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# Collective responses of flocking sheep to a herding dog

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Group-living organisms commonly exhibit collective escape responses, yet how information flows among group members in these events remains an open question. Here, we study the collective responses of a sheep flock to a shepherd dog in a driving task between two well-defined target points. We collected high-resolution spatiotemporal data from 14 sheep and the dog, using Ultra-Wide-Band tags attached to each individual. We find that the spatial positions of sheep along the front-back axis of the group's velocity strongly correlate with their impact on the collective movement. Our analyses reveal that, even though the dog chases the sheep flock from behind, directional information on shorter time scales propagates from the front of the group towards the rear; further, the dog adjusts its movement in response to the flock's dynamics. We introduce an agent-based model that captures key data features. Specifically, in response to chasing, the sheep change their spatial relative positions less frequently and exhibit a transfer of directional information flow from front to back; this pattern disappears in the absence of chasing. Our study reveals some general insights into how directional information propagates in escaping animal groups.

Keywords: Collective behavior, Flocking, Sheep, Shepherd dog, Herding, Escape behavior

## I. INTRODUCTION

The ability of groups of organisms to detect threats or predator attacks and then coordinate their collective movements to escape is observed in many species living in groups such as swarms of insects [1], schools of fish [2–5], flocks of birds [6–10], and herds of mammals [11–13]. These patterns of collective motion often confuse the predator and increase the survival of the prey [14–20] (for detailed review, see [21]).

These properties, sometimes referred as a form of collective intelligence [22, 23], emerge at the group level from specific behavioral interactions between individuals [24–32]. Studying these interactions can provide insight into the way information spreads across groups of organisms in response to predator attacks and into the mechanisms by which animals coordinate their actions [33–38]. This knowledge is also fundamental to understanding how selective pressure acting at the individual level promotes flocking behaviors [15, 19, 39–43].

Studying collective escape phenomena in the field is a challenging task. Predator attacks are not only unpredictable but also rare events. Simultaneously obtaining data on the trajectories of the predator and individuals within the group during these attacks can be extremely complex. To overcome these difficulties, some studies simulate threats and instigate collective responses via various methods, such as a human approaching antelopes [13] or robotic models of predators approaching a flock of birds [44] or a school of fish [45].

Collective responses can also be investigated via the system of sheep herding, where interactions of a flock of sheep with a herding dog offer the opportunity to study

the impact of a controlled threat on the collective movements of an animal group [46]. As a matter of fact, herding dogs have retained only some sequences of the predation behavior of wild canids. They display motor behavioral patterns such as searching and orienting, fixing, following, approaching, and finally chasing that are observed in related wild canids such as wolves and coyotes. But unlike the complete sequence characteristic of these species, the capture and killing of prey are absent in herding dogs [47]. Moreover, while predators typically aim to separate target individuals from the herd, sheepdogs are trained to maintain flock cohesion. However, several studies have reported that in the presence of a dog, sheep exhibit fearful behavior [48, 49] and their level of stress increases alongside an increase in plasma cortisol concentration [50], suggesting that sheep perceive a herding dog as a threat. Since the behavior of the dog is controlled by the shepherd, it is thus possible to carry out a large number of replications of the same experimental situation.

Using a similar setup, King et al. [46] have studied the response of a sheep flock to a herding dog. The analyses of individuals' trajectories, revealed that as the dog approaches, the sheep tend to move towards the center of the flock, a behavior consistent with the selfish-herd hypothesis. Moreover, in large sheep flocks ( $N = 100$ ) without any external threat, sheep alternate between a slow grazing phase, during which the group spreads out, and fast packing events, during which sheep imitate the behavior of their neighbors and run toward the center of the group, thus increasing group density [51]. However, how exactly the information flows among sheep flock members remains unclear.

Here, we investigate the collective responses of a flock of sheep to the behavior of a herding dog focusing particularly on how information spreads within the flock. As the dog gets closer to the flock, it induces an avoidance reaction from the sheep. We analyze how this behavioral reaction to the perceived threat propagates within the flock and affects the collective movements of sheep. In our experiments, a trained border collie was responding to the verbal commands of the shepherd and used to guide a flock of sheep ( $N = 14$ ) from an initial location to a target location (Fig. 1a). We collected the positions and orientation of all sheep, the dog and the shepherd with a Ultra wide band-based real-time location system during several dozen of trips performed by the flock. We first analyze the collective movements of the flock when interacting with the dog. We then analyze the directional correlation between the dog and the flock, as well as among the individual sheep, to determine how information propagates within the flock. We finally used a modified version of a shepherding model to show that simple interaction rules between sheep, and between sheep and the dog can reproduce key features of collective escape response and information flow observed in our data.

## II. RESULTS

### A. Collective behavior of sheep and their reaction to the dog

Fig. 1b shows the trajectories of the  $N = 14$  sheep (blue lines) and the dog (red) over a 26-seconds herding event, and the instantaneous positions of each individual at 6 equispaced instants of time  $t_1, \dots, t_6$ . During this particular event, the sheep move away from the dog while remaining quite cohesive, with the dog staying behind the flock and exhibiting a zigzag motion (see also Supplementary video S1 and Supplementary video S2).

We characterize the sheep collective behavior using three observables: the group cohesion  $C$ , given by the mean radius of the group, the polarization  $P$ , which measures the degree of alignment of the individual sheep, and the elongation  $E$ , which measures the ratio length/width of the sheep flock with respect to its direction of motion (see Supplementary Fig.1). The position of the dog is described by the relative position of the dog with respect to the barycenter (or group centroid) of the flock in the direction of motion of the flock, and the distance of the dog to the rear sheep in the flock in the direction of motion of the group (Fig. 1d).

We are first interested in describing how the sheep responds to the presence and the movements of the dog. Fig. 2a shows that, during the sequence depicted in Fig. 1b, sheep speed is about  $1.3 \text{ ms}^{-1}$ , smaller than the dog mean speed,  $2 \text{ ms}^{-1}$ . Sheep remain highly cohesive during the drive,  $C \approx 1.2 \text{ m}$ , which corresponds the typical body length of sheep (Fig. 2b); they remain

well aligned, with  $P(t) > 0.6$  all the time (Fig. 2c), which is substantially above the expected polarization value of  $N$  non-interacting individuals,  $P_0 \approx 1/\sqrt{N} = 0.27$  ([52]). Flock adopt an oblong shape perpendicular to the direction of motion, with  $E(t)$  smaller than 1 most of the time (Fig. 2b).

The dog always remains behind the flock barycenter and almost always behind every sheep with respect to the direction of motion of the flock, i.e.  $\bar{y}_{\text{RD}}(t) > 0$  most of the time (Fig. 2d), and at a distance to the barycenter ( $d_{\text{DB}}(t)$ ) that varies  $\approx 3\text{--}5 \text{ m}$  (Fig. 2d). The dog performs wide zigzags in the field (Fig. 1b), which are lateral movements with respect to the direction of motion of the flock, with  $\bar{x}_{\text{D}}$  displaying wide oscillations between negative (when the dog is at the left side of flock direction of motion) and positive (when the dog is at the right side) values, with an amplitude often larger than 2 m (Fig. 2e). These oscillations are also visible in the trajectory of the flock, as shown by the changes of variation of its direction of motion given by the barycenter heading  $\phi_{\text{B}}$  (Fig. 2e).

To know the extent to which these behavioral features can be generalized, we have measured the probability density functions (PDF) of the observables, defined above, over all herding events (Fig. 2f-j). Indeed, the two PDFs of sheep speed and dog speed are quite similar, although the dog often reaches speed values that are quite larger than those of the sheep (see the bump at  $2 \text{ ms}^{-1}$  in the red curve in Fig. 2f). However, dog speed is more often lower than sheep speed, with a peak of  $v_{\text{D}}$  located at  $0.8 \text{ ms}^{-1}$ , below the location of the peak of  $v_{\text{B}}$  at  $0.9 \text{ ms}^{-1}$ . In turn, the dog often reaches a speed higher than  $2 \text{ ms}^{-1}$ , yielding a mean speed of  $1.5 \text{ ms}^{-1}$ , slightly higher than the mean speed of sheep,  $1.3 \text{ ms}^{-1}$  (Fig. 2f).

The flock remains cohesive, with a mean radius  $\langle C \rangle = 1.21 \text{ m}$  ( $\sim$ body length),  $\text{SD} = 0.34 \text{ m}$ , with a peak in elongation at  $E = 0.8$  (Fig. 2g), and highly polarized,  $\langle P \rangle = 0.85$ ,  $\text{SD} = 0.17$  (Fig. 2h). The distance between the flock's barycenter and the dog varies over a wide range, from  $d_{\text{BD}} \approx 3$  to  $7 \text{ m}$  (Fig. 2i). The dog is well behind the flock in the direction of motion of the flock, typically at a distance between  $\bar{y}_{\text{RD}} \approx 1$  and  $4 \text{ m}$  from the rear sheep (Fig. 2i), and only in a small number of cases the dog surpasses the rear sheep ( $\bar{y}_{\text{RD}} < 0$ ). The wide lateral oscillations of the dog have a typical amplitude similar to the one observed in the illustrative sequence shown in Fig. 1b, from  $-4$  to  $2 \text{ m}$ , and can be even more pronounced, with  $\bar{x}_{\text{D}}$  ranging from  $-6$  to  $6 \text{ m}$  (Fig. 2j). Note that the negative/positive asymmetry is simply due to the limited number of experiments, as no left/right asymmetry is expected in sheep or dog behavior.

