

A peer-reviewed version of this preprint was published in PeerJ on 10 April 2014.

[View the peer-reviewed version](https://peerj.com/articles/344) (peerj.com/articles/344), which is the preferred citable publication unless you specifically need to cite this preprint.

Rands SA, Muir H, Terry NL. 2014. Red deer synchronise their activity with close neighbours. PeerJ 2:e344 <https://doi.org/10.7717/peerj.344>

1 **Red deer synchronise their activity with close neighbours**

2

3 Sean A. Rands*, Hayley Muir†, and Naomi Terry†

4

5 †HM and NT contributed equally to this work

6 *author for correspondence

7

8

9 School of Biological Sciences, University of Bristol, Bristol, UK

10

11

12

13 **ABSTRACT**

14

15 Models of collective animal behaviour frequently make assumptions about the effects of
16 neighbours on the behaviour of focal individuals, but these assumptions are rarely
17 tested. One such set of assumptions is that the switch between active and inactive
18 behaviour seen in herding animals is influenced by the activity of close neighbours,
19 where neighbouring animals show a higher degree of behavioural synchrony than would
20 be expected by chance. We tested this assumption by observing the simultaneous
21 behaviour of paired individuals within a herd of red deer *Cervus elaphus*. Focal
22 individuals were more synchronised with their two closest neighbours than with the
23 third closest or randomly selected individuals from the herd. Our results suggest that the
24 behaviour of individual deer is influenced by immediate neighbours. Even if we assume

25 that there are no social relationships between individuals, this suggests that the
26 assumptions made in models about the influence of neighbours may be appropriate.

27

28

29 **INTRODUCTION**

30

31 Many animals form groups at some point in their life cycle. In most cases, these groups
32 occur because there is some benefit from being in the group to each of its members
33 (Krause & Ruxton 2002), suggesting that the behaviour of each individual must in part
34 be both influenced by and directed towards behaving as part of the group. Models of
35 collective behaviour (Camazine et al. 2001; Sumpter 2010) frequently consider the
36 behaviours of groups that emerge from the combined actions of the individuals within
37 the group. These models are good at creating simulations of groups that appear to
38 behave in very similar ways to what is seen in nature, but very different models can
39 produce similar phenomena. In order to identify which modelled processes are
40 appropriate, it is essential to challenge these models with empirical data. However, the
41 noisiness of biological systems increases the difficulty of testing whether the interaction
42 rules used in these models are appropriate (Mann 2011).

43

44 Many of the models and associated empirical studies that describe collective behaviour
45 typically consider individuals that are influenced by other group members who are in
46 close proximity, either within a physical 'metric' distance of a focal individual (Couzin
47 et al. 2002; Herbert-Read et al. 2011; Rands et al. 2004, 2006; Romey & Vidal 2013), or
48 according to a topologically-defined network of interacting individuals (Bode et al.

49 2011a; Camperi et al. 2012; Nagy et al. 2010). Other influential models of movement
50 involve changes in behavioural states, considering the departure and leadership
51 decisions made by groups of moving animals (Fernandez & Deneubourg 2011; Pillot et
52 al. 2011; Sueur et al. 2011), where the behavioural state change experienced by
53 individuals is the switch from being static to moving. Other studies of behavioural state
54 changes have considered how local interactions govern changes between being vigilant
55 and non-vigilant (Beauchamp et al. 2012), or being active and inactive according to
56 both social facilitation and metabolic requirements (Ruckstuhl & Kokko 2002).
57
58 Given this wide variety of models exploring collective behaviour, empirical tests
59 exploring the individual behaviours driving observed collective behaviours are patchy
60 in their coverage. Much research effort has been devoted to exploring how decision-
61 making and leadership processes are connected and distributed within groups (Conradt
62 & List 2009; Dyer et al. 2009; King & Cowlshaw 2009). Specific consideration of the
63 effects of inter-neighbour interactions have explored individual decisions made during
64 group movement according to metric (Herbert-Read et al. 2011; Ramseyer et al. 2009)
65 or topological distance to neighbours (Ballerini et al. 2008; Nagy et al. 2010), and there
66 have been a number of studies exploring leaving decisions (Sueur et al. 2011). Fewer
67 studies have considered changes in behavioural state within a group. Several have
68 considered how neighbours influence the vigilance patterns of groups (Beauchamp
69 2009). Most tests of the models exploring changes in activity in response to metabolic
70 requirements and the behaviour of neighbours (Ruckstuhl & Kokko 2002) have focused
71 on how difference in energetic requirements can lead to sexual segregation (Aivaz &
72 Ruckstuhl 2011; Michelena et al. 2008; Yearsley & Pérez-Barberia 2005), non-

