental importance in animal societies. Studies on nonhuman animal social systems often aggregate social interaction event data into a single network within a particular time frame. Analysis of the resulting network can provide a useful insight into the overall extent of interaction. However, through aggregation, information is lost about the order in which interactions occurred, and hence the sequences of actions over time. Many research hypotheses relate directly to the sequence of actions, such as the recency or rate of action, rather than to their overall volume or presence. Here, we demonstrate how the temporal structure of social interaction sequences can be quantified from disaggregated event data using the relational event model (REM). We first outline the REM, explaining why it is different from other models for longitudinal data, and how it can be used to model sequences of events unfolding in a network. We then discuss a case study on the European jackdaw, *Corvus monedula*, in which temporal patterns of persistence and reciprocity of action are of interest, and present and discuss the results of a REM analysis of these data. One of the strengths of a REM analysis is its ability to take into account different ways in which data are collected. Having explained how to take into account the way in which the data were collected for the jackdaw study, we briefly discuss the application of the model to other studies. We provide details of how the models may be fitted in the R statistical software environment and outline some recent extensions to the REM framework.
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The application of social network analysis to nonhuman animal societies has attracted a great deal of interest over the last decade (Croft, James, & Krause, 2008; Sih, Hanser, & McHugh, 2009; Wey, Blumstein, Shen, & Jordán, 2008; Whitehead, 2008). Who interacts with whom and the local (for example, cliques in the network) and global (overall) network structures that these interactions produce are of central importance for key issues in ecology and evolution (Krause, Croft, & James, 2007). There is great interest in linking observed patterns in animal social networks to such processes to understand, for example, how disease is transmitted within a population or how cooperation is maintained (Croft et al., 2008; Sih et al., 2009; Wey et al., 2008). To date, however, researchers have tended to aggregate data on social interactions over time into a single, static, network within a particular time frame (Croft et al., 2008), even if the observations were originally made for individual, disaggregated, events (Faust & Skvoretz, 2002; Freeman, Freeman, & Romney, 1992). Aggregate event network data indicate which individuals interacted, and possibly how often. However, through aggregation, information is lost about the order in which such interactions occurred, and hence the sequences or patterns of actions over time. While some research questions relate to the overall number, or the presence, of interactions between individuals in a particular time frame, many questions relate directly to the sequence of actions (Blonder, Wey, Dornhaus, James, & Sih, 2012; Pinter-Wollman et al., 2013).

The importance of considering temporal dynamics in studies of animal social networks has been highlighted by a number of recent review papers (Blonder et al., 2012; Pinter-Wollman et al., 2013). Several empirical studies have begun to consider the temporal structure of animal social networks, particularly in the context of

information diffusion and disease transmission (Blonder & Dornhaus, 2011). In these studies, the temporal patterns of social interactions have clear consequences for the likelihood of an individual gaining access to information, or being exposed to disease. Other approaches to the study of temporal networks relate to the development or stability of social relationships through time, for example comparing the structure of time-aggregated networks over different sampling periods (Croft et al., 2011; Hobson, Avery, & Wright, 2013).

Analysis of the dynamics of social interaction is particularly useful in addressing questions about social processes unfolding between individuals within group settings, such as a dominance hierarchy, reviewed in Stevens and Gilby (2004). An analysis of disaggregated events would shed light on how that dominance hierarchy came to be, possibly through persistence of winning (Jennings, Carlin, & Gammell, 2009).

There is great value in applying statistical models, such as the relational event model (REM) for social action (Butts, 2008), to time-ordered animal social interaction data to test hypotheses that relate to the ordering of events or actions within a sampling period (Rendell & Gero, 2014). The REM was originally developed in the social sciences by Butts (2008) to investigate the timing or order of events in human interactions, such as conversations or communications. Here, we show how the REM can be applied to animal social network data that are based on interactions (events) between individual animals. We illustrate the application of the REM with a case study.

Our aim here is thus to demonstrate the potential of the REM for studying animal social behaviour as it unfolds in time. We explain how the REM can be used to test explicit hypotheses about such aspects of animal behaviour, while taking into account the way in which the data were collected, and the possible actions that can occur in the sequence of events. From a practical perspective, we also explain how REMs can be fitted and the data prepared for modelling using particular packages within the R statistical environment (R Core Team, 2013).

THE REM AND OTHER APPROACHES FOR LONGITUDINAL AND NETWORK ANALYSIS

The REM allows a comparison of patterns of actions through time across different individuals in a network. We explain the theoretical background to the REM in more detail in the Methods.

The REM is distinct from other established models and methods for longitudinal and network analysis, and the data requirements are also different. Typical nonparametric sequence analysis treats whole sequences as the units of analysis (Abbott, 1995). These methods either wholly aggregate events, thus losing the temporal aspects of the data, make comparisons about deviations across average tendencies, or examine where common sequences are conserved, such as in genomic sequence alignment (Mount, 2001). The REM treats the events (microbehaviours) as the units of analysis and uses sufficient statistics (statistics that summarize the values of the sample data without loss of information from the sample) to model the event dynamics directly.