Fig. 3 shows the impact of these wide lateral oscillations in the PDF of the angles with which the barycenter of the flock and the dog perceive each other. The PDF of the angle between the direction of the barycenter and the dog is wide, with values of  $|\psi_{\text{BD}}|$  greater than  $120^\circ$  being quite frequent, implying that the dog

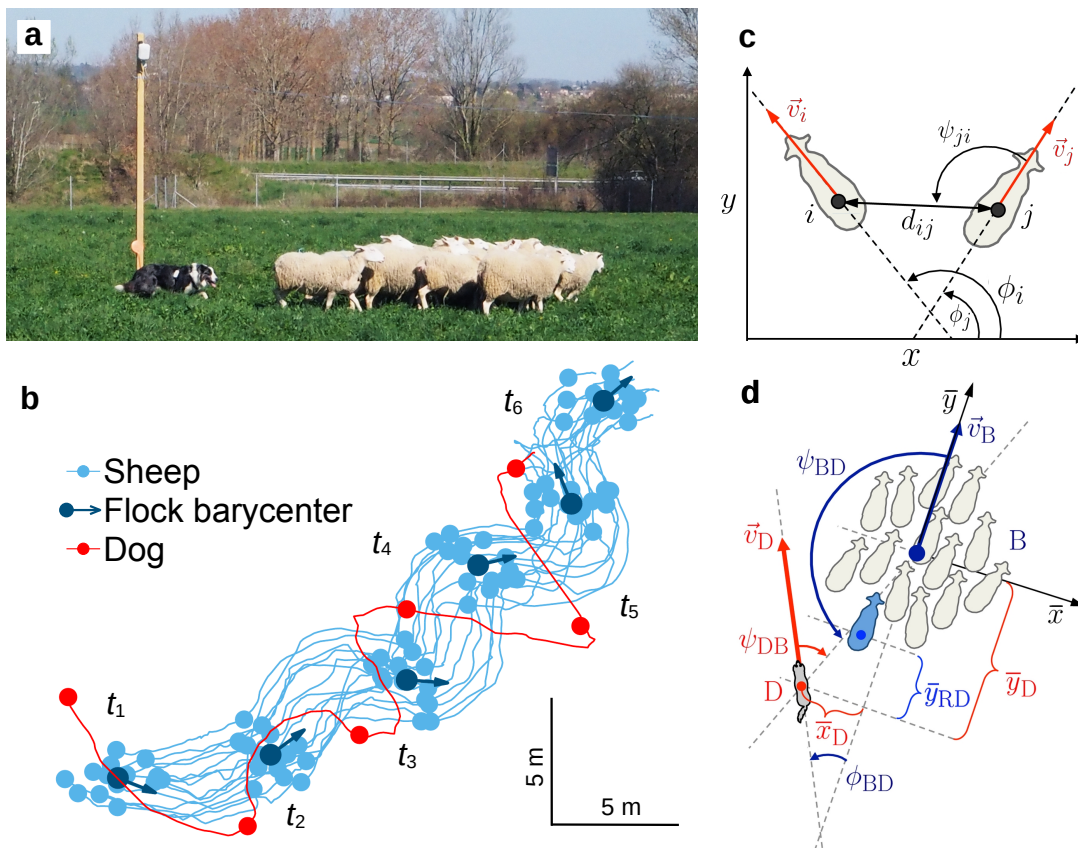


FIG. 1. **Experimental design and quantitative analysis of the collective responses of a flock of sheep to a herding dog.** (a) Flock of 14 females merino sheep (*Ovis aries*) and sheepdog (*Border collie*), equipped with Ubisense tags to track their positions while moving in a field of  $80\text{ m} \times 50\text{ m}$ , passing in front of a pole on which a Ubisense Ultra Wide Band sensor is fixed. (b) Trajectories (solid lines) of the 14 sheep (light blue) and the dog (red) along 26 seconds of a driving event, with their positions (circles) shown each 5 s and labeled from  $t_1$  to  $t_6$ . The position of the barycenter of the flock and its instantaneous direction of motion for every 5 s are shown in dark blue. (c) Solid black dots represents the position of sheep obtained from the UWB tags and the sheep is shown only as a schematic. Velocity vectors  $\vec{v}_i$  and  $\vec{v}_j$ , with their heading angles  $\phi_i$  and  $\phi_j$ , of two sheep  $i$  and  $j$  respectively; the angle,  $\psi_{ji}$ , with which sheep  $j$  perceives sheep  $i$ , and the distance between them  $d_{ij}$ . (d) Velocity vector of barycenter of the flock  $\vec{v}_B$ , velocity vector of the dog  $\vec{v}_D$ , heading difference between both vectors  $\phi_{BD}$ , angle the barycenter has to turn to perceive the dog  $\psi_{BD}$ , position of the dog  $(\bar{x}_D, \bar{y}_D)$  in the system of reference of the barycenter and in the direction of motion of the flock (given by  $\vec{v}_B$ ), and distance of the rear sheep of the flock (sheep in blue color) to the dog, in the direction of motion of the flock,  $\bar{y}_{RD}$ .

201 is behind the flock; conversely, the flock is ahead of the  
 202 dog most of the times, although the distribution is relatively  
 203 wide (Fig. 3a). Similarly, the PDF of the alignment  
 204 between the barycenter of the flock and the dog  
 205 headings is relatively wide, having practically the same  
 206 shape than  $|\psi_{DB}|$ , showing frequent misalignments larger  
 207 than  $\phi_{BD} = 45^\circ$  (Fig. 3b).

208 We also calculate the turning rate,  $\delta\phi_i = \phi_i(t + \Delta t) -$   
 209  $\phi_i(t)$ , of the barycenter of the flock and that of the dog  
 210 as a function of  $\psi_{DB}$  and  $\psi_{BD}$  respectively. The turning  
 211 rate of barycenter of the flock ( $\delta\phi_B$ ) is close to 0 when the  
 212 dog is behind the sheep ( $|\psi_{BD}| \approx 180^\circ$ ), but turns in the  
 213 opposite direction of dog as  $|\psi_{BD}|$  decreases, *i.e.* when  
 214 the dog moves towards the flanks of the flock (Figure  
 215 4a).

216 Moreover, during herding events the dog turns towards

217 the barycenter of the flock, and its turning rate ( $\Delta\phi_D$ ) is  
 218 proportional to dog's viewing angle ( $\psi_{DB}$ ); in response  
 219 to orders given by the shepherd, the dog performs en-  
 220 veloping movements to the right or left, until sometimes  
 221 its direction of movement is perpendicular to that of the  
 222 flock (Fig. 4b). There is also a notable correlation be-  
 223 tween the speeds of the dog and the barycenter, and  
 224 the flock becomes less cohesive as sheep move at higher  
 225 speeds (Supplementary Fig.2). We find that both dog  
 226 speed and barycenter speed increase or decrease simulta-  
 227 neously, suggesting a mutual influence between the dog  
 228 and the sheep (Supplementary Fig.3). In the next sec-  
 229 tion, we delve further into revealing the influence between  
 230 the dog and the sheep at fine time scales.

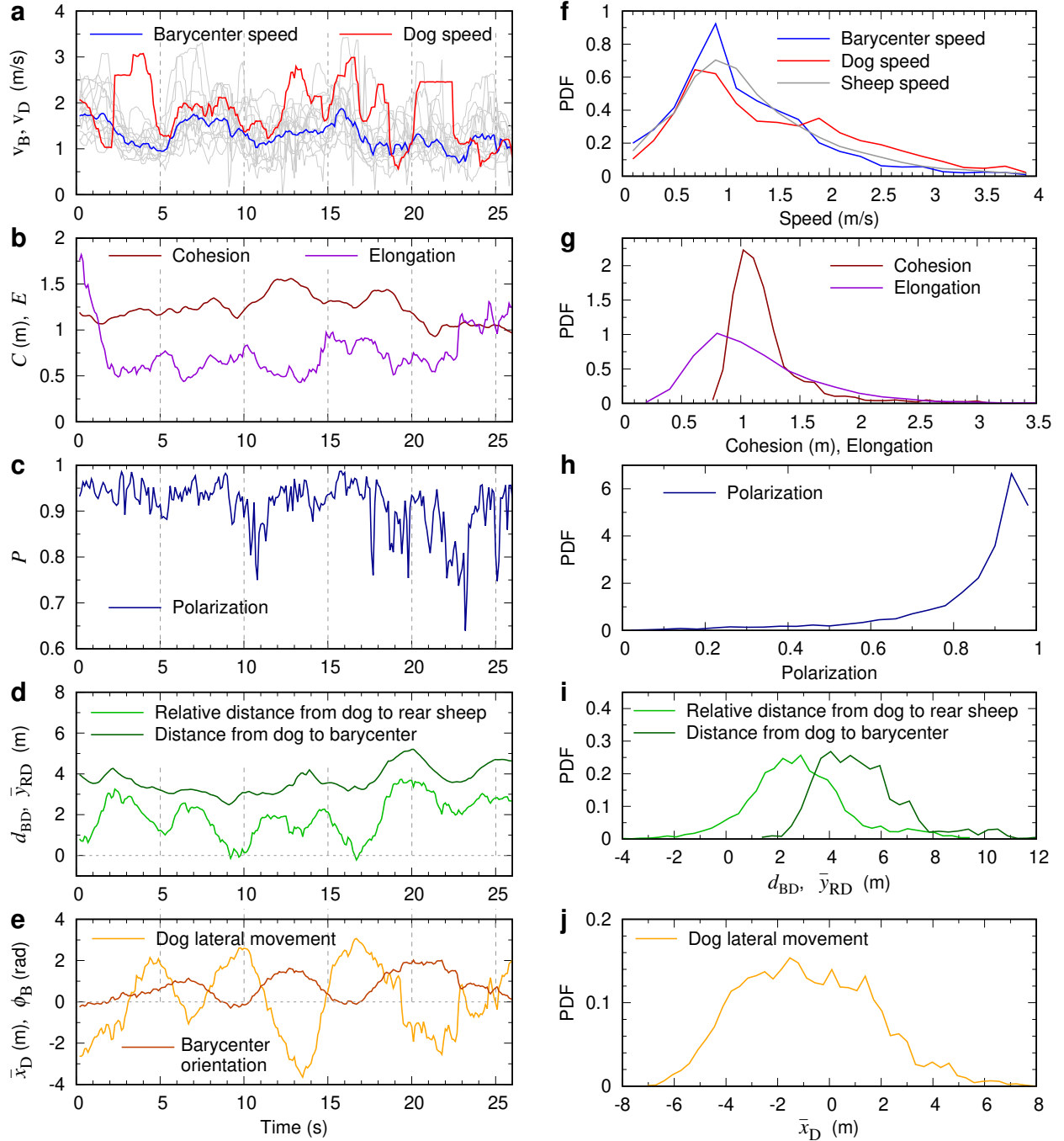


FIG. 2. Time series and probability density functions of the observables characterizing collective behavior of sheep and their reaction to the dog. (a) Speed of the barycenter of the flock  $v_B(t)$  (light blue), dog  $v_D(t)$  (magenta), and individual sheep (gray lines). (b) Cohesion  $C(t)$  (brown) and elongation  $E(t)$  (purple). (c) Polarization  $P(t)$  (dark blue). (d) Relative distance  $\bar{y}_{RD}(t)$  from the dog to rear sheep in the direction of motion of the flock, given by velocity vector of the barycenter (green), and distance  $d_{BD}(t)$  from barycenter to the dog (dark-green). (e) Lateral movement of the dog with respect to the direction of motion of the flock  $\bar{x}_D$  (orange), and orientation of the barycenter  $\phi_B(t)$ . Vertical gray dashed lines in a-e show the instants of time shown in Fig. 1b. (f-j) Probability density function (PDF) corresponding to the observables shown in the left column. Mean  $\pm$  SD values:  $\langle C \rangle = 1.21 \pm 0.34$  m ( $\sim$ body length);  $\langle P \rangle = 0.85 \pm 0.17$ ;  $\langle v_B \rangle = 1.3 \pm 0.002$   $\text{ms}^{-1}$ ;  $\langle v_D \rangle = 1.5 \pm 0.01$   $\text{ms}^{-1}$ ; Mode of  $E = 0.8$ . While the time series a-e are based on trajectories shown in Fig. 1b, the PDFs f-j are constructed using data from all the drives.

