ARTICLE

Herding mechanisms to maintain the cohesion of a harem group: two interaction phases during herding

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Abstract

In animal groups, individual interactions achieve coordinated movements to maintain cohesion. In horse harem groups, herding is a behavior in which males chase females from behind; it is considered to assist with group cohesiveness. However, the mechanisms by which the individuals move to maintain group cohesion are unknown. We applied novel non-invasive methods of drone filming and video tracking to observe horse movements in the field with high temporal and spatial resolution. We tracked all group members and drew trajectories. We analyzed the movements of females and found two phases of interactions based on their timing of movement initiation. The females that moved first were those nearest to the herding male, while the movement initiation of the later females was determined by the distance from the nearest moving female, not by the distance from the herding male. These interactions are unique among animal group movements and might represent a herding mechanism responsible for maintaining group cohesion. This might be due to long-term stable relationships within a harem group and strong social bonds between females. This study showed that the combination of drone filming and video tracking is a useful method for analyzing the movements of animals simultaneously in high resolution.

Keywords Drone · Video tracking · Herding · Interaction of individuals · Movement · Horses

Introduction

In animal groups, member behavior is coordinated between individuals of the same species to escape threats, access resources, and maintain cohesion. The global positioning system (GPS) tracking and video tracking software enable the plotting of individual positions and analysis of individual behaviors during group movement at a high spatial–temporal resolution (see Herbert-Read 2016 for a review). This allows for an in-depth assessment of individual interactions and

behavioral mechanisms of group movements. However, most previous studies were conducted in laboratory settings and not in the natural environment of the organisms being studied (see Herbert-Read 2016; Strandburg-Peshkin et al. 2018 for reviews). While GPS is the most common method used for tracking individual movements in the wild, it requires capturing individuals for affixing loggers or sensors. Video filming using drones (unmanned aerial system) is gaining attention as a method that is relatively less invasive and less expensive, but is sufficiently accurate, for recording animal behavior (Christie et al. 2016; Inoue et al. 2018). This method allows data collection from animals without physically contacting them for affixing loggers and/or collars, thus representing a method suitable for video recording a large number of individuals simultaneously in the wild without the need to capture them. Recently, Torney et al. (2018) filmed groups of caribous using drones, and demonstrated that they were able to track individuals within the groups and investigate their interactions during migration, using the object tracking software. To the best of our knowledge, this is the only study to have applied these new video filming methods for analyzing the interactions of individuals during

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group movement in the wild. In this study, we applied these new methods, which combine video filming using drones and video tracking software to track individuals and investigate group movement of feral horses (*Equus caballus*).

Feral horses form long-term socially stable harem groups that are not common in many other ungulates, except plains zebra (*E. quagga*), mountain zebra (*E. zebra*), and Asiatic wild ass (*E. hemionus*) (Klingel 1974), and forest buffalo (*Syncerus caffer nanus*) (Melletti et al. 2007). These harem groups are composed of either one or a few males with multiple unrelated females and their immature offspring, and the females are considered to form strong social bonds between each other (Rubenstein 1994; Cameron et al. 2009; Stanley et al. 2018). We focused on individual movements during the herding behavior of the male, where the male chases the females from behind, which is considered to maintain group cohesion (Fig. 1; Feh 2005). However, the mechanism by which the movements of individuals maintain group cohesion is unknown, and the movement of horse groups during herding is different from their normal movements (Krueger et al. 2014; Bourjade et al. 2015). It is also unusual compared to the movements of other animal groups. The male initiation of movement from behind in horses contrasts the interactions found in birds or fishes (Lukeman et al. 2010; Nagy et al. 2010; Herbert-Read et al. 2011; Katz et al. 2011), where the leader at the front initiates the movement of followers.

Female–male interactions during such movements are similar to interspecific interactions, such as sheep–sheepdog or predator–prey interactions (Muro et al. 2011; Strömbom et al. 2014), which invoke the roles of chaser and escaper; however, a male horse is not a predator of a female horse. In addition, individuals in horse harem groups have long-term stable social relationships, unlike most animal species that have been observed in previous group movement studies

Fig. 1 Herding by a male horse. A male horse chases a female horse with his ears pressed back flat and his head lowered close to the ground. © Shinya Yamamoto

with high temporal and spatial resolution (Lukeman et al. 2010; Nagy et al. 2010; Sárová et al. 2010; Herbert-Read et al. 2011; Katz et al. 2011). Thus, the group movement in horse herding might differ from the movements of other animals observed in previous studies. Studying the group movement of horses during herding might provide us with new insights into the movements of animal groups.

As the first step towards analyzing the movement of a horse group during herding, we tracked individual movements, combining video filming using drones and video tracking software, and investigated male–female and female–female interactions to determine the mechanisms that maintain group cohesion. We determined which individuals within the group affected the movement initiation of females, considering the distance between individuals calculated by their two-dimensional coordinates tracked by the video tracking software.

