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ARTICLE

A mathematical model of herding in horse-harem group

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Abstract
In animal groups, individual interactions achieve coordinated movements to maintain cohesion. In horse-harem groups, herding is a behaviour in which stallions chase mares from behind; it is considered to assist with group cohesiveness. The mechanisms of the group cohesion were studied using the methods of drone filming and video tracking during herding and two phases of interactions were found based on the mares' timing of movement initiation. The study shows that mares that move first are those nearest to the stallion; while the movement initiation of the later mares is determined by the distance from the nearest moving mare. Thus, as a second step to the full understanding of group cohesion, we propose a mathematical model of mares herded by a harem stallion, which is a modification of a sheep model during shepherding. Our model is a linear combination of the five components: inertia, repulsion from the stallion, short-range repulsion, synchronisation attraction, and attraction to the centre of the group. We tune the parameters of our proposed models based on the data and successfully reproduce the movements and directional trends of the mares.

Keywords Math model · Herding · Interaction of individuals · Movement · Horses

Introduction

Many species across the animal kingdom exhibit different forms of collective motions under various circumstances. Some maintain a cohesive group through subtle interactions among conspecifics (Ballerini et al. 2008; Nagy et al. 2010; Petit et al. 2009) and others perform group aggregation and evasion in the face of a threat to lower the risk of predation (Hamilton 1971; King et al. 2012; Strömbom et al. 2014).

To examine their strategies, animal groups have been tracked remotely with high spatial and temporal resolutions (Herbert-Read 2016) using advanced technologies such as GPS technology (Ákos et al. 2014; Nagy et al. 2010; Strandburg-Peshkin et al. 2015), imaging algorithms (Grünbaum et al. 2005; Lukeman et al. 2010; Yamanaka and Takeuchi 2018) and unmanned aerial vehicles (Christie et al. 2016; Inoue et al. 2018). For example, GPS devices attached to animals uncovered leader–follower relationships within the group during motion, that is, certain individuals within a group of pigeons contribute more to the decision-making during their flight; while others consistently copy movements (Nagy et al. 2010). In another example, roles in a group of pet dogs may change while out walking, but the relationships among conspecifics are stable in the long term (Ákos et al. 2014). In many other animal groups, leadership and decision-making are determined by the fitness of the group in mind (Fischhoff et al. 2007). In the cases where GPS devices are difficult or impossible to attach, computer vision has paved the way to track animal motion. Recording collective motion of surf scoters by still cameras enabled their overall dynamics to be inferred by creating a Newtonian model, where their motion was resolved into a sum of simple forces of interaction among individual animals (Lukeman et al. 2010).

The examples above considered the interactions among conspecifics in detail. Mechanisms involving group aggregation, however, have seldom been studied. An example is herding. In the case of a shepherd dog and sheep, herding involves the movement of the shepherd dog and the aggregation of a group of sheep with the intention to collect and move the group in a certain direction (Strömbom et al. 2014). While herding, different forces of interaction come into play, reflecting the dynamics of the movements of the sheep and the two crucial strategies employed by the dog to complete the task. This model heuristically explains the

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herding of sheep by a shepherd dog as a model comprising self-propelled particle with a constant speed. Although the strategies of the dog can be explained in the framework of reinforcement learning (Go et al. 2016), dogs may be trained by humans to perform the herding task (Rooney and Cowan 2011; Savalois et al. 2013; Greenebaum 2010). In the case of horses, a stallion chases mares to herd them (Krueger et al. 2014). Herding among horses is thought to be performed primarily by the stallion (Berger 1977; Feh 2005; Ransom and Cade 2009) for protection from other individuals/groups (Boyd and Keiper 2005; Waring 1983), for group cohesiveness with the aim of long-term social relationships with members of the group (Feh 2005), or to drive the group from a certain location for various reasons. Animals in the wild, like feral horses, naturally acquire the instinct to herd in the absence of human instruction, unlike many breeds of dogs, which are trained by humans (Rooney and Cowan 2011; Savalois et al. 2013; Greenebaum 2010). Herding is one event where movements of the mares and stallion are at the most dynamic stage. Individual-level interactions, such as herding, have implications related to group-level coordination and cohesiveness in socially stable animal groups (Ringhofer et al. 2017).

Several anecdotal accounts of the herding of horses are available. Many studies are qualitative in nature and describe the physical attributes of stallion behaviour while herding mares (Ginther et al. 2002). These reports include descriptions of the position of the ears or the general posture of the horse while performing tasks (Feh 2005; Ginther et al. 2002). In addition to these qualitative aspects of herding, a quantitative treatment is preferable to obtain an overall understanding of the behaviour.

With the commercialisation of unmanned aerial vehicles, or drones, tracking and analysing animals, endangered or otherwise, in restricted spaces or in the wild have been a growing trend (Inoue et al. 2018) in animal behaviour research. Coupled with tracking software (Brown and Cox 2009; Swierczek et al. 2011; Yamanaka and Takeuchi 2018; Yokoi et al. 2016), this relatively new method offers a non-invasive way to track and analyse animal groups discreetly in their natural habitat (Christie et al. 2016). Since ground observations may have a potential source of error (Bourjade et al. 2009), aerial observations using a drone are preferable for obtaining an unbiased view of absolute movements of the animals in question. In addition, horses live in vast open areas, which makes it possible to locate all their absolute positions from the air. Our previous work using drones, for example, succeeded in collecting movements of mares during a herding event of feral horses initiated by a stallion using drones (Ringhofer et al. 2019).