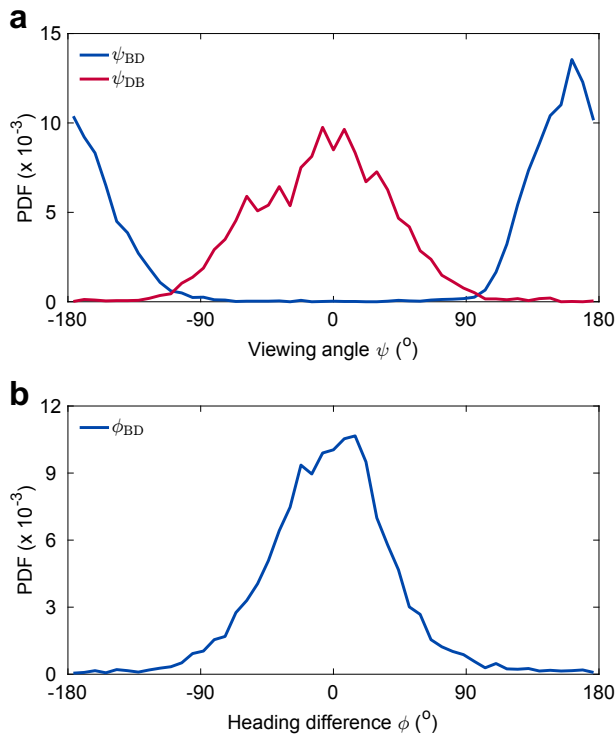


FIG. 3. **Relative angular positions and headings of the barycenter of the flock and the dog.** Probability density functions (PDF) of (a) the respective viewing angles  $\psi_{BD}$  and  $\psi_{DB}$  with which the barycenter (blue) and the dog (red) perceive each other, and (b) their heading angle difference  $\phi_{BD} = \phi_D - \phi_B$  (blue).

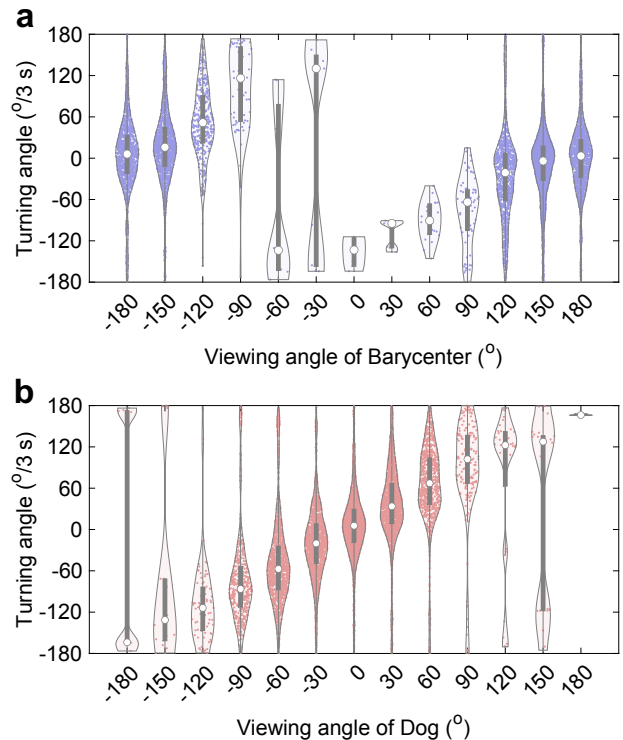


FIG. 4. **Turning rates of the barycenter of the flock and the dog.** Turning angle over 3 s of the barycenter of the flock (a) and the dog (b) with respect to their corresponding viewing angles  $\psi_{BD}$  and  $\psi_{DB}$ , respectively. In all plots, purple and orange dots represent the observed turning rates for a given viewing angle, white dots correspond to the median, and the thick vertical line corresponds to the limits of the first and third quartiles, respectively

## B. Directional correlations and hierarchical dynamics

231  
232

233 In our experiments, the dog actively steers the flock  
234 between two designated points in the field. During these  
235 events, we aim to explore both the influence of dog be-  
236 havior on the direction of sheep movement and how the  
237 behavior of an individual sheep affects the direction of  
238 movement of its neighbors. We infer that an individ-  
239  $j$  follows  $i$  if  $j$  consistently copies  $i$ 's direction with  
240 some time delay, denoted by  $\tau_{ij}$ . To identify this leader-  
241 follower relationship, we follow the methods described in  
242 [53–55] and calculate the cross-correlation function be-  
243 tween orientations of  $i$  and  $j$ , henceforth referred to as  
244 directional correlation (Fig. 5a,b; see also Supplemen-  
245 tary Section 1 and Supplementary Fig.4).

246 We then construct a directed leader-follower network  
247 for each herding event based on the pairwise  $\tau_{ij}$  values  
248 computed for that herding event. In such a network, each  
249 node represents the dog or an individual sheep, and a di-  
250 rected edge is drawn from the follower to the leader. We  
251 infer the ‘leadership hierarchy’ of an individual by com-  
252 puting the indegree (defined as the number of incoming  
253 edges into a node) for the node representing the individ-  
254 ual on the network. The higher the indegrees (or, in other  
255 words, the number of followers), the higher the position

256 in the leadership hierarchy.

257 Here, we note that, for a given pair, a leader-follower  
258 relationship may not always exist. Unless one individ-  
259 ual in the pair consistently copies the direction of the  
260 other, the strength of directional correlation will be neg-  
261 ligible. However, in our data, we do observe consistent  
262 leader-follower pairs within each herding event. Figure 5c  
263 shows the leader-follower network observed during one of  
264 the herding events and Supplementary Fig.5. shows the  
265 networks observed during other herding events. To un-  
266 derstand the leader-follower relationship further, we over-  
267 lay the network on a reference frame whose origin is the  
268 barycenter of the sheep flock. Furthermore, in Fig.5c,  
269 the node’s size is proportional to its indegree and thus  
270 reflects its position in the leadership hierarchy.

271 We observe that sheep in the front of the flock are char-  
272 acterized by a higher indegree (bigger node size) com-  
273 pared to the sheep located in the back, lastly followed  
274 by the dog. In other words, the sheep at the front is the  
275 highest in the directional leadership hierarchy. Further-  
276 more, although the dog drives the flock, it is the lowest  
277 in the leadership hierarchy. This suggests that the dog  
278 continuously adjusts its direction based on sheep motion.



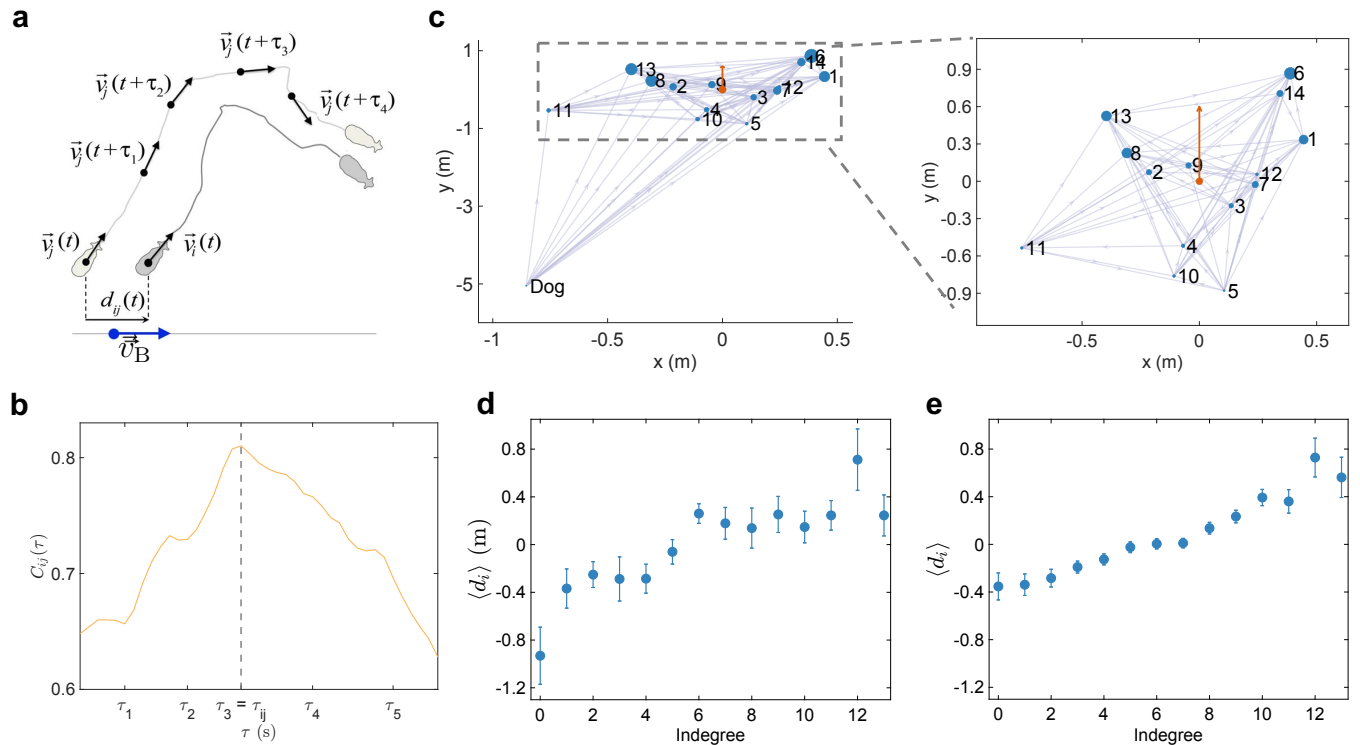


FIG. 5. **Hierarchical leader-follower relationships.** (a) Graphical representation of directional correlation analysis.  $d_{ij}$  is the projected relative distance ( $\vec{r}_i - \vec{r}_j$ ) between individuals  $i$  and  $j$  onto the direction of motion of the sheep flock ( $\vec{v}_B$ ) at time,  $t$ . (b) Representative directional correlation function  $C_{ij}(\tau)$  between 2 sheep during one of the herding events.  $\tau_{ij} = \tau_3$  is the time delay at which  $C_{ij}$  is maximum. (c) Leader-follower network of one of the drives. Nodes labeled from 1-14 are sheep, and labels remain the same throughout the experiment. Nodes are plotted on a reference frame in which the barycenter (orange dot) is at origin facing north. Edges between nodes are drawn from followers to leaders, with the size of each node being proportional to the number of its followers. (d-e) Relationship between the average relative spatial position (mean  $d_i \pm \text{SE}$ ) and the hierarchical leadership network obtained from all herding events in the data (d) and the model (e). Indegree serves as a proxy for hierarchy, where individuals with a high indegree are higher in the hierarchy.

