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**Using the Relational Events Model (REM)
to Investigate the Temporal Dynamics of
Animal Social Networks.**

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Abstract

Social dynamics are of fundamental importance in animal societies. Studies on non-human 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 Events 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. We outline some recent extensions to the REM framework.

Keywords: Animal Social Behaviour; Event Data; Jackdaw; Longitudinal Network; Social Network Analysis; Reciprocity; Temporal Network Analysis.

1 Introduction

The application of social network analysis to non-human animal societies has attracted a great deal of interest over the last decade (Croft et al., 2008; Whitehead, 2008; Wey et al., 2008; Sih et al., 2009). 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 et al., 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 co-operation is maintained within a population (Croft et al., 2008; Wey et al., 2008; Sih et al., 2009). 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 (Freeman et al., 1992; Faust and Skvoretz, 2002). 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. Whilst 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 (Pinter-Wollman et al., 2013; Blonder et al., 2012).

The importance of considering temporal dynamics in studies of animal social networks has been highlighted by a number of recent review papers (Pinter-Wollman et al., 2013; Blonder et al., 2012). 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 and 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 (Hobson et al., 2013; Croft et al., 2011).

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 et al., 2009).

There is great value in applying statistical models, such as the Relational Events 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 and 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, developed by Butts (2008), can be applied to animal social network data that is 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, whilst 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).

1.1 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 - the theoretical background to the REM is explained in more detail in Section 2.

REM is distinct from other established models and methods for longitudinal and network analysis, and the data requirements are also different. Typical non-parametric 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 (micro-behaviours) as the units of analysis and uses sufficient statistics (statistics that summarise 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; called *loops* in network terms. Adapting an argument of Goffman (1967) to animal behaviour, actions amongst animals over time can be seen as series of discrete events where one animal directs a behaviour at one or more of the other animals in their 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 possible 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. Firstly, these include Temporal Exponential Random Graph Models (TERGMs) (Hanneke et al., 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 et al., 2014). Secondly, 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 temporal ERGMs 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 Section 2, we provide a brief theoretical outline of the REM, and explain how it may be fitted, as well

as the necessary data preparation. In Section 3, we discuss our illustrative empirical case study. In Section 4 we draw conclusions on the results of our case study, and discuss how the REM could be 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.

2 The Relational Event Model (REM) for social action

2.1 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 (2015) for details of other generalisations.

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 ; $s(a) = i$

$j \in \mathfrak{R}$: is the ‘‘Receiver’’ of event a ; $r(a) = j$

$k \in C$: is the ‘‘Action type’’ (category) of event a ; $c(a) = k$

$t \in R$: is the ‘‘Time of event’’ the order in which the event transpired.

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

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

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 generalised to incorporate exogenous events in Marcum and Butts (2015), follows a piecewise constant hazard under a mixture of Poisson distributions. Current implementations support a variety of estimation methods commonly used in generalised linear models including: maximum likelihood, Markov Chain Monte Carlo, Bayesian sampling-importance-resampling, and Bayesian method of posterior modes.

2.2 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 patterns of animal behaviour, including sending, receiving, reciprocity, and persistence of action. It also be possible to specify and fit REMs investigate patterns 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 if 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 non-significant 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 a lot of 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 potential 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 Events Model*, may be fitted with `rem(...)` and is used for our two examples. 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 of 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 animal 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 pre-packaged summaries of event sequences, such as conversational dynamics (Gibson, 2003) and thus makes it quite 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 an individual animal is observed by the researcher 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, as illustrated in Figure 1 below. 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 (i), or whether another animal, including B or C, grooms A (ii), but if B grooms C or vice-versa this is not directly observed by the researcher (iii), 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 non-observable 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. Support constraints can be set up in the `informR` package, as Marcum and Butts (2015) explain in more detail.

