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Group behaviours and individual spatial sorting before departure predict the dynamic of collective movements in horses

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1 INTRODUCTION

2 Animals that live in groups face the daily challenge to decide where and when the
3 group should move. By moving together, they maintain group cohesiveness which brings
4 them several advantages: protection from predators, information about feeding sites, resources
5 defence (Alexander 1974; Danchin et al. 2008). Therefore, group members need to seek a
6 consensus by making a decision collectively. Consensus decision can be either shared or
7 unshared (Conradt & Roper, 2005). In shared consensus decision, all group members
8 contribute to the decision outcome, either equally (regardless of individual characteristics) or
9 partially (some individuals have a greater influence, Pyritz et al. 2011). In unshared
10 consensus, one particular individual decides systematically where and when the group should
11 go. It is, however, more interesting to consider a spectrum from shared consensus to unshared
12 consensus rather than a binary distinction.

13 In the study of mechanisms underlying such collective decisions, a frequent approach
14 is to identify the type of consensus by seeking for individuals that could play a key role
15 during decision-making processes (Petit, Gautrais, Leca, Theraulaz, & Deneubourg, 2009).
16 Specific individuals, either old, high-ranking or of a specific sex, have been reported to
17 occupy the position of leaders in various species (King, Douglas, Huchard, Isaac, &
18 Cowlshaw, 2008; Schaller, 1963). However, there are as many studies, if not more, that
19 found that leadership is rather distributed among group members (King et al. 2009; Petit &
20 Bon 2010). Moreover, what one calls a leader is usually the individual that took the vanguard
21 position during collective movements although there is no evidence that this individual
22 decided for others (Bourjade, Thierry, Hausberger, & Petit, 2015). For instance, in one of the
23 most cited examples of despotic leadership (i.e. unshared consensus decision), the dominant
24 male in mountain gorillas (*Gorilla gorilla berengei*: Schaller 1963), the departure of the
25 silverback has been reported to be preceded by grunts emitted by other group members

26 suggesting a rather shared decisional process (Stewart & Harcourt, 1994). However, this
27 requires looking beyond the time of departure as decision-making processes may occur
28 beforehand and the influence of all group members measured.

29 Indeed, studies on collective movements rarely took into account the events preceding
30 collective movements. However, the arousal state, or “mood” (Ward & Zahavi, 1973), of
31 individuals may influence the dynamic of the impending collective movements in terms of
32 number of participants or joining duration. For instance, group dispersion has been shown to
33 influence the number of participants in mammals (white-faced capuchin, *Cebus capucinus*:
34 Leca, Gunst, Thierry, & Petit, 2003; Tonkean macaque, *Macaca tonkeana* and rhesus
35 macaque, *Macaca mulatta*: Sueur & Petit, 2008; sheep, *Ovis aries* and cattle, *Bos taurus*:
36 Ramseyer, Boissy, Dumont, & Thierry, 2009; Ramseyer, Thierry, Boissy, & Dumont, 2009;
37 European bison, *Bison bonasus*: Ramos, Petit, Longour, Pasquaretta, & Sueur, 2015) and
38 birds (black-headed gulls, *Larus ridibundus*: de Schutter 1997; domestic goose, *Anser anser*:
39 Ramseyer et al. 2008), fish (Damsel fish, *Dascyllus aruanus*: Ward et al. 2013). Some
40 individuals can also display behaviour that indicates their motivation to move, for instance by
41 moving away from group members in the desired direction (Hamadryas baboon, *Papio h.*
42 *hamadryas*, Kummer 1968). In domestic geese, sheep, cattle and bison, the number of
43 participants increased with the number of individuals heading in the direction of the
44 movement (Ramseyer et al. 2008; Ramseyer, Boissy, Dumont, & Thierry, 2009; Ramseyer,
45 Thierry, Boissy, & Dumont, 2009; Ramos et al. 2015). In some species, this number increased
46 with the number of vocalizers (meerkat, *Suricata suricatta*: Bousquet et al. 2011; African
47 elephant, *Loxodonta Africana*: O’Connell-Rodwell et al. 2012; African wild dog, *Lycaon*
48 *pictus*: Walker et al. 2017; red-fronted lemur, *Eulemur rufifrons*: Sperber et al. 2019). In
49 several species of primates, the number of individuals moving on few meters towards a
50 specific direction before departure influenced the final decision of the group (Kummer,

51 1968a; Selmann, Majolo, Schülke, & Ostner, 2013; Strandburg-Peshkin, Farine, Couzin, &
52 Crofoot, 2015; Sueur, Deneubourg, & Petit, 2010).

53 Such predeparture behaviours have been viewed as a preparation for collective
54 movements (Ramseyer, Boissy, Dumont, et al., 2009). However, to be valid, this assumption
55 must be tested by at least verifying that the observed behaviours are specific to the context of
56 collective movements. One solution, for instance, is to compare predeparture behavioural
57 patterns with behavioural patterns exhibited during control periods that did not precede a
58 collective movement. Such method is commonly used in studies on the function of post-
59 conflict behaviours that compare matched-control periods with post-conflict periods to deem
60 the observed behavioural pattern, a reconciliation process (e.g. white-face capuchins: Leca,
61 Fornasieri, & Petit, 2002; domestic horses: Cozzi, Sighieri, Gazzano, Nicol, & Baragli, 2010).
62 However, so far, such an approach has never been used in the context of collective
63 movements and predeparture behaviours. In this study, we applied it to this context using
64 domestic horses, *Equus ferus caballus*, as a model.

65 Horses are highly-social species that form long-lasting bonds (Waring, 2003).
66 Distributed leadership has been reported with an influence of individual characteristics (age:
67 Tyler, 1972; dominance rank: Krueger, Flauger, Farmer, & Hemelrijk, 2014; personality:
68 Briard, Dorn, & Petit, 2015). However, in both Przewalski (*Equus f. przewalskii*, Bourjade et
69 al. 2015) and domestic horses (Briard et al 2015; Briard et al. 2017), the characteristics of the
70 initiator did not explain variation in recruitment success (e.g. number of followers or joining
71 speed). Moreover, predeparture behaviours such as moving away from the group or
72 maintaining a peripheral position occur in Przewalski horses (Bourjade et al. 2009, 2015) and
73 may indicate negotiation processes due to higher conflict of interests as they correlate with
74 longer recruitment phase (Bourjade et al., 2009). In such a context, exploring the predeparture
75 period appears necessary to understand the collective decision-making of horses. This study

76 aimed to investigate whether: (1) predeparture behaviours can be observed in domestic horses
77 and if so, whether the observed behavioural patterns (2) are specific to the context of
78 collective movements by comparing them to control periods and (3) can explain the dynamic
79 of ensuing collective movements. Based on previous studies in Przewalski horses (Bourjade
80 et al. 2015) and other ungulates (e.g. Ramseyer, Boissy, Dumont, & Thierry, 2009;
81 Ramseyer, Thierry, Boissy, & Dumont, 2009), we expect to see, as departure gets closer, an
82 increase in the arousal of the group. This could manifest itself through an increase in activity,
83 a decrease in group dispersion or the alignment of group members towards the direction of the
84 future collective movement. If such behavioural patterns exist and are specific to predeparture
85 periods, we do not expect to observe them in control periods. However, if we do not find any
86 differences between predeparture and control periods, then predeparture behaviours cannot be
87 deemed as preparatory (i.e. an anticipation of a future collective movement).

88

89 **MATERIAL AND METHODS**

90 **Animals and Environment**

91 The focal groups were bred at La Ferme de Bonjacques, a horse husbandry located in
92 eastern France (48°06'00.0"N, 6°06'01.0"E, 305m). Both groups were composed of 9 mares
93 of various breeds aged from 9 to 28 years old for group 1 and 3 to 22 years old for group 2
94 (see SI Appendix A for more details). All horses were individually recognisable by their
95 morphology, coat colours and white markings. Both groups were kept on hilly pastures (group
96 1: 8 ha, group 2: 11 ha) composed of large grassland areas with vegetation forming natural,
97 shaded shelters. Due to the relief and the vegetation, individuals were never able to see the
98 entire pasture from any given point. A river, allowing individuals to have free access to water
99 crossed both pastures increasing the number of distinct zones. Both groups had access to a salt
100 lick stone and group 1 had access to a hayrack (2x2m) but spent less than 10% of the total

101 observation period eating from it. Both groups had been accustomed to human presence
102 during a preliminary observation month.