279 Consequently, we expect that the sheep in the front  
 280 influences the group's direction and, in turn, the dog's di-  
 281 rection.

282 To quantify the influence of individuals located at  
 283 the front of the flock on the direction of its move-  
 284 ments, we calculated the average distance of sheep from  
 285 its neighbors projected onto the group velocity,  $d_{ij} =$   
 286  $\langle (\vec{x}_j - \vec{x}_i) \cdot \vec{v}_{\text{flock}} \rangle_t$ , and  $d_i = \frac{1}{N} \sum_j d_{ij}$ , where  $N$  is the  
 287 number of sheep (Fig. 5a). For all sheep that are in  
 288 the front of the group,  $d_i > 0$ , and consequently,  $d_i < 0$   
 289 for sheep at the back. As noted earlier, we use the in-  
 290 degree of a node as a proxy for its directional influence.  
 291 So, we calculate  $d_i$  for all individuals with a given inde-  
 292 gree. This informs us about the average spatial position  
 293 of all sheep with the same indegree. In simple terms,  
 294 it indicates where the sheep is located (front or back of  
 295 the group center) for a given indegree. We find a strong  
 296 correlation between  $d_i$  and the indegree of a node, con-  
 297 firming that sheep located in the front of the flock influ-  
 298 ence the direction of motion of the group, and in turn, on  
 299 dog movement (Fig.5d, Pearson correlation for indegree  
 300 versus  $\langle d_i \rangle$ ,  $\rho = 0.85$ ,  $P = 0.00004$ ). In addition, Sup-

301plementary Fig.6 shows that some individuals are consis-  
 302tently found at the front of the group during the different  
 303 herding events.

### 304 C. Modeling the collective response of the flock to 305 the herding dog

306 To better understand how information propagates  
 307 within the flock as a result of social interactions among  
 308 sheep and their interactions with the dog, we use a mod-  
 309 ified version of a herding model developed by Strömbom  
 310 et al [56]. The model is described in detail in Materials  
 311 and Methods, and the values of the parameters used in  
 312 the model are listed in Supplementary Table 1. Fig. 6  
 313 shows the results of extensive numerical simulations of  
 314 the model (see also Supplementary Videos 3 and 4). We  
 315 find that group properties such as cohesion (Fig. 6a),  
 316 elongation (Fig. 6b), polarization (Fig. 6c) and relative  
 317 distance between dog to rear sheep (Fig. 6d) are all in  
 318 qualitative agreement with experimental data. The lat-  
 319 eral movement of the dog ( $\vec{x}_D$ ) shows a (weak) bimodal

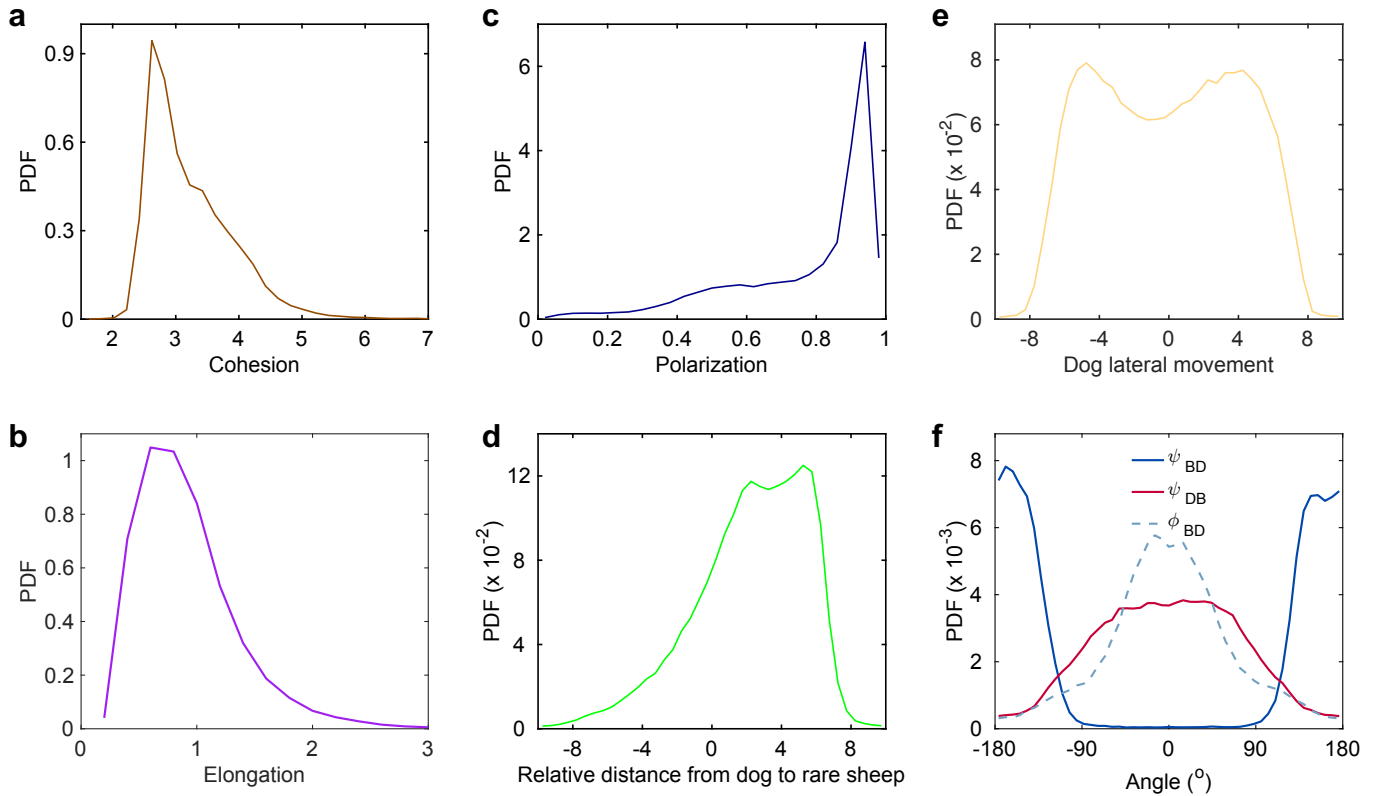


FIG. 6. **Simulation results of the shepherding model.** Probability density functions (a-f): (a) Cohesion. (b) Elongation. (c) Polarization. (d) Relative distance  $\bar{y}_{RD}$  from the dog to rear sheep in the direction of motion of the flock. (e) Lateral movement of the dog with respect to the direction of motion of the flock,  $\bar{x}_D$ . (f) Viewing angles  $\psi_{BD}$  and  $\psi_{DB}$  with which the barycenter and the dog perceive each other, and their heading angle difference  $\phi_{BD} = \phi_D - \phi_B$ .

distribution in model simulations (Fig. 6e), while the real data shows a broad unimodal distribution (Fig. 2j); we speculate that this minor difference could be due to higher noise in the real data. Additionally, we find that the PDFs of the viewing angle of the barycenter and the dog, and the difference in heading angles between barycenter and the dog, all qualitatively agree with experiments (Fig. 6f).

Importantly, we construct the interaction network in model simulations using the same protocol as described in Section II B. Here too, we find that individuals in the front of the flock are more often influential in directional decisions, with the dog consistently adjusting its direction in agreement with experimental observations (Fig. 5e, also see Supplementary Section 2 and Supplementary Fig.7 for the robustness of the results to model assumptions).

Furthermore, we aim to understand if the observed pattern of information propagation from front to back results from a constant perturbation induced by the dog or if it merely emerges as a consequence of social interaction between sheep. We first construct a null model of collective movement wherein we exclude the dog from the herding model. In the null model, sheep follow the same behavioral rules as in the herding model. However, in the null model, sheep do not graze but always move at a

constant speed (see Supplementary Section 3 for details). Here, when we construct the interaction network based on directional correlations, we do not find any leader-follower pairs. Even when they exist, there are only 2-3 pairs of leader-followers. The leader-follower network is not as highly connected as the one observed in the real data or the herding model (see Supplementary Fig.8).

In the herding model too, we note that there is no built hierarchy between the individuals in the model; further, as individuals do not occupy a fixed spatial position within the flock, we would expect that there would be no consistent leader-follower pairs. In contrast to these expectations but consistent with real sheep data, in the presence of a constant perturbation, such as a herding dog, we observe a hierarchical transfer of directional information of group motion (Fig.5e). This is likely because once a perturbation event starts, individuals' relative locations do not change, resulting in individuals located at the front of the flock having more influence on its direction of motion but only when they are consistently herded by the dog. Lastly, it is important to note that the last position occupied by the dog in the hierarchy with respect to sheep is not explicitly coded in the model but emerges as a result of the interactions between the dog and sheep.



### III. DISCUSSION

We investigated the collective responses of a flock of merino sheep interacting with a herding dog. Specifically, we study (1) the influence of the dog on the direction of sheep movement and (2) the impact of individual sheep both on their neighbors and the dog. Through the analysis of high-resolution spatiotemporal tracking data of both the dog (acting as a threat or stressor) and the sheep, we characterize the collective response of the flock and offer insights on the hierarchical nature of directional information flow.

In our experiments, we observe a highly polarized and cohesive sheep flock throughout the herding events. Additionally, we observe alignment between the flock and the dog. We emphasize that the groups are not only highly cohesive but also exhibit high polarization. Moreover, as the dog increases its speed, the group increases its speed while being highly polarized but less cohesive. The increase in group cohesion observed in our experiments when sheep interact with the dog is consistent with the mechanisms that reduce predation risks, such as the selfish herd effect [46] or group defense [21]. However, recent studies indicate that an increase in group cohesion alone may not adequately explain the anti-predatory benefits of group living, especially when groups exhibit synchronous collective motion as observed in our sheep flock experiments [9, 19, 44]. Furthermore, computational models suggest that when the speeds of predators and prey are comparable, individuals aligning with neighbors rather than moving towards the group center are less likely to be captured [57].

Through the analysis of time delays of directional correlations, we identify a clear hierarchy among sheep in terms of their directional influence on the flock. We find that the average spatial position of a sheep along the front-back axis of group velocity strongly correlates with its influence on group movement. In other words, although the flock is continuously chased by the dog, we find that the dog aligns its movement direction, on short time scales ( $\sim$  seconds), with that of the flock, with the directional information flowing from front of the flock to the rear and then to the dog. While this appears counter-intuitive, in a previous study, Early et al. [58] speculated that the dog's adjustment was based on the flock's movement in a yard. This unexpected directional hierarchy likely results from the proximity between the dog and the flock in confined sheep's yards, which allows the flock to move in its intended direction while the dog adapts to the herd on a short time scale.

We also observe that some sheep find themselves typically in the front of the group while others are typically in the rear. We suggest that this spatial heterogeneity in sheep positions within the flock may arise from differences in individual reactivity to dogs [59], with the individuals that are most sensitive to the presence of the dog are those who are at the front of the flock, thus initiating the directional changes. As an interesting contrast,

in a recent study on sheep flocks in the absence of any threat [60], all sheep had an equal probability of being at the front of the group.