A group of n animals can be thought of as a network comprising n individuals, whose actions relate to one another as a series of (disaggregated) events. Actions may often be between pairs of individuals (dyads) in the network, although higher-order interactions, such as triads, are also possible. Self-directed actions (for example, self-grooming) may also occur; these are called loops in network terms. Adapting an argument of Goffman (1967) to animal behaviour, actions among animals over time can be seen as series of discrete events where one animal directs its behaviour at one or more of the other animals in its environment.

Each row of the disaggregated event data represents an event, where an action takes place. The exact time of the event may also be recorded. Covariate information, such as the sex of the focal individual, is often available. Where several actions are possible for a particular event, the action type may be known, and may be treated as an event covariate, or modelled directly as a categorical variable.

Other models for dynamic networks focus on aggregate changes in the whole network structure over time. First, these include temporal exponential random graph models (TERGMs; Hanneke, Fu, & Xing, 2010), for which efficient and unbiased estimation routines were first proposed by Desmarais and Cranmer (2010, 2012), implemented in the xergm package for R (Leifeld, Cranmer, & Desmarais, 2014). Second, these involve each actor evaluating their utility for forming and dissolving ties (i.e. stochastic actor oriented models (SAOMs) usually fitted with the software SIENA (Snijders, 2005)). The minimal data for REM involve only multiple observations of time-ordered events, and thus have much less specific data requirements than sequence analysis, which needs multiple observations of whole sequences, or TERGMs and SAOMs, which require single complete network data from at least two points in time. The family of models employed by the REM framework is related to the event history (or failure/survival/life table) analysis (Mills, 2011) in that each potential action is assumed to have a piecewise constant hazard (the rate of occurrence, given everything that has transpired up to that point; Butts, 2008). As these statistics are hazards, they directly estimate the rate of event occurrence. The REM framework is thus a useful general tool for the analysis of social behavioural processes that unfold in time.

The remainder of this article is structured as follows. In the Methods, we provide a brief theoretical outline of the REM, and explain how it may be fitted, as well as the necessary data preparation. In the case study section, we describe the specification and results of a REM analysis of the jackdaw data. In the Discussion, we draw conclusions on the results of our case study, and discuss how the REM could be used in other studies of animal social behaviour over time. We also briefly outline some extensions to the models we present, and recent areas of development of the REM.

METHODS

Background

A detailed description of the REM can be found in Butts (2008), where he derives two likelihoods for the model: one for interval (exact-timed) event data and one for ordinal event data. Here we outline the model framework for the ordinal case; however, readers should refer to Butts (2008), Marcum (2012) and Marcum and Butts (2014) for details of other generalizations.

The definition of the REM begins with tuples for each action, a (a tuple is a data structure consisting of multiple parts).

Define relational event tuples: $a = (i, j, k, t)$, where:

$i \in S$: is the 'Sender' of event a; $s(a) = i$; S is the set of possible senders.

$j \in \Re$: is the 'Receiver' of event a; $r(a) = j$; $\Re$ is the set of possible receivers.

$k \in C$: is the 'Action type' (category) of event a; $c(a) = k$; C is the set of actions.

$t \in R$: is the 'Time of event' the order in which the event transpired, in study period R.

Then, under a piecewise constant latent hazard model, dynamics are governed by the rate function:

$$\lambda\Big(s(a),r(a),c(a),X_a,A_t,\theta\Big) = \exp\Big[\lambda_0 + \theta^T u\Big(s(a),r(a),c(a),X_a,A_t\Big)\Big]$$
(1)

where:

$\lambda()$, λ_0: are rates; the latter is the baseline rate of action, which is fixed at 0 at the beginning and end of the observation.

X_a: are covariates relating to the action; these could include characteristics of the action and/or the animal.

A_t: is the sequence of past action.

u: is a vector of sufficient statistics.

θ: are the REM model coefficients associated with u.

The likelihood of the REM, which is fully derived in Butts (2008) and generalized to incorporate exogenous events in Marcum and Butts (2014), follows a piecewise constant hazard under a mixture of Poisson distributions. Current implementations support a variety of estimation methods commonly used in generalized linear models including: maximum likelihood, Markov Chain Monte Carlo, Bayesian sampling importance resampling and Bayesian method of posterior modes.

Specifying and Fitting the REM

REMs can be fitted to data for which the exact time of an event is available, for example events extracted from video data, or to ordered data, as in our case study. In the REM it is possible to estimate coefficients for different kinds of behaviour, including sending, receiving, reciprocity and persistence of action. It is also possible to specify and fit REMs and investigate kinds of behaviour involving different types of action, such as animal A grooming animal B, followed by (or preceded by) B attacking A.