103

104 **Observation Procedure**

105 Groups were observed and filmed for about two months for a total of 184 hrs for group
106 1 and 112 hrs for group 2. Two observers approached horses on foot up to a maximal distance
107 of about 20m and used handheld two-way radios to communicate when separated. Each of
108 them had a camera to ensure that the entire group was continuously filmed. Over the
109 observation period, one of the observers also recorded every 5 min by instantaneous scan
110 sampling (Altmann, 1974) the position of every individual using a pair of telemetric
111 binoculars (precision: 1m) and a compass (precision: 1°). The observer stayed still throughout
112 the scan and attributed for each horse a distance in meter (horse-observer distance) and an
113 angle in degree by pointing the compass towards each horse and placing the orienting arrow
114 on the magnetic needle to read the value. During those scans, the observer also recorded the
115 activity (inactive: at rest - standing with a flexed foot or recumbent- or active: all other
116 activities) and the orientation of each individual according to four noticeable and fixed points
117 in the environment at 90° or 180° of one another.

118

119 **Data Scoring**

120 Two persons watched the videos and recorded the identity and the behaviour of every
121 individual initiating or joining a collective movement. Before they could score different
122 videos, we ensured inter-observer concordance by asking them to score the same videos and
123 comparing their results until they reached 95% concordance (Caro, Roper, Young, & Dank,
124 1979).

125

126 **Initiation and joining latencies**

127 Departure was defined by the movement of an initiator, that is, any individual that first
128 travels at least 20 m in less than 20 s outside the group without pausing and with its neck kept
129 above the horizontal position (Bourjade et al., 2009; Briard et al., 2015). Then, any horse
130 moving away from the group with its neck kept above the horizontal position and in the same
131 direction as the initiator was identified as a follower. For each follower, we defined a joining
132 latency by calculating the time between an initiation and the moment an individual joined it
133 (i.e. first step taken in the same direction as the initiator). Using these latencies, we
134 determined the joining rank of individuals for each collective movement (i.e. from 1, the
135 initiator, to 9, the last follower). A collective movement begins with a start attempt and ends
136 with the arrival of the last follower (Petit and Bon 2010; Briard et al. 2015). We defined the
137 goal area as sites in which all animals stopped walking and started a new activity such as
138 foraging or resting. We defined a predeparture period as those corresponding to the period
139 between the end of the preceding collective movement and the initiation of the focal
140 movement. However, we decided to stop only up to 60 minutes before departure because the
141 sample size for more distant scans was too small (less than 5 events per group). We recorded
142 for group 1 and 2, 56 and 73 initiations respectively, 43 and 50 of them involving the entire
143 group and with all individuals always visible from 60 minutes before initiation to the end of
144 the collective movement. So, the analysis focused on these 43 and 50 events.

145

146 **Group behaviour before departure**

147 During these 60 minutes preceding initiation, we measured five different group
148 behaviours using scans performed every 5 minutes: number of inactive individuals, number of
149 goal-oriented individuals, distance to goal area, dispersion, and density at the front of the
150 group (see Table 1 for definitions). Since initiation is relatively unpredictable, we never had a

151 scan of the group performed at the exact moment the initiator started to move. Therefore, the
152 scans at 0 min (*i.e.* first step of the initiator) were completed using video recordings. Then,
153 preceding scans obtained from direct observation were categorized into half-open 5-min time
154 intervals (e.g.]0-5min],]5-10min], etc.). From angle and distances values obtained by
155 instantaneous scan sampling using the telemetric binoculars and the compass, we were able to
156 calculate individual xy-coordinates: $X_i = \cos(\alpha_i) \times d_i$ and $Y_i = \sin(\alpha_i) \times d_i$ with α_i the angle
157 in radian and d_i the distance in meters. Since the goal area could not be anticipated, we
158 defined its angle and distance every 5 minutes based on the video recordings, the individual
159 angle and distance of the focal scan and a cadastral plan of the pasture. The xy-coordinates of
160 the group barycenter were equal to the mean of individual xy-coordinates, $X_{bc} = \sum x_i / N$, and
161 $Y_{bc} = \sum y_i / N$, with $N = 9$. The index of group dispersion was equal to the squared deviations
162 from the barycenter divided by N , $D = \sum \sqrt{[(X_i - X_{bc})^2 + (Y_i - Y_{bc})^2]} / N$. Finally, with a similar
163 formula $D_{ia} = \sqrt{[(X_i - X_a)^2 + (Y_i - Y_a)^2]}$ with X_a and Y_a the xy-coordinates of the goal area, we
164 calculated individual distances to the goal area and attributed a topological rank based on
165 topological distances (*i.e.* rank 1 is attributed to the closest individual). The front of the group
166 was determined using the closest individual to the goal area as a referential. The density at the
167 front of the group was calculated using the number of individuals within a 10-meters radius
168 around the referential.

169

170 **Statistical analysis**

171 The effect of time on the five different group behaviours was investigated using Linear
172 Mixed-Effects Models for dispersion (after a log-transformation due to a right-skewed
173 distribution) and distance to goal area (LMM, R package nlme v. 3.1-140, Pinheiro et al.
174 2020) or Generalized Linear Mixed-Models with a Poisson distribution for group activity,
175 orientation and front density (glmmPQL R package MASS v7.3-51.4, Venables & Ripley

176 2002). Given the relationship between the distance to goal area and time, we used a quadratic
177 fit ($y \sim x + I(x^2)$). Finally, we used as a random factor the identity of each collective movement
178 nested within the group identity and added a correlation structure (corAR1) to take into
179 account the sequential dependence of observations.

180 To assess if group behaviour could predict the imminence of a collective movement,
181 we compared the predeparture periods with control periods. These control periods were taken
182 off scans performed at least 60 minutes away from any collective movements. We only used 5
183 time categories (from 0 to 60 min before departure, with 15-min intervals) to ensure sufficient
184 sample size per time category ($N_0 = 101$, $N_{15} = 103$, $N_{30} = 104$, $N_{45} = 92$, $N_{60} = 70$). Since
185 there is no initiation to be used as a referential, we randomly assigned a fifth of the scans to
186 the time category 0 min. Then, based on their timing, preceding scans were assigned to one of
187 the four remaining time categories, i.e. [15-10[, [30-25[, [45-40[or [60-55[min before
188 category 0 min. Isolated scans, that could not be connected to a time category 0 min, were
189 discarded. For orientation, because we did not have any referential direction for the control
190 periods, we used the direction adopted by the majority in each time category 0 min to then
191 look at the number of individuals that had adopted this direction over the previous time
192 categories (*i.e.* from 10 min to 60 min before). Finally, since front density and group distance
193 to the goal area were measures that rely on the existence of a goal area, they were not
194 compared to control periods. We compared the effect of time on these three behaviours during
195 control periods using similar models than for the predeparture period (see above for details).
196 As independent variables, we used time (from 0 to 60 min before departure) with an
197 interaction with a binary variable called period type (0 = predeparture; 1 = control).

198 To assess the influence of predeparture behaviours on the dynamic of the collective
199 movements (*i.e.* the speed and joining order), we conducted two types of analyses. For the
200 duration of the joining phase, we used a linear mixed-effect model (LMM) with the five group

201 behaviours as independent factors (i.e. dispersion, density, activity, orientation and distance to
202 the goal area; Table 1) and the log-transformed latency of the last follower as the dependent
203 variable (continuous data with a right-skewed distribution). Dispersion and density at the
204 front were log-transformed to linearize their relationship with the dependent variable and
205 facilitate the interpretation of the model's coefficients. We tested this model at 3 different
206 moments: at initiation, 25-30 min and 55-60 min before departure. We used the multimodel
207 inference method (R package MuMIn v.1.43.6; Barton 2019) to determine which candidate
208 model best explained the dynamic of the joining phase. Models were first compared according
209 to their Akaike's information criterion (AIC) corrected for small sample size (AICc) and then
210 ranked by their weights (AICw; Burnham & Anderson 2002). When the AICc of the
211 candidate models differed by less than 2 units, we accepted the one with the lowest AICc as
212 the best-fit model. We also calculated the evidence ratio between the presented models with
213 the lowest AICc score and that of interest following the formula described in Burnham and
214 Anderson (2002). For the joining order, we used a linear model approach to study the
215 temporal link between topological ranks before departure (*i.e.* topological distance to goal
216 area) and joining ranks during collective movements (R package lme4 v.1.1-21; Bates et al.
217 2015). We particularly looked at the evolution of the slope.