Our previous work (Ringhofer et al. 2019) examined inter-individual distances and timing of movement initiation, and qualitatively described their collective motions based on their reaction to their nearest moving individuals; however, it remains to be investigated how horses achieve coordination and cohesion during a herding event. To understand its mechanism, more intensive investigation incorporating attraction/repulsion models with various parameters is necessary. The previous results imply that the movement of mares can be explained by a zonal model such as a sheep model during shepherding (Strömbom et al. 2014) since zones are determined by the distances. Thus, we propose a quantitative model based on a heuristic model of herding of sheep by a shepherd dog (Strömbom et al. 2014), that is, the motion is a linear combination of various forces, with modification due to the differences in the properties of motion between sheep and mares.

Materials and methods

Subjects

The incidents of mare herding analysed in this work is the same as those in our previous work (Ringhofer et al. 2019). They were obtained by filming from a drone (Phantom 3 Advanced and Mavic Pro, DJI China) in Serra D'Arga, Portugal (8° 42′ N, 41° 48′ E). The feral horse habitat includes grass fields, shrubs, forest and shrub areas, where more than 210 individuals (excluding foals) live. Our focal group was a harem group comprising one stallion, five mares and one foal filmed in 2016 and one stallion, six mares (one newly joined), one filly (the foal of 2016, which grew) and two foals in 2017.

Data were taken during the breeding season (June–July) in 2016 and 2017. The focal group was recorded every 30 min using a drone, which took off approximately 10–30 m from the horses and flew at a height of about 75 m for 10–15 min until the battery was depleted, when the weather condition allowed. All mares were identified as well as the time points when herding began and ended. Observations lasted 6–9 h a day, and 3–10 flights of the drone were acquired per day for 30 days. Herding by a stallion occurs rarely and at a very short time. A total of 12 instances were observed over a period of 59 hours of video recording.

Length of time of herding varied from 3 to 23 s, with a mean herding time of 11.08 s and a standard deviation of 6.42 s. All instances of herding were manually identified from the high-resolution video. Herding began when the stallion lowered its head with its ears pinned to the back (Feh 2005; Ginther et al. 2002) and ended when its head returned its normal position. All movements of the stallion and the mares were tracked and analysed only during instances of herding. In this study, we focused on the stallion and the mares that were regular members of the harem group and were involved in group social interactions.

Image processing

A total of 12 instances of herding were recorded among the video clips. To reduce the effects of drone movements such as rotation and tilting due to wind and other factors, the videos were preprocessed for stabilisation using the Warp Stabilizer function in Adobe Premiere Pro. The resulting stabilised videos had a frame rate of 30 frames per second.

After the preprocessing, each of the mares in the video was tracked frame by frame using Tracker (Brown and Cox 2009), a free video-analysis software built on the Java framework. Two additional stationary objects on the ground (rocks) were also tracked to ensure no further rotation or tilting remained. Any such drone movements were mathematically corrected using rotation matrices.

Differences in drone heights during video recording and the movement of the herd from one point to another result in videos shot in different locations. While analysing the videos, we have set the point of origin to be the lowest left pixel. All mare motions are relative to this point of origin, and differences in coordinates from video to video should not pose any problem. Tracker then gave the x and y coordinates of individual mares, where the scales of videos with different heights were normalised with the stallion's body length (BL) in each video as the standard unit. As we do not know the exact body length measurements of the mares and the stallion, the body length of the stallion is chosen as the reference measurement, which is constant through all observations. The body length of the stallion is measured from the withers to just before the tail. All succeeding quantities, like distances travelled, are measured according to the body length of the stallion.

Finally, the tracked positions of the individual mares were postprocessed as below using MatLab (release R2017b). To smoothen the data and reduce the effects of noise from the measurements, data was filtered using a Butterworth filter with order 2 and a sampling frequency of 30 Hz (Fig. 1). Thus, in the succeeding parts of this paper, one timestep is equivalent to one-thirtieth (1/30) of a second. The filtered data were used to calculate various characteristics of horse movements such as the speed and orientation.

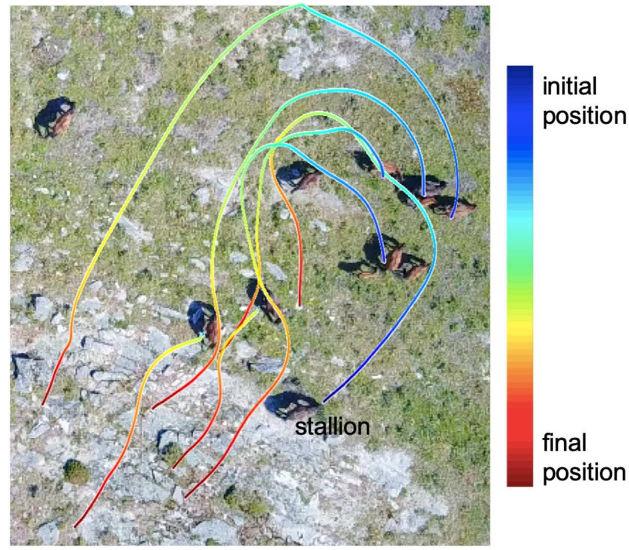

Fig. 1 Extracted trajectories of the harem during a herding instance superimposed on a drone video screen shot. Starting points of the trajectories coincide with the initial positions of the stallion or mare. Herding lasted for 23 s for this instance

Model

Our model for feral mares during herding by a stallion is based on the model for sheep during shepherding by a shepherd dog (Strömbom et al. 2014), where the sheep model assumes a constant speed and the direction of motion is determined by a linear combination of the following components: inertia, a repulsive force from the shepherd dog, a short-range repulsive force, an attractive force to the centre of the group (centre of mass, COM) and a random noise. Different from a sheep, however, a mare moves with a variable speed (Fig. 2) and hence, our model directly expresses this variation of speed. By adding another component, our model is a linear combination of the following components: inertia, repulsion from the stallion, short-range repulsion, medium-range attraction, synchronisation attraction, and attraction to the COM.