Materials and methods

Study area and data collection

Serra d'Arga, an 825-m high mountain in northern Portugal (8° 42′ N, 41° 48′ E), includes a grassy field, rocky ground, forest, and shrub areas within an area of 4493 ha (see Matsuzawa 2017 and Ringhofer et al. 2017 for details). We observed a harem group in 2016 and 2017, within approximately 24 identified harem groups including more than 210 individuals (excluding foals). This focal harem group comprised one male, five females, and one foal in 2016, and one male, six females (one newly joined), one sub-adult female (the foal of 2016, which grew), and two foals in 2017. All individuals in this harem group were identified and named. Data were collected during the breeding and birth season in June and July of 2016 and 2017. The harem group was recorded every 30 min using drones (Phantom 3 Advanced and Mavic Pro, DJI China) taking off at a distance of approximately 10–30 m from the horses and flying at an altitude of 75 m for 10–15 min until battery depletion. We recorded the positions of each identified individual and noted time points when herding occurred. Observations lasted for 6–9 h a day and 3–10 flights were acquired daily for 30 days. A total of 59 h of video footage was recorded.

Data analysis

We recorded 13 herding behavior events, with sufficient duration for analysis in 10 of the 13 events (Table S1). The pre-processing of the videos for stabilization was performed using Adobe Premiere Pro, with a resulting frame rate of 30 fps (details in electronic supplementary material). The identified individuals were tracked using Tracker (Tracker 5.0.3 21, https

://www.physlets.org/tracker). We focused on the adult male and females who were the regular members of the harem group and were involved in group social interactions. The male body length (BL), from the base of the tail to the base of the neck, was used as the unit of length across all videos. The reason for not using the nose-to-tail length as BL was that the head orientation varied depending on the posture of the horses, and the length from the nose to the tail changed accordingly. However, the distance from the base of the neck to the base of the tail was relatively constant and always straight even the head orientation changed, when viewed from above via the drone. The drone's ground height varied because of the difference in ground tilt, and the scale of the images was different in each video file (i.e., the length of a pixel represented a different absolute length in the real environment), because no standard object of known size could be placed in the images. In addition, we do not know the exact body length of the horses. Thus, we used BL as a unit of length, which was supposed to be constant during the observation. Using these measurements, we tracked the movements of the male and target females frame-by-frame during the herding events. As some female group members were far from the male and did not react to herding, we categorized the females as target and non-target females. The target females were defined as foraging individuals that began to move after the male initiated herding and continued in front of the male throughout the herding event. This was because herding was mostly observed when the females were foraging, and in few situations, when the females were already moving before the initiation of herding by the male, it was impossible to clearly identify whether the movement was caused only by herding. Herding initiation was defined as an event when the male assumed the posture of herding, with a lowered neck during approach to the females. Herding end was defined as an event when the male raised his neck or began foraging. The tracked positions of individuals in two-dimensional coordinates were analyzed in Matlab (MATLAB R2017b) to draw trajectories.

For statistical analysis of the influence of the herding male and other moving females on the movement initiation of target females, R (R × 64 3.5.0, https://www.Rproject.org) was used. A generalized linear mixed model (GLMM) was used with the binomial error structure (when the target females moved, it was scored as 1, and when they did not move, it was scored as 0) and logit link function, including the distance from the herding male and the distance from the nearest moving female as fixed effects and the identity of the horse as a random effect to conduct a likelihood ratio test. The distance between individuals was calculated using their two-dimensional coordinates as follows:

The time point when a target female began to move (take a step forward) and continued moving throughout herding was defined as the starting point of the movement of a female.

Results

We tracked the trajectories of the male and target females in 10 herding events (Fig. 2, See supplementary video for an example of a herding event). During herding events, the target females did not start to move simultaneously, but instead started to move in sequence. The first females started to move 2.79 ± 1.34 s (mean $\pm$ SE, $n = 10$) after the male initiated herding, the second females started to move 1.69 ± 0.46 s ($n = 8$) after the first females, the third females started to move 2.05 ± 0.76 s ($n = 4$) after the second females, the fourth females started to move 0.27 ± 0.10 s ($n = 3$) after the third females, and the fifth females started to move 5.47 ± 1.99 s ($n = 3$) after the fourth females.