218 Before conducting analysis, all variables when included in the same model were
219 screened for excessive correlations ($r > 0.7$) and collinearity ($VIF > 10$, Dormann et al. 2013).
220 All statistical analyses were performed in R version 3.6.1 (R Core Team 2019). The
221 significance threshold was set at $\alpha=0.05$.

222

223 **Ethical Statement**

224 Our observations were carried out in full accordance with the ethical guidelines of our
225 research institution and comply with the European legislation for animal welfare. This study

226 has been conducted with the approval of our local ethical committee (reference:
227 AL/19/17/02/13).

228

229 **RESULTS**

230 **Evolution of predeparture behavioural patterns over time**

231 To assess variations during the 60 min period preceding departure, we compared
232 various behaviours that were recorded every 5 minutes. We found that all analysed variables
233 displayed significant changes over time (Figure 1). The number of goal-oriented individuals
234 and the density at the front increased over time during the predeparture period (GLMM,
235 orientation: $\beta \pm SE = 0.019 \pm 0.002$, $t_{584} = 8.690$, $P < 0.001$; GLMM, density: $\beta \pm SE = 0.008$
236 ± 0.002 , $t_{584} = 5.351$ $P = 0.02$; Figure 1) while dispersion and the number of inactive
237 individuals decreased (LMM, dispersion: $\beta \pm SE = -0.093 \pm 0.035$, $t_{584} = -2.62$, $P = 0.01$;
238 GLMM, group activity: $\beta \pm SE = -0.019 \pm 0.003$, $t_{584} = -5.638$, $P < 0.001$, Figure 1). Group
239 distance to goal area exhibited a quadratic relationship with time. Groups moved away from
240 the future destination before getting closer (LMM, distance to goal area, β (time) $\pm SE = -$
241 0.342 ± 0.102 , $t_{584} = -3.364$, $P < 0.001$, β (time²) $\pm SE = -0.004 \pm 0.002$, $t_{584} = -2.595$ $P =$
242 0.01). This means that before departure and as the initiation is getting closer, individuals
243 become more active, oriented towards the future goal, reduce interindividual distances,
244 notably at the front of the group, and starts to move towards the goal.

245 **Comparison with control periods**

246 To assess if the above variables could indicate the imminence of a collective
247 movement, we compared predeparture periods with control periods. We found that similarly
248 to predeparture periods, the number of individuals oriented in the same direction increased

249 over time during the control period (ANOVA, time x period type: $\text{Chisq} = 2.577, P = 0.11$)
250 and within the same range (ANOVA, period type: $\text{Chisq} = 0.0385, P = 0.844$). Contrary to
251 orientation, during control periods, time did not have the same effect on the number of
252 individuals of inactive individuals (ANOVA: $\text{Chisq} = 22.005, P < 0.001$), which stayed
253 constant (GLMM, time x period type: $\beta \pm \text{SE} = 0.024 \pm 0.005, P < 0.001$; Figure 2). In
254 addition, control periods were characterized, on average, by more inactive individuals than
255 during predeparture periods (GLMM, period type: $\beta \pm \text{SE} = 0.77 \pm 0.24, t_{537} = 4.678, P <$
256 0.001 ; Figure 2). The temporal pattern of group dispersion during control periods did not
257 significantly differ from predeparture period (ANOVA, time x period type: $\text{Chisq} = 0.0012, P$
258 $= 0.97$). However, dispersion in control periods was, on average, three-times higher than in
259 predeparture periods suggesting a much lower group cohesion outside the context of
260 collective movements (LMM, period type: $\beta \pm \text{SE} = 55.60 \pm 4.18, P < 0.001$; Figure 2).

261 Finally, we also observed that during the predeparture period, the number of inactive
262 individuals was significantly correlated to the number of individuals oriented in the same
263 direction (Pearson $r = -0.15, P < 0.001, N = 678$) and the dispersion (Pearson $r = -0.13, P <$
264 $0.001, N = 678$) contrary to the control periods (activity - orientation, Pearson $r = -0.03, P =$
265 $0.59, N = 364$; activity - dispersion, Pearson $r = -0.09, P = 0.16, N = 470$).

266

267 **Predeparture behaviours predict the duration of the joining phase**

268 At initiation, multimodel inference showed that the best model to explain the duration
269 of the joining phase (*i.e.* latency of the last follower) included dispersion alone (conditional
270 average LMM: $\beta \pm \text{SE} = 0.740 \pm 0.141, z = 5.172, p < 0.001, \text{RVI} = 1$; Table S2). The more
271 dispersed the individuals were, the longer it took for group members to follow (Figure 3a). At
272 25-30 min, the best model for the latency of the last follower included the density at the front
273 alone (conditional average LMM: $\beta \pm \text{SE} = -0.633 \pm 0.303, z = 2.090, p = 0.037$; relative

274 variable importance, RVI=0.61; Figure 3b, Table S2), meaning that the more individuals
275 gathered at the front during the predeparture period, the faster the joining phase was (Figure
276 3b). However, the two next models could not be excluded from the top-ranked models
277 ($\Delta AICc < 2$) and therefore dispersion was also a good predictor of the duration of the joining
278 phase (conditional average LMM: $\beta \pm SE = 0.596 \pm 0.289$, $z = 2.066$, $P = 0.039$; RVI = 0.60;
279 Figure 3c, Table S2). At 55-60 min, the best model included the dispersion alone (conditional
280 average LMM: $\beta \pm SE = 1.098 \pm 0.316$, $z = 3.473$, $P < 0.001$, RVI=0.98; Table S2) meaning
281 that the more gathered the individuals were 60 minutes before departure, the faster the joining
282 phase was (Figure 3d). The three other variables, *i.e.* activity, orientation and distance to the
283 goal area, were never included in the top-ranked models (activity RVI < 0.14, orientation RVI
284 < 0.06, distance to the goal area RVI < 0.01).

285

286 **Spatial organization before departure predicts joining order**

287 We explored the evolution over time of spatial positions before departure as a function
288 of the joining rank during collective movements. As shown by figure 4, there is a relationship
289 between individual distances to the goal area at departure (LM [initiation] $\beta \pm SE = 0.46 \pm$
290 0.03 , $R^2 = 0.21$, $P < 0.0001$) and up to 30-40 minutes before departure (LM [30-35 min], $\beta \pm$
291 $SE = 0.11 \pm 0.049$, $R^2 = 0.01$, $P = 0.027$). The slope starts to increase around 30-35 minutes
292 before departure as well as the match between the linear regression and the mean value,
293 suggesting that the correlation between the spatial position and the future joining rank is
294 increasing over time (see Table S3 in supplemental material). This result also indicates that
295 individual spatial position before departure is likely to predict how quickly a horse will join
296 the ensuing collective movement.

297

298 **DISCUSSION**

299 We found evidence that the dynamic of collective movements, from direction to
300 joining duration and order could be predicted by group behaviours exhibited before departure.
301 Our findings support the idea that decision-making begins well before departure. This
302 therefore means that the first departed individual is likely to be the mere catalyser of an
303 already-begun collective phenomenon and highlights the absolute necessity to look beyond
304 the timing of initiation to understand collective decision-making processes in animal societies.