A typical starting point in the modelling process is to include parameters for each individual in the network in the REM, allowing each animal to have its own specific rate of sending and receiving actions in the model, to test whether there is any evidence of differential rates of sending and receiving actions. For a network of n animals there are potentially n specific rates of sending and n rates of receiving actions. When we set up the model using a particular animal as the 'reference animal', significant positive coefficients for any other animals in the network indicate higher rates of sending or receiving a particular action than for the reference animal. Significant negative coefficients indicate the converse, and nonsignificant coefficients indicate they can be thought of as similar to the reference animal with respect to sending or receiving actions.

Allowing for specific sending and receiving of actions in the REM makes the model valuable for estimating specific effects for each animal, but typically requires many model parameters. Setting up the REM with a reference animal requires $2 \times (n - 1)$ parameters for the fixed effects for sending and for receiving actions; for large networks and/or short sequences, this potentially large number of model parameters should be considered in terms of model complexity given the available data. It may be possible to reduce the number of model parameters to common sending and receiving effects, as detailed in Butts (2010). When comparing fitted REMs, we use the Bayesian information criterion (BIC) to assess their relative goodness of fit and additionally report pseudo-R^2 measures (these are based on one minus the ratio of the null and fitted likelihoods).

REMs may be fitted in the statistical environment R (R Core Team, 2013), using the package relevent (Butts, 2010). Within this package, there are two modelling commands: rem(…) and rem.dyad(…). The function rem(…) is a more general command for modelling with considerable flexibility for specifying multiple action types, loops, and allowing for different study designs through the use of event support constraints. The egocentric relational event model may be fitted with rem(…) and is used for the case study analysis. Use of the rem(…) command in relevent generally requires a fair amount of data preparation prior to modelling, which can be achieved using the informR package (Marcum, 2012). informR allows for a lot of flexibility in setting up the data for identifying particular sequences in the relational event data, making it invaluable for answering research questions about sequences and recency of events in studies of behaviour. The other modelling command in the relevent package is rem.dyad(…). This is much more limited in its flexibility as a model command than rem(…), but has the advantage of prepackaged summaries of event sequences, such as conversational dynamics (Gibson, 2003) and thus it is very powerful for simple dyadic models.

The sampling used in the study design should be taken into account in the modelling process. In many cases, focal sampling is used, where the researcher observes an individual animal for a set period of time, possibly at random, or possibly through opportunity or convenience. This means the researcher only observed events associated with the focal animal (Fig. 1). If we label the focal animal as 'A' and two other animals, 'B' and 'C', and the researcher (observer) as 'Obs', and use the example of grooming, the researcher can see whether A grooms another animal, including B or C (Fig. 1a), or whether another animal, including B or C, grooms A (Fig. 1b), but if B grooms C or vice versa this is not directly observed by the researcher (Fig. 1c), even if such events occur. Therefore, prior to modelling, we must set up the data such that only those actions that could have been observed for any given event by the researcher are considered in the possible set of actions, and exclude
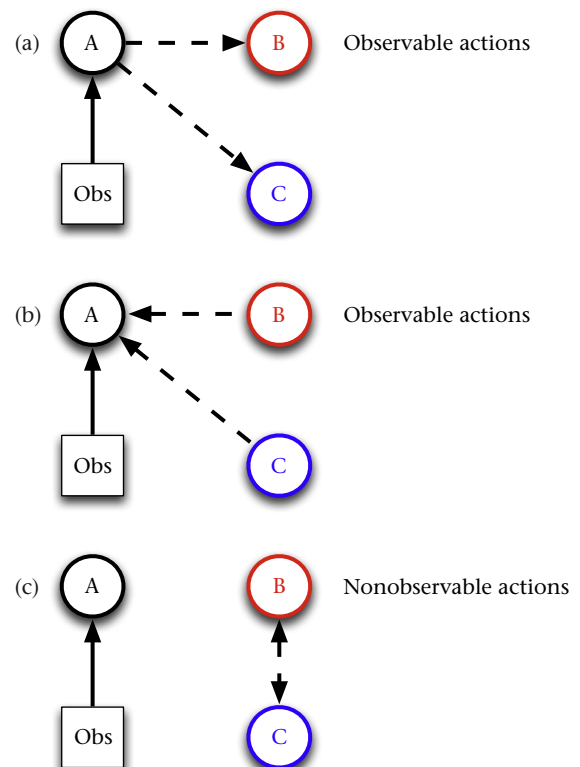

Figure 1. (a) Animal A directs its actions to animals B or C; the observer (Obs) records these actions as animal A sending behaviour. (b) Animals B or C direct their actions to animal A; the observer records these actions as animal A receiving behaviour. (c) Animals B and C interact; the observer is focusing on animal A, and hence does not observe or record the actions of animals B and C.

nonobservable actions. We do this using a set of support constraints, where a binary indicator system is used to evaluate and restrict which actions are possible, or observable, at any given moment in the event history. For example, an event that is observable by the researcher at a particular point in the sequence is associated with a support constraint value of 1 and a nonobservable event is associated with a value of 0. Support constraints can be set up in the informR package, as Marcum and Butts (2014) explain in more detail.

