

Red deer synchronise their activity with close neighbours

Models of collective animal behaviour frequently make assumptions about the effects of neighbours on the behaviour of focal individuals, but these assumptions are rarely tested. One such set of assumptions is that the switch between active and inactive behaviour seen in herding animals is influenced by the activity of close neighbours, where neighbouring animals show a higher degree of behavioural synchrony than would be expected by chance. We tested this assumption by observing the simultaneous behaviour of paired individuals within a herd of red deer *Cervus elaphus*. Focal individuals were more synchronised with their two closest neighbours than with the third closest or randomly selected individuals from the herd. Our results suggest that the behaviour of individual deer is influenced by immediate neighbours. Even if we assume that there are no social relationships between individuals, this suggests that the assumptions made in models about the influence of neighbours may be appropriate.

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

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

3 †HM and NLT contributed equally to this work

4 *author for correspondence

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

6 INTRODUCTION

7 Many animals form groups at some point in their life cycle. In most cases, these groups occur
8 because there is some benefit from being in the group to each of its members ([Krause & Ruxton](#)
9 [2002](#)), suggesting that the behaviour of each individual must in part be both influenced by and
10 directed towards behaving as part of the group. Models of collective behaviour ([Camazine et al.](#)
11 [2001](#); [Sumpter 2010](#)) frequently consider the behaviours of groups that emerge from the
12 combined actions of the individuals within the group. These models are good at creating
13 simulations of groups that appear to behave in very similar ways to what is seen in nature, but
14 very different models can produce similar phenomena. In order to identify which modelled
15 processes are appropriate, it is essential to challenge these models with empirical data. However,
16 the noisiness of biological systems increases the difficulty of testing whether the interaction rules
17 used in these models are appropriate ([Mann 2011](#)).

18 Many of the models and associated empirical studies that describe collective behaviour typically
19 consider individuals that are influenced by other group members who are in close proximity,
20 either within a physical ‘metric’ distance of a focal individual ([Couzin et al. 2002](#); [Herbert-Read](#)
21 [et al. 2011](#); [Rands et al. 2004, 2006](#); [Romey & Vidal 2013](#)), or according to a topologically-
22 defined network of interacting individuals ([Bode et al. 2011a](#); [Camperi et al. 2012](#); [Nagy et al.](#)
23 [2010](#)). Other influential models of movement involve changes in behavioural states, considering
24 the departure and leadership decisions made by groups of moving animals ([Fernandez &](#)
25 [Deneubourg 2011](#); [Pillot et al. 2011](#); [Sueur et al. 2011](#)), where the behavioural state change
26 experienced by individuals is the switch from being static to moving. Other studies of
27 behavioural state changes have considered how local interactions govern changes between being
28 vigilant and non-vigilant ([Beauchamp et al. 2012](#)), or being active and inactive according to both

29 social facilitation and metabolic requirements ([Ruckstuhl & Kokko 2002](#)).

30 Given this wide variety of models exploring collective behaviour, empirical tests exploring the
31 individual behaviours driving observed collective behaviours are patchy in their coverage. Much
32 research effort has been devoted to exploring how decision-making and leadership processes are
33 connected and distributed within groups ([Conradt & List 2009](#); [Dyer et al. 2009](#); [King &
34 Cowlshaw 2009](#)). Specific consideration of the effects of inter-neighbour interactions have
35 explored individual decisions made during group movement according to metric ([Herbert-Read et
36 al. 2011](#); [Ramseyer et al. 2009](#)) or topological distance to neighbours ([Ballerini et al. 2008](#); [Nagy
37 et al. 2010](#)), and there have been a number of studies exploring leaving decisions ([Sueur et al.
38 2011](#)). Fewer studies have considered changes in behavioural state within a group. Several have
39 considered how neighbours influence the vigilance patterns of groups ([Beauchamp 2009](#)). Most
40 tests of the models exploring changes in activity in response to metabolic requirements and the
41 behaviour of neighbours ([Ruckstuhl & Kokko 2002](#)) have focused on how difference in energetic
42 requirements can lead to sexual segregation ([Aivaz & Ruckstuhl 2011](#); [Michelena et al. 2008](#);
43 [Yearsley & Pérez-Barberia 2005](#)), non-synchronous behaviour ([Šárová et al. 2007](#)), group
44 cohesion ([Conradt 1998](#)), and group-size effects on activity ([Gautrais et al. 2007](#)). However,
45 although these models assume that behavioural state is influenced by the actions of close
46 neighbours, little has been done to test this empirically. Evidence is suggested by a study of cattle
47 *Bos taurus* synchronising their lying behaviour, where their posture is more likely to be similar to
48 neighbouring individuals compared to the rest of the herd ([Stoye et al. 2012](#)). However, there is
49 scope for much more exploration of the assumptions behind models considering how the
50 proximity of individuals to others can influence switches in their behavioural state. In this study,
51 we asked whether the behaviours of individual red deer *Cervus elaphus* living in a managed herd
52 are influenced by their neighbours. Individual deer spend large parts of their lives near or within

