

1 **USING THE RELATIONAL EVENTS MODEL (REM) TO INVESTIGATE THE TEMPORAL**
2 **DYNAMICS OF ANIMAL SOCIAL NETWORKS.**

3 Mark Tranmer (University of Manchester, UK)*,

4 Christopher Steven Marcum (National Institutes of Health, USA),

5 F. Blake Morton (University of Stirling, UK),

6 Darren P. Croft (University of Exeter, UK),

7 Selvino R. de Kort (Manchester Metropolitan University, UK).

8 Social dynamics are of fundamental importance in animal societies. Studies on non-
9 human animal social systems often aggregate social interaction event data into a single
10 network within a particular time frame. Analysis of the resulting network can provide a
11 useful insight into the overall extent of interaction. However, through aggregation,
12 information is lost about the order in which interactions occurred, and hence the
13 sequences of actions over time. Many research hypotheses relate directly to the
14 sequence of actions, such as the recency or rate of action, rather than to their overall
15 volume or presence. Here, we demonstrate how the temporal structure of social
16 interaction sequences can be quantified from disaggregated event data using the
17 Relational Events Model (REM). We first outline the REM, explaining why it is different
18 from other models for longitudinal data, and how it can be used to model sequences of
19 events unfolding in a network. We then discuss a case study on the European jackdaw
20 (*Corvus monedula*), in which temporal patterns of persistence and reciprocity of action
21 are of interest, and present and discuss the results of a REM analysis of these data.

22 One of the strengths of a REM analysis is its ability to take into account different ways in
23 which data are collected. Having explained how to take into account the way in which
24 the data were collected for the jackdaw study, we briefly discuss the application of the
25 model to other studies. We provide details of how the models may be fitted in the R
26 statistical software environment. We outline some recent extensions to the REM
27 framework.

28 **Keywords:** Animal Social Behaviour; Event Data; Jackdaw; Longitudinal Network;
29 Social Network Analysis; Reciprocity; Temporal Network Analysis, Food sharing.

30 * Corresponding Author: Mark Tranmer, CMIST, Social Statistics, University of
31 Manchester, M13 9PL, UK. mark.tranmer@manchester.ac.uk

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33 The application of social network analysis to non-human animal societies has attracted a
34 great deal of interest over the last decade (Croft et al., 2008; Whitehead, 2008; Wey et
35 al., 2008; Sih et al., 2009). Who interacts with whom, and the local (for example, cliques
36 in the network) and global (overall) network structures that these interactions produce
37 are of central importance for key issues in ecology and evolution (Krause et al., 2007).
38 There is great interest in linking observed patterns in animal social networks to such
39 processes to understand, for example, how disease is transmitted within a population,
40 or how co-operation is maintained (Croft et al., 2008; Wey et al., 2008; Sih et al., 2009).
41 To date, however, researchers have tended to aggregate data on social interactions over
42 time into a single, static, network within a particular time frame (Croft et al., 2008), even
43 if the observations were originally made for individual, disaggregated, events (Freeman
44 et al., 1992; Faust and Skvoretz, 2002). Aggregate event network data indicate which
45 individuals interacted, and possibly how often. However, through aggregation,
46 information is lost about the order in which such interactions occurred, and hence the
47 sequences or patterns of actions over time. Whilst some research questions relate to
48 the overall number, or the presence, of interactions between individuals in a particular
49 time-frame, many questions relate directly to the sequence of actions (Blonder et al.,
50 2012; Pinter-Wollman et al., 2013).

51 The importance of considering temporal dynamics in studies of animal social networks
52 has been highlighted by a number of recent review papers (Blonder et al., 2012; Pinter-
53 Wollman et al., 2013). Several empirical studies have begun to consider the temporal
54 structure of animal social networks, particularly in the context of information diffusion
55 and disease transmission (Blonder and Dornhaus, 2011). In these studies, the temporal
56 patterns of social interactions have clear consequences for the likelihood of an
57 individual gaining access to information, or being exposed to disease. Other approaches
58 to the study of temporal networks relate to the development or stability of social
59 relationships through time. For example, comparing the structure of time-aggregated
60 networks over different sampling periods (Croft et al., 2011; Hobson et al., 2013).