The setting should also be taken into account via support constraints when modelling the relational event data. The setting is the context in which observable events can occur given the study design. In the case of food sharing, an animal cannot transfer a food item if it does not have a food item to transfer at any given moment. Moreover, if the animal eats a food item it has just found, it no longer has this item to transfer. As a further example, if animals are being focally sampled for their grooming behaviour in two separate enclosures, animals in the first enclosure cannot groom animals in the second enclosure, and vice versa.

CASE STUDY

Background

De Kort, Emery and Clayton (2006) studied a group of 12 European jackdaws, which received 28 randomized feeding trials on different days in 2003. These authors aggregated the events into two static networks: the first for the time frame of the first half of the study period (first 14 trials) and the second for the time frame of the second half of the study period (trials 15–28). The birds were all living in one large aviary, having been taken from several nests after at least a week from hatching. The nestlings were hand-raised until nutritional independence, and were grouped in four nestboxes. Individuals in the same nestbox were not necessarily siblings. For the feeding trials, one bird at a time received 10 morsels of food consecutively, after which, a second bird received 10 morsels, etc., until all birds had received the same treatment. The order in which individuals received morsels was randomized before each trial. For each trial, the morsels alternated between sweetcorn and the larvae of the wax moth, *Galleria mellonella*. Birds did not receive these morsels outside the feeding trials. For each morsel provided to a focal bird, it was recorded whether a bird ate the morsel, transferred it to another bird, or dropped it on the floor, thus, for equation (1), there are three categories of action for each morsel. For each trial, exact-timing information is not available, but the order of events is known.

Our research questions are as follows. Is there any evidence in the observed disaggregated event data that persistence and reciprocity of action are more likely than we would expect by chance? If so, what is the frequency of these events given past actions, and how soon in the sequence are such actions repeated? How do these actions relate to exogenous factors, such as sex and food type? Other approaches for modelling animal interactions over time, especially with time-aggregated data will not allow us to answer all of these questions, or will only provide partial answers. For example, other methods do not allow us to assess how soon in the sequence actions are repeated in a time-ordered sequence of events.

The network in our case study is fairly small, 12 jackdaws, although a long sequence of event data was collected, comprising 3168 events. The REM could also be used with much larger networks, where such data are available. We fitted REMs to these data to test for persistence and reciprocity of action in terms of food sharing among the network of birds. We also investigated whether the patterns of action were different for two birds raised in the same nestbox, compared with two birds, each from a different nestbox. The order of observed events is of interest in this example because the closeness or distance of food sharing events in the sequence relates to whether the birds rely on memory to direct their actions; events more distant in the sequence require longer memory retention from the bird transferring the food. Corvids are known to have excellent memory (Bednekoff, Balda, Kamil, & Hile, 1997). The number of times a persistent action from one bird to another leads to a reciprocal food transfer can also be investigated with the REM. Food sharing is of great interest to evolutionary biologists, because it suggests the existence of altruism, or it requires difficult-to-explain phenomena such as reciprocation and temporal discounting (Stephens, McLinn, & Stevens, 2002). It is also of interest to anthropologists because food sharing is often regarded as being fundamental to the evolution of complex cognition in many animal species, including humans (de Waal, 1996). In our case study, the animals are in captivity. While in this environment, their behaviour may differ from animals in the wild. However, food sharing is part of the animals' natural behaviour repertoire.

Specifying and Fitting the REM

De Kort et al. (2006) analysed their two static networks of aggregate events with descriptive measures such as frequencies of transfer, and with permutation tests, such as the tauKr statistic (Hemelrijk, 1990). These authors found that jackdaws shared food with more than one other individual, and a high percentage (26%) was initiated by the donor, especially compared with primates, where active giving is exceedingly rare (de Kort, Emery, & Clayton, 2003, 2006). Furthermore, the frequency of food sharing and the number of recipients were both reduced in the second time frame, compared with the first (von Bayern, de Kort, Clayton, & Emery, 2007). While the results of their aggregated analysis answer particular questions about the overall food sharing behaviour of the birds for a particular time period, other questions, such as those on the recency of reciprocal action, or the rate of persistent action, can be answered via an analysis of the disaggregated event data with the REM. The egocentric REM can be used to test for differential food sharing behaviour among the birds.

In our REMs, we follow the path of each morsel as it enters the system until it leaves the system, i.e. it is eaten or dropped by a particular bird. We treat the introduction of morsels to particular birds in each trial as exogenous events, randomized by trial and bird, and assume that these initiate event histories.

