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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

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

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

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

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

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

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

MATERIAL AND METHODS

Animals and Environment

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

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

Observation Procedure

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

Data Scoring

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

Initiation and joining latencies

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

Group behaviour before departure

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

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

Statistical analysis

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

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

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

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

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

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

Ethical Statement

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

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

RESULTS

Evolution of predeparture behavioural patterns over time

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

Comparison with control periods

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

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

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

Predeparture behaviours predict the duration of the joining phase

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

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

Spatial organization before departure predicts joining order

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

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

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

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

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

Predeparture behaviours and joining dynamic

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

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

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

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

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

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

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

Conclusion

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

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

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TABLES

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

FIGURE LEGENDS

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

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

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

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

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

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

Each window corresponds to a time category (from $t = 0$ min, the initiation, to $t = 55 - 60$ min). Boxplots represent the distribution of topological distances to the goal area as a function of the future joining rank (e.g. joining rank 1 is the initiator, joining rank 2 the first follower, etc.). The thick curvy black line represents the mean topological rank for each joining rank and the thin straight black line represents the linear regression.

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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