Zonal models have been used in various modelling studies (Couzin et al. 2002, 2005; Huth and Wissel 1992; Lukeman et al. 2010) to describe a region in space where interactions take place with a target individual. With horses having a field of vision of nearly 360 degrees (Brooks and Matthews 2005), zonal models seem to be an appropriate choice to describe the interactions with a target horse as there is almost no blind spot. Our choice of zones and forces of interactions reflect the results of concurrent studies where synchronisation of movements among mares occurs (Ringhofer et al. 2019).

Note that the random-noise component was omitted since the trajectories of horses were sufficiently smooth. In addition, all the components were normalised to allow our coefficients to be bounded and compared reasonably.

We let M_i be the position of mare i and S be the position of the stallion, from which the following forces are calculated.

Inertia

An inertial force H_i is introduced since a mare tends to move in its previous direction.

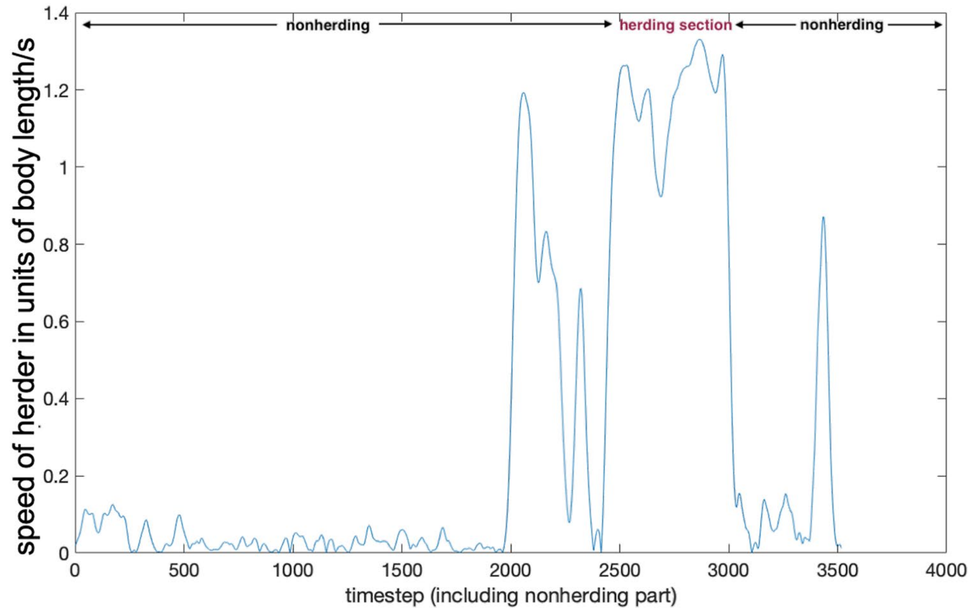

Fig. 2 An example of variable speed of a mare during herding

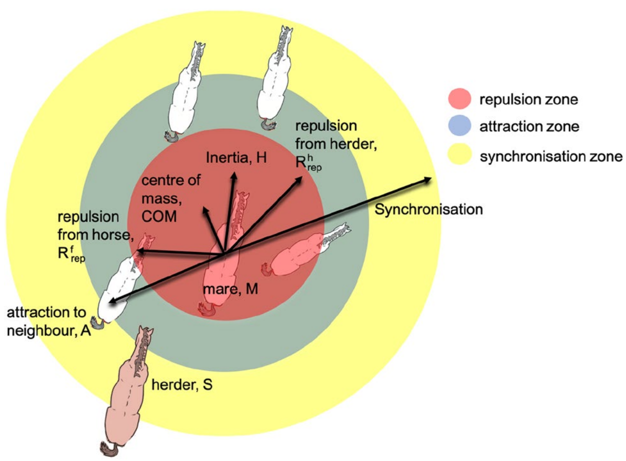

Fig. 3 Schematic diagram of the zones and forces of interaction experienced by a mare while being herded by a stallion

Repulsion from the stallion

When a mare is within a certain distance d_{rep} from the stallion, she experiences a force of repulsion directed away from the stallion, $R^h_{i,\text{rep}} = S - M_i$.

Short-range repulsion

A mare experiences a force of repulsion from other mares when they are within the repulsion zone, $R^f_{i,\text{rep}} = \frac{1}{n_{\text{rep}}} \sum_{j=1}^{n_{\text{rep}}} \frac{M_i - M_j}{|M_i - M_j|}$, where n_{rep} is the number of mares within the zone (Fig. 3). This means that a mare tends to retain an exclusive zone around her (Lukeman et al. 2010).

Medium-range attraction

A mare experiences a force of attraction from other mares when they are within the attraction zone, $A_{i,\text{att}} = \frac{1}{n_{\text{att}}} \sum_{j=1}^{n_{\text{att}}} \frac{M_j - M_i}{|M_j - M_i|}$, where n_{att} is the number of mares within the zone (Fig. 3). This means that an individual likes to match its direction to her specific zone (Lukeman et al. 2010).

Synchronisation attraction

A mare matches her direction with the nearest moving mare within a set region (Fig. 3). This means that a moving mare may be escaping from a danger (Lukeman et al. 2010).

Attraction to the COM

Mares experience a force of attraction towards the group's COM, $C_i = \text{COM} - M_i$, since divergent positions increase the risk of predation.