While it is clear that individuals located in front had a greater directional influence on the herd, we did not observe a significant correlation between the spatial position of an individual and its influence on the speed changes of neighboring sheep (Supplementary Section 4 and Supplementary Fig.9). This could be explained by the fact that as the flock maintains its cohesion during the herding events, it is imperative that individuals move at a similar speed. Therefore, there may be no preferred position within the flock to influence the group's speed or that of any other flock member. However, as shown in [38, 61], the directional changes in escape events do appear to depend on the spatial location of individuals since those on the periphery have more degrees of freedom to alter the direction of motion.

Our findings are consistent with observations in mobbing flocks interacting with a fixed ground-based predator model, in which individuals influencing the group's direction of motion were located at the front [62]. Similar front-to-back directional information flows have also been reported in homing pigeons, merino sheep and meerkats exhibiting directed collective motion, although individuals were not subjected to an external threat [54, 60, 63]. On the other hand, in jackdaw flocks exhibiting synchronized motion but without any perturbation, the birds influencing the group's direction were not only found at the front or edges but also at the rear [62]. In meerkat groups in motion, the individuals in front do not influence the speed of the group [63]. All this suggests that it is essential to consider the ecological context when inferring the social or hierarchical influence of individuals on each other in animal groups.

We strengthen our inferences using a computational model to show that sheep following simple interaction rules (*i.e.*, repulsion from the dog and a tendency to move towards nearby neighbors and align with them), can reproduce collective response patterns similar to those observed in our experiments. Specifically, we observed a correlation between the average spatial position of sheep within the group and their hierarchy in directional influence. While certain individuals are often observed at the front of the group in experiments, the model suggests that individuals don't need to be at a fixed spatial positions within the flock to obtain the experimentally observed pattern of correlation between the spatial position of sheep and its hierarchical influence in the movement direction. In addition, using a null model, we also show the presence of a constant external perturbation that drives away the flock, such as a herding dog, is a must to produce the hierarchical directional influence from front to back. These observations suggest simple interaction rules of collecting and driving can reproduce the empirically observed patterns. Furthermore, the observed hierarchy in sheep is likely to be found more generally, beyond the specific shepherd system we studied, at least in small

486 herds.

487 Our observations also reveal that the flock is often elon-  
 488 gated perpendicular to the group velocity. This finding  
 489 contrasts with expectations from fish schools, where ob-  
 490 long formations (*i.e.* the group is elongated along its di-  
 491 rection of motion) are considered to provide protection  
 492 against predation [64]. The analysis of the herding model  
 493 shows that group elongation is determined by the rela-  
 494 tive strengths of attraction ( $w_{Att}$ ) and orientation ( $w_{Ali}$ ).  
 495 The model predicts that if the orientation strength is  
 496 lower than the attraction strength, the mode of elonga-  
 497 tion occurs at values less than 1 (Supplementary Fig.10);  
 498 indicating that in sheep flocks, the strength of attraction  
 499 is relatively higher than that of alignment. However, we  
 500 emphasize that the alignment strength remains large to  
 501 maintain a high degree of polarization observed in data,  
 502 suggesting that both cohesion and highly directed motion  
 503 are likely crucial for predator avoidance.

504 In our study, we used only one sheep flock and the same  
 505 dog across all trials. However, different groups display  
 506 variation in collective properties such as cohesion, polar-  
 507 isation, group speed and information transfer [65]. Ad-  
 508 ditionally, predators vary in attack rate and time spent  
 509 near the prey, demonstrating that predators differ in their  
 510 response to prey [66]. Therefore, these factors can affect  
 511 the generalisability of our results. While we partially ad-  
 512 dress this issue by developing a computational model to  
 513 complement our findings, we note that to strengthen the  
 514 generality of the conclusions, future studies could con-  
 515 sider using various sheep flocks and dogs of the same  
 516 breed, as well as different breeds.

517 In all our analyses, we only focused on the flock dynam-  
 518 ics when the sheep were actively chased by the sheepdog.  
 519 Thus, we did not study the dynamic interactions between  
 520 sheep during grazing and threat detection. Recent stud-  
 521 ies on fish schools in the laboratory and blackbuck herds  
 522 in the wild show a consistent pattern that the initial prop-  
 523 agation of threat information across the group is often  
 524 mediated by changes in speed [13, 67]. Future studies  
 525 could incorporate a grazing phase followed by introducing  
 526 a threat to better understand the role of speed changes  
 527 during collective escape in sheep flocks. Additionally,  
 528 in our computational model, we assumed alignment in-  
 529 teractions between sheep; however, some empirical stud-  
 530 ies didn't find evidence for velocity matching [28, 29].  
 531 Computational models have also demonstrated that em-  
 532 pirically observed group properties can be reproduced  
 533 without requiring explicit alignment interactions [68–70].  
 534 Therefore, a logical continuation would be to reconstruct  
 535 the interaction rules between sheep, and between sheep  
 536 and the dog directly from the UWB data. Interaction  
 537 rules between individuals have been directly character-  
 538 ized in various species of schooling fish [32, 71].

539 Using a similar method and considering that Ubisense  
 540 tags are both user-friendly and cost-effective, one can  
 541 characterize and quantify interaction rules within this  
 542 system as well. Such insights will enable the development  
 543 of enhanced herding models with applications spanning

544 various fields, including the creation of robots designed  
 545 for environmental cleaning, crowd management, guiding  
 546 groups of exploratory robots and bio-herding [72, 73].

## 547 IV. MATERIALS AND METHODS

### 548 A. Herding experiments

549 **Ethics.** Experiments were approved by the local  
 550 Ethics Committee for Animal Science and Health and  
 551 were performed at the experimental domain of Langlade  
 552 (INRA, UMR 1388 GenPhySE), Pomportuzat, France,  
 553 under permit APAFiS SSA 2017 005 in agreement with  
 554 the French legislation.  
 555

556 **Study species:** 14 female merino sheep (*Ovis aries*)  
 557 aged 4 years and with a mean body weight of 75  
 558 kg and mean body length of 1.2 m were used in the  
 559 experiments. We also used an 8 years old border collie  
 560 specially trained to herd sheep and whose behavior  
 561 during the experiments was managed by a professional  
 562 handler (Fig. 1a).  
 563

564 **Tracking system:** We used a real-time location  
 565 system developed by Ubisense based on Ultra-Wide  
 566 Band (UWB) signals triangulation [74] to track the  
 567 movement trajectories of each sheep, the dog and the  
 568 shepherd. Each sheep was equipped with two tags  
 569 attached by a clip to the fleece along the axis of the  
 570 vertebral column, which made it possible to get both  
 571 the position and the orientation of the animal. The  
 572 dog and his handler were also equipped with four and  
 573 two tags respectively (Supplementary Fig.11). Ubisense  
 574 tags are miniaturized circuits powered with batteries  
 575 that operate in 6–8 GHz frequency band for localization  
 576 and emit UWB wave trains that are then received and  
 577 processed by a set of sensors. In our experiments, the  
 578 tracking system included 8 sensors uniformly distributed  
 579 around the experimental pasture and fixed 3 m from the  
 580 ground. The sensors are UWB signal receivers connected  
 581 through low-latency Ethernet cables to a server that  
 582 processes sensor data into tags position. Each tag is  
 583 localized at 2Hz with a typical error of less than 30cm.  
 584

585 **Herding events:** Experiments were performed on a  
 586 flat rectangular pasture of 80 m length and 50 m width.  
 587 The task consisted for the shepherd and his dog to *drive*  
 588 the flock between two locations A and B, 60 m apart. We  
 589 performed a total of 26 round trips during which the flock  
 590 was driven from place A to place B and then brought back  
 591 to place A, located in the middle of the enclosure, to min-  
 592 imize any potential boundary effects (see Supplementary  
 593 Fig.12). Each round trip lasted 2 minutes on average.  
 594 The controlled movement phases of the flock were inter-  
 595 spersed with five rest periods of 30 to 60 minutes each  
 596 to allow the dog to recover and maintain sufficient mo-  
 597 tivation to carry out the task. During the experiments,

sheep were not continuously exposed to the dog and spent most of the time at rest in a more or less random spatial configuration. In turn, the sheep move and align with each other in the dog's presence. Supplementary Fig.13 shows the two phases that can be identified in the whole set of data captured during the experiments: an active phase, where both speed and alignment are high, and a passive phase, where both speed and alignment are small. Supplementary Fig.14 also shows that speed and alignment are positively correlated. We, therefore, focus our analysis on the active phase during which the dog was driving the sheep and staying behind the flock relative to its direction of movement.

While staying in this position, it may happen that the dog regularly alternates its direction of movement from left to right and vice versa, following the shepherd's orders. Finally, most of the time, the shepherd remained motionless on one side of the field and gave his orders to the dog.

**Quantification of collective behavior:** We denote by  $\vec{r}_i(x_i, y_i)$  and  $\vec{v}_i(v_x^i, v_y^i)$  the position and velocity vectors of individuals, respectively, with  $i = 1, \dots, N$  for the sheep,  $i = D$  for the dog and  $i = B$  for the barycenter (or, group centroid) of the sheep flock given by  $\vec{r}_B(t) = (1/N) \sum_{i=1}^N \vec{r}_i(t)$ . We consider that the heading of an individual is given by its direction of motion, *i.e.*, by the angle of its velocity vector  $\phi_i = \text{ATAN2}(v_y^i, v_x^i)$  (Figs. 1c, d).

Then, we define the group cohesion  $C$  and the group polarization  $P$  as follows:

$$C(t) = \frac{1}{N} \sum_{i=1}^N d_{Bi}, \quad P(t) = \frac{1}{N} \left\| \sum_{i=1}^N \frac{\vec{v}_i(t)}{v_i(t)} \right\|,$$

where  $v_i(t) = \|\vec{v}_i(t)\|$  is the speed of individual  $i$  and  $d_{Bi} = \|\vec{r}_i(t) - \vec{r}_B(t)\|$  is the distance between the barycenter and  $i$ .

The viewing angle of  $i$  defined as the angle with which  $i$  perceives  $j$ , quantifies how much the velocity vector  $\vec{v}_i$  has to turn to point towards  $j$ ,  $\psi_{ij} = \theta_{ij} - \phi_i$ , where  $\theta_{ij} = \text{ATAN2}(y_j - y_i, x_j - x_i)$  is the angle that the vector going from  $i$  to  $j$  forms with the horizontal x-axis. The alignment of two individuals is measured by the difference of their headings,  $\phi_{ij} = \phi_j - \phi_i$ . Positive angles are measured counterclockwise, and negative angles are measured clockwise.