When we analyzed the influence of the herding male and other moving females on the movement initiation of the target females, the females that moved first after herding initiation were those nearest to the herding male (Fig. 3). The first females started to move when the herding male approached at a distance of 7.96 ± 0.95 BL (mean $\pm$ SE, $n = 10$). The movement initiation of the second and subsequent females was determined by the distance from the nearest moving female, rather than by the distance from the herding male (GLMM with binomial error structure and logit link function, conducted with likelihood ratio test: $Z = 1.000$, $P = 0.313$ for the distance from the herding male, and $Z = -2.464$, $P = 0.003$ for the distance from the moving female, $n = 37$; Table 1). In addition, in six specific cases, the females did not start to move even when the herding male was closer to them than the moving females; however, these females started to move later, when the moving females approached within a certain distance. The second and subsequent females started to move when the moving females approached at a distance of 4.28 ± 0.63 BL.

Discussion

Our study tracked the movements of individuals in a harem group of horses using drone filming and video tracking. In this study, we showed that a combination of these methods
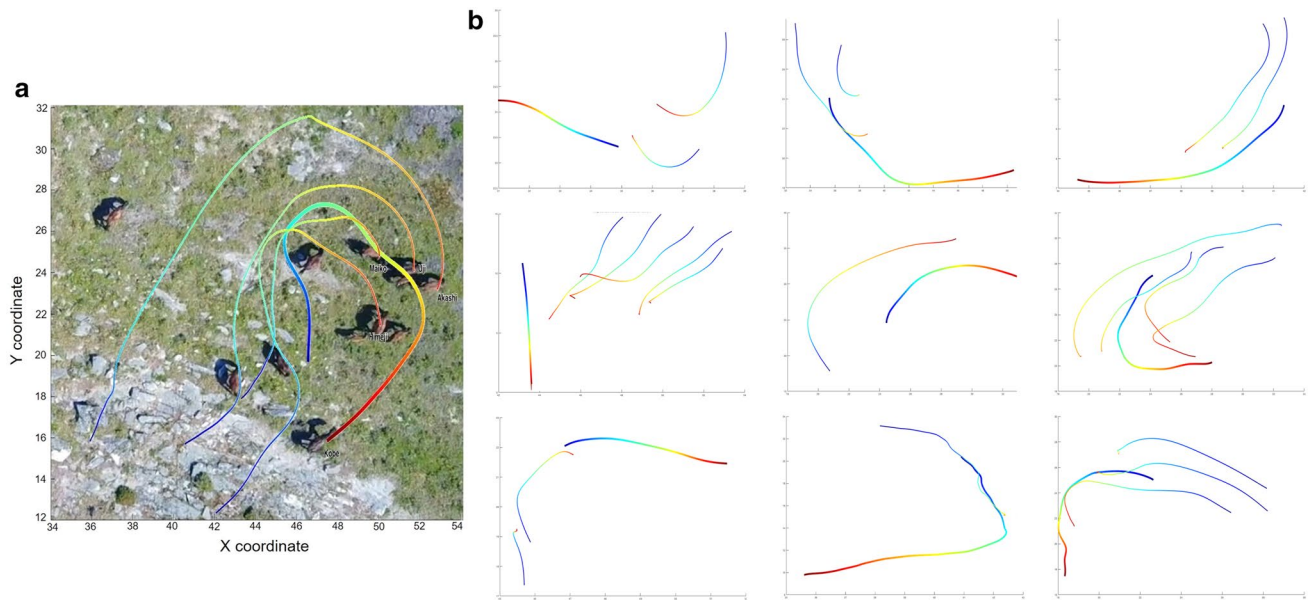
$$\text{Distance between } A \text{ and } B = \sqrt{\left((x \text{ coordinate of } A - x \text{ coordinate of } B)^2 + (y \text{ coordinate of } A - y \text{ coordinate of } B)^2\right)}.$$

Fig. 2 **a** View from the camera of the drone, showing trajectories of the male and target females during one herding event. **b** Trajectories of the male and target females in all herding events. The trajectory of the male is represented using a thick line. Color change indicates the course of time. The starting and ending points of the movement are shown in red and blue, respectively
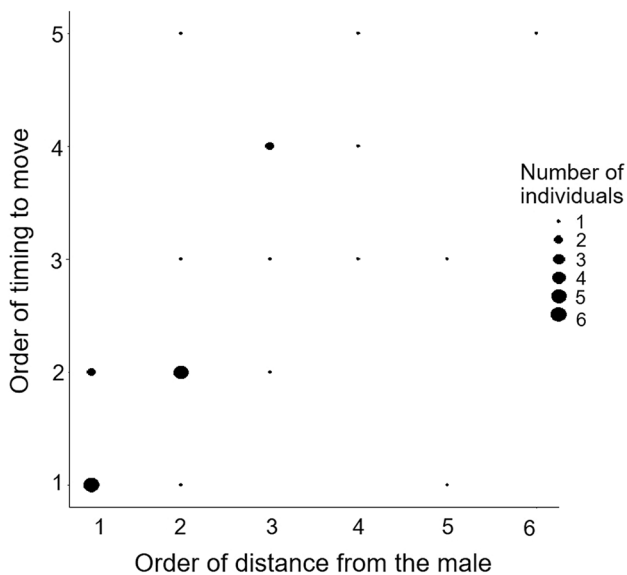