Once a bird receives a morsel, it may be eaten by the initial receiver, it may be dropped on the floor or it may be transferred to another bird. Here, we treat the latter action type as a 'food transfer'. Because we have the order of events but not the exact timing, we use an ordinal likelihood with multiple action types, to reflect the three possible actions for each morsel.

We used informR in R to prepare the data for the REM analysis, introducing support constraints to take into account the bird that is offered the food item in each trial; only the bird that is offered the morsel can immediately eat it, and the item can only be dropped on the floor initially by the bird being offered the morsel. The support constraints ensure that the model estimates are only based on the subset of events that are possible at any particular time. The general use of support constraints in REMs is discussed in more detail in Marcum and Butts (2014). Furthermore, we incorporate exogenous events between the initiation and termination of each trial to take into account that trials took place on different days.

We explore four types of behavioural effects here, using the REM:

(1) whether each individual bird has its own specific rate of transferring food;

(2) whether nestbox homophily (familiarity of birds from the same nestbox) is associated with particular food sharing behaviour;

(3) reciprocity and persistence of food sharing: how quickly these actions occur, or are repeated in the sequence of events;

(4) whether food-sharing behaviour is different for the two different food types.

In Model 1 (M1), 13 fixed effects were fitted to compare the relative tendency for a bird to initially eat the morsel rather than transferring it or dropping it on the floor. Because there are 12 birds, each of which has an opportunity to eat, share or drop a morsel during the various trials, 12 of the fixed effects are for the birds (B1-B12) to transfer the morsel, and the 13th is for dropping the morsel on the floor. Eating the morsel is the reference category. Positive coefficients would suggest that the bird is more likely to transfer the morsel (or drop it on floor) than to eat it. Negative coefficients indicate that the bird is likely to immediately eat the morsel rather than give it away or drop it.

Some birds were raised in the same nestbox. Model 2 (M2) extends M1 to include a nestbox homophily term that compares the likelihood of an exchange between any two birds raised in the same nestbox to any two birds not raised in the same nestbox. A positive coefficient here indicates greater within-nestbox homophily than between-nestbox heterophily in terms of food sharing behaviour. In Model 3 (M3) we investigate persistence of action and reciprocity by adding three statistics to the model. The first, PoA, measures persistence of action with respect to food sharing. The second models the tendency for reciprocity to occur at any time during the event history. The third models the tendency for reciprocity to occur more or less recently in event history, given that a reciprocal encounter has been initiated.

De Kort et al. (2006) found evidence of differential behaviour when sharing wax moth larvae, compared with sweetcorn; in particular, they found that wax moth larvae were more likely to be shared by the birds. Hence in M4, we add covariate terms that differentiate between whether the focal morsel was sweetcorn or a wax moth larva, although we introduce the food types as interaction terms for the different birds in our example to investigate whether there is differential preference for food type among the 12 birds; an alternative way to model this difference overall would be to simply add a corn covariate as a main effect.

REM Results

Throughout the study period, the jackdaws transferred 11.1% of food items to one another. We initially included the sex of the bird as an exogenous covariate in the REM, and the results suggested that jackdaws did not share more food between the sexes than within them, but this is probably a result of a biased sex ratio in

Table 1
Relational event model results for jackdaw food sharing

Estimate	M1			M2			M3			M4		
	B	SD	SL	B	SD	SL	B	SD	SL	B	SD	SL
B1	−4.128	0.161	***	−4.340	0.166	***	−6.799	0.236	***	−5.998	0.253	***
B2	−4.976	0.243	***	−5.205	0.247	***	−6.529	0.313	***	−5.510	0.344	***
B3	−3.854	0.141	***	−4.061	0.146	***	−5.501	0.262	***	−4.484	0.285	***
B4	−4.460	0.190	***	−4.893	0.201	***	−6.822	0.286	***	−5.780	0.301	***
B5	−5.393	0.302	***	−5.680	0.306	***	−7.391	0.360	***	−6.748	0.449	***
B6	−4.567	0.201	***	−4.850	0.206	***	−6.693	0.275	***	−5.887	0.314	***
B7	−3.983	0.150	***	−4.268	0.158	***	−5.857	0.252	***	−4.828	0.272	***
B8	−5.637	0.334	***	−5.957	0.338	***	−7.463	0.364	***	−6.326	0.367	***
B9	−3.817	0.139	***	−4.247	0.155	***	−4.832	0.400	***	−3.538	0.429	***
B10	−5.304	0.289	***	−5.738	0.297	***	−7.135	0.323	***	−6.396	0.385	***
B11	−5.062	0.259	***	−5.485	0.267	***	−7.519	0.380	***	−6.821	0.471	***
B12	−3.764	0.135	***	−4.195	0.150	***	−7.323	0.349	***	−6.269	0.367	***
floor	−3.523	0.115	***	−3.523	0.115	***	−6.540	0.217	***	−5.596	0.221	***
hom				0.861	0.109	***	0.228	0.156		0.157	0.178	
PoA							2.261	0.121	***	1.984	0.124	***
recip							−0.397	0.239		−0.550	0.283	
recenXrecip							0.003	<0.001	***	0.004	0.001	***
B1.Corn										−2.849	0.668	***
B2.Corn										−3.647	0.850	***
B3.Corn										−3.531	0.676	***
B4.Corn										−3.936	0.914	***
B5.Corn										−2.208	0.810	**
B6.Corn										−2.760	0.702	***
B7.Corn										−3.503	0.654	***
B8.Corn										−10.522	26.398	
B9.Corn										−5.359	1.273	***
B10.Corn										−2.451	0.743	***
B11.Corn										−2.514	0.898	**
B12.Corn										−3.951	1.134	***
floor.Corn										−11.177	25.681	
hom.Corn										0.286	0.381	
PoA.Corn										1.107	0.377	**
recip.Corn										0.435	0.553	
recenXrecip.Corn										−0.003	0.001	***
BIC	4656.627			4604.662			2805.765			2809.678		
Pseudo−R^2	0.712			0.717			0.832			0.841		