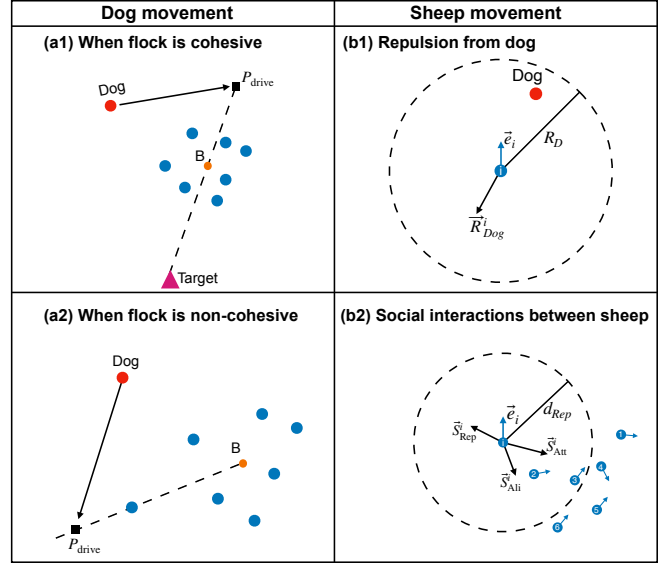
The average behavior of the flock is described by the velocity vector of the barycenter  $\vec{v}_B$  (Fig. 1b, dark blue arrow). This vector defines the ordinate axis of an oriented system of reference centered on B (Fig. 1d). Denoting the variables in this system of reference with a bar, we have, for  $i = 1, \dots, N, D$ :

$$\bar{x}_i = -d_{Bi} \sin \psi_{Bi}, \quad \bar{y}_i = d_{Bi} \cos \psi_{Bi}.$$

The length and the width of the group in its direction of motion can then be easily expressed using these

variables, so that the elongation can be defined as

$$E(t) = \frac{\max_{i=1, \dots, N} \{\bar{y}_i(t)\} - \min_{i=1, \dots, N} \{\bar{y}_i(t)\}}{\max_{i=1, \dots, N} \{\bar{x}_i(t)\} - \min_{i=1, \dots, N} \{\bar{x}_i(t)\}}.$$



**FIG. 7. Schematic representation of the interaction rules in the computational model for (a) dog and (b) sheep.** At each time step, the dog's position is updated based on whether: **(a1)** the flock is cohesive (*i.e.* the distance of the farthest sheep from the barycenter (B) is less than  $l_{sep}$ ), or **(a2)** non-cohesive (*i.e.* the distance of the farthest sheep from the barycenter is greater than  $l_{sep}$ ). The dog moves in a straight line at a constant speed,  $v_D$ , if it is farther than  $d_{Rep}$  distance from all agents. Otherwise, it moves at  $0.05v_D$ . **(b1)** Sheep move away (along  $\vec{R}_{Dog}^i$ ) from the dog if it is within distance  $R_D$ . Sheep repel from their neighbors that are within a distance of  $d_{Rep}$  along  $\vec{S}_{Rep}^i$ . Sheep align and attract towards a set of randomly chosen neighbors among those they can perceive. For example in **(b2)**, the focal sheep can perceive five nearest neighbors ( $k = 5$ , marked 1-5). The focal sheep is attracted towards the average direction,  $\vec{S}_{Att}^i$ , of four randomly chosen neighbors ( $n_{Att} = 4$ , sheep marked 1-4 in this case) and aligns ( $\vec{S}_{Ali}^i$ ) with one of those chosen neighbor ( $n_{Ali} = 1$ , sheep marked 4 in this case). We set  $k = 10$ ,  $n_{Att} = 5$ , and  $n_{Ali} = 1$  in our simulations (see Materials and Methods). The resulting heading vector of sheep  $i$  is a linear weighted combination of repulsion from the dog, collision avoidance, attraction towards neighbors, orientation towards neighbors, each with their corresponding weights given by  $w_{Dog}$ ,  $w_{Rep}$ ,  $w_{Att}$ , and  $w_{Ali}$  respectively. We set  $R_d = 12$ ,  $R_a = 2$ ,  $w_{Dog} = 1$ ,  $w_{Rep} = 2$ ,  $w_{Att} = 1.5$ ,  $w_{Ali} = 1.3$ ,  $\alpha = 0.5$ ,  $e = 0.5$ ,  $v_S = 1 \text{ ms}^{-1}$ , and  $v_{Dog} = 1.5 \text{ ms}^{-1}$  in our simulations.

The sign of  $\bar{x}_i$  reveals the side where individual  $i$  is located with respect to the direction of motion of the sheep flock, and  $\bar{x}_i$  shows how far the individual is from this direction. In particular,  $\bar{x}_D(t)$  reflects the lateral oscillations of the dog with respect to the direction of motion of the flock. Along this direction, the distance of the dog to the barycenter of the flock is given by  $-\bar{y}_D$ ,

660 and the distance of the dog to the rear sheep of the flock  
661 by  $\bar{y}_{RD} = \bar{y}_R - \bar{y}_D$ , where  $R$  refers to the rear sheep in  
662 this direction, that is,  $\bar{y}_R \leq \bar{y}_i$  for all  $i$ . Negative values  
663 of  $-\bar{y}_D$  and  $\bar{y}_{RD}$  mean respectively that the dog is in  
664 front of the barycenter or in front of the rear sheep.

665

## 666 B. Agent-based herding model

667 We use a discrete-time model, adopted from [56], where  
668 the positions of individuals change at equispaced time  
669 instants  $t^n = n\Delta t$ ,  $\Delta t = 1$  s.

670 **Sheep:** At a given time  $t^n$ , each individual sheep  $i$  is  
671 located at  $\vec{r}_i^n$  and moves to the point  $\vec{r}_i^{n+1}$  given by

$$672 \quad \vec{r}_i^{n+1} = \vec{r}_i^n + l\vec{e}(\phi_i^{n+1}), \quad (1)$$

673 where  $\vec{e}(\phi_i^{n+1})$  is the unit vector in the direction of  $\phi_i^{n+1}$   
674 and  $l (= v_S\Delta t)$  is the length traveled during this pe-  
675 riod. The angle  $\phi_i^{n+1}$  is the sheep heading's angle during  
676 this  $n$ -th time step and is given by the direction of the  
677 weighted additive combination of the vector director of  
678 the previous time step  $\vec{e}(\phi_i^n)$ , an additive noise ( $\vec{N}_i^n$ ), and  
679 the vectors corresponding to the external interactions to  
680 which the sheep is subject,

$$681 \quad \vec{U}_i^{n+1} = \alpha\vec{e}(\phi_i^n) + \vec{S}_{\text{social}}^{i,n} + \vec{R}_{\text{Dog}}^{i,n} + \epsilon\vec{N}_i^n, \quad (2)$$

682 where  $\vec{S}_{\text{social}}^{i,n}$  are the social interactions between sheep  
683 and  $\vec{R}_{\text{dog}}^{i,n}$  the repulsion from the dog. We assume that in-  
684 teractions between individuals can be expressed by linear  
685 functions that do not depend on the distance separating  
686 individuals.

687 Usually, in self-propelled particle models, agents align  
688 and attract with *all* the nearest, topological or metric  
689 neighbors [75]. However, recent studies have shown that  
690 in a moving animal group, each individual does not in-  
691 teract with all its neighbors but only with a small num-  
692 ber of them. For instance, it has been shown that fish  
693 selectively interact with their most or two most influen-  
694 tial neighbors [52, 76, 77] or just one randomly chosen  
695 neighbor [78, 79]. Sheep are also shown to select which  
696 neighbors they interact with [80]. Inspired by these em-  
697 pirical observations, we introduce a key modification in  
698 the model: sheep perceives a limited number of its near-  
699 est neighbors ( $k$ ), among which only a few of them have  
700 an impact on its behavior [81].

701 Thus, a number  $n_{\text{Att}}$  of these neighbors, chosen ran-  
702 domly, are considered to attract the sheep, and to con-  
703 tribute equally to the strength of the attraction ( $S_{\text{Att}}^i$ )  
704 and a number  $n_{\text{Ali}} \leq n_{\text{Att}}$ , and sampled randomly from  
705 the  $n_{\text{Att}}$  attracting ones, are considered to act on the  
706 alignment of the sheep ( $S_{\text{Ali}}^i$ ), all of them with the same  
707 intensity. Finally, the sheep is repulsed by every sheep  
708 closer than a short distance  $d_{\text{Rep}}$ , and this, with the same  
709 intensity. Thus, social interactions between sheep are de-

scribed as follows:

$$711 \quad \vec{S}_{\text{Att}}^i = \frac{w_{\text{Att}}}{n_{\text{Att}}} \sum_{j=1}^{n_{\text{Att}}} \frac{\vec{r}_j - \vec{r}_i}{\|\vec{r}_j - \vec{r}_i\|}, \quad (3)$$

$$712 \quad \vec{S}_{\text{Ali}}^i = \frac{w_{\text{Ali}}}{n_{\text{Ali}}} \sum_{j=1}^{n_{\text{Ali}}} \vec{e}_j, \quad (4)$$

$$713 \quad \vec{S}_{\text{Rep}}^i = -\frac{w_{\text{Rep}}}{n_{\text{Rep}}} \sum_{j=1}^{n_{\text{Rep}}} \frac{\vec{r}_j - \vec{r}_i}{\|\vec{r}_j - \vec{r}_i\|}, \quad (5)$$

714 where each interaction has a positive weight  $w$ .

715 When the dog is closer than a distance  $R_D$ , the sheep  
716 is repulsed in the opposite direction according to

$$717 \quad \vec{R}_{\text{Dog}}^i = -w_{\text{Dog}} \frac{\vec{r}_{\text{Dog}} - \vec{r}_i}{\|\vec{r}_{\text{Dog}} - \vec{r}_i\|}, \quad (6)$$

718 where  $w_{\text{dog}}$  is a positive weight.

719 As in [56], we also assume that all sheep maintain a  
720 minimum distance of  $d_{\text{Rep}}$  from each other at all times to  
721 avoid collisions. Sheep move at speed  $v_S$  via social inter-  
722 actions (align with and are attracted to their neighbours)  
723 only when the dog is within a distance  $R_D$ . Otherwise,  
724 the sheep remain in a 'grazing' phase and do not move.

725 **Dog:** Sheepdogs are typically controlled by a shep-  
726 herd, who wishes to drive the flock from one point to  
727 another by using the dog as a repulsive stimulus that  
728 makes the individual sheep move away from it. We are  
729 interested in situations where the sheep are grouped in a  
730 flock, and the sheepdog is positioned at one side of the  
731 flock. Then, the shepherd adjusts the position of the dog  
732 to make the flock travel towards a target point  $T$ . For  
733 simplicity, we assume that the dog moves straight with  
734 constant speed  $v_D = 1.5 \text{ ms}^{-1}$ , unless a sheep is closer  
735 than a short distance  $l_a$ , in whose case the dog slows  
736 down to  $v_D = 0.05 \text{ ms}^{-1}$ .