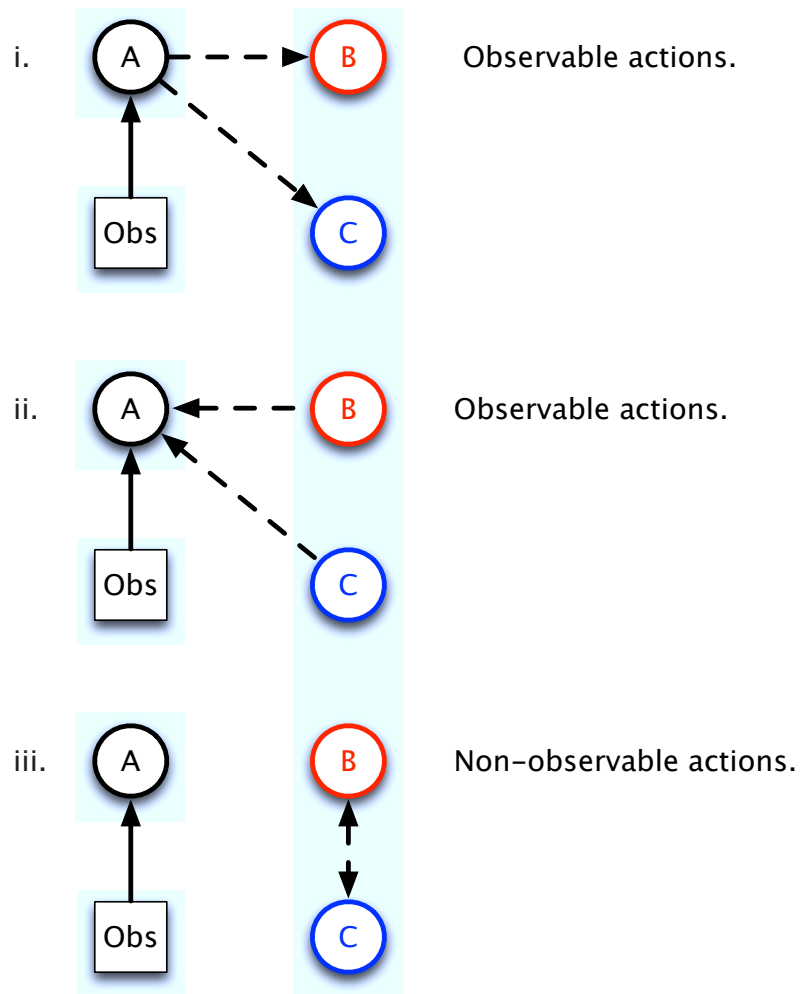


Fig. 1: Observable and non-observable actions in focal sampling. A, B and C are animals; Obs is the Observer.

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 such an item to transfer. Another 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.

3 Case study

3.1 Introduction

de Kort et al. (2006) studied a group of twelve European jackdaws, who received 28 randomised 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 nest-boxes. Individuals in the same nest-box were not necessarily siblings. For the feeding trials, one bird at a time received ten morsels of food consecutively, after which, a second bird received 10 morsels, etc., until all birds had received the same treatment. The order that individuals received morsels was randomised before each trial. For each trial, the morsels alternated between sweetcorn or 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 known, 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 is more likely than we would expect by chance? If so, what is the frequency of these events given past action, and how quickly are such actions repeated? How do these actions relate to exogenous factors? 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 quickly 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 fit REMs to these data to test for persistence and reciprocity of action in terms of food-sharing amongst the network of birds. We also investigate whether the patterns of action are different for two birds raised in the same nest-box, compared with two birds, each from a different nest-box. 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 et al., 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 et al., 2002). It is also of interest to anthropologists because food sharing is often regarded as being fundamental to the evolution of complex cognition many animal species, including humans (de Waal, 1996). In our case study, the animals are in captivity. Whilst in this environment, their behaviour may differ from animals in the wild. However, food sharing is part of the animals' natural behaviour repertoire.

3.2 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, mostly initiated by the donor, and that in the second time-frame, the frequency of food sharing and the number of recipients were both reduced, compared with the first time-frame. Whilst 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 on those of 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 ego-centric REM can be used to test for differential food-sharing behaviour amongst the birds.

In our REMs, we follow the path of each morsel as it enters the system until it leaves the system; until it is eaten or dropped by a particular bird. We treat the introduction of morsels to particular birds in each trial as exogenous events, randomised by trial and bird, and assume that these initiate event histories. Once a bird receives a morsel, it may be eaten by initial receiver, it may be dropped on the floor, or it may be transferred to another bird. Here, we treat

any such 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 which bird 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 constants in REMs is discussed in more detail in Marcum and Butts (2015). Furthermore, we incorporate exogenous events between the initiation and termination of each trial to take into account that trials took place on different days.

See Marcum and Butts (2015) for more discussion of support constraints.

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

1. The behaviour of individual birds.
2. Whether nest-box-homophily (familiarity of birds from the same nest-box) 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), thirteen 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 twelve birds, each of which has an opportunity to eat, share or drop a morsel during the various trials, twelve of

the fixed effects are for the birds to transfer the morsel, and the thirteenth 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 common nest-boxes. Model 2 (M2), extends M1 to include a nest-box-homophily term that compares the likelihood of an exchange between any two birds raised in a common nest-box to any two birds not raised in common nest-boxes. A positive coefficient here indicates greater within-nest-box-homophily than between-nest-box-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 persistency 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, 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 amongst the twelve birds, an alternative way to model this difference overall would be to simply add a corn covariate as a main effect.

Tab. 1: Relational Events Model Results for Jackdaw Food-Sharing.