M1 − M4 are models 1 − 4. The SD are standard deviations about the posterior modes. Significance level (SL): asterisks are asymptotically equivalent to probabilities associated with a Z statistic. Thus ** and *** refer to significance levels of approximately 1% and 0.1%, respectively.

these data: there are 10 male birds and only two females. Therefore, we do not have enough power in our data to detect sex differences and so we did not consider the sex of the birds further in these analyses.

In Table 1, the negative fixed-effect coefficients from M1 suggest that all 12 birds prefer to eat the morsel, rather than to transfer or drop it. However, as the result for the estimate of the nestbox homophily term (hom) in M2 shows, two jackdaws raised in the same nestbox are more than twice as likely to share food with one another than two jackdaws from different nestboxes; the hazard (relative rate) of sharing for two birds from the same nestbox is multiplied by $e^{0.8614} = 2.37$, all other things being equal. M3 provides evidence that strong persistence of action is involved in the feeding process, as shown by the estimate of PoA. The hazard that a bird will repeat whatever it just did is multiplied by $e^{2.26}$; a roughly 10-fold increase, net of the baseline hazards of occurrence. As a corollary, there is very little evidence of reciprocity as the estimate of recip indicates. However, when reciprocity does occur, it is more likely to happen immediately than further along in the chain of events, as the positive recency coefficient estimate for recenXrecip suggests. The nestbox homophily effect for hom disappears in the presence of persistence and recency effects in M3, suggesting that there is an interaction between these terms, and that reciprocity is confined to birds from the same nestbox.

The results for M4, in which food types are compared, suggest that wax moth larvae are particularly valued as a social commodity. Jackdaws are more likely to immediately share wax moth larvae than sweetcorn, and more likely to eat sweetcorn than wax moth larvae, as the negative fixed effects coefficients for sweetcorn (the terms with .Corn in the name) suggest; the latter finding is consistent with the findings of de Kort et al. (2006). Having sweetcorn also drives birds to persist in their actions to a greater extent, and in the rare occurrence of reciprocity, that type of exchange tends to happen later in the event history than those involving sharing wax moth larvae. We conclude this because of the negative recenXrecip.Corn coefficient. That is, wax moth larvae are more likely to be shared, and exchanges are more likely to be quickly reciprocated than those involving the transfer of sweetcorn. Statistically, M3 has the best fit to the data, although M4 has a comparable BIC value to M3 given that it includes 17 additional parameters; both M3 and M4 have much smaller values of BIC than the preceding models.

DISCUSSION

We have demonstrated the potential of the REM for modelling the temporal structure of animal social interactions, allowing an investigation of reciprocity and persistence of behaviour. We can assess whether this repetition or reciprocation of action tends to happen early in the sequence of events that follow the original action, or later in the sequence. We have shown that the REM is a flexible approach for studying social behaviour as it unfolds in time, and how support constraints can be used to allow for the study design and for the possible actions that can occur. We have explained how these models can be fitted in the statistical software R.

Having illustrated the application of the model with our case study, we think that the REM will be more generally useful in studies of animal social behaviour, where disaggregated event data are available. When covariates can be incorporated into the model, such as the sex and kinship of each animal, these allow hypotheses involving homophily (similarity of characteristics) or heterophily (difference) to be tested. Future work may also consider alternative low-level social processes that may be at play here, such as how the sequence of behavioural events is affected by the presence of a predator at some point in the sequence.