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

66 There is great value in applying statistical models, such as the Relational Events Model
67 (REM) for social action (Butts, 2008), to time ordered animal social interaction data to
68 test hypotheses that relate to the ordering of events or actions within a sampling period
69 (Rendell and Gero, 2014). The REM was originally developed in the social sciences by
70 Butts (2008) to investigate the timing or order of events in human interactions, such as
71 conversations or communications. Here, we show how the REM, developed by Butts
72 (2008), can be applied to animal social network data that is based on interactions
73 (events) between individual animals. We illustrate the application of the REM with a
74 case study.

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

82 *The REM, and other approaches for longitudinal and network analysis*

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

86 REM is distinct from other established models and methods for longitudinal and
87 network analysis, and the data requirements are also different. Typical non-parametric

88 sequence analysis treats whole sequences as the units of analysis (Abbott, 1995). These
89 methods either wholly aggregate events, thus losing the temporal aspects of the data,
90 make comparisons about deviations across average tendencies, or examine where
91 common sequences are conserved, such as in genomic sequence alignment (Mount,
92 2001). The REM treats the events (micro-behaviours) as the units of analysis and uses
93 sufficient statistics (statistics that summarise the values of the sample data without loss
94 of information from the sample) to model the event dynamics directly.

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

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

108 Other models for dynamic networks focus on aggregate changes in the whole network
109 structure over time. Firstly, these include Temporal Exponential Random Graph Models
110 (TERGMs) (Hanneke et al., 2010), for which efficient and unbiased estimation routines
111 were first proposed by Desmarais and Cranmer (2010, 2012), implemented in the
112 `xergm` package for R (Leifeld et al., 2014). Secondly, these involve each actor
113 evaluating their utility for forming and dissolving ties (i.e., Stochastic Actor Oriented
114 Models (SAOMs) usually fitted with the software, SIENA (Snijders, 2005)). The minimal
115 data for REM involve only multiple observations of time-ordered events, and thus have

116 much less specific data requirements than sequence analysis, which needs multiple
117 observations of whole sequences, or TERGMs and SAOMs, which require single
118 complete network data from at least two points in time. The family of models employed
119 by the REM framework is related to the event history (or failure/survival/life-table)
120 analysis (Mills, 2011) in that each potential action is assumed to have a piecewise
121 constant hazard (the rate of occurrence, given everything that has transpired up to that
122 point) (Butts, 2008). As these statistics are hazards, they directly estimate the rate of
123 event occurrence. The REM framework is thus a useful general tool for the analysis of
124 social behavioural processes that unfold in time.

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

132 **METHODS**

133 *Background*

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

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

141

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

143 $i \in S$: is the "Sender" of event a ; $s(a) = i$; S is the set of possible senders.

144 $j \in \mathfrak{R}$: is the "Receiver" of event a ; $r(a) = j$; \mathfrak{R} is the set of possible receivers.

145 $k \in C$: is the "Action type" (category) of event a ; $c(a) = k$; C is the set of actions.

146 $t \in R$: is the "Time of event" the order in which the event transpired, in study period R .

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

$$149 \lambda(s(a), r(a), c(a), X_a, A_t, \theta) = \exp[\lambda_0 + \theta^T u(s(a), r(a), c(a), X_a, A_t)] \quad (1)$$

150 Where:

151 $\lambda()$, λ_0 : are rates; the latter is the baseline rate of action, which is fixed at 0 at the
152 beginning and end of the observation.

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

155 A_t : is the sequence of past action.

156 u : is a vector of sufficient statistics.

157 θ : are the REM model coefficients associated with u .

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

164

165 *Specifying and Fitting the REM*

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

172 A typical starting point in the modelling process is to include parameters for each
173 individual in the network in the REM; allowing each animal to have its own specific rate
174 of sending and receiving actions in the model, to test if there is any evidence of
175 differential rates of sending and receiving actions. For a network of n animals there are
176 potentially n specific rates of sending and n rates of receiving actions. When we set up
177 the model using a particular animal as the “reference animal”, significant positive
178 coefficients for any other animals in the network indicate higher rates of sending or
179 receiving a particular action than for the reference animal. Significant negative
180 coefficients indicate the converse, and non-significant coefficients indicate they can be
181 thought of as similar to the reference animal with respect to sending or receiving
182 actions.