53 large herds ([Clutton-Brock & Albon 1989](#)), and therefore are ideal for addressing how changes in
54 individual activity tie in with group-level behaviour. We hypothesised that deer that were
55 topologically closer within the herd were more likely to be synchronised than would be expected
56 when comparing two individuals randomly selected from different locations within the herd.

57 **MATERIALS AND METHODS**

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

61 The herd studied was housed in an enclosed 40.5 hectare deer park in the Ashton Court Estate,
62 Bristol, England, composed of open grassland, with scattered patches of woodland. The herd is a
63 population of *c.* 99 individuals of mixed age and sex, and its management and husbandry is
64 conducted by Bristol City Council (the exact herd size was not known at the time of observation).
65 Except for rutting periods, the enclosure is accessible to the general public, and the deer are
66 habituated to the presence of humans and dogs. Permissions were not required for these
67 observational studies, which occurred during the hours the public had access to the park. All
68 observations were conducted within 10-100m of the focal individuals, using binoculars where
69 appropriate: for habituation, observers were in position for recording at least five minutes before
70 observations started.

71

72 The study coincided with the rutting season of the deer, with stags often solitary and with greatly
73 reduced feeding, and therefore likely to display very different behaviours to the rest of the herd

74 ([Clutton-Brock & Albon 1989](#); [Pépin et al. 2009](#)). Males with antlers (approximately eleven
75 individuals) were therefore excluded from the observations. The study focussed on females and
76 young males that had not yet segregated from their maternal group, which were likely to display
77 behaviour similar to the females ([Clutton-Brock & Albon 1989](#)).

78 Prior to the study described, an ethogram was constructed for individual behaviour within the
79 herd, differentiating between grazing, standing, walking, running, interacting, laying with head
80 down, laying with head alert, and laying whilst ruminating. Within the analysis, these were
81 reclassified as a combined dichotomous behaviours. Individuals were classified as ‘active’ if they
82 were grazing, standing, walking, running, and interacting, and ‘resting’ if they were conducting
83 one of the other behaviours.

84 For a single observation period, a focal individual was randomly selected from the herd. A two
85 figure random number was generated, and, considering the visible deer in the observer’s field of
86 vision, the focal deer was selected by counting linearly from leftmost or rightmost visible deer
87 (where the direction of counting was selected by a coin toss, and where a count was discarded if
88 the random number selected was larger than the number of deer visible: this randomisation
89 technique may have introduced some unavoidable bias towards individuals on the side of the herd
90 closest to the observer, but, ignoring outlying stags, most of the herd was visible and countable
91 during the sampling period and this bias should therefore have been minimal). Selected focal
92 individuals were watched for twenty minutes. If the herd was disturbed by a human presence in
93 the middle of the observation period, the observation was aborted and the data discarded. In total,
94 eighteen complete observations of twenty minutes were conducted, over four days in October
95 2012; an additional two planned observations were started but aborted early due to disturbance,
96 and have not been included in the analysis. All observations were conducted within 1200 and

97 1630h, outside of the dawn and dusk peaks of activity frequently shown by red deer ([Clutton-](#)
98 [Brock et al. 1982](#)).

99 Over an observation period, the behaviour of the focal individual was recorded every minute.
100 Simultaneously, the behaviour of the first, second and third closest individual in the herd to the
101 focal were also recorded (where the identities of these individuals could change between the
102 recording events as the deer moved within the herd). At the same time, the behaviour of a
103 different randomly selected control individual within the herd was also recorded (selected using
104 the randomisation technique described above from what remained of the herd after the focal and
105 three nearest neighbours had been excluded, and ignoring rutting stags as stated above), where
106 the identity of the control individual was independently chosen at each recording event.