One of the strengths of modelling with the REM is that the study design and sampling method can be taken into account through the support constraints, making it useful for a range of sample designs and settings. For example, Morton et al. (2013) observed the grooming behaviour of capuchin monkeys, *Sapajus apella*, in two enclosures located in Edinburgh Zoo, U.K. (Macdonald & Whiten, 2011). They comprised an East group, with eight monkeys and a West group, with 10 monkeys. These authors were interested in whether monkeys reciprocated grooming, and persisted in their grooming actions. Because they are in two separate enclosures, monkeys from the East group cannot groom or be groomed by animals in the West group. Focal sampling was used in the study design, and one observer, who alternated between the East and West enclosures, collected all the data. For full details of the study design, see Morton et al. (2013). Rather than analyse the data for each of these small networks separately for each enclosure, thus reducing statistical power, a joint REM could be fitted that pools the estimates from each focal monkey's event history. To take into account impossible actions between enclosures, individual and enclosure-specific support constraints could be specified on the set of possible observable actions at any given point in time. These would disallow grooming from one enclosure to the next or grooming of oneself, as possible actions. This would ensure that the correct set of possible actions for each observed event was used in the model estimation.

Although we did not focus on them in this paper, the REM has the potential for modelling more complex dynamics in networks. Perhaps the most important of these are Gibson's conversational dynamics (Gibson, 2003, 2005). These were originally developed in the area of (human) conversation as participation shifts (or p-shifts), where, for example, the action of one individual A to another B is followed by a group reaction, or by the interaction by two other individuals in the group that are not A or B. In the context of animal behaviour, and using grooming as an example, these p-shifts would include such sequences of events as: A grooms B, B subsequently grooms another animal in the network that is not A, or A grooms B, and subsequently C grooms D. In Table 1 of Gibson (2003), such p-shifts are listed in four categories of behaviour: 'turn-receiving', 'turn-claiming', 'turn-usurping', and 'turn-continuing'. These p-shifts can be modelled in the REM framework via the relevent package in R (Butts, 2010), allowing more sophisticated hypotheses about temporal dynamics of animal social networks to be tested.

We used a single-level version of the REM. A multilevel version has recently been proposed (DuBois, Butts, McFarland, & Smyth, 2013). The multilevel version could be useful, for example, when we have 10 or more groups (such as multiple enclosures) for which we want to identify common patterns of action by modelling the entire data set, for statistical efficiency. Such an approach would allow each group to be identified for inference.

Another recent development in the general area of REMs is in the stochastic blockmodeling of relational event dynamics (DuBois, Butts, & Smyth, 2013). These authors develop approaches for modelling the stochastic equivalence of nodes in static networks, such as stochastic blockmodels (Nowicki & Snijders, 2001), to the dynamic context. DuBois, Butts, and Smyth, (2013) use this approach to identify latent clusters in the network in which there are similar dynamics of network interaction. They show, through a variety of empirical examples involving human network dynamics, evidence of different numbers of latent clusters (K^* in their terminology), ranging from two to 10. We think such approaches could be also valuable in identifying latent clusters in dynamic social networks for animals.

Acknowledgments

References

Abbott, A. (1995). Sequence analysis: new methods for old ideas. *Annual Review of Sociology, 21*, 93–113.

von Bayern, A. M., de Kort, S. R., Clayton, N. S., & Emery, N. J. (2007). The role of food-and object-sharing in the development of social bonds in juvenile jackdaws (*Corvus monedula*). *Behaviour, 144*(6), 711–733.

Bednekoff, P. A., Balda, R. P., Kamil, A. C., & Hile, A. G. (1997). Long-term spatial memory in four seed-caching corvid species. *Animal Behaviour, 53*(2), 335–341.

Blonder, B., & Dornhaus, A. (2011). Time-ordered networks reveal limitations to information flow in ant colonies. *PloS One, 6*(5), e20298.

Blonder, B., Wey, T. W., Dornhaus, A., James, R., & Sih, A. (2012). Temporal dynamics and network analysis. *Methods in Ecology and Evolution, 3*(6), 958–972.

Butts, C. T. (2008). A relational event framework for social action. *Sociological Methodology, 38*(1), 155–200.

Butts, C. T. (2010). *relevent: Relational event models.* R package version 1.0. http://CRAN.R-project.org/package=relevent.

Croft, D. P., Edenbrow, M., Darden, S. K., Ramnarine, I. W., van Oosterhout, C., & Cable, J. (2011). Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology, 65*(12), 2219–2227.

Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks.* Princeton, NJ: Princeton University Press.

Desmarais, B. A., & Cranmer, S. J. (2010). Consistent confidence intervals for maximum pseudolikelihood estimators. In *Proceedings of the Neural Information Processing Systems Workshop on Computational Social Science and the Wisdom of Crowds* (pp. 1–4). http://www.unc.edu/~skylerc/Skyler/Research_files/BootMPLE.pdf.

Desmarais, B. A., & Cranmer, S. J. (2012). Statistical mechanics of networks: estimation and uncertainty. *Physica A: Statistical Mechanics and its Applications, 391*(4), 1865–1876.