305

306 **The specificity of pre-departure behavioural patterns**

307 During the hour prior departure, group behaviours changed over time. The number of inactive
308 individuals progressively decreased, traducing a progressive arousal of the group (see Ward &
309 Zahavi 1973 for a definition of the “mood of the roost”). Simultaneously to this increase, the
310 number of individuals gathered at the front and oriented towards the future collective
311 movement increased over time. We also observed, a reduction of dispersion and distance to
312 the future goal area before departure. The slight increase in group distance to the goal area
313 before its decrease is likely to be due to the configuration of the environment the studied
314 group lived in (i.e. limited space and destinations). Such gathering at the group periphery and
315 synchronisation of behaviours before departure have been reported in many species (Boinski
316 & Garber, 2000; Kummer, 1968a; Ramseyer, Boissy, Dumont, et al., 2009; Ramseyer,
317 Thierry, Boissy, et al., 2009; Strandburg-Peshkin et al., 2015) and were suggested as a
318 preparation to collective movements. However, to be valid, this assumption needed to be
319 tested by at least verifying that these modifications are not found outside the context of
320 collective movements. Thanks to the comparison with control periods and more definitively
321 than previous studies, we can conclude on the specificity of predeparture periods. On one
322 hand, we found that the temporal increase in activity and cohesion was specific to

323 predeparture periods. During control periods, the activity level stayed relatively constant and
324 group cohesion was much lower. Finally, we found that only during predeparture periods did
325 the number of goal-oriented individuals correlate with the number of inactive individuals and
326 the group dispersion. Therefore, the specificity of predeparture periods lies in the co-
327 occurrence of multiple patterns: a progressive decrease in the number of inactive individuals
328 associated with a low dispersion and a high degree of synchronization in terms of orientation.
329 Nevertheless, the differences between the indices characterizing the states of the group
330 (number of inactive individuals or dispersion) during the control and pre-departure phase raise
331 the question of the temporal evolution of these indices. For example, concerning the
332 dispersion, two extreme hypotheses can be formulated: a monotonic or a sudden decrease
333 when the group passes from the state observed during the control period to the pre-departure
334 period. An abrupt decrease would suggest that the adoption of a pre-departure configuration is
335 itself a social phenomenon (e.g. governed by mimetism; Sumpter, 2010). This dynamic
336 towards the pre-departure also raises the question of links between the pre-departure state and
337 the probability of initiating a movement and its success : are these probabilities governed by
338 the same cause as that governing the adoption of the predeparture configuration or do they
339 depend on the state/configuration of the group? New observations are needed to decipher
340 between these different hypotheses.

341 On the other hand, we found that the temporal pattern of group orientation in pre-departure
342 period is not different from the observed patterns during control periods. Such pattern
343 indicates that individuals maintain their orientation over multiple time steps (i.e inertia). As a
344 consequence, the probability that orientations are identical decreases with time (i.e. as we
345 move away from the initiation period). Moreover, social species are known to respond to the
346 behaviours of group members, such as body posture and orientation, by adopting the same
347 behaviours themselves, a process known as social facilitation or allelomimetism (Clayton,

348 1978; Conradt & Roper, 2000; Deneubourg & Goss, 1989). In herbivores, such
349 synchronization has often been observed outside the context of collective movements
350 (Benham, 1982; Côté, Schaefer, & Messier, 1997; Gautrais, Michéna, Sibbald, Bon, &
351 Deneubourg, 2007; Rands, Muir, & Terry, 2014; Stoye, Porter, & Stamp Dawkins, 2012).
352 Therefore, during predeparture periods the increasing number of individuals oriented in the
353 same direction predicts the direction of a potential collective movement but not an impending
354 group departure. The absence of difference between the predeparture and the control periods,
355 both in terms of dynamics and magnitude, puts into perspective the interpretation of the
356 progressive orientation of group members before departure. Such phenomenon is often
357 viewed as a preparation if not a negotiation or a voting process (Kummer, 1968b; Ramos et
358 al., 2015; Ramseyer, Boissy, Dumont, et al., 2009; Ramseyer et al., 2008; Ramseyer, Thierry,
359 et al., 2009; Strandburg-Peshkin et al., 2015; Sueur et al., 2010) and the resulting dynamics as
360 the consequence of the degree of consensus before departure. However, in the absence of
361 control, the causal relationship between the degree of common orientation before departure
362 and recruitment during collective movements should be interpreted cautiously. Here our
363 results suggest that the choice of destination could result from the global dynamics rather than
364 an a priori choice.

365

366 **Predeparture behaviours and joining dynamic**

367 Interestingly, the behaviours that were specific to the predeparture periods and could
368 predict the imminence of a departure were not the ones that predicted the joining dynamic.
369 Indeed, the cohesion of the group, i.e. dispersion and density at the front, was the only factor
370 that had a significant impact on the duration of the joining process. Our results confirmed
371 those of previous studies on dispersion and recruitment in primates (Leca et al., 2003; Sperber

372 et al., 2019; Sueur & Petit, 2008) and birds (Ramseyer et al., 2008) but partially matched
373 those in heifers and ewes (Ramseyer, Boissy, Dumont, et al., 2009; Ramseyer, Thierry,
374 Boissy, et al., 2009). In these latter studies, the authors found an effect of dispersion but also
375 of orientation and activity at different times. The methodological differences make the
376 comparison quite difficult since they analysed only collective movements that occurred when
377 the individuals were aggregated within a certain perimeter before departure.

378 We also showed that before departure individuals that were closer to the front and
379 therefore to the future goal area joined the collective movement earlier. On one hand, the
380 spatial position of individuals may affect their capacity to initiate as demonstrated by Dyer et
381 al. (2009) in groups of humans. They showed that peripheral individuals were more likely to
382 move freely away from the group than central individuals. On the other hand, the progressive
383 movement of an individual towards the front of the group may act both as a conspicuous cue
384 of motivation and help to recruit group members. Similar results have been reported in
385 Przewalski horses (Bourjade et al., 2009) and other animal societies (Boinski & Garber, 2000;
386 Kummer, 1968a; Ramseyer, Boissy, Dumont, et al., 2009; Ramseyer, Thierry, et al., 2009;
387 Strandburg-Peshkin et al., 2015; Sueur et al., 2010). It has been suggested that front-to-back
388 positioning within animal groups can be the consequences of behavioural or motivational
389 differences between group members (Couzin, Krause, James, Ruxton, & Franks, 2002).
390 Individual differences in activity level (Homing pigeons, *Columbia livia*, Pettit et al. 2015),
391 age (red-fronted lemurs, *Eulemur rufifrons*, Sperber et al. 2019), satiation (roach, *Rutilus*
392 *rutilus*, Krause 1993), dominance (Hemelrijk, 1998) or in social attraction (domestic horses,
393 *Equus f. caballus* Briard et al. 2015) have shown to explain patterns of positioning within the
394 group. In addition to motivational differences, social preferences and/or shared phenotypes
395 (e.g. phenotypic assortativity, Krause, James, Franks, & Croft, 2014) could underlie such
396 spatial positioning and differences in reactivity to an individual's departure. Indeed, it has

397 been shown in numerous social species that social preferences and phenotypic similarities
398 effect on how individuals are spatially organized (Briard et al., 2015; Godde, Humbert, Côté,
399 Réale, & Whitehead, 2013) and how they influence one another (i.e. selective mimetism,
400 Sueur, Petit, & Deneubourg, 2009).

401 The effect of both group cohesion and spatial positioning before departure on the
402 joining dynamic suggests that even in case of high synchronisation in terms of activity or
403 orientation, interindividual distances greatly affect recruitment. As a consequence of spatial
404 sorting and group cohesion, individuals differ in their neighbourhood size (i.e. how many
405 conspecifics an individual interacts with, Farine et al. 2017), which could affect their
406 propensity to react to the initiator departure. In our study, since the initiator is among the
407 closest to the front, it also means that individuals far from the goal area are far from the
408 initiator. Therefore, it is possible that in domestic horses, as in a flock of birds under attack by
409 a peregrine falcon (Ballerini et al., 2008), the propagation of information (i.e. departure of the
410 initiator) and the reaction of individuals depended on distances. Such nearest neighbour effect
411 was also found to underlie spatial organisation during collective movement in wild primates
412 (Farine et al., 2016; Sperber et al., 2019) and activity synchronisation in red deer (Rands et al.
413 2014). Interestingly, until now, such effect was only identified in dense and large groups of
414 animals where one individual is unlikely to see all its conspecifics.

415 Many questions remain to be addressed concerning the exact rules that underpin
416 decision-making processes during collective movements in domestic horses. First of all, we
417 could not study the effect of predeparture behaviours on the number of followers as the
418 majority of recorded events involved the entire group. However, in numerous species
419 including horses (Bourjade et al., 2009; Krueger et al., 2014; Petit et al., 2009; Sueur & Petit,
420 2008), individuals can fail to recruit any group member and often have to renounce to depart
421 from the group. Using such unsuccessful departures as well as control periods that only differ

422 from predeparture periods by one parameter (e.g. dispersion) would provide useful insights on
423 why an initiation succeeds or fails and help understand decision-making processes. Moreover,
424 although it is clear that interindividual distances are at stake, even in this small-scale system,
425 our study did not allow us to disentangle between motivational differences and local
426 information transmission. Indeed, we did not record enough events during which the initiator
427 was not the closest to the goal. Experiments with trained individuals that would depart from
428 the group following a cue (Gérard, Valençon, Poulin, & Petit, 2020; Pillot et al., 2010)
429 would allow recording a sufficient number of events where the initiator holds various spatial
430 position. It could then be determined which differences in motivation or local information
431 transmission are decisive. Finally, we had to rely on discrete data to study the dynamic of
432 predeparture behaviours. With the rise of technology (e.g. GPS collars, drones, automatic
433 tracking software), continuous data could be collected allowing more advanced statistical
434 analysis, which could help uncover new behavioural patterns.