Parameter estimation

For simplicity, we denote the x and y components of the forces enumerated above at each timestep, $T = 1, 2, \cdots t$, as $F^{(T)}_{x1}, F^{(T)}_{y1}, \ldots, F^{(T)}_{x6}, F^{(T)}_{y6}$. Likewise, the corresponding x and y components of the velocity of each mare at timestep T is given by $v^{(T)}_x, v^{(T)}_y$. Our model can be written as a linear combination of forces of the form

$$c_1 \left[F^{(T)}_{x1}, F^{(T)}_{y1}\right] + \cdots + c_6 \left[F^{(T)}_{x6}, F^{(T)}_{y6}\right] = \left[v^{(T)}_x, v^{(T)}_y\right], \quad (1)$$

or

$$\begin{bmatrix} F_{x1}^{(1)}, & F_{x2}^{(1)}, & \cdots, & F_{x6}^{(1)} \\ F_{y1}^{(1)}, & F_{y2}^{(1)}, & \cdots, & F_{y6}^{(1)} \\ & \vdots, & \ddots & \\ F_{x1}^{(t)}, & F_{x2}^{(t)}, & \cdots, & F_{x6}^{(t)} \\ F_{y1}^{(t)}, & F_{y2}^{(t)} & \cdots, & F_{y6}^{(t)} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \\ \vdots \\ c_6 \end{bmatrix} = \begin{bmatrix} v_x^{(1)} \\ v_y^{(1)} \\ \vdots \\ v_x^{(t)} \\ v_y^{(t)} \end{bmatrix}, \tag{2}$$

or simply $\mathbf{Fc} = \mathbf{v}$. $\mathbf{F}$ comprises the components of the interaction, namely, F_{x1}^t and F_{y1}^t refer to the x and y components of the force of inertia. F_{x2}^t, F_{y2}^t correspond to the force of repulsion from the herder, F_{x3}^t, F_{y3}^t are to the short-range repulsion from neighbours, F_{x4}^t, F_{y4}^t correspond to the medium-range attraction to neighbours, F_{x5}^t, F_{y5}^t are to synchronisation attraction, and finally F_{x6}^t, F_{y6}^t correspond to the force of attraction towards the centre of mass.

The coefficients $\mathbf{c} = [c_1, c_2, c_3, c_4, c_5, c_6]$ correspond to the parameters of the enumerated forces above, respectively. Finally, $\mathbf{v}$ comprises the velocities of the individual mares.

The coefficients should be estimated from the observed data. To do this, the coefficients $\mathbf{c}$ were chosen so that we minimised the sum of the squared difference between the model, $\mathbf{Fc}$, and the measurements, $\mathbf{v}$, subject to the condition that the coefficients are non-negative. Mathematically, we can express this as

$$\underset{\mathbf{c}}{\operatorname{argmin}} \, ||\mathbf{Fc} - \mathbf{v}||_2, \quad \text{subject to} \quad \mathbf{c} \geq \mathbf{0}. \tag{3}$$

Note that only moving horses were considered in the estimation of the coefficients.

The coefficients of the components were estimated using the data and the trajectories reproduced by the model were compared with the observed trajectories. For the estimation of coefficients, two cases were considered: in the first case, each mare in each herding instance has a specific coefficient set; in the second case, each mare has the same coefficient set in all herding instances, which is called the shared coefficients in the following.

The other parameters of our model were heuristically identified from the data sets as follows: The radius of repulsion is based on the mean distances of the mares to the group's centre of mass during the herding event. This gives us an idea of the spacing among individual mares. During herding, it is observed that the spatial distribution of the mares tend to be more compact, but still keep a certain distance from each other during the motion. For this region, we assign 4 BL. The region of synchronisation, on the other hand, was chosen by computing the distance between the two farthest mares in motion with the same heading. For this region, we assigned a value of 10 BL. Finally, the value for the region of attraction is chosen arbitrarily to be the midpoint of the two mentioned regions above. Here, we assign 7 BL. Finally, the herder detection distance, d_{rep}, is the distance between the herder and the mare when the mare begins to move. Comparing all herding events we have, we heuristically chose 9 BL, the maximum among these observed distances to represent this parameter.

Videos were carefully observed using the Tracker software, and distances among mares were measured. For example, when mares appear to have diverged from each other during a herding instance, the values were noted and were considered to be part of the zone of repulsion.

Evaluation

The trajectories reproduced using the model were evaluated in terms of the root-mean-square error,

$$\text{RMSE} = \sqrt{\sum_t \left(\hat{M}_i(t) - M_i(t)\right)^2}, \tag{4}$$

where $\hat{M}_i(t)$ is the predicted position of mare i at time t and t runs the times during each herding.

Results

Properties of data

By applying the image processing in Sect. 2.1 to our data, we obtained 12 sequences of herding.

The initial spatial distributions of mares varied widely, for example, the most compact initial spatial distribution had a mean pairwise distance of 3.671 BL with a standard deviation (SD) of 1.175 BL; while the most disperse initial spatial distribution had a mean pairwise distance of 31.779 BL with an SD of 13.075 BL. The length of the sequences were between 4.67 and 23.3 s, with an average of 14.48 s with an SD of 6.82 s. In the following sections, we label the individual mares observed both in 2016 and 2017 to be mares 1–5; while, the mare only observed in 2017 to be mare 6.

Model with specific coefficients

When the coefficients were calculated for each mare in each herding instance, the RMSEs of the model obtained from the observed data were almost within 2 BL (Fig. 4).

These RMSEs were sufficiently small to reproduce the observed data (Fig. 5).

The average RMSE in this model was 0.90 BL with an SD of 0.81 BL.