183 Allowing for specific sending and receiving of actions in the REM makes the model
184 valuable for estimating specific effects for each animal, but typically requires many
185 model parameters. Setting up the REM with a reference animal requires $2 \times (n - 1)$
186 parameters for the fixed effects for sending and for receiving actions; for large networks
187 and/or short sequences, this potential large number of model parameters should be
188 considered in terms of model complexity given the available data. It may be possible to
189 reduce the number of model parameters to common sending and receiving effects, as
190 detailed in (Butts, 2010). When comparing fitted REMs, we use the Bayesian Information
191 Criterion (BIC) to assess their relative goodness of fit and additionally report pseudo-R2
192 measures (these are based on one minus the ratio of the null and fitted likelihoods).

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

209 The sampling used in the study design should be taken into account in the modelling
210 process. In many cases, focal sampling is used, where the researcher observes an
211 individual animal for a set period of time, possibly at random, or possibly through
212 opportunity or convenience. This means the researcher only observed events associated
213 with the focal animal (Fig. 1). If we label the focal animal as “A” and two other animals,
214 “B” and “C”, and the researcher (observer) as “Obs”, and use the example of grooming,
215 the researcher can see whether A grooms another animal, including B or C (i), or
216 whether another animal, including B or C, grooms A (ii), but if B grooms C or vice-versa
217 this is not directly observed by the researcher (iii), even if such events occur. Therefore,
218 prior to modelling, we must set up the data such that only those actions that could have
219 been observed for any given event by the researcher are considered in the possible set
220 of actions, and exclude non-observable actions. We do this using a set of support
221 constraints, where a binary indicator system is used to evaluate and restrict which

222 actions are possible, or observable, at any given moment in the event history. For
223 example, an event that is observable by the researcher at a particular point in the
224 sequence is associated with a support constraint value of 1 and an unobservable event
225 is associated with a value of 0. Support constraints can be set up in the `informR`
226 package, as Marcum and Butts (2014) explain in more detail.

227 ***** Figure 1: Observable Actions in Focal Sampling (about here) *****

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

236 **CASE STUDY**

237 *Background*

238 de Kort et al. (2006) studied a group of twelve European jackdaws, who received 28
239 randomised feeding trials on different days in 2003. These authors aggregated the
240 events into two static networks: the first for the time frame of the first half of the study
241 period (first 14 trials) and the second for the time frame of the second half of the study
242 period (trials 15-28). The birds were all living in one large aviary, having been taken from
243 several nests after at least a week from hatching. The nestlings were hand-raised until
244 nutritional independence, and were grouped in four nest-boxes. Individuals in the same
245 nest-box were not necessarily siblings. For the feeding trials, one bird at a time received
246 ten morsels of food consecutively, after which, a second bird received 10 morsels, etc.,
247 until all birds had received the same treatment. The order that individuals received
248 morsels was randomised before each trial. For each trial, the morsels alternated

249 between sweet corn and the larvae of the wax moth, *Galleria mellonella*. Birds did not
250 receive these morsels outside the feeding trials. For each morsel provided to a focal
251 bird, it was recorded whether a bird ate the morsel, transferred it to another bird, or
252 dropped it on the floor, thus, for Equation (1), there are three categories of action for
253 each morsel. For each trial, exact-timing information is not available, but the order of
254 events is known.

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

264 The network in our case study is fairly small, 12 jackdaws, although a long sequence of
265 event data was collected, comprising 3168 events. The REM could also be used with
266 much larger networks, where such data are available. We fit REMs to these data to test
267 for persistence and reciprocity of action in terms of food sharing amongst the network
268 of birds. We also investigate whether the patterns of action are different for two birds
269 raised in the same nest-box, compared with two birds, each from a different nest-box.
270 The order of observed events is of interest in this example because the closeness or
271 distance of food sharing events in the sequence relates to whether the birds rely on
272 memory to direct their actions; events more distant in the sequence require longer
273 memory retention from the bird transferring the food. Corvids are known to have
274 excellent memory (Bednekoff et al., 1997). The number of times a persistent action from
275 one bird to another leads to a reciprocal food transfer can also be investigated with the
276 REM. Food sharing is of great interest to evolutionary biologists, because it suggests the
277 existence of altruism, or it requires difficult-to-explain phenomena such as reciprocation

278 and temporal discounting (Stephens et al., 2002). It is also of interest to anthropologists
279 because food sharing is often regarded as being fundamental to the evolution of
280 complex cognition in many animal species, including humans (de Waal, 1996). In our
281 case study, the animals are in captivity. Whilst in this environment, their behaviour may
282 differ from animals in the wild. However, food sharing is part of the animals' natural
283 behaviour repertoire.