73 synchronous behaviour (Šárová et al. 2007), group cohesion (Conradt 1998), and group-
74 size effects on activity (Gautrais et al. 2007). However, although these models assume
75 that behavioural state is influenced by the actions of close neighbours, little has been
76 done to test this empirically. Evidence is suggested by a study of cattle *Bos taurus*
77 synchronising their lying behaviour, where their posture is more likely to be similar to
78 neighbouring individuals compared to the rest of the herd (Stoye et al. 2012). However,
79 there is scope for much more exploration of the assumptions behind models considering
80 how the proximity of individuals to others can influence switches in their behavioural
81 state. In this study, we asked whether the behaviours of individual red deer *Cervus*
82 *elaphus* living in a managed herd are influenced by their neighbours. Individual deer
83 spend large parts of their lives near or within large herds (Clutton-Brock & Albon
84 1989), and therefore are ideal for addressing how changes in individual activity tie in
85 with group-level behaviour. We hypothesised that deer that were topologically closer
86 within the herd were more likely to be synchronised than would be expected when
87 comparing two individuals randomly selected from different locations within the herd.

88

89

90 **MATERIALS AND METHODS**

91

92 The work described is purely observational, conforming with UK law and ASAB/ABS
93 guidelines on animal experimentation. Ethical approval was given by the University of
94 Bristol Ethical Review Group (University Investigation Number UB/12/035).

95

96 The herd studied was housed in an enclosed 40.5 hectare deer park in the Ashton Court

97 Estate, Bristol, England, composed of open grassland, with scattered patches of
98 woodland. The herd is a population of *c.* 99 individuals of mixed age and sex, and its
99 management and husbandry is conducted by Bristol City Council. Except for rutting
100 periods, the enclosure is accessible to the general public, and the deer are habituated to
101 the presence of humans and dogs. Permissions were not required for these observational
102 studies, which occurred during the hours the public had access to the park. All
103 observations were conducted within 10-100m of the focal individuals, using binoculars
104 where appropriate: for habituation, observers were in position for recording at least five
105 minutes before observations started.

106
107 The study coincided with the rutting season of the deer, with stags often solitary and
108 with greatly reduced feeding, and therefore likely to display very different behaviours to
109 the rest of the herd (Clutton-Brock & Albon 1989; Pépin et al. 2009). Males with antlers
110 were therefore excluded from the observations. The study focussed on females and
111 young males that had not yet segregated from their maternal group, which were likely to
112 display behaviour similar to the females (Clutton-Brock & Albon 1989).

113
114 Prior to the study described, an ethogram was constructed for individual behaviour
115 within the herd, differentiating between grazing, standing, walking, running, interacting,
116 laying with head down, laying with head alert, and laying whilst ruminating. Within the
117 analysis, these were reclassified as a combined dichotomous behaviours. Individuals
118 were classified as 'active' if they were grazing, standing, walking, running, and
119 interacting, and 'resting' if they were conducting one of the other behaviours.

120

121 For a single observation period, a focal individual was randomly selected from the herd.
122 A two figure random number was generated, and, considering the visible deer in the
123 observer's field of vision, the focal deer was selected by counting linearly from leftmost
124 or rightmost visible deer (where the direction of counting was selected by a coin toss,
125 and where a count was discarded if the random number selected was larger than the
126 number of deer visible). Selected focal individuals were watched for twenty minutes. If
127 the herd was disturbed by a human presence in the middle of the observation period, the
128 observation was aborted and the data discarded. In total, eighteen complete observations
129 of twenty minutes were conducted, over four days in October 2012. All observations
130 were conducted within 1200 and 1630h, outside of the dawn and dusk peaks of activity
131 frequently shown by red deer (Clutton-Brock et al. 1982).