	M1			M2			M3			M4		
	B	SD		B	SD		B	SD		B	SD	
B1	-4.1281	0.1614	***	-4.3404	0.1656	***	-6.7993	0.2364	***	-5.9977	0.2532	***
B2	-4.9759	0.2434	***	-5.2052	0.2465	***	-6.529	0.3126	***	-5.5099	0.3435	***
B3	-3.8544	0.1415	***	-4.0608	0.146	***	-5.5007	0.2622	***	-4.4841	0.2849	***
B4	-4.4595	0.1901	***	-4.8934	0.2013	***	-6.8215	0.2864	***	-5.7796	0.3006	***
B5	-5.3929	0.3022	***	-5.6803	0.306	***	-7.3905	0.3601	***	-6.7481	0.449	***
B6	-4.5672	0.201	***	-4.8502	0.2065	***	-6.6934	0.275	***	-5.8865	0.3136	***
B7	-3.983	0.1504	***	-4.2679	0.1578	***	-5.857	0.2515	***	-4.8282	0.2724	***
B8	-5.637	0.3339	***	-5.9574	0.338	***	-7.4628	0.3643	***	-6.3255	0.3667	***
B9	-3.8166	0.1388	***	-4.2473	0.1537	***	-4.8318	0.4001	***	-3.5383	0.4289	***
B10	-5.3044	0.2894	***	-5.7376	0.2969	***	-7.1351	0.3234	***	-6.396	0.3847	***
B11	-5.0619	0.259	***	-5.4848	0.267	***	-7.5194	0.3804	***	-6.8207	0.4714	***
B12	-3.7636	0.1352	***	-4.1953	0.1504	***	-7.3229	0.3498	***	-6.2694	0.3674	***
floor	-3.5233	0.1149	***	-3.5233	0.1149	***	-6.5397	0.2174	***	-5.5964	0.2214	***
hom				0.8614	0.1086	***	0.2277	0.1557		0.1573	0.1783	
PoA							2.2605	0.1213	***	1.9835	0.124	***
recip							-0.3968	0.2386		-0.5499	0.283	.
recenXrecip							0.0028	0.0004	***	0.0037	0.0005	***
B1.Corn										-2.8489	0.6675	***
B2.Corn										-3.6471	0.8501	***
B3.Corn										-3.5305	0.6758	***
B4.Corn										-3.936	0.914	***
B5.Corn										-2.2079	0.8104	**
B6.Corn										-2.7602	0.702	***
B7.Corn										-3.5032	0.6537	***
B8.Corn										-10.5216	26.3976	
B9.Corn										-5.359	1.2731	***
B10.Corn										-2.4507	0.7431	***
B11.Corn										-2.5135	0.8977	**
B12.Corn										-3.9508	1.1337	***
floor.Corn										-11.1766	25.6814	
hom.Corn										0.2855	0.3814	
PoA.Corn										1.1074	0.3767	**
recip.Corn										0.4352	0.5527	
recenXrecip.Corn										-0.0032	0.0009	***
BIC	4656.627			4604.662			2805.765			2809.678		
Pseudo R^2	0.712			0.717			0.832			0.841		

The SD are standard deviations about the posterior modes. The stars are asymptotically equivalent to probabilities associated with a Z statistic. Thus: *, ** and *** refer to significance levels of approximately 5%, 1% and 0.1%, respectively.

3.2.1 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 biased sex ratio in these data: there are ten male birds and only two females; 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 twelve birds prefer to eat the morsel, rather than to transfer or drop it. However, as the result for the estimate of the nest-box-homophily term (`hom`) in M2 shows, two jackdaws raised in the same nest-box are more than twice as likely to share food with one another than two jackdaws, each from the a different nest-box; the hazard (relative rate) of sharing for two birds from the same nest-box is multiplied by $e^{.8614} = 2.36$, all other things being equal. M3 provides evidence that strong persistence of action is involved in the feeding process, as shown by the estimates of Persistence of Action, `PoA`. The hazard that a bird will repeat whatever it just did is multiplied by $e^{2.26}$; a roughly tenfold 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 nest-box-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 nest-box.

The results for M4, in which food types are compared, suggest that wax moth larvae are particularly valued as a social commodity. Corvids 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 seventeen additional parameters; both M3 and M4 have much smaller values of BIC than the preceding models.

4 Conclusions

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, and how past action is associated with the recency of the action that follows. 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 such models can be fitted in the statistical software, R.

Having illustrated the application of the models with our two examples, 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 in 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 in two enclosures located in Edinburgh Zoo (Macdonald and Whiten, 2011). They comprised an East group, with 8 monkeys and a West group, with 10 monkeys. These authors were interested in whether monkeys reciprocate grooming, and persist 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 all the data were collected by one observer, who alternated between the East and West enclosures. 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 model can 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 were specified on the set of possible observable actions at any given point in time. These disallow grooming from one enclosure to the next or grooming of oneself, as possible actions. This ensures that the correct set of possible actions for each observed event are 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), thirteen 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 et al., 2013a). The multilevel version could be useful, for example, when we have multiple groups (such as multiple enclosures) for which we want to identify common patterns of action by modelling the entire dataset, 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 et al., 2013b). These authors develop approaches for modelling the stochastic equivalence on nodes in static networks, such as stochastic blockmodels (Nowicki and Snijders, 2001), to the dynamic context. DuBois et al. (2013b) used 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 2 to 10. We think such approaches could be also valuable in identifying latent clusters in dynamic social networks for animals.

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