107 Synchronisation between individuals was calculated as the proportion of the observations where
108 the focal and test individual were both active or both inactive. Data were compared with
109 Friedman tests. Because there was some change that focal individuals were re-selected by chance,
110 we acknowledge that there could be some degree of pseudoreplication in the dataset. To explore
111 this, we generated a full set of Friedman tests where all possible combinations of up to five of the
112 focal individuals were excluded from the analysis. *Post-hoc* tests were conducted for the
113 comparison of synchronisation at different proximities, using two-tailed Wilcoxon signed-ranks
114 tests assuming a normal approximation with continuity corrections, with the *post-hoc*
115 significance value adjusted to $p = 0.009$ using a Bonferroni correction. All analyses were
116 conducted with R 3.0 ([R Development Core Team 2013](#)).

117 **RESULTS AND DISCUSSION**

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

127 We used a dichotomous classification for behaviour, following the differentiation between
128 ‘active’ and ‘passive’ behaviours used by Ruckstuhl & Kokko (2002). Using a dichotomous
129 classification means that an underlying degree of ‘synchronisation’ can occur by chance.
130 Individual deer were active for 73.11% of their time during the period observed (calculated by
131 combining the individual datasets collected for focal, neighbour and control individuals). If we
132 assume that all deer acted independently, we can estimate that if we were to pick two individuals
133 at random, they would be conducting the same action 60.68% of the time. This corresponds with
134 the dotted line shown in Fig. 1, which falls near the middle of the control results. The three close
135 neighbours were much more likely to be synchronised than this random estimate, suggesting that
136 their individual behaviours are at least partially influenced by each other. We acknowledge that
137 the dichotomous scheme that we use may be falsely classifying some behaviours as similar (e.g.
138 one member of an ‘active’ pair might be grazing whilst its partner is running). However, our
139 dichotomous classification follows the differentiation between ‘active’ and ‘passive’ behaviours

140 used by Ruckstuhl & Kokko ([2002](#)). We would suggest that individuals conducting resting
141 behaviours may have to invest more energy and expose themselves to a potentially greater risk of
142 predation if they have to suddenly switch to one of the ‘active’ behaviours than if they were
143 switching between two different ‘active’ behaviours or two different ‘resting’ behaviours.
144 Therefore, considering just two behavioural states may be sufficient to try and pick apart broad
145 patterns of synchronisation.

146 In considering the three nearest neighbours to a focal individual at a given moment in time, it was
147 necessary to ignore a few factors which may have an effect on each individual’s behaviour.
148 Firstly, the identity of each neighbour is likely to have changed over the course of consecutive
149 observations of a focal deer. However, if we are interested in demonstrating that proximity is a
150 factor driving behavioural synchronisation, this is not an issue as it is how the actions of the focal
151 individual correlate with its unidentified neighbours that is important. Secondly, the observations
152 do not account for inter-neighbour distance, where individuals in physically close proximity may
153 be more likely to be synchronised. However, we are considering a topological relationship here
154 (as is considered by [Ballerini et al. 2008](#); [Nagy et al. 2010](#)) rather than a metric distance: it would
155 be illuminating to observe whether increased physical proximity increases synchronisation, but
156 the logistics of field observation made this too difficult to observe accurately. Thirdly, because
157 this is an observational study, we are unable to separate whether synchronisation of activity is
158 occurring in response to neighbour behaviour from whether some local effect is driving the
159 behaviour instead: for example, deer that are close together may be more likely to be grazing
160 because the quality of the local patch of grass available to them is better than that experienced by
161 more distant individuals. Similarly, because we are looking at correlations, we are unable to
162 separate mechanisms that may be causing local synchronisation from the observed behaviour:
163 synchronisation could be occurring because key individuals are driving the local behaviours

164 within the herd ([King & Cowlshaw 2009](#); [Rands 2011](#)). To move from observing correlations to
165 picking apart how synchronisation works, we would need to conduct experimental manipulations
166 of the herd, such as by changing local forage quality or by removing possible key individuals
167 from the herd.

168 The synchronisation behaviour we describe does not account for social relationships between the
169 individuals. Local social networks are likely to strongly influence substructures within groups
170 ([Bode et al. 2011b](#); [Sueur et al. 2011](#)), and being able to identify individuals and assay their
171 interaction behaviour over longer periods of time may give us a much clearer indication of the
172 behavioural dynamics of the herd. Similarly, we did not account for how differences in the
173 physiological state ([Rands et al. 2003, 2006, 2008](#)) or social status ([Rands 2011](#)) of individuals
174 could be influencing their need to copy the behaviour of others. There is still a great need to
175 properly link models and empirical work considering how social foraging behaviour can
176 influence group behaviour ([Marshall et al. 2012](#)), and in particular we urge further careful studies
177 of the effects of neighbour proximity in order to explore these neglected assumptions implicit
178 within many models.