132
133 Over an observation period, the behaviour of the focal individual was recorded every
134 minute. Simultaneously, the behaviour of the first, second and third closest individual in
135 the herd to the focal were also recorded (where the identities of these individuals could
136 change between the recording events as the deer moved within the herd). At the same
137 time, the behaviour of a different randomly selected control individual within the herd
138 was also recorded (selected from what remained of the herd after the focal and three
139 nearest neighbours had been excluded), where the identity of the control individual was
140 independently chosen at each recording even.

141
142 Synchronisation between individuals was calculated as the proportion of the
143 observations where the focal and test individual were both active or both inactive. Data
144 were compared with Freidman tests. Because there was some change that focal

145 individuals were re-selected by chance, we acknowledge that there could be some
146 degree of pseudoreplication in the dataset. To explore this, we generated a full set of
147 Friedman tests where all possible combinations of up to five of the focal individuals
148 were excluded from the analysis. *Post-hoc* tests were conducted for the comparison of
149 synchronisation at different proximities, using two-tailed Wilcoxon signed-ranks tests
150 assuming a normal approximation with continuity corrections, with the *post-hoc*
151 significance value adjusted to $p = 0.009$ using a Bonferroni correction. All analyses
152 were conducted with *R* 3.0 (R Development Core Team 2013).

153

154

155 **RESULTS AND DISCUSSION**

156

157 Deer are less likely to be synchronised as they become socially further away from a
158 focal individual ($\chi^2_3 = 21.36, p < 0.001$; Fig. 1). Because deer could not be individually
159 identified, there is some chance that some pseudoreplication has occurred, with focal
160 deer being resampled by chance. However, randomly removing data (all possible
161 combinations of up to five focal individuals were removed) had no effect upon these
162 results (the range of p values obtained fell in the range 0.000005-0.018). *Post hoc* tests
163 demonstrated that focal individuals were more synchronised with first and second
164 closest neighbours than with control deer (Fig. 1), but the increased synchronisation
165 with the third-closest neighbour compared to the control ($p = 0.011$) was not significant
166 after applying Bonferroni corrections.

167

168 We used a dichotomous classification for behaviour, following the differentiation

169 between 'active' and 'passive' behaviours used by Ruckstuhl & Kokko (2002). Using a
170 dichotomous classification means that an underlying degree of 'synchronisation' can
171 occur by chance. Considering the entire dataset, individual deer were active for 73.11%
172 of their time during the period observed. If we assume that all deer acted independently,
173 we can estimate that if we were to pick two individuals at random, they would be
174 conducting the same action 60.68% of the time. This corresponds with the dotted line
175 shown in Fig. 1, which falls near the middle of the control results. The three close
176 neighbours were much more likely to be synchronised than this random estimate,
177 suggesting that their individual behaviours are at least partially influenced by each
178 other. We acknowledge that the dichotomous scheme that we use may be falsely
179 classifying some behaviours as similar (e.g. one member of an 'active' pair might be
180 grazing whilst its partner is running). However, our dichotomous classification follows
181 the differentiation between 'active' and 'passive' behaviours used by Ruckstuhl &
182 Kokko (2002). We would suggest that individuals conducting resting behaviours may
183 have to invest more energy and expose themselves to a potentially greater risk of
184 predation if they have to suddenly switch to one of the 'active' behaviours than if they
185 were switching between two different 'active' behaviours or two different 'resting'
186 behaviours. Therefore, considering just two behavioural states may be sufficient to try
187 and pick apart broad patterns of synchronisation.