435

436 **Conclusion**

437 We demonstrate that decision-making during collective movements is a continuous
438 process that starts before departure in domestic horses. The use of control periods, a first in
439 the context of collective movements and predeparture behaviours, highlights the specificity of
440 periods preceding collective movements and how animals communicate their willingness to
441 move to other group members. Moreover, we showed that a behaviour often presented as
442 preparatory, i.e. interindividual alignment, was not specific to predeparture and occurred just
443 as often in other contexts. Finally, our work suggests that similarly to dense and large groups,
444 interindividual distances are a key aspect of decision-making processes in small and loose
445 groups. Taken together our results clearly emphasise the necessity to look beyond the event of

446 initiation and to take into account the role of local interactions to catch the whole decision-
447 making processes during collective movements of group-living species.

448

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638

639

640 **TABLES**

641

Table 1 – Behavioural variables of the predeparture period used in analyses

Behaviours	Definition
Group activity	Number of inactive individuals i.e. at rest, standing with a flexed foot or recumbent.

Group orientation	Number of individuals oriented in the direction of the movement defined as the bisecting line of 45° sector. For the control period, the referential direction was the direction chosen by the majority of individuals within the time category 0 and was subsequently used in the preceding time categories.
Group distance to the goal area	Distance in meters between the arrival area and the barycentre of the group based on xy-coordinates.
Group dispersion	Mean distance in meters between each horse and the barycentre of the group base on the xy-coordinates, i.e. $D = \sum \sqrt{[(X_i - X_{bc})^2 + (Y_i - Y_{bc})^2]} / N$
Density at the front of the group	Number of individuals within 10m away from the front of the group. The front is defined by the distance of the closest individual to the arrival area

642

643

644 **FIGURE LEGENDS**

645

646 **Figure 1** – Patterns of (a) orientation, (b) density at the group front, (c) dispersion, (d) distance to goal
 647 area and (e) activity, in the 60 min period preceding departures of the entire group.

648 The mean and standard errors are represented for each type of behaviour and time categories. The red
 649 line represents the linear (orientation, front density, dispersion and activity) and quadratic regression
 650 (distance to goal). From 0 min to 60 min, $N = 93, N = 63, N = 73, N = 63, N = 55, N = 54, N = 47, N$
 651 $= 43, N = 35, N = 36, N = 30$ and $N = 32$.

652

653 **Figure 2** - Comparison of the evolution of group behaviour, (a) orientation, (b) activity and (c)
 654 dispersion, between predeparture periods (dark grey) and control periods (light grey).

655 Graphs represent the mean and standard errors for each type of behaviour and time categories. From 0
 656 min to 60 min, control periods, $N = 101, N = 103, N = 104, N = 92$ and $N = 70$. From 0 min to 60
 657 min, predeparture periods, $N = 93, N = 63, N = 54, N = 35$ and $N = 32$.

658

659 **Figure 3** - Relationships between the joining latency of the last follower and (a) the dispersion at
660 departure, (b) the density at the group front and (c) the dispersion, 30 minutes before departure, (d) the
661 dispersion 60 minutes before departure. Solid lines of corresponding colours show the line of best fit
662 in the linear mixed-effects model and shade areas standard errors.

663

664 **Figure 4** - Temporal evolution of the relationship between spatial position before departure and
665 joining rank during collective movements.

666 Each window corresponds to a time category (from $t = 0$ min, the initiation, to $t = 55 - 60$ min).

667 Boxplots represent the distribution of topological distances to the goal area as a function of the future
668 joining rank (e.g. joining rank 1 is the initiator, joining rank 2 the first follower, etc.). The thick curvy
669 black line represents the mean topological rank for each joining rank and the thin straight black line
670 represents the linear regression.

671

672

ACKNOWLEDGEMENTS

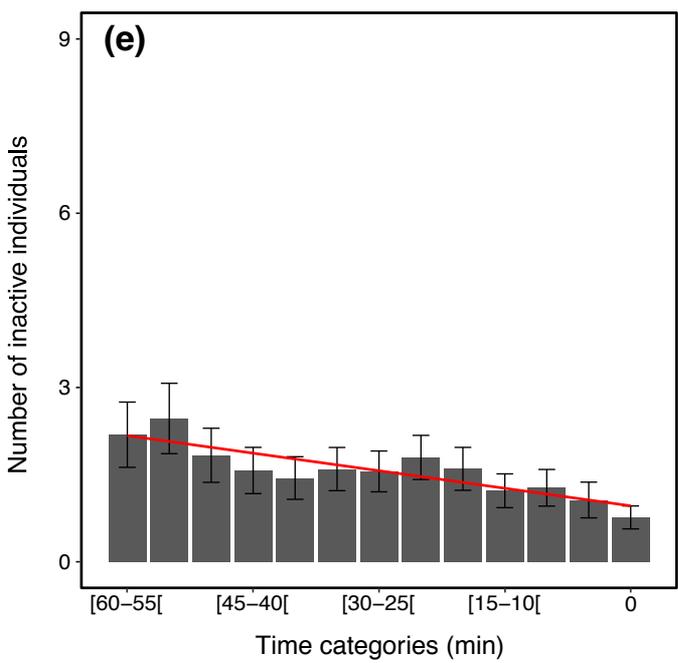
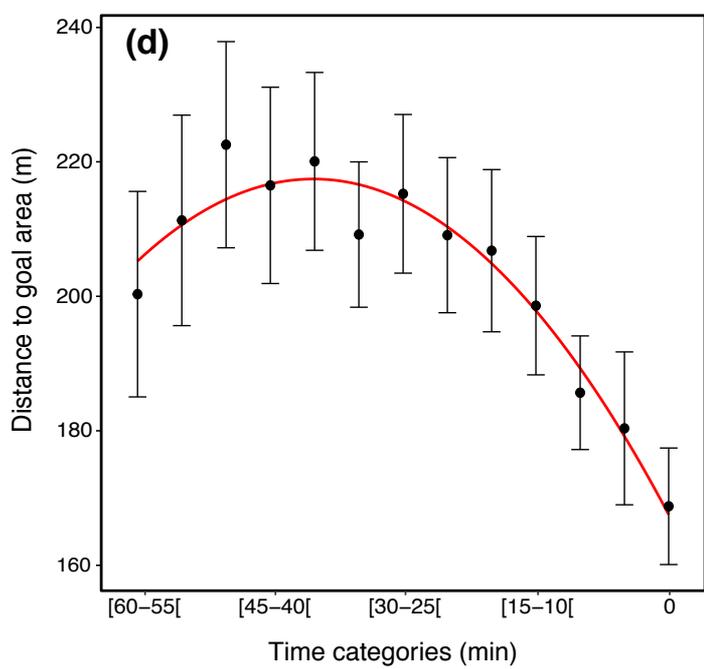
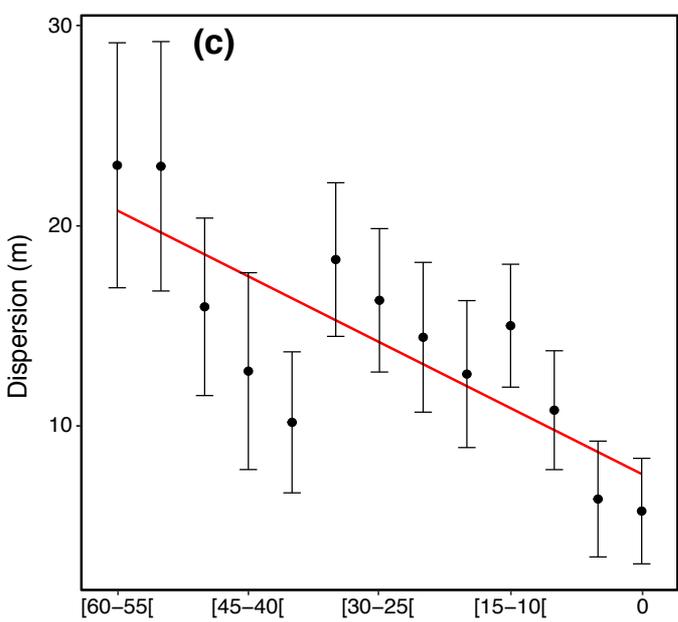
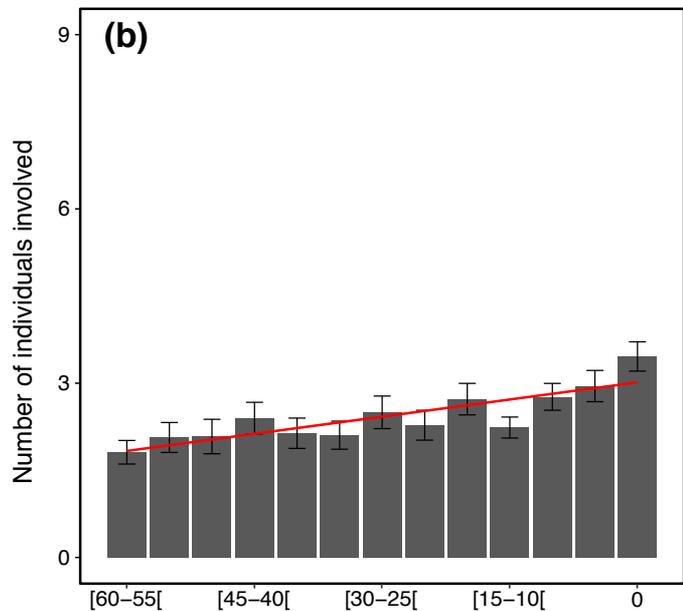
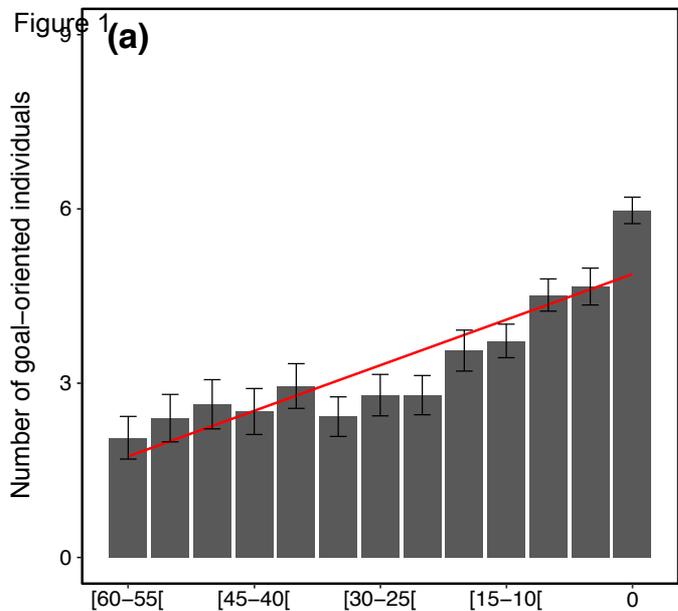
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AUTHORS' CONTRIBUTIONS