179 This study demonstrates that individual deer are more likely to synchronise their activity with
180 their closer neighbours when compared to more distant neighbours and the wider herd. This
181 provides support for the spatial assumptions used in models of activity synchronisation
182 ([Ruckstuhl & Kokko 2002](#)). Similar patterns were seen in small herds of cattle ([Stoye et al.](#)
183 [2012](#)), but the current study demonstrates that these assumptions may also be applicable to much
184 larger herds of animals.

185 **ACKNOWLEDGEMENTS**

186 Andrew Robins and four anonymous referees who commented on earlier versions of this
187 manuscript are thanked.

188 **REFERENCES**

- 189 Aivaz AN, and Ruckstuhl KE. 2011. Costs of behavioral synchrony as a potential driver behind
190 size-assorted grouping. *Behavioral Ecology* 22:1353-1363.
- 191 Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, Giardina I, Lecomte V, Orlandi A,
192 Parisi G, Procaccini A et al. . 2008. Interaction ruling animal collective behavior depends
193 on topological rather than metric distance: evidence from a field study. *Proceedings of the*
194 *National Academy of Sciences of the USA* 105:1232-1237.
- 195 Beauchamp G. 2009. Sleeping gulls monitor the vigilance behaviour of their neighbours. *Biology*
196 *Letters* 5:9-11.
- 197 Beauchamp G, Alexander P, and Jovani R. 2012. Consistent waves of collective vigilance in
198 groups using public information about predation risk. *Behavioral Ecology* 23:368-374.
- 199 Bode NWF, Franks DW, and Wood AJ. 2011a. Limited interactions in flocks: relating model
200 simulations to empirical data. *Journal of the Royal Society Interface* 8:301-304.
- 201 Bode NWF, Wood AJ, and Franks DW. 2011b. Social networks and models for collective motion
202 in animals. *Behavioral Ecology and Sociobiology* 65:117-130.
- 203 Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, and Bonabeau E. 2001. *Self-*
204 *organization in biological systems*. Princeton: Princeton University Press.
- 205 Camperi M, Cavagna A, Giardina I, Parisi G, and Silvestri E. 2012. Spatially balanced
206 topological interaction grants optimal cohesion in flocking models. *Interface Focus*
207 2:715-725.
- 208 Clutton-Brock TH, and Albon SD. 1989. *Red deer in the highlands*. Gloucester: BSP Professional
209 Books.
- 210 Clutton-Brock TH, Guinness FE, and Albon SD. 1982. *Red deer: behavior and ecology of two*
211 *sexes*. Chicago: Chicago University Press.

- 212 Conradt L. 1998. Could asynchrony in activity between the sexes cause intersexual social
213 segregation in ruminants? *Proceedings of the Royal Society B* 265:1359-1363.
- 214 Conradt L, and List C. 2009. Group decisions in humans and animals: a survey. *Philosophical*
215 *Transactions of the Royal Society B* 364:719-742.
- 216 Couzin ID, Krause J, James R, Ruxton GD, and Franks NR. 2002. Collective memory and spatial
217 sorting in animal groups. *Journal of Theoretical Biology* 218:1-11.
- 218 Dyer JRG, Johansson A, Helbing D, Couzin ID, and Krause J. 2009. Leadership, consensus
219 decision making and collective behaviour in humans. *Philosophical Transactions of the*
220 *Royal Society B* 364:781-789.
- 221 Fernandez AA, and Deneubourg J-L. 2011. On following behaviour as a mechanism for
222 collective movement. *Journal of Theoretical Biology* 284:7-15.
- 223 Gautrais J, Michelena P, Sibbald A, Bon R, and Deneubourg J-L. 2007. Allelomimetic
224 synchronization in Merino sheep. *Animal Behaviour* 74:1443-1454.
- 225 Herbert-Read JE, Perna A, Mann RP, Schaerf TM, Sumpter DJT, and Ward AJW. 2011. Inferring
226 the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences*
227 *of the USA* 108:18726-18731.
- 228 King AJ, and Cowlshaw G. 2009. Leaders, followers, and group decision-making.
229 *Communicative and Integrative Biology* 2:147-150.
- 230 Krause J, and Ruxton GD. 2002. *Living in groups*. Oxford: Oxford University Press.
- 231 Mann RP. 2011. Bayesian inference for identifying interaction rules in moving animal groups.
232 *PLoS One* 6:e22827.
- 233 Marshall HH, Carter AJ, Rowcliffe JM, and Cowlshaw G. 2012. Linking social foraging
234 behaviour with individual time budgets and emergent group-level phenomena. *Animal*
235 *Behaviour* 84:1295-1305.
- 236 Michelena P, Gautrais J, Gérard J-F, Bon R, and Deneubourg J-L. 2008. Social cohesion in