188

189 In considering the three nearest neighbours to a focal individual at a given moment in
190 time, it was necessary to ignore a few factors which may have an effect on each
191 individual's behaviour. Firstly, the identity of each neighbour is likely to have changed
192 over the course of consecutive observations of a focal deer. However, if we are

193 interested in demonstrating that proximity is a factor driving behavioural
194 synchronisation, this is not an issue as it is how the actions of the focal individual
195 correlate with its unidentified neighbours that is important. Secondly, the observations
196 do not account for inter-neighbour distance, where individuals in physically close
197 proximity may be more likely to be synchronised. However, we are considering a
198 topological relationship here (as is considered by Ballerini et al. 2008; Nagy et al. 2010)
199 rather than a metric distance: it would be illuminating to observe whether increased
200 physical proximity increases synchronisation, but the logistics of field observation made
201 this too difficult to observe accurately. Thirdly, because this is an observational study,
202 we are unable to separate whether synchronisation of activity is occurring in response to
203 neighbour behaviour from whether some local effect is driving the behaviour instead:
204 for example, deer that are close together may be more likely to be grazing because the
205 quality of the local patch of grass available to them is better than that experienced by
206 more distant individuals. Similarly, because we are looking at correlations, we are
207 unable to separate mechanisms that may be causing local synchronisation from the
208 observed behaviour: synchronisation could be occurring because key individuals are
209 driving the local behaviours within the herd (King & Cowlshaw 2009; Rands 2011). To
210 move from observing correlations to picking apart how synchronisation works, we
211 would need to conduct experimental manipulations of the herd, such as by changing
212 local forage quality or by removing possible key individuals from the herd.

213

214 The synchronisation behaviour we describe does not account for social relationships
215 between the individuals. Local social networks are likely to strongly influence
216 substructures within groups (Bode et al. 2011b; Sueur et al. 2011), and being able to

217 identify individuals and assay their interaction behaviour over longer periods of time
218 may give us a much clearer indication of the behavioural dynamics of the herd.
219 Similarly, we did not account for how differences in the physiological state (Rands et al.
220 2003, 2006, 2008) or social status (Rands 2011) of individuals could be influencing
221 their need to copy the behaviour of others. There is still a great need to properly link
222 models and empirical work considering how social foraging behaviour can influence
223 group behaviour (Marshall et al. 2012), and in particular we urge further careful studies
224 of the effects of neighbour proximity in order to explore these neglected assumptions
225 implicit within many models.

226
227 This study demonstrates that individual deer are more likely to synchronise their
228 activity with their closer neighbours when compared to more distant neighbours and the
229 wider herd. This provides support for the spatial assumptions used in models of activity
230 synchronisation (Ruckstuhl & Kokko 2002). Similar patterns were seen in small herds
231 of cattle (Stoye et al. 2012), but the current study demonstrates that these assumptions
232 may also be applicable to much larger herds of animals.