737 At each time step, the dog's position is updated as  
738 a function of the position of the barycenter of the flock  
739 with respect to the target point, so that the repulsion  
740 that the dog exerts on the sheep points towards the tar-  
741 get. Thus, the dog moves towards a point  $P_{\text{drive}}$  such  
742 that the barycenter of flock  $B$  lies between  $P_{\text{drive}}$  and  
743 the target  $T$ , ensuring that the three points are aligned  
744 and that a distance  $l_{\text{drive}}$  separates  $P_{\text{drive}}$  from  $B$  (Fig.  
745 7). If an individual sheep  $S_i$  separates from the flock  
746 more than a distance  $l_{\text{sep}}$ , the dog has to make it to re-  
747 turn to the group. Then,  $P_{\text{drive}}$  is defined in the same  
748 way but considering that the barycenter of the flock is  
749 the target and  $S_i$  is the sheep to be driven. Once the  
750 sheep is back in the group, the dog returns to drive the  
751 flock towards the target.

752 The point  $P_{\text{drive}}$  is then given by

$$753 \quad \vec{r}_{P_{\text{drive}}} = \begin{cases} \vec{r}_B - l_{\text{drive}} \frac{\vec{r}_T - \vec{r}_B}{\|\vec{r}_T - \vec{r}_B\|} & \text{if } R \leq l_{\text{sep}}, \\ \vec{r}_{i^*} - l_{\text{drive}} \frac{\vec{r}_B - \vec{r}_{i^*}}{\|\vec{r}_B - \vec{r}_{i^*}\|} & \text{if } \|\vec{r}_{i^*} - \vec{r}_B\| > l_{\text{sep}}, \end{cases}$$

where  $i^*$  is the most distant sheep from the barycenter, *i.e.*,  $\|\vec{r}_{i^*} - \vec{r}_B\| \geq \|\vec{r}_i - \vec{r}_B\|$  for all  $i = 1, \dots, N$ .

**A modified model:** To test the robustness of the model results, we also consider a modified model in which  $R_D$  does not cover the entire flock. Under this condition,

to ensure that the flock remains cohesive and polarised, we assume that sheep social interactions (attraction and alignment) are always present among sheep, regardless of the dog's position. Further, we assume that the sheep also copy their neighbor's speed. Further details of the model and results are presented in SM Section 2.

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- [1] William L Romey, Amy L Smith, and Jerome Buhl. Flash expansion and the repulsive herd. *Animal Behaviour*, 110:171–178, 2015.
- [2] Tony J Pitcher and Christopher J Wyche. Predator-avoidance behaviours of sand-eel schools: why schools seldom split. In *Predators and prey in fishes: Proceedings of the 3rd biennial conference on the ethology and behavioral ecology of fishes, held at Normal, Illinois, USA, May 19–22, 1981*, pages 193–204. Springer, 1983.
- [3] Paolo Domenici and Robert S Batty. Escape manoeuvres of schooling clupea harengus. *Journal of Fish Biology*, 45: 97–110, 1994.
- [4] Leif Nøttestad and Bjørn Erik Axelsen. Herring schooling manoeuvres in response to killer whale attacks. *Canadian Journal of Zoology*, 77(10):1540–1546, 1999.
- [5] Carolina Doran, David Bierbach, Juliane Lukas, Pascal Klamser, Tim Landgraf, Haider Klenz, Marie Habedank, Lenin Arias-Rodriguez, Stefan Krause, Pawel Romanczuk, et al. Fish waves as emergent collective antipredator behavior. *Current Biology*, 32(3):708–714, 2022.
- [6] Claudio Carere, Simona Montanino, Flavia Moreschini, Francesca Zoratto, Flavia Chiarotti, Daniela Santucci, and Enrico Alleva. Aerial flocking patterns of wintering starlings, *sturnus vulgaris*, under different predation risk. *Animal Behaviour*, 77(1):101–107, 2009.
- [7] Andrea Procaccini, Alberto Orlandi, Andrea Cavagna, Irene Gardina, Francesca Zoratto, Daniela Santucci, Flavia Chiarotti, Charlotte K. Hemelrijk, Enrico Alleva, Giorgio Parisi, and Claudio Carere. Propagating waves in starling, *Sturnus vulgaris*, flocks under predation. *Animal Behaviour*, 82(4):759–765, 10 2011.
- [8] RF Storms, Claudio Carere, Francesca Zoratto, and CK Hemelrijk. Complex patterns of collective escape in starling flocks under predation. *Behavioral Ecology and Sociobiology*, 73:1–10, 2019.
- [9] Marina Papadopoulou, Hanno Hildenbrandt, Daniel WE Sankey, Steven J Portugal, and Charlotte K Hemelrijk. Self-organization of collective escape in pigeon flocks. *PLoS Computational Biology*, 18(1):e1009772, 2022.
- [10] Marina Papadopoulou, Hanno Hildenbrandt, Daniel WE Sankey, Steven J Portugal, and Charlotte K Hemelrijk. Emergence of splits and collective turns in pigeon flocks under predation. *Royal Society Open Science*, 9(2): 211898, 2022.
- [11] Christopher C Shank. Cooperative defense by bighorn sheep. *Journal of Mammalogy*, 58(2):243–244, 1977.
- [12] Andres J. Novaro, Claudio A. Moraga, Cristobal Briceño, Martin C. Funes, and Andrea Marino. First records of culpeo (*lycalopex culpaeus*) attacks and cooperative defense by guanacos (*lama guanicoe*). *Mammalia*, 73(2): 148–150, 2009.
- [13] Akanksha Rathore, Bhavya Deepti Vadavalli, Vivek Jadhav, Kavita Isvaran, and Vishwesh Guttal. Leadership and information transfer in groups escaping a (simulated) threat in the wild. *bioRxiv*, pages 2023–07, 2023.
- [14] Colin R Tosh, Andrew L Jackson, and Graeme D Ruxton. The confusion effect in predatory neural networks. *The American Naturalist*, 167(2):E52–E65, 2006.
- [15] Randal S Olson, Arend Hintze, Fred C Dyer, David B Knoester, and Christoph Adami. Predator confusion is sufficient to evolve swarming behaviour. *Journal of The Royal Society Interface*, 10(85):20130305, 2013.
- [16] Laurie Landeau and John Terborgh. Oddity and the ‘confusion effect’ in predation. *Animal Behaviour*, 34(5): 1372–1380, 1986.
- [17] Anne E Magurran. The adaptive significance of schooling as an anti-predator defence in fish. *Annales Zoologici Fennici*, pages 51–66, 1990.
- [18] Will Cresswell. Flocking is an effective anti-predation strategy in redshanks, *tringa totanus*. *Animal Behaviour*, 47(2):433–442, 1994.
- [19] Christos C Ioannou, Vishwesh Guttal, and Iain D Couzin. Predatory fish select for coordinated collective motion in virtual prey. *Science*, 337(6099):1212–1215, 2012.
- [20] Callum Duffield and Christos C Ioannou. Marginal predation: do encounter or confusion effects explain the targeting of prey group edges? *Behavioral Ecology*, 28(5): 1283–1292, 2017.
- [21] Christos C Ioannou. Grouping and predation. *Encyclopedia of Evolutionary Psychological Science*, pages 3574–3580, 2021.
- [22] Iain Couzin. Collective minds. *Nature*, 445(7129):715, 2007.
- [23] Mehdi Moussaid, Simon Garnier, Guy Theraulaz, and Dirk Helbing. Collective information processing and pattern formation in swarms, flocks, and crowds. *Topics in Cognitive Science*, 1(3):469–497, 2009.
- [24] Scott Camazine, Jean-Louis Deneubourg, Nigel R Franks, James Sneyd, Guy Theraulaz, and Eric Bonabeau. *Self-Organization in Biological Systems*. Princeton university press, 2001.
- [25] David JT Sumpter. *Collective Animal Behavior*. Princeton University Press, 2010.
- [26] James E Herbert-Read. Understanding how animal groups achieve coordinated movement. *Journal of Experimental Biology*, 219(19):2971–2983, 2016.
- [27] M. Ballerini, N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Gardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini, M. Viale, and V. Zdravkovic. Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proceedings of the National Academy of Sciences of the United States of America*, 105(4):1232–1237, 2008.