Model with shared coefficients

When the coefficients were calculated for each mare in all herding instances, the RMSEs of the model obtained from

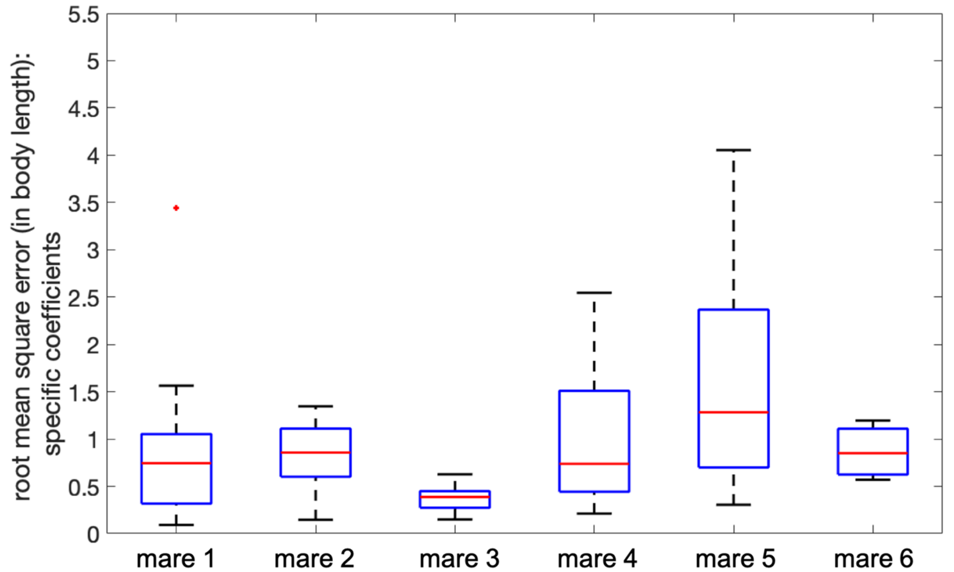

Fig. 4 Distribution of the RMSE for each mare using specific coefficients

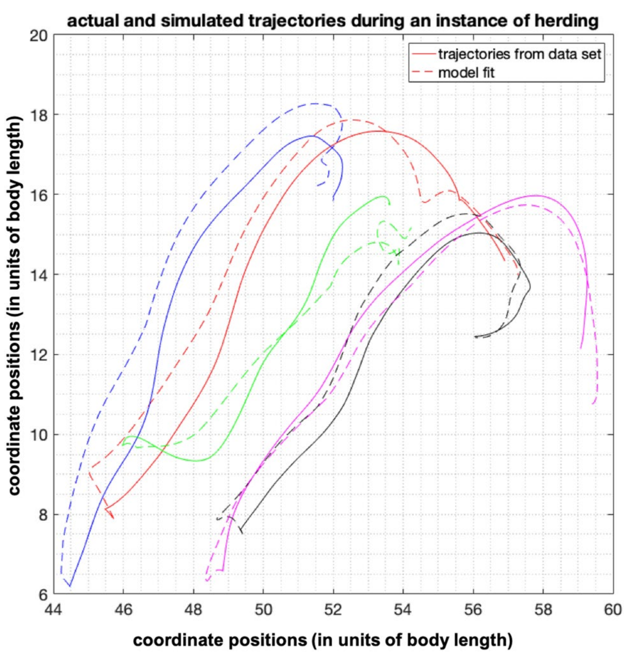

Fig. 5 Comparison of actual mare trajectories with the best-fit model using specific coefficients

the observed data were much larger than those of the first model (Fig. 6).

The second model had a larger mean of 1.68 BL and an SD of 1.04 BL. Although these RMSEs were larger than those of the first model, their trajectories were of similar shapes to the observed data (Fig. 7).

To confirm the similarity of the trajectories, we calculated the directional error at each time t, defined as

$$1 - \frac{\mathbf{v}_m \cdot \mathbf{v}_d}{|\mathbf{v}_m||\mathbf{v}_d|}, \tag{5}$$

where $\mathbf{v}_m$ and $\mathbf{v}_d$ are the velocity vectors of each mare in the model and actual trajectories, respectively. As a result, the directional errors of the mares were sufficiently small almost everywhere (Fig. 8) and the average error over all moving mares across all herding instances was 0.031.

Comparison between the two models

We introduced two ways of estimating the coefficients, specific coefficients and shared coefficients. To determine which is better, we examined their distribution by visualisation using principal component analysis (PCA). We found that the coefficient vectors of the mares have a large variation, implying that the model overfits the observed data if it has specific coefficients (Fig. 9).

To examine variation in coefficients of the mares, we compared their coefficient vectors (Table 1), which appeared to be widely distributed. This wide distribution was confirmed by the hierarchical clustering of the coefficient vectors plotted in a dendrogram (Fig. 10). We see very varied coefficients among the individual mares which highlights the different forces of interactions happening during a herding event. Another possibility is that these coefficients may indicate forms of relationships among individuals within the harem such as siblings. This may also suggest dominance, friendship, or relative location among mares when responding to the herding by the stallion.