- 237 groups of sheep: effect of activity level, sex composition and group size. *Applied Animal*
238 *Behaviour Science* 112:81-93.
- 239 Nagy M, Ákos Z, Biro D, and Vicsek T. 2010. Hierarchical group dynamics in pigeon flocks.
240 *Nature* 464:890-893.
- 241 Pépin D, Morellat N, and Goulard M. 2009. Seasonal and daily walking activity patterns of free-
242 rearing adult red deer (*Cervus elaphus*) at the individual level. *European Journal of*
243 *Wildlife Research* 55:479-486.
- 244 Pillot M-H, Gautrais J, Arrufat P, Couzin ID, Bon R, and Deneubourg JL. 2011. Scalable rules for
245 coherent group motion in a gregarious vertebrate. *PLoS One* 6:e14487.
- 246 R Development Core Team. 2013. *R: a language and environment for statistical computing*.
247 Vienna: R Foundation for Statistical Computing.
- 248 Ramseyer A, Thierry B, Boissy A, and Dumont B. 2009. Decision-making processes in group
249 departures of cattle. *Ethology* 115:948-957.
- 250 Rands SA. 2011. The effects of dominance on leadership and energetic gain: a dynamic game
251 between pairs of social foragers. *PLoS Computational Biology* 7:e1002252.
- 252 Rands SA, Cowlshaw G, Pettifor RA, Rowcliffe JM, and Johnstone RA. 2003. The spontaneous
253 emergence of leaders and followers in a foraging pair. *Nature* 423:432-434.
- 254 Rands SA, Cowlshaw G, Pettifor RA, Rowcliffe JM, and Johnstone RA. 2008. The emergence of
255 leaders and followers in foraging pairs when the qualities of individuals differ. *BMC*
256 *Evolutionary Biology* 8:51.
- 257 Rands SA, Pettifor RA, Rowcliffe JM, and Cowlshaw G. 2004. State-dependent foraging rules
258 for social animals in selfish herds. *Proceedings of the Royal Society B* 271:2613-2620.
- 259 Rands SA, Pettifor RA, Rowcliffe JM, and Cowlshaw G. 2006. Social foraging and dominance
260 relationships: the effects of socially mediated interference. *Behavioral Ecology and*
261 *Sociobiology* 60:572-581.

- 262 Romey WL, and Vidal JM. 2013. Sum of heterogeneous blind zones predict movements of
263 simulated groups. *Ecological Modelling* 258:9-15.
- 264 Ruckstuhl KE, and Kokko H. 2002. Modelling sexual segregation in ungulates: effects of group
265 size, activity budgets and synchrony. *Animal Behaviour* 64:909-914.
- 266 Šárová R, Špinka M, and Panamá JLA. 2007. Synchronization and leadership in switches
267 between resting and activity in a beef cattle herd – a case study. *Applied Animal
268 Behaviour Science* 108:327-331.
- 269 Stoye S, Porter MA, and Dawkins MS. 2012. Synchronized lying in cattle in relation to time of
270 day. *Livestock Science* 149:70-73.
- 271 Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM, Williams
272 LM, Zinner D, and Aureli F. 2011. Collective decision-making and fission-fusion
273 dynamics: a conceptual framework. *Oikos* 120:1608-1617.
- 274 Sumpter DJT. 2010. *Collective animal behavior*. Princeton: Princeton University Press.
- 275 Yearsley JM, and Pérez-Barberia FJ. 2005. Does the activity budget hypothesis explain sexual
276 segregation in ungulates? *Animal Behaviour* 69:257-267.

Figure 1

Boxplot showing the proportion of time that behaviour of the focal individual was synchronised with neighbours of differing social distances.

Significant pairwise *post-hoc* tests are shown.