- [28] Yael Katz, Kolbjørn Tunstrøm, Christos C. Ioannou, Cristián Huepe, and Iain D. Couzin. Inferring the structure and dynamics of interactions in schooling fish. *Proceedings of the National Academy of Sciences of the United States of America*, 108(46):18720–18725, 2011.
- [29] James E. Herbert-Read, Andrea Perna, Richard P. Mann, Timothy M. Schaerf, David J.T. Sumpter, and Ashley J.W. Ward. Inferring the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences of the United States of America*, 108(46):18726–18731, 2011.
- [30] Jacques Gautrais, Francesco Ginelli, Richard Fournier, Stéphane Blanco, Marc Soria, Hugues Chaté, and Guy Theraulaz. Deciphering Interactions in Moving Animal Groups. *PLoS Computational Biology*, 8(9), 2012.
- [31] James G Puckett, Douglas H Kelley, and Nicholas T Ouellette. Searching for effective forces in laboratory insect swarms. *Scientific Reports*, 4(1):4766, 2014.
- [32] Daniel S Calovi, Alexandra Litchinko, Valentin Lecheval, Ugo Lopez, Alfonso Pérez Escudero, Hugues Chaté, Clément Sire, and Guy Theraulaz. Disentangling and modeling interactions in fish with burst-and-coast swimming reveal distinct alignment and attraction behaviors. *PLoS Computational Biology*, 14(1):e1005933, 2018.
- [33] J E Treherne and W A Foster. Group transmission of predator avoidance behaviour in a marine insect: the Trafalgar effect. *Animal Behavior*, 29:911–917, 1981.
- [34] David Sumpter, Jerome Buhl, Dora Biro, and Iain Couzin. Information transfer in moving animal groups. *Theory in Biosciences*, 127:177–186, 2008.
- [35] Stefano Marras, Robert S. Batty, and Paolo Domenici. Information transfer and antipredator maneuvers in schooling herring. *Adaptive Behavior*, 20(1):44–56, 2012.
- [36] Nils Olav Handegard, Kevin M. Boswell, Christos C. Ioannou, Simon P. Leblanc, Dag B. Tjøstheim, and Iain D. Couzin. The dynamics of coordinated group hunting and collective information transfer among schooling prey. *Current Biology*, 22(13):1213–1217, 2012.
- [37] Daniel S Calovi, Ugo Lopez, Paul Schuhmacher, Hugues Chaté, Clément Sire, and Guy Theraulaz. Collective response to perturbations in a data-driven fish school model. *Journal of The Royal Society Interface*, 12(104):20141362, 2015.
- [38] Valentin Lecheval, Li Jiang, Pierre Tichit, Clément Sire, Charlotte K Hemelrijk, and Guy Theraulaz. Social conformity and propagation of information in collective returns of fish schools. *Proceedings of the Royal Society B: Biological Sciences*, 285(1877):20180251, 2018.
- [39] Vishwesa Guttal and Iain D. Couzin. Social interactions, information use, and the evolution of collective migration. *Proceedings of the National Academy of Sciences of the United States of America*, 107(37):16172–16177, 2010.
- [40] William D Hamilton. Geometry for the selfish herd. *Journal of Theoretical Biology*, 31(2):295–311, 1971.
- [41] Randal S Olson, David B Knoester, and Christoph Adami. Evolution of swarming behavior is shaped by how predators attack. *Artificial Life*, 22(3):299–318, 2016.
- [42] James E Herbert-Read, Emil Rosén, Alex Szorkovszky, Christos C Ioannou, Björn Rogell, Andrea Perna, Indar W Ramnarine, Alexander Kotrschal, Niclas Kolm, Jens Krause, et al. How predation shapes the social interaction rules of shoaling fish. *Proceedings of the Royal Society B: Biological Sciences*, 284(1861):20171126, 2017.
- [43] Pascal P Klamser and Pawel Romanczuk. Collective predator evasion: Putting the criticality hypothesis to the test. *PLoS Computational Biology*, 17(3):e1008832, 2021.
- [44] Daniel W.E. Sankey, Rolf F. Storms, Robert J. Musters, Timothy W. Russell, Charlotte K. Hemelrijk, and Steven J. Portugal. Absence of “selfish herd” dynamics in bird flocks under threat. *Current Biology*, 31(14):3192–3198, 7 2021.
- [45] Giovanni Polverino, Vrishin R. Soman, Mert Karakaya, Clelia Gasparini, Jonathan P. Evans, and Maurizio Porfiri. Ecology of fear in highly invasive fish revealed by robots. *iScience*, 25(1):103529, 1 2022.
- [46] Andrew J King, Alan M Wilson, Simon D Wilshin, John Lowe, Hamed Haddadi, Stephen Hailes, and A Jennifer Morton. Selfish-herd behaviour of sheep under threat. *Current Biology*, 22(14):R561–R562, 2012.
- [47] Raymond Coppinger and Mark Feinstein. *How dogs work*. University of Chicago Press, 2020.
- [48] Caroline Lee, Else Verbeek, Rebecca Doyle, and Melissa Bateson. Attention bias to threat indicates anxiety differences in sheep. *Biology Letters*, 12(6):20150977, 2016.
- [49] Jessica E Monk, Dana LM Campbell, and Caroline Lee. Future application of an attention bias test to assess affective states in sheep. *Animal Production Science*, 63(6):523–534, 2023.
- [50] R Kilgour and H de Langen. Stress in sheep resulting from management practices. *Proceedings of the New Zealand Society of Animal Production*, 26(1):83–90, 1990.
- [51] Francesco Ginelli, Fernando Peruani, Marie-Hélène Pilot, Hugues Chaté, Guy Theraulaz, and Richard Bon. Intermittent collective dynamics emerge from conflicting imperatives in sheep herds. *Proceedings of the National Academy of Sciences of the United States of America*, 112(41):12729–12734, 2015.
- [52] Liu Lei, Ramón Escobedo, Clément Sire, and Guy Theraulaz. Computational and robotic modeling reveal parsimonious combinations of interactions between individuals in schooling fish. *PLoS Computational Biology*, 16(3):e1007194, 2020.
- [53] Dirk Bumann and Jens Krause. Front individuals lead in shoals of three-spined sticklebacks (*gasterosteus aculeatus*) and juvenile roach (*rutilus rutilus*). *Behaviour*, 125(3-4):189–198, 1993.
- [54] Máté Nagy, Zsuzsa Ákos, Dora Biro, and Tamás Vicsek. Hierarchical group dynamics in pigeon flocks. *Nature*, 464(7290):890–893, 2010.
- [55] Ariana Strandburg-Peshkin, Danai Papageorgiou, Margaret C Crofoot, and Damien R Farine. Inferring influence and leadership in moving animal groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1746):20170006, 2018.
- [56] Daniel Strömbom, Richard P. Mann, Alan M. Wilson, Stephen Hailes, A. Jennifer Morton, David J.T. Sumpter, and Andrew J. King. Solving the herding problem: Heuristics for herding autonomous, interacting agents. *Journal of the Royal Society Interface*, 11(100):20140719, 2014.
- [57] Daniel WE Sankey. ‘selfish herders’ finish last in mobile animal groups. *Proceedings of the Royal Society B*, 289(1985):20221653, 2022.



- [58] Jonathan Early, Jessica Aalders, Elizabeth Arnott, Claire Wade, and Paul McGreevy. Sequential analysis of livestock herding dog and sheep interactions. *Animals*, 10(2):352, 2020.
- [59] GJ Syme and Lesley A Syme. The concept of spatial leadership in farm animals: an experiment with sheep. *Animal Behaviour*, 23:921–925, 1975.
- [60] Luis Gómez-Nava, Richard Bon, and Fernando Peruani. Intermittent collective motion in sheep results from alternating the role of leader and follower. *Nature Physics*, 18(12):1494–1501, 2022.
- [61] Alessandro Attanasi, Andrea Cavagna, Lorenzo Del Castello, Irene Giardina, Asja Jelic, Stefania Melillo, Leonardo Parisi, Oliver Pohl, Edward Shen, and Massimiliano Viale. Emergence of collective changes in travel direction of starling flocks from individual birds’ fluctuations. *Journal of The Royal Society Interface*, 12(108):20150319, 2015.
- [62] Hangjian Ling, Guillam E McIvor, Joseph Westley, Kasper Van der Vaart, Jennifer Yin, Richard T Vaughan, Alex Thornton, and Nicholas T Ouellette. Collective turns in jackdaw flocks: kinematics and information transfer. *Journal of the Royal Society Interface*, 16(159):20190450, 2019.
- [63] Baptiste Averly, Vivek H. Sridhar, Vlad Demartsev, Gabriella Gall, Marta Manser, and Ariana Strandburg-Peshkin. Disentangling influence over group speed and direction reveals multiple patterns of influence in moving meerkat groups. *Scientific Reports*, 12(1), 12 2022.
- [64] Dirk Bumann, Jens Krause, and Dan Rubenstein. Mortality risk of spatial positions in animal groups: the danger of being in the front. *Behaviour*, 134(13-14):1063–1076, 1997.
- [65] Hannah EA MacGregor and Christos C Ioannou. Collective motion diminishes, but variation between groups emerges, through time in fish shoals. *Royal Society Open Science*, 8(10):210655, 2021.
- [66] Andrew W Szopa-Comley, Callum Duffield, Indar W Ramnarine, and Christos C Ioannou. Predatory behaviour as a personality trait in a wild fish population. *Animal Behaviour*, 170:51–64, 2020.
- [67] James E Herbert-Read, Camille Buhl, Feng Hu, Ashley JW Ward, and David JT Sumpter. Initiation and spread of escape waves within animal groups. *Royal Society Open Science*, 2(4):140355, 2015.
- [68] Pawel Romanczuk, Iain D Couzin, and Lutz Schimansky-Geier. Collective motion due to individual escape and pursuit response. *Physical Review Letters*, 102(1):010602, 2009.
- [69] Vishweshha Guttal, Pawel Romanczuk, Stephen J Simpson, Gregory A Sword, and Iain D Couzin. Cannibalism can drive the evolution of behavioural phase polyphenism in locusts. *Ecology letters*, 15(10):1158–1166, 2012.
- [70] Daniel Strömbom and Catherine Futerma. An alignment-free explanation for collective predator evasion in moving animal groups. *Dynamics*, 3(4):793–802, 2023.
- [71] R Escobedo, V Lecheval, V Pappaspyros, F Bonnet, F Mondada, Clément Sire, and Guy Theraulaz. A data-driven method for reconstructing and modelling social interactions in moving animal groups. *Philosophical Transactions of the Royal Society B*, 375(1807):20190380, 2020.
- [72] Marco Dorigo, Guy Theraulaz, and Vito Trianni. Swarm robotics: Past, present, and future. *Proceedings of the IEEE*, 109(7):1152–1165, 2021.
- [73] Andrew J King, Steven J Portugal, Daniel Strömbom, Richard P Mann, José A Carrillo, Dante Kalise, Guido de Croon, Heather Barnett, Paul Scerri, Roderich Groß, et al. Biologically inspired herding of animal groups by robots. *Methods in Ecology and Evolution*, 14(2):478–486, 2023.
- [74] Marc-Olivier Killijian, Matthieu Roy, Gilles Trédan, and Christophe Zanon. Souk: social observation of human kinetics. In *Proceedings of the 2013 ACM International Joint Conference on Pervasive and Ubiquitous Computing*, pages 193–196, 2013.
- [75] Tamás Vicsek and Anna Zafeiris. Collective motion. *Physics Reports*, 517(3):71–140, 2012.
- [76] Li Jiang, Luca Giuggioli, Andrea Perna, Ramón Escobedo, Valentin Lecheval, Clément Sire, Zhangang Han, and Guy Theraulaz. Identifying influential neighbors in animal flocking. *PLoS Computational Biology*, 13(11):e1005822, 2017.
- [77] Robert C Hinz and Gonzalo G de Polavieja. Ontogeny of collective behavior reveals a simple attraction rule. *Proceedings of the National Academy of Sciences of the United States of America*, 114(9):2295–2300, 2017.
- [78] Jitesh Jhawar, Richard G Morris, UR Amith-Kumar, M Danny Raj, Tim Rogers, Harikrishnan Rajendran, and Vishweshha Guttal. Noise-induced schooling of fish. *Nature Physics*, 16(4):488–493, 2020.
- [79] Andreu Puy, Elisabet Gimeno, Jordi Torrents, Palina Bartashevich, M Carmen Miguel, Romualdo Pastor-Satorras, and Pawel Romanczuk. Selective social interactions and speed-induced leadership in schooling fish. *Proceedings of the National Academy of Sciences of the United States of America*, 121(18):e2309733121, 2024.
- [80] Hadrien-Matthieu Gascuel, Fernando Peruani, and Richard Bon. Identifying interaction neighbours in animal groups. *Animal Behaviour*, 174:97–104, 2021.
- [81] Vivek Jadhav, Vishweshha Guttal, and Danny Raj Masila. Randomness in the choice of neighbours promotes cohesion in mobile animal groups. *Royal Society Open Science*, 9(3):220124, 2022.

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**Code and data availability:** The codes for all the analyses and the computational model are available on the GitHub repository: <https://github.com/tee-lab/collective-responses-of-flocking-sheep-to-herding-dog.git>.

**Author contributions:** GT designed the experi-

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