LB collected field data, participated in the design of the study, carried out the statistical analysis and drafted the manuscript; OP and JLD supervised and coordinated the study, participated in the data analysis and helped draft the manuscript. All authors gave final approval for publication.



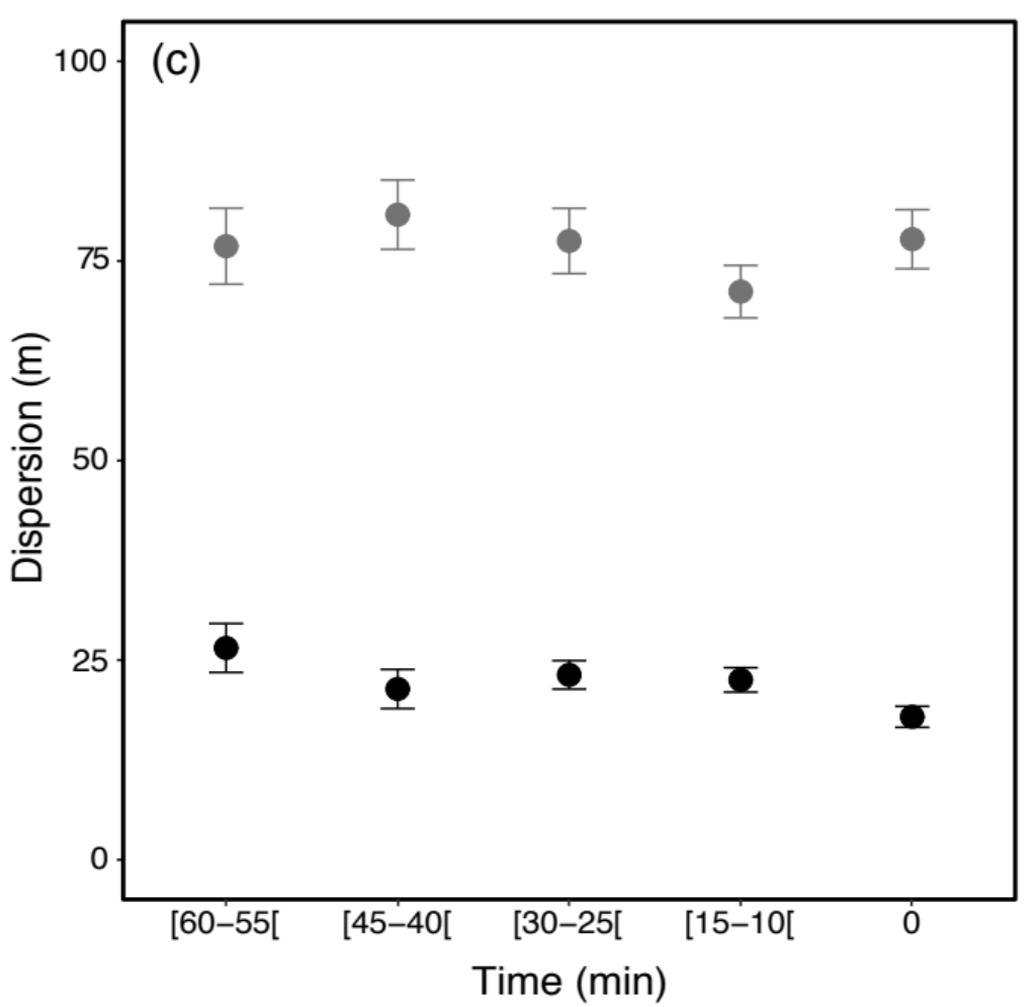
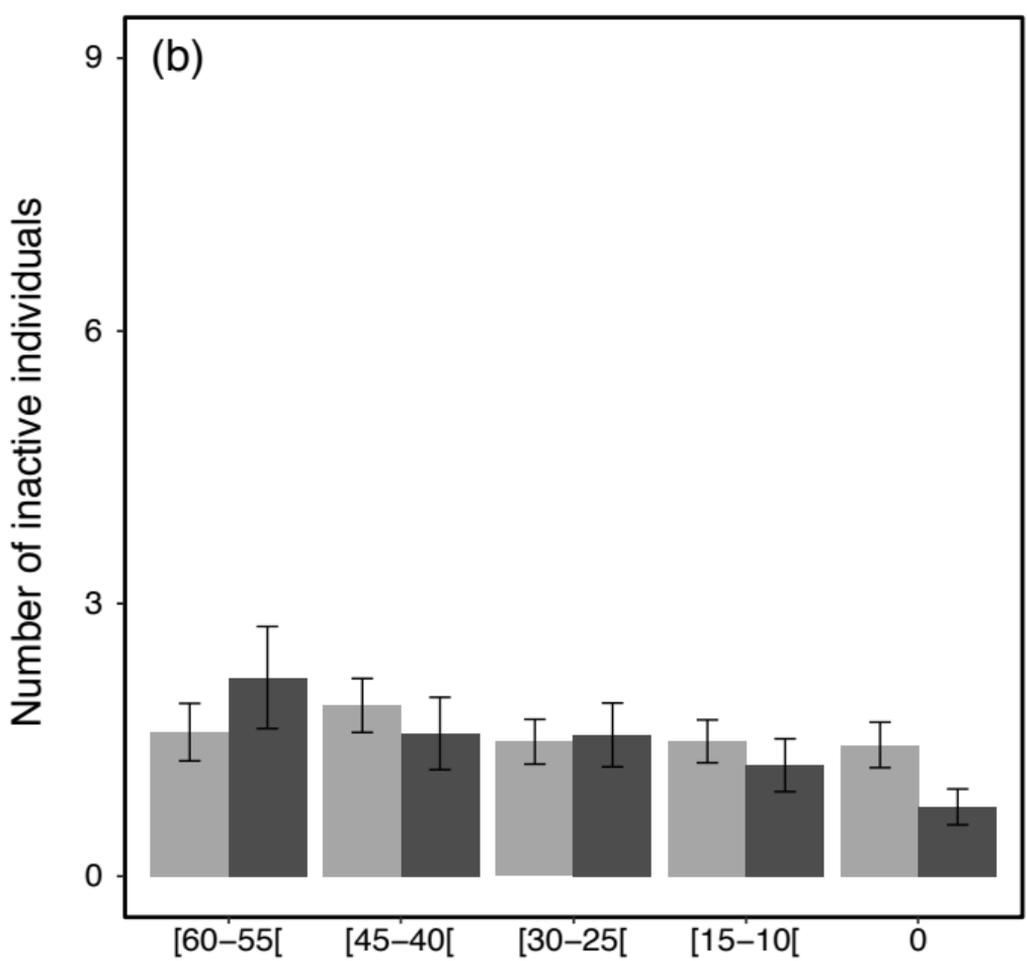
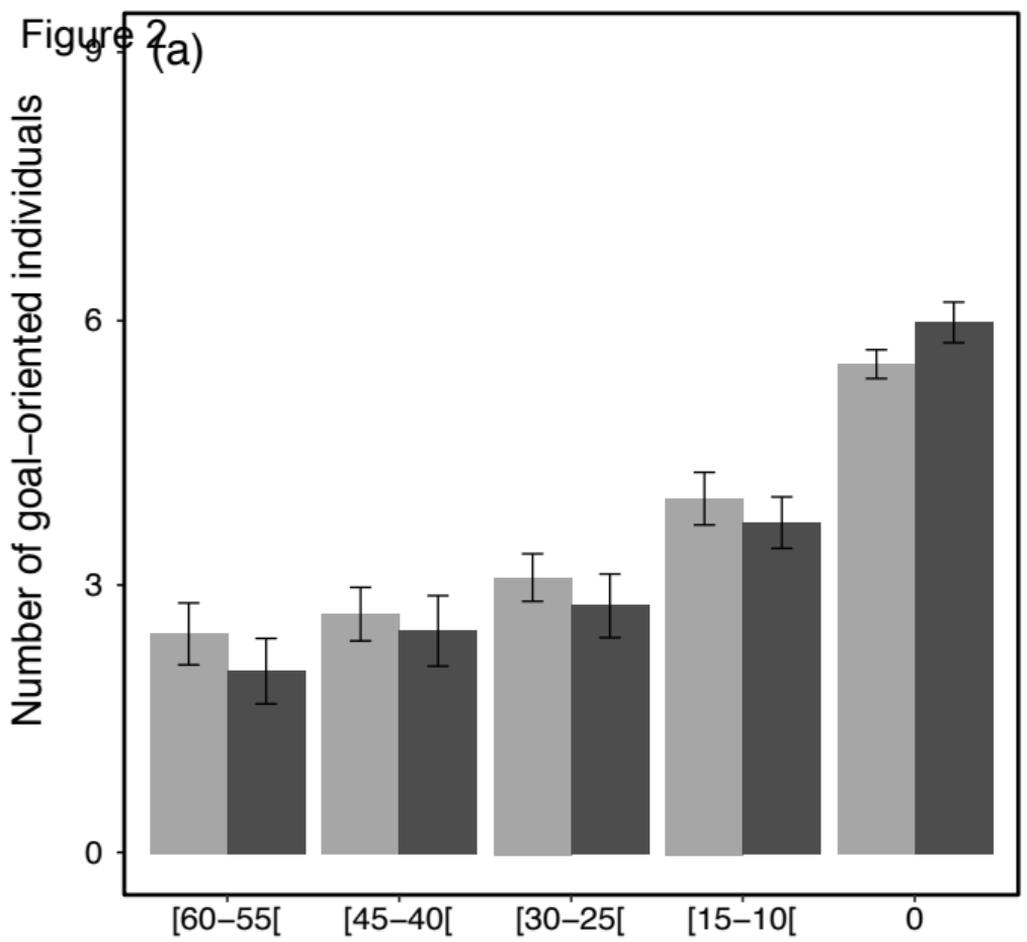


