

# 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**

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## 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. Except for rutting periods, the enclosure is accessible to the  
65 general public, and the deer are habituated to the presence of humans and dogs. Permissions were  
66 not required for these observational studies, which occurred during the hours the public had  
67 access to the park. All observations were conducted within 10-100m of the focal individuals,  
68 using binoculars where appropriate: for habituation, observers were in position for recording at  
69 least five minutes before observations started.

70

71 The study coincided with the rutting season of the deer, with stags often solitary and with greatly  
72 reduced feeding, and therefore likely to display very different behaviours to the rest of the herd  
73 ([Clutton-Brock & Albon 1989](#); [Pépin et al. 2009](#)). Males with antlers were therefore excluded

74 from the observations. The study focussed on females and young males that had not yet  
75 segregated from their maternal group, which were likely to display behaviour similar to the  
76 females ([Clutton-Brock & Albon 1989](#)).

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

83 For a single observation period, a focal individual was randomly selected from the herd. A two  
84 figure random number was generated, and, considering the visible deer in the observer’s field of  
85 vision, the focal deer was selected by counting linearly from leftmost or rightmost visible deer  
86 (where the direction of counting was selected by a coin toss, and where a count was discarded if  
87 the random number selected was larger than the number of deer visible). Selected focal  
88 individuals were watched for twenty minutes. If the herd was disturbed by a human presence in  
89 the middle of the observation period, the observation was aborted and the data discarded. In total,  
90 eighteen complete observations of twenty minutes were conducted, over four days in October  
91 2012. All observations were conducted within 1200 and 1630h, outside of the dawn and dusk  
92 peaks of activity frequently shown by red deer ([Clutton-Brock et al. 1982](#)).

93 Over an observation period, the behaviour of the focal individual was recorded every minute.  
94 Simultaneously, the behaviour of the first, second and third closest individual in the herd to the  
95 focal were also recorded (where the identities of these individuals could change between the

96 recording events as the deer moved within the herd). At the same time, the behaviour of a  
97 different randomly selected control individual within the herd was also recorded (selected from  
98 what remained of the herd after the focal and three nearest neighbours had been excluded), where  
99 the identity of the control individual was independently chosen at each recording even.

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

## 110 **RESULTS AND DISCUSSION**

111 Deer are less likely to be synchronised as they become socially further away from a focal  
112 individual ( $\chi^2_3 = 21.36$ ,  $p < 0.001$ ; Fig. 1). Because deer could not be individually identified, there  
113 is some chance that some pseudoreplication has occurred, with focal deer being resampled by  
114 chance. However, randomly removing data (all possible combinations of up to five focal  
115 individuals were removed) had no effect upon these results (the range of  $p$  values obtained fell in

116 the range 0.000005-0.018). *Post hoc* tests demonstrated that focal individuals were more  
117 synchronised with first and second closest neighbours than with control deer (Fig. 1), but the  
118 increased synchronisation with the third-closest neighbour compared to the control ( $p = 0.011$ )  
119 was not significant after applying Bonferroni corrections.

120 We used a dichotomous classification for behaviour, following the differentiation between  
121 ‘active’ and ‘passive’ behaviours used by Ruckstuhl & Kokko (2002). Using a dichotomous  
122 classification means that an underlying degree of ‘synchronisation’ can occur by chance.  
123 Considering the entire dataset, individual deer were active for 73.11% of their time during the  
124 period observed. If we assume that all deer acted independently, we can estimate that if we were  
125 to pick two individuals at random, they would be conducting the same action 60.68% of the time.  
126 This corresponds with the dotted line shown in Fig. 1, which falls near the middle of the control  
127 results. The three close neighbours were much more likely to be synchronised than this random  
128 estimate, suggesting that their individual behaviours are at least partially influenced by each  
129 other. We acknowledge that the dichotomous scheme that we use may be falsely classifying some  
130 behaviours as similar (e.g. one member of an ‘active’ pair might be grazing whilst its partner is  
131 running). However, our dichotomous classification follows the differentiation between ‘active’  
132 and ‘passive’ behaviours used by Ruckstuhl & Kokko (2002). We would suggest that individuals  
133 conducting resting behaviours may have to invest more energy and expose themselves to a  
134 potentially greater risk of predation if they have to suddenly switch to one of the ‘active’  
135 behaviours than if they were switching between two different ‘active’ behaviours or two different  
136 ‘resting’ behaviours. Therefore, considering just two behavioural states may be sufficient to try  
137 and pick apart broad patterns of synchronisation.

138 In considering the three nearest neighbours to a focal individual at a given moment in time, it was

139 necessary to ignore a few factors which may have an effect on each individual's behaviour.  
140 Firstly, the identity of each neighbour is likely to have changed over the course of consecutive  
141 observations of a focal deer. However, if we are interested in demonstrating that proximity is a  
142 factor driving behavioural synchronisation, this is not an issue as it is how the actions of the focal  
143 individual correlate with its unidentified neighbours that is important. Secondly, the observations  
144 do not account for inter-neighbour distance, where individuals in physically close proximity may  
145 be more likely to be synchronised. However, we are considering a topological relationship here  
146 (as is considered by [Ballerini et al. 2008](#); [Nagy et al. 2010](#)) rather than a metric distance: it would  
147 be illuminating to observe whether increased physical proximity increases synchronisation, but  
148 the logistics of field observation made this too difficult to observe accurately. Thirdly, because  
149 this is an observational study, we are unable to separate whether synchronisation of activity is  
150 occurring in response to neighbour behaviour from whether some local effect is driving the  
151 behaviour instead: for example, deer that are close together may be more likely to be grazing  
152 because the quality of the local patch of grass available to them is better than that experienced by  
153 more distant individuals. Similarly, because we are looking at correlations, we are unable to  
154 separate mechanisms that may be causing local synchronisation from the observed behaviour:  
155 synchronisation could be occurring because key individuals are driving the local behaviours  
156 within the herd ([King & Cowlshaw 2009](#); [Rands 2011](#)). To move from observing correlations to  
157 picking apart how synchronisation works, we would need to conduct experimental manipulations  
158 of the herd, such as by changing local forage quality or by removing possible key individuals  
159 from the herd.

160 The synchronisation behaviour we describe does not account for social relationships between the  
161 individuals. Local social networks are likely to strongly influence substructures within groups  
162 ([Bode et al. 2011b](#); [Sueur et al. 2011](#)), and being able to identify individuals and assay their

163 interaction behaviour over longer periods of time may give us a much clearer indication of the  
164 behavioural dynamics of the herd. Similarly, we did not account for how differences in the  
165 physiological state ([Rands et al. 2003, 2006, 2008](#)) or social status ([Rands 2011](#)) of individuals  
166 could be influencing their need to copy the behaviour of others. There is still a great need to  
167 properly link models and empirical work considering how social foraging behaviour can  
168 influence group behaviour ([Marshall et al. 2012](#)), and in particular we urge further careful studies  
169 of the effects of neighbour proximity in order to explore these neglected assumptions implicit  
170 within many models.

171 This study demonstrates that individual deer are more likely to synchronise their activity with  
172 their closer neighbours when compared to more distant neighbours and the wider herd. This  
173 provides support for the spatial assumptions used in models of activity synchronisation  
174 ([Ruckstuhl & Kokko 2002](#)). Similar patterns were seen in small herds of cattle ([Stoye et al.](#)  
175 [2012](#)), but the current study demonstrates that these assumptions may also be applicable to much  
176 larger herds of animals.

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# 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.