233

234

235 **ACKNOWLEDGEMENTS**

236

237 Three anonymous referees who commented on earlier versions of this manuscript are
238 thanked.

239

240

241 REFERENCES

242

- 243 Aivaz AN, and Ruckstuhl KE. 2011. Costs of behavioral synchrony as a potential driver
244 behind size-assorted grouping. *Behavioral Ecology* 22:1353-1363.
- 245 Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, Giardina I, Lecomte V,
246 Orlandi A, Parisi G, Procaccini A et al. . 2008. Interaction ruling animal
247 collective behavior depends on topological rather than metric distance: evidence
248 from a field study. *Proceedings of the National Academy of Sciences of the USA*
249 105:1232-1237.
- 250 Beauchamp G. 2009. Sleeping gulls monitor the vigilance behaviour of their
251 neighbours. *Biology Letters* 5:9-11.
- 252 Beauchamp G, Alexander P, and Jovani R. 2012. Consistent waves of collective
253 vigilance in groups using public information about predation risk. *Behavioral*
254 *Ecology* 23:368-374.
- 255 Bode NWF, Franks DW, and Wood AJ. 2011a. Limited interactions in flocks: relating
256 model simulations to empirical data. *Journal of the Royal Society Interface*
257 8:301-304.
- 258 Bode NWF, Wood AJ, and Franks DW. 2011b. Social networks and models for
259 collective motion in animals. *Behavioral Ecology and Sociobiology* 65:117-130.
- 260 Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, and Bonabeau E.
261 2001. *Self-organization in biological systems*. Princeton: Princeton University
262 Press.
- 263 Camperi M, Cavagna A, Giardina I, Parisi G, and Silvestri E. 2012. Spatially balanced
264 topological interaction grants optimal cohesion in flocking models. *Interface*
265 *Focus* 2:715-725.
- 266 Clutton-Brock TH, and Albon SD. 1989. *Red deer in the highlands*. Gloucester: BSP
267 Professional Books.
- 268 Clutton-Brock TH, Guinness FE, and Albon SD. 1982. *Red deer: behavior and ecology*
269 *of two sexes*. Chicago: Chicago University Press.
- 270 Conradt L. 1998. Could asynchrony in activity between the sexes cause intersexual
271 social segregation in ruminants? *Proceedings of the Royal Society B* 265:1359-
272 1363.
- 273 Conradt L, and List C. 2009. Group decisions in humans and animals: a survey.
274 *Philosophical Transactions of the Royal Society B* 364:719-742.
- 275 Couzin ID, Krause J, James R, Ruxton GD, and Franks NR. 2002. Collective memory
276 and spatial sorting in animal groups. *Journal of Theoretical Biology* 218:1-11.
- 277 Dyer JRG, Johansson A, Helbing D, Couzin ID, and Krause J. 2009. Leadership,
278 consensus decision making and collective behaviour in humans. *Philosophical*
279 *Transactions of the Royal Society B* 364:781-789.
- 280 Fernandez AA, and Deneubourg J-L. 2011. On following behaviour as a mechanism for
281 collective movement. *Journal of Theoretical Biology* 284:7-15.
- 282 Gautrais J, Michelena P, Sibbald A, Bon R, and Deneubourg J-L. 2007. Allelomimetic
283 synchronization in Merino sheep. *Animal Behaviour* 74:1443-1454.
- 284 Herbert-Read JE, Perna A, Mann RP, Schaerf TM, Sumpter DJT, and Ward AJW. 2011.
285 Inferring the rules of interaction of shoaling fish. *Proceedings of the National*
286 *Academy of Sciences of the USA* 108:18726-18731.