DuBois, C., Butts, C. T., McFarland, D., & Smyth, P. (2013). Hierarchical models for relational event sequences. *Journal of Mathematical Psychology, 57*(6), 297–309.

DuBois, C., Butts, C. T., & Smyth, P. (2013). Stochastic blockmodeling of relational event dynamics. In C. M. Carvalh, & P. Ravikumar (Eds.), *Proceedings of the Sixteenth International Conference on Artificial Intelligence and Statistics* (pp. 238–246).

Faust, K., & Skvoretz, J. (2002). Comparing networks across space and time, size and species. *Sociological Methodology, 32*, 267–299.

Freeman, L. C., Freeman, S. C., & Romney, A. K. (1992). The implications of social structure for dominance hierarchies in Red Deer (*Cervus elaphus* L.). *Animal Behaviour, 44*(2), 239–245.

Gibson, D. R. (2003). Participation shifts: order and differentiation in group conversation. *Social forces, 81*(4), 1335–1380.

Gibson, D. R. (2005). Taking turns and talking ties: networks and conversational interaction. *American Journal of Sociology, 110*(6), 1561–1597.

Goffman, E. (1967). *Interaction ritual: essays on face-to-face interaction.* Piscataway, NJ: Aldine.

Hanneke, S., Fu, W., & Xing, E. P. (2010). Discrete temporal models of social networks. *Electronic Journal of Statistics, 4*, 585–605.

Hemelrijk, C. (1990). A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. *Journal of Theoretical Biology, 143*(3), 405–420.

Hobson, E. A., Avery, M. L., & Wright, T. F. (2013). An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. *Animal Behaviour, 85*(1), 83–96.

Jennings, D. J., Carlin, C. M., & Gammell, M. P. (2009). A winner effect supports third-party intervention behaviour during fallow deer (*Dama dama*) fights. *Animal Behaviour, 77*(2), 343–348.

de Kort, S. R., Emery, N. J., & Clayton, N. S. (2003). Food offering in jackdaws (*Corvus monedula*). *Naturwissenschaften, 90*(5), 238–240.

de Kort, S. R., Emery, N. J., & Clayton, N. S. (2006). Food sharing in jackdaws, *Corvus monedula*: what, why and with whom? *Animal Behaviour, 72*(2), 297–304.

Krause, J., Croft, D., & James, R. (2007). Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology, 62*(1), 15–27.

Leifeld, P., Cranmer, S. J., & Desmarais, B. A. (2014). *xergm: Extensions for exponential random graph models.* R package version 1.1. http://CRAN.R-project.org/package=xergm.

Macdonald, C., & Whiten, A. (2011). The 'Living Links to Human Evolution' Research Centre in Edinburgh Zoo: a new endeavour in collaboration. *International Zoo Yearbook, 45*(1), 7–17.

Marcum, C. S. (2012). *informR: R tools for creating sequence statistics.* R package version 1.0.04. http://CRAN.R-project.org/package=informR.

Marcum, C. S., & Butts, C. T. (2014). Creating sequence statistics for egocentric relational events models using informr. *Journal of Statistical Software*, 1–35.

Mills, M. (2011). *Introducing survival and event history analysis.* Thousand Oaks, CA: Sage.

Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S. F., Thierry, B., Paukner, A., et al. (2013). Personality structure in brown capuchin monkeys (*Sapajus apella*): comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp.*), and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology, 127*(3), 282.

Mount, D. (2001). *Bioinformatics: Sequence and genome analysis.* Cold Spring Harbor, NY: Cold Spring Harbor Press.

Nowicki, K., & Snijders, T. A. B. (2001). Estimation and prediction for stochastic block structures. *Journal of the American Statistical Association, 96*(455), 1077–1087.

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., et al. (2013). The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology, 25*(2), 242–255.

R Core Team. (2013). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Rendell, L., & Gero, S. (2014). The behavioral ecologist's essential social networks cookbook: comment on Pinter-Wollman et al (2013). *Behavioral Ecology, 25*(2), 257–258.

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology, 63*(7), 975–988.

Snijders, T. A. B. (2005). Models for longitudinal network data. In P. J. Carrington, J. Scott, & S. Wasserman (Eds.), *Models and methods in social network analysis* (pp. 215–247). New York, NY: Cambridge University Press.

Stephens, D. W., McLinn, C. M., & Stevens, J. R. (2002). Discounting and reciprocity in an iterated prisoner's dilemma. *Science, 298*(5601), 2216–2218.

Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for non-kin food sharing: timing and currency of benefits. *Animal Behaviour, 67*(4), 603–614.

de Waal, F. B. (1996). *Good natured.* Harvard, MA: Harvard University Press.

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour, 75*(2), 333–344.

Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis.* Chicago, IL: University of Chicago Press.