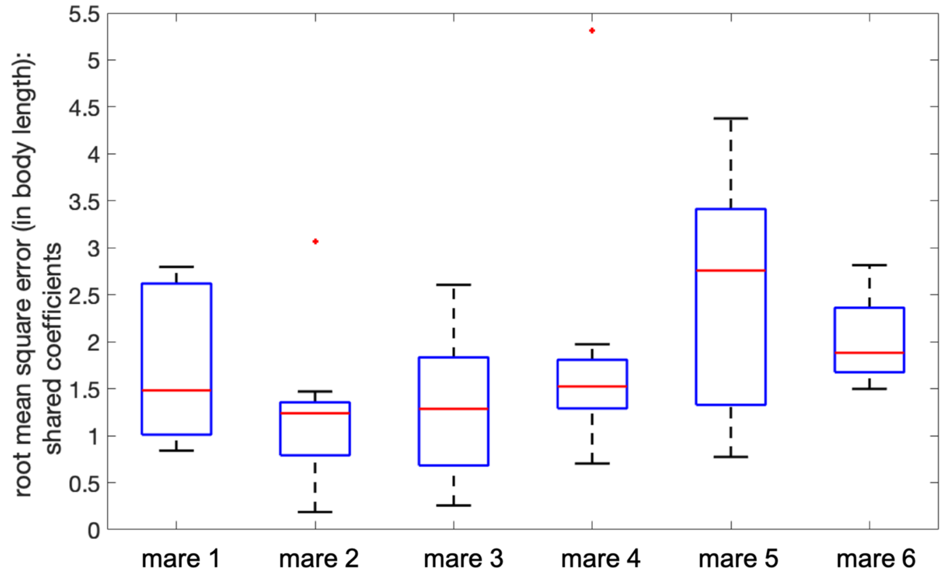

Fig. 6 Distribution of the RMSE for each mare using shared coefficients for one mare

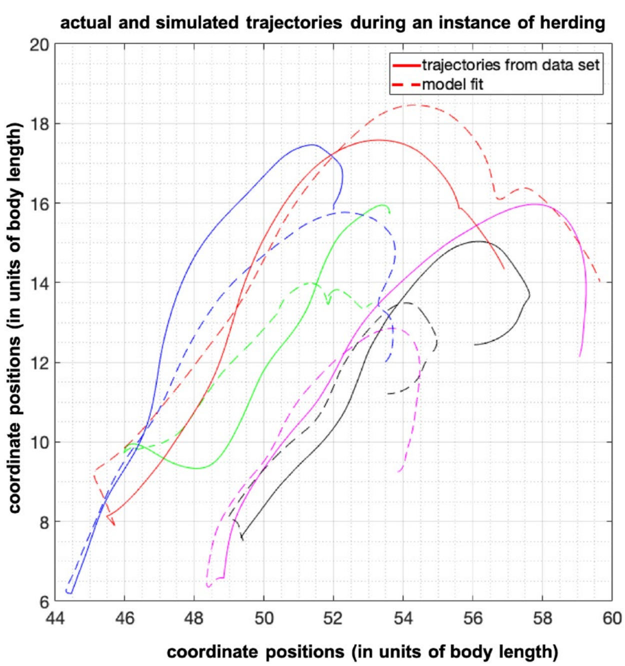

Fig. 7 Comparison of actual mare trajectories with the model using shared coefficients for each mare across herding instances

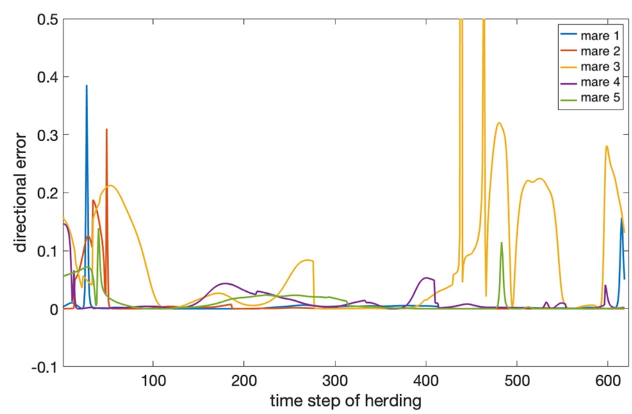

Fig. 8 Directional errors in one herding instance

Simplification of the model

Our model consists of six components based on the previous models in (Lukeman et al. 2010; Strömbom et al. 2014; Couzin et al. 2002), which is consistent with the previous findings (Krueger et al. 2014). However, the medium-range attraction took values of zero for four mares and less than 0.03 for the other two mares. Furthermore, coefficients of the synchronisation attraction are relatively low compared to other forces of interaction. Since each component is normalised, the values express the contribution to the movement, and that both medium-range attraction and synchronisation provide little effect on the movement. This suggests that both medium-range attraction and synchronisation attraction are redundant; in other words, they can be removed from the model. To confirm this hypothesis, we modified our model by removing these forces and calculated the root mean square error (RMSE) of the simplified model (Fig. 11). As a result, the RMSE was still 1.69 BL with a standard deviation of 1.02 BL. Thus, we can ignore the both medium-range attraction and synchronisation forces. The resulting coefficients of the corresponding forces are presented in Table 2, and they understandably similar to the values presented in Table 1.