- 287 King AJ, and Cowlshaw G. 2009. Leaders, followers, and group decision-making.
 288 *Communicative and Integrative Biology* 2:147-150.
- 289 Krause J, and Ruxton GD. 2002. *Living in groups*. Oxford: Oxford University Press.
- 290 Mann RP. 2011. Bayesian inference for identifying interaction rules in moving animal
 291 groups. *PLoS One* 6:e22827.
- 292 Marshall HH, Carter AJ, Rowcliffe JM, and Cowlshaw G. 2012. Linking social
 293 foraging behaviour with individual time budgets and emergent group-level
 294 phenomena. *Animal Behaviour* 84:1295-1305.
- 295 Michéna P, Gautrais J, Gérard J-F, Bon R, and Deneubourg J-L. 2008. Social cohesion
 296 in groups of sheep: effect of activity level, sex composition and group size.
 297 *Applied Animal Behaviour Science* 112:81-93.
- 298 Nagy M, Ákos Z, Biro D, and Vicsek T. 2010. Hierarchical group dynamics in pigeon
 299 flocks. *Nature* 464:890-893.
- 300 Pépin D, Morellat N, and Goulard M. 2009. Seasonal and daily walking activity
 301 patterns of free-rearing adult red deer (*Cervus elaphus*) at the individual level.
 302 *European Journal of Wildlife Research* 55:479-486.
- 303 Pillot M-H, Gautrais J, Arrufat P, Couzin ID, Bon R, and Deneubourg JL. 2011.
 304 Scalable rules for coherent group motion in a gregarious vertebrate. *PLoS One*
 305 6:e14487.
- 306 R Development Core Team. 2013. *R: a language and environment for statistical*
 307 *computing*. Vienna: R Foundation for Statistical Computing.
- 308 Ramseyer A, Thierry B, Boissy A, and Dumont B. 2009. Decision-making processes in
 309 group departures of cattle. *Ethology* 115:948-957.
- 310 Rands SA. 2011. The effects of dominance on leadership and energetic gain: a dynamic
 311 game between pairs of social foragers. *PLoS Computational Biology*
 312 7:e1002252.
- 313 Rands SA, Cowlshaw G, Pettifor RA, Rowcliffe JM, and Johnstone RA. 2003. The
 314 spontaneous emergence of leaders and followers in a foraging pair. *Nature*
 315 423:432-434.
- 316 Rands SA, Cowlshaw G, Pettifor RA, Rowcliffe JM, and Johnstone RA. 2008. The
 317 emergence of leaders and followers in foraging pairs when the qualities of
 318 individuals differ. *BMC Evolutionary Biology* 8:51.
- 319 Rands SA, Pettifor RA, Rowcliffe JM, and Cowlshaw G. 2004. State-dependent
 320 foraging rules for social animals in selfish herds. *Proceedings of the Royal*
 321 *Society B* 271:2613-2620.
- 322 Rands SA, Pettifor RA, Rowcliffe JM, and Cowlshaw G. 2006. Social foraging and
 323 dominance relationships: the effects of socially mediated interference.
 324 *Behavioral Ecology and Sociobiology* 60:572-581.
- 325 Romey WL, and Vidal JM. 2013. Sum of heterogeneous blind zones predict movements
 326 of simulated groups. *Ecological Modelling* 258:9-15.
- 327 Ruckstuhl KE, and Kokko H. 2002. Modelling sexual segregation in ungulates: effects
 328 of group size, activity budgets and synchrony. *Animal Behaviour* 64:909-914.
- 329 Šárová R, Špinka M, and Panamá JLA. 2007. Synchronization and leadership in
 330 switches between resting and activity in a beef cattle herd – a case study.
 331 *Applied Animal Behaviour Science* 108:327-331.
- 332 Stoye S, Porter MA, and Dawkins MS. 2012. Synchronized lying in cattle in relation to
 333 time of day. *Livestock Science* 149:70-73.
- 334 Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM,

335 Williams LM, Zinner D, and Aureli F. 2011. Collective decision-making and
 336 fission-fusion dynamics: a conceptual framework. *Oikos* 120:1608-1617.
 337 Sumpter DJT. 2010. *Collective animal behavior*. Princeton: Princeton University Press.
 338 Yearsley JM, and Pérez-Barberia FJ. 2005. Does the activity budget hypothesis explain
 339 sexual segregation in ungulates? *Animal Behaviour* 69:257-267.
 340
 341

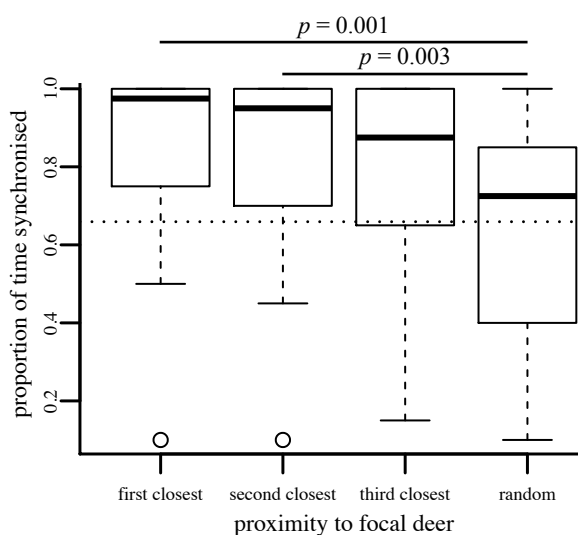
342

343

344

345

346



347

348

349 FIGURE 1. Boxplot showing the proportion of time that behaviour of the focal
 350 individual was synchronised with neighbours of differing social distances. Significant
 351 pairwise *post-hoc* tests are shown.