284 *Specifying and Fitting the REM.*

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

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

302 Once a bird receives a morsel, it may be eaten by the initial receiver, it may be dropped
303 on the floor, or it may be transferred to another bird. Here, we treat the latter action
304 type as a "food transfer". Because we have the order of events but not the exact timing,

305 we use an ordinal likelihood with multiple action types, to reflect the three possible
306 actions for each morsel.

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

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

- 317 1. Whether each individual bird has its own specific rate of transferring food.
- 318 2. Whether nest-box-homophily (familiarity of birds from the same nest-box) is
319 associated with particular food sharing behaviour.
- 320 3. Reciprocity and persistence of food sharing: how quickly these actions occur, or
321 are repeated in the sequence of events.
- 322 4. Whether food sharing behaviour is different for the two different food types.

323 In Model 1 (M1), thirteen fixed effects were fitted to compare the relative tendency for
324 a bird to initially eat the morsel rather than transferring it, or dropping it on the floor.
325 Because there are twelve birds, each of which has an opportunity to eat, share or drop a
326 morsel during the various trials, twelve of the fixed effects are for the birds to transfer
327 the morsel, and the thirteenth is for dropping the morsel on the floor. Eating the morsel
328 is the reference category. Positive coefficients would suggest that the bird is more likely
329 to transfer the morsel (or drop it on floor) than to eat it. Negative coefficients indicate
330 that the bird is likely to immediately eat the morsel rather than give it away or drop it.

331 Some birds were raised in common nest-boxes. Model 2 (M2), extends M1 to include a
332 nest-box-homophily term that compares the likelihood of an exchange between any two
333 birds raised in a common nest-box to any two birds not raised in common nest-boxes. A
334 positive coefficient here indicates greater within- nest-box-homophily than between-
335 nest-box-heterophily in terms of food sharing behaviour. In Model 3 (M3) we investigate
336 persistence of action and reciprocity by adding three statistics to the model. The first,
337 $P_{\circ A}$, measures persistency of action with respect to food sharing. The second models
338 the tendency for reciprocity to occur at any time during the event history. The third
339 models the tendency for reciprocity to occur more or less recently in event history,
340 given that a reciprocal encounter has been initiated.

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

349 *REM results.*

350 Throughout the study period, the jackdaws transferred 11.1% of food items to one
351 another. We initially included the sex of the bird as an exogenous covariate in the REM,
352 and the results suggested that jackdaws did not share more food between the sexes
353 than within them, but this is probably a result of biased sex ratio in these data: there are
354 ten male birds and only two females. Therefore, we do not have enough power in our
355 data to detect sex differences and so we did not consider the sex of the birds further in
356 these analyses.

357 In Table 1, the negative fixed effect coefficients from M1 suggest that all twelve birds
358 prefer to eat the morsel, rather than to transfer or drop it. However, as the result for

359 the estimate of the nest-box-homophily term (`hom`) in M2 shows, two jackdaws raised
360 in the same nest-box are more than twice as likely to share food with one another than
361 two jackdaws, each from the a different nest-box; the hazard (relative rate) of sharing
362 for two birds from the same nest-box is multiplied by $e^{.8614} = 2.36$, all other things being
363 equal. M3 provides evidence that strong persistence of action is involved in the feeding
364 process, as shown by the estimate of `PoA`. The hazard that a bird will repeat whatever it
365 just did is multiplied by $e^{2.26}$; a roughly tenfold increase, net of the baseline hazards of
366 occurrence. As a corollary, there is very little evidence of reciprocity as the estimate of
367 `recip` indicates. However, when reciprocity does occur, it is more likely to happen
368 immediately than further along in the chain of events, as the positive recency coefficient
369 estimate for `recenXrecip` suggests. The nest-box-homophily effect for `hom`
370 disappears in the presence of persistence and recency effects in M3, suggesting that
371 there is an interaction between these terms, and that reciprocity is confined to birds
372 from the same nest-box.