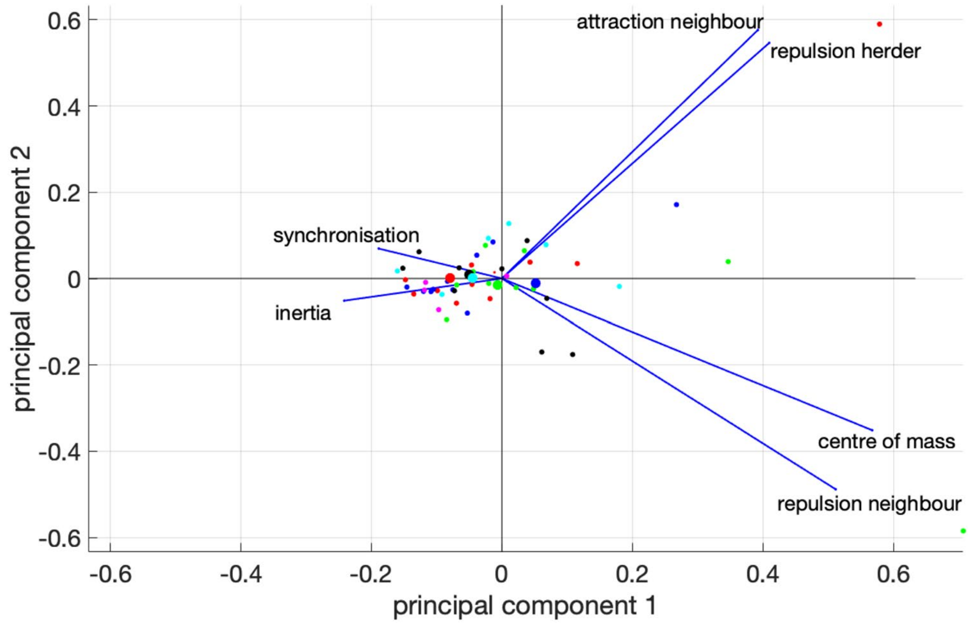

Fig. 9 Distribution of estimated coefficient vectors after PCA. Small circles show specific coefficients and large circles show shared coefficients. Each colour indicates a different individual

Table 1 Coefficients of the forces obtained using six-component model with shared coefficients

Horse identity	Inertia, c_1	Repulsion from herder, c_2	Short-range repulsion, c_3	Medium-range attraction, c_4	Synchronisation attraction, c_5	Attraction to COM, c_6
1	0.600	0.009	0	0	0.134	0.051
2	0.499	0.183	0.033	0	0.083	0.036
3	0.353	0.399	0.204	0.024	0.015	0.592
4	0.595	0.359	0.230	0	0.125	0.423
5	0.912	0.399	0.037	0	0	0.287
6	0.677	0.272	0	0.027	0	0.298

Discussion

In this study, we proposed a mathematical model to explain the motion of mares as a response to a herding stallion. The model is a linear combination of six components based on the previous models in (Lukeman et al. 2010; Strömbom et al. 2014; Couzin et al. 2002) and modified so that the velocity is not constant. The coefficients of the six components were calculated by non-negative least-squares optimisation from the observed data in two ways. The coefficients in the first way were calculated for each individual in each herding instance, and those in the second way were calculated for each individual in all herding instances. As a result, the model with specific coefficients reproduced the observed trajectories more closely than the model with shared coefficients.

Our current study has considered only a relatively small harem of horses in their natural habitat during the stallion's herding. This means that the forces of interactions are among individuals at a local level and that the group movements initiated by others such as the stallion in a different group, mares and fillies are not analysed here. Our model may work even for such movements in a local level. In a group level or in the case when a far greater number of horses are in the same area, horses are self-organised through interaction and make a hierarchical structure, where a leader–follower relationship appears even among harems and zone effects among individuals are important (Ozogány and Vicsek 2015; Ferdinandy et al. 2017). We will extend our model to such cases in the future.

Our mare model is based on the sheep model of shepherding and consists of several forces with coefficients and zones (Strömbom et al. 2014). The difference from the original model is the usage of a variable speed and parameters such as coefficients and zone sizes.

Our current work deals with a stallion herding mares within the same species. We have drawn similarities to from intra-species herding behaviour specifically in the case of dog driving sheep to a target. This suggests that the model can be extended to other species.