Figure 3

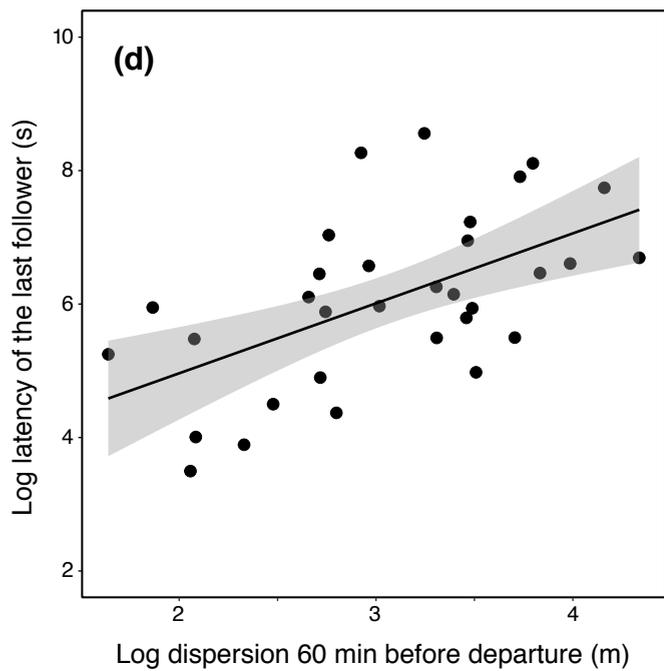
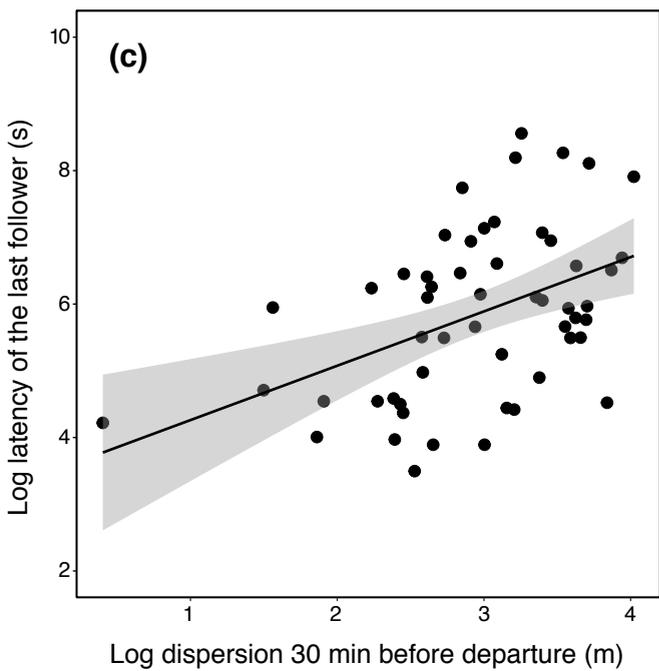
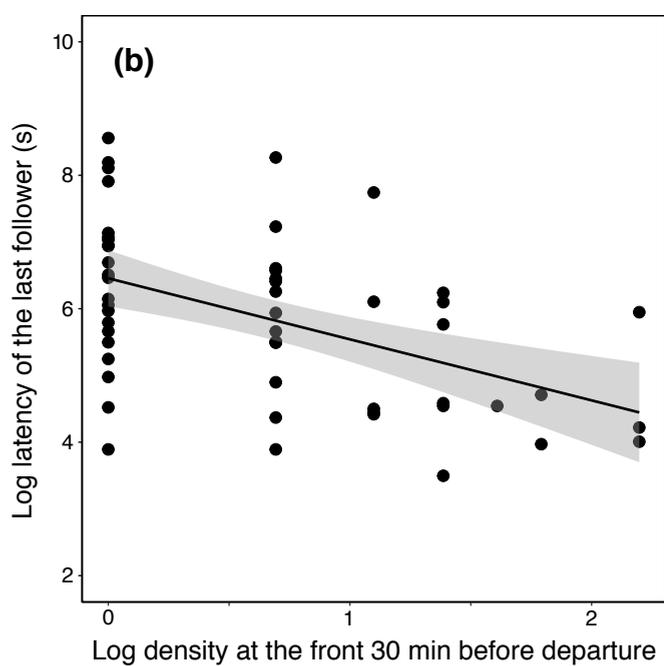
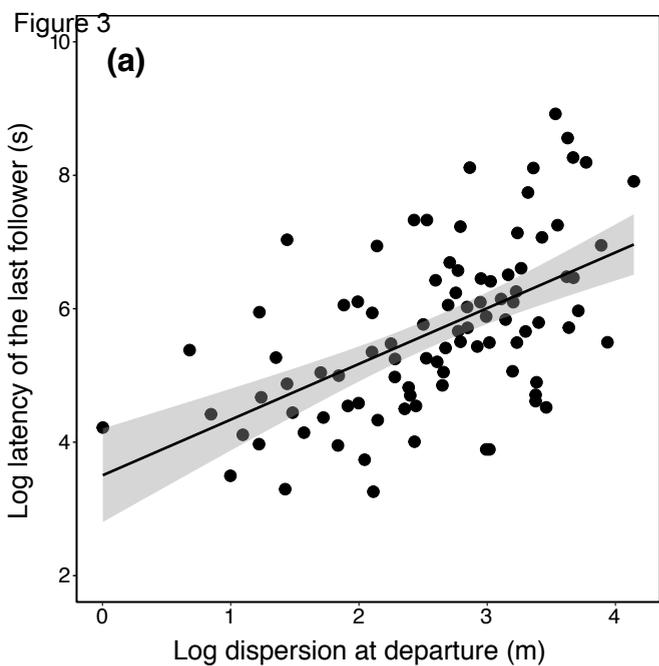
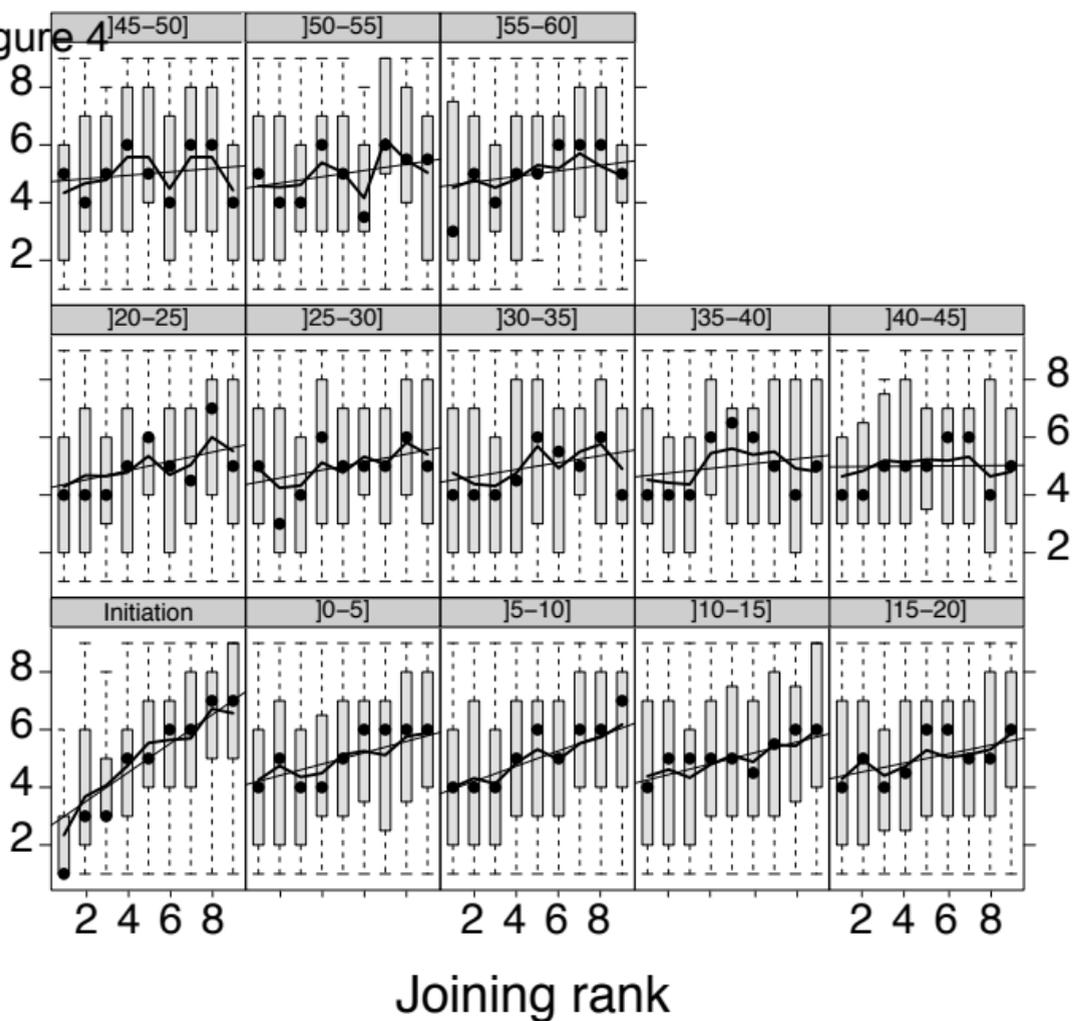


Figure 4

Topological distance to arrival area



Supplementary material

Table S1 - Table reporting characteristics of each horse (group, breed, age)

Group	Individual	Breed	Age (yr)
1	Gr	WP	18
	Ha	AB	17
	Is	WP	16
	Ju	WP	15
	Li	AB	13
	Ma	PT	12
	Pa	AB	9
	Su	PT	28
	Ve	PT	27
2	Re	FB	7
	Ti	PT	5
	Tq	FB	5
	Tx	HT	22
	Uc	PT	4
	Ul	FB	4
	Vk	FB	3
	Vo	FB	3
	Vt	HT	3

Breeds: NF=New Forest; WP=Welsh Pony; FB=French Breed; PT=Pony Type; HT=Horse Type; AB=Arabian Breed

Table S2 - Model selections with Akaike's information criterion corrected for small sample size (AICc) for the models used to examine the influence of predeparture behaviours on the duration of the joining phase (*i.e.* latency of the last follower). The degree of freedom (df), the weights (wi) and the evidence ratio (E/R) for each model are also indicated. The full model comprised dispersion, group activity, group orientation, front density and distance to the goal area as independent variables. The identity of the initiator was used as a random factor. Models in bold represent the best-fit models for each dependent variable ($\Delta\text{AICc} < 2$).