373 ***** Table 1 about here *****

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

388

389 **DISCUSSION**

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

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

406 One of the strengths of modelling with the REM is that the study design and sampling
407 method can be taken into account through the support constraints, making it useful for
408 a range of sample designs and settings. For example, Morton et al. (2013) observed the
409 grooming behaviour of capuchin monkeys in two enclosures located in Edinburgh Zoo
410 (Macdonald and Whiten, 2011). They comprised an East group, with 8 monkeys and a
411 West group, with 10 monkeys. These authors were interested in whether monkeys
412 reciprocated grooming, and persisted in their grooming actions. Because they are in two
413 separate enclosures, monkeys from the East group cannot groom or be groomed by
414 animals in the West group. Focal sampling was used in the study design, and one
415 observer, who alternated between the East and West enclosures, collected all the data.

416 For full details of the study design see Morton et al. (2013). Rather than analyse the data
417 for each of these small networks separately for each enclosure, thus reducing statistical
418 power, a joint REM could be fitted that pools the estimates from each focal monkey's
419 event history. To take into account impossible actions between enclosures, individual
420 and enclosure-specific support constraints could be specified on the set of possible
421 observable actions at any given point in time. These would disallow grooming from one
422 enclosure to the next or grooming of oneself, as possible actions. This would ensure that
423 the correct set of possible actions for each observed event were used in the model
424 estimation.

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

439 We used a single level version of the REM. A multilevel version has recently been
440 proposed (DuBois et al., 2013a). The multilevel version could be useful, for example,
441 when we have, say, ten or more groups (such as multiple enclosures) for which we want
442 to identify common patterns of action by modelling the entire dataset, for statistical
443 efficiency. Such an approach would allow each group to be identified for inference.

444 Another recent development in the general area of REMs is in the stochastic
445 blockmodeling of relational event dynamics (DuBois et al., 2013b). These authors
446 develop approaches for modelling the stochastic equivalence on nodes in static
447 networks, such as stochastic blockmodels (Nowicki and Snijders, 2001), to the dynamic
448 context. DuBois et al. (2013b) used this approach to identify latent clusters in the
449 network in which there are similar dynamics of network interaction. They show, through
450 a variety of empirical examples involving human network dynamics, evidence of
451 different numbers of latent clusters (K^{\square} in their terminology), ranging from 2 to 10. We
452 think such approaches could be also valuable in identifying latent clusters in dynamic
453 social networks for animals.

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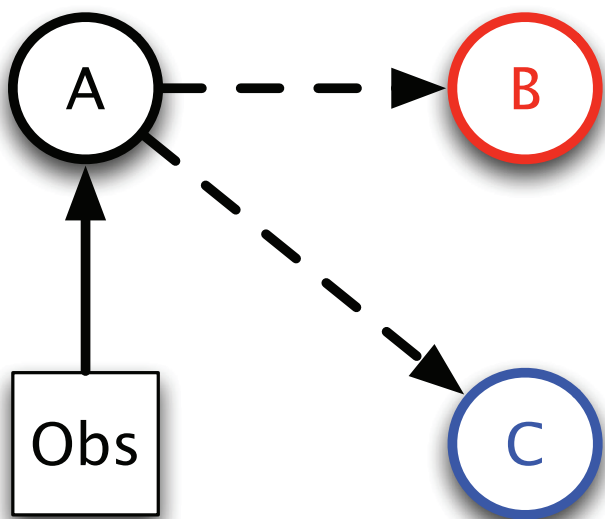
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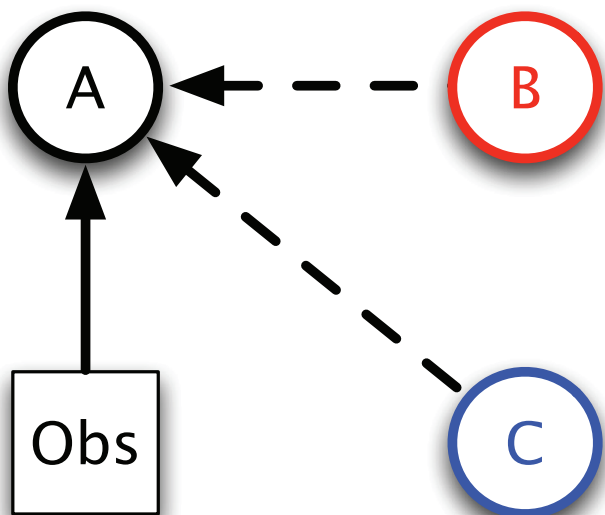
Figure

i.