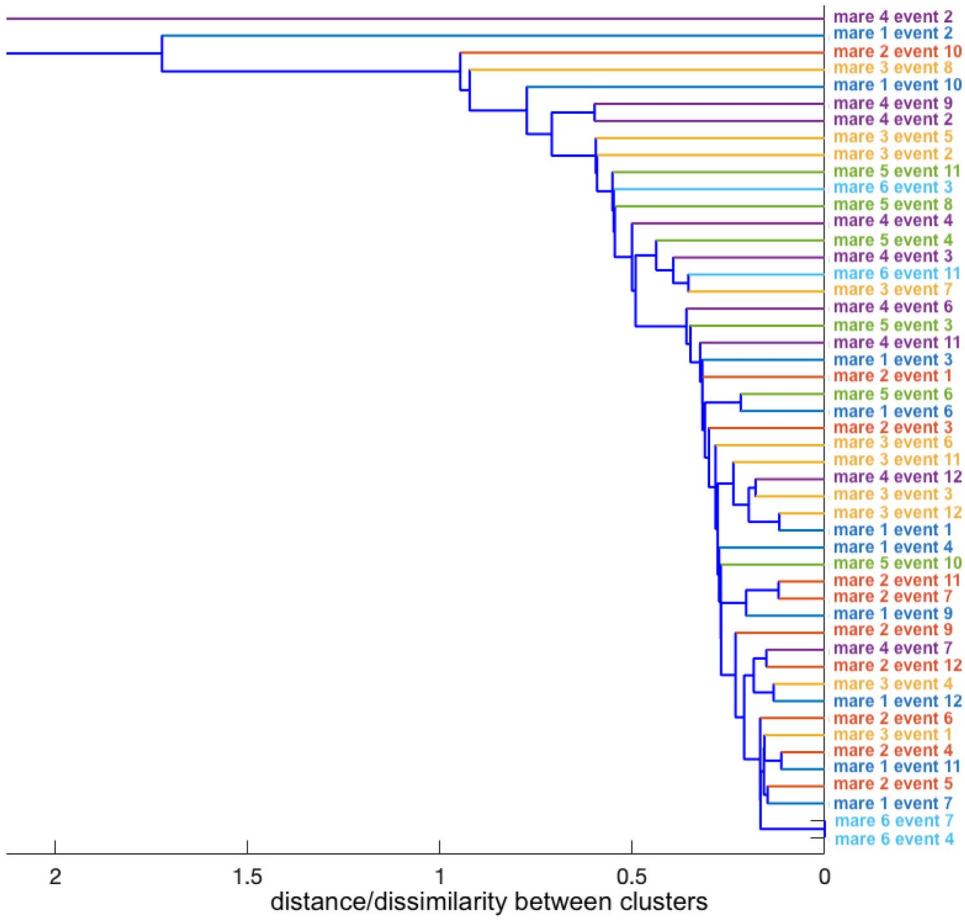

Fig. 10 Hierarchical clustering of mares based on the specific coefficient model

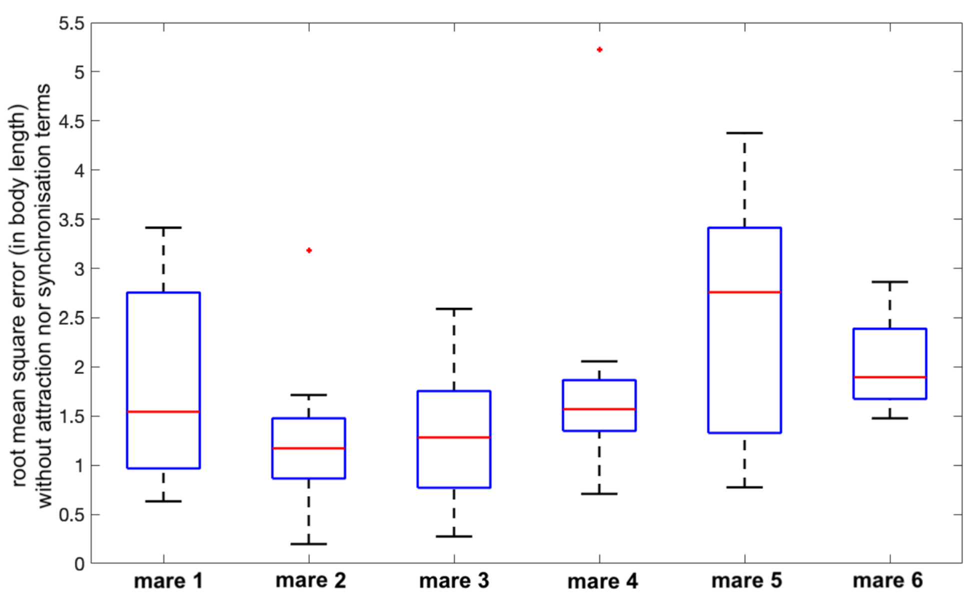

Fig. 11 Distribution of errors when both the attraction and synchronisation terms are removed

In fact, a classical model for a homogeneous group called BOID (bird-oid object) also introduced similar forces to explain a flock of birds, that is, separation, alignment and cohesion (Reynolds 1987).

In this model, the zones (Ferdinandy et al. 2017) are critical for distance-dependent interactions. The zones induce our previous finding in (Ringhofer et al. 2017) that the mares that move first are those nearest to the stallion

Table 2 Coefficients of the forces obtained using four-component model with shared coefficients

Horse identity	Inertia, c_1	Repulsion from herder, c_2	Short-range repulsion, c_3	Attraction to COM, c_6
1	0.600	0.029	0	0.058
2	0.510	0.193	0.030	0.037
3	0.355	0.403	0.209	0.620
4	0.608	0.365	0.205	0.426
5	0.912	0.398	0.037	0.287
6	0.675	0.281	0	0.330

and the rest are initiated by the moving mares, not the stallion.

Leader–follower relationship is affected by not only spatial factors but also social factors that are different individually (Syme and Syme 1975; Squires and Daws 1975; Herbert-Read 2016). Our models (both specific and shared coefficients) are made up of coefficients with a degree of variability which may be attributed to differences in the responses of the mares during the herding activity. These may include different mares being targeted for herding or differences in the order of movement (Ringhofer et al. 2017; Bourjade et al. 2009). Since our model with shared coefficients reproduced only the trends of the observed trajectories, we need to investigate more data into the future.

Conclusion

To understand the mechanism of the collective motions of mares during a herding event by a stallion, especially, how the effects of inter-individual distances and timing of movement initiation found in (Ringhofer et al. 2017) appear, we proposed a mathematical model that describes their inter-individual interactions by four components with zonal effects: inertia, repulsion from the stallion, short-range repulsion, and attraction to the COM. This is a modification of the previous models in (Lukeman et al. 2010; Strömbom et al. 2014; Couzin et al. 2002) so that it allows a variable velocity. The model quantitatively reproduced the observed trajectories under the assumption that each mare in each herding instance has a specific coefficient set for the components. We also reproduced the trajectories under the assumption that each mare has the same coefficient set in all herding instances. We found that the first model is superior in that it was able to reproduce the trajectories with less deviation from the data. The second model is still able to capture the trends of the motions of the mares, but with greater root mean square error compared to the previous.

Our coefficients analysis in both models suggests differences in the movements of the mares may be due to the differences in the spatial and social factors of the individuals during the event.

We acknowledge that the model still has errors in the scale and should be improved. In addition, the motion of the stallion was obtained from the observation in this study and may be modelled as a function of the mare positions. These are open issues for future study. Nonetheless, the present study provides a strong tool for understanding the collective behaviour of a group of animals from the point of view individual interactions.

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Compliance with ethical standards

Conflict of interest The authors declared that they have no competing interests.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. The field observations complied with the guidelines for animal studies in the wild issued by the Wildlife Research Center of Kyoto University, Japan.

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