Model terms	df	AICc	ΔAICc	wi	E/R
<i>At departure</i>					
Full model	8	309.7	29.51	0	∞
Log (dispersion)	4	280.2	0	0.785	1
Log (dispersion) + log (front density)	5	284.0	3.77	0.119	6.60
Null model (intercept only)	3	300.1	19.83	0	∞
<i>30 min before departure</i>					
Full model	8	190.0	19.05	0	∞
Log (front density)	4	170.9	0	0.341	1
Log (dispersion)	4	171.2	0.30	0.294	1.16
Log (front density) + Log (dispersion)	5	172.3	1.32	0.071	4.80
Null model (intercept only)	3	178.0	7.01	0.010	34.1
<i>60 min before departure</i>					
Full model	8	131.3	27.87	0	∞
Log (dispersion)	4	103.4	0	0.700	1
Log (dispersion) + log (front density)	5	106.3	2.91	0.164	4.27
Null model (intercept only)	3	112.3	8.88	0.008	87.5

Table S3 – Temporal evolution of the link between topological distances before departure and joining order during collective movement

Time categories	Estimate (slope)	SE	R²	p-value
Initiation	0.459	0.031	0.21	< 0.0001
0 - 5 min	0.175	0.041	0.029	< 0.0001
5 – 10 min	0.259	0.038	0.066	< 0.0001
10 – 15 min	0.161	0.041	0.024	0.0001
15 – 20 min	0.146	0.044	0.019	0.0011
20 – 25 min	0.163	0.045	0.025	0.0003
25 – 30 min	0.158	0.045	0.023	0.0005
30 – 35 min	0.108	0.049	0.009	0.0269
35 – 40 min	0.085	0.051	0.005	0.0933
40 – 45 min	-0.025	0.056	-0.003	0.6600
45 – 50 min	0.049	0.056	-0.007	0.3806
50 – 55 min	0.083	0.061	0.003	0.1724
55 – 60 min	0.064	0.059	0.007	0.2730