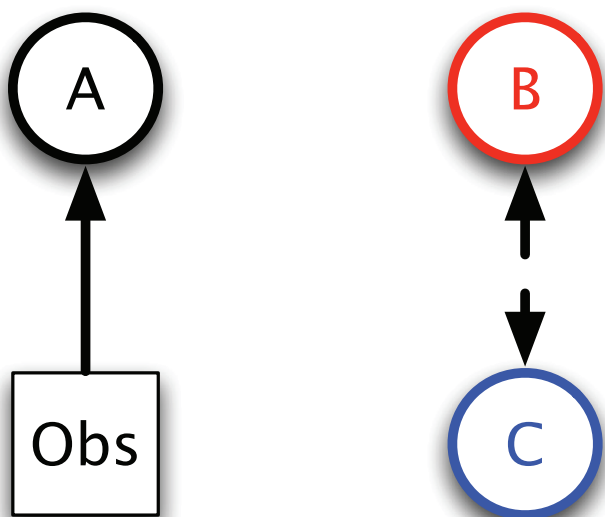
Observable actions.

ii.



Observable actions.

iii.



Non-observable actions.

Table

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

Estimate:	M1			M2			M3			M4		
	B	SD	Sig.	B	SD	Sig.	B	SD	Sig.	B	SD	Sig.
B1	-4.128	.161	***	-4.340	.166	***	-6.799	.236	***	-5.998	.253	***
B2	-4.976	.243	***	-5.205	.247	***	-6.529	.313	***	-5.510	.344	***
B3	-3.854	.141	***	-4.061	.146	***	-5.501	.262	***	-4.484	.285	***
B4	-4.460	.190	***	-4.893	.201	***	-6.822	.286	***	-5.780	.301	***
B5	-5.393	.302	***	-5.680	.306	***	-7.391	.360	***	-6.748	.449	***
B6	-4.567	.201	***	-4.850	.206	***	-6.693	.275	***	-5.887	.314	***
B7	-3.983	.150	***	-4.268	.158	***	-5.857	.252	***	-4.828	.272	***
B8	-5.637	.334	***	-5.957	.338	***	-7.463	.364	***	-6.326	.367	***
B9	-3.817	.139	***	-4.247	.155	***	-4.832	.400	***	-3.538	.429	***
B10	-5.304	.289	***	-5.738	.297	***	-7.135	.323	***	-6.396	.385	***
B11	-5.062	.259	***	-5.485	.267	***	-7.519	.380	***	-6.821	.471	***
B12	-3.764	.135	***	-4.195	.150	***	-7.323	.349	***	-6.269	.367	***
floor	-3.523	.115	***	-3.523	.115	***	-6.540	.217	***	-5.596	.221	***
hom				.861	.109	***	.228	.156		.157	.178	
PoA							2.261	.121	***	1.984	.124	***
recip							-.397	.239		-.550	.283	
recenXrecip							.003	<.001	***	.004	.001	***
B1.Corn										-2.849	.668	***
B2.Corn										-3.647	.850	***
B3.Corn										-3.531	.676	***
B4.Corn										-3.936	.914	***
B5.Corn										-2.208	.810	**
B6.Corn										-2.760	.702	***
B7.Corn										-3.503	.654	***
B8.Corn										-10.522	26.398	
B9.Corn										-5.359	1.273	***
B10.Corn										-2.451	.743	***
B11.Corn										-2.514	.898	**
B12.Corn										-3.951	1.134	***
floor.Corn										-11.177	25.681	
hom.Corn										.286	.381	
PoA.Corn										1.107	.377	**
recip.Corn										.435	.553	
recenXrecip.Corn										-.003	.001	***
BIC	4656.627			4604.662			2805.765			2809.678		
Pseudo R²	.712			.717			.832			.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.