Fig. 3 Distance from the male when the first female began to move, and the moving order of target females. Each dot represents the number of target females (*n*=26 in total)

Table 1 The influence of the distance from the herding male and from the nearest moving female on decisions to start moving in the second and subsequent females during herding (*n*=37). A generalized linear mixed model (GLMM) was used with the binomial error structure (when the target females moved, it was scored as 1, and when it did not move, it was scored as 0, for every time point when a focal target female started to move) and logit link function, including the distance from the herding male and from the nearest moving female as fixed effects and the identity of the horse as a random effect to conduct a likelihood ratio test. We used BL (the body length of the male) as the unit of length

Fixed effect	Estimate	SE	X^2_1	Z	P
Distance from the herding male	0.158	0.158	1.018	1	0.313
Distance from the nearest moving female	− 0.385	0.156	8.581	− 2.464	0.003*

*Significant at $P < 0.01$

provides an effective method for analyzing the movements of individuals in a social group simultaneously at high temporal and spatial resolution. These methods are useful for studying the simultaneous movement of a large number of individuals of animal species without physically contacting them.

We found that the females that moved first were those nearest to the herding male at the beginning of the herding behavior and that the movement initiation of the second and subsequent females was determined by the distance from the nearest moving female, rather than by the distance from the herding male. This indicates that the trigger for movement initiation varied between the females that moved first and the females that moved later during the herding process. This might be due to changes in interactions over time.

There is some possibility that the order of the movement of females might be caused by the individual differences, such as in the personalities, social relationship with others, age, or breeding stage. It was suggested in the 1970s that not only spatial factors but also certain social factors might affect leadership and followership in the movement of animal groups (Syme and Syme 1975; Squires and Daws 1975). Many recent studies suggest the influence of individual differences on the movement of animal groups (see Herbert-Read 2016; Strandburg-Peshkin et al. 2018 for reviews). Observational studies of groups of herbivores, for example, show that leadership and/or followership are related to individual differences, such as in age (cattle: Reinhardt 1983, Sueur et al. 2018; European bison: Ramos et al. 2015), sex (European bison: Ramos et al. 2015), breeding stage (plains zebras: Fischhoff et al. 2007), dominance (horses: Krueger et al. 2014; cattle: Reinhardt 1983, Sárová et al. 2010, Sueur et al. 2018), affinity (horses: Briard et al. 2015, cattle: Sueur et al. 2018), and personality (horses: Briard et al. 2015). However, such influence of individual differences is not particularly relevant to our study. If some of these individual differences in female horses strongly affect their movement initiation in the group, the females might have to initiate the movement regardless of their distance from the herding male or other moving females in the group; however, the females that moved first were the ones nearest to the male, and the second and the subsequent females started to move when the moving females approached them. In addition, there was no significant difference between females in the number of times they became the target of herding (Himeji: 6, Tarumi: 4, Akashi: 5, Maiko: 6, Kakogawa: 5 among the individuals during the whole observation period, see Table S1 for the detail). Thus, in explaining the movement of a harem group during herding, the distance between other individuals and their activities (herding or moving) can be considered to be more important than the individual differences between females for initiating the movement of females. However, we still do not know how the affinities of females influence their spatial position when they start to move. Further, individual differences can influence the spatial position of group members during movement (Sárová et al. 2010; Farine et al. 2016); however, we still do not know whether differences between females influence their spatial position during movement when all of the target females move. In addition, the inconsistent results of previous studies of herbivore movements might reflect differences in environmental settings (they have mostly being conducted in unnatural settings) and the inaccuracy of the analytical techniques (most studies have not analyzed in sufficiently high spatio-temporal resolutions). Thus, to investigate the influence of individual differences on the spatial position of individuals during movement, further studies are needed using novel techniques of present study to gather more data on group movement of horses in natural settings, and analyzing the data through agent-based modeling accounting for the socio-ecological data of individuals.

The two different phases of interactions in a horse group during herding differ from the interactions of other animal species, such as ants, fishes, birds, and cattle (ants: Franks and Richardson 2006, fishes: Herbert-Read et al. 2011; Katz et al. 2011, birds: Lukeman et al. 2010; Nagy et al. 2010, cattle: Šárová et al. 2010), and might be a mechanism for the maintenance of group cohesiveness in a harem group of horses. These movements also differ from the movements in interspecific chaser–escaper relationships (wolf–prey: Muro et al. 2011, sheep dog–sheep: Strömbom et al. 2014) and intraspecific leader–follower relationships (birds: Lukeman et al. 2010; Nagy et al. 2010, fishes: Herbert-Read et al. 2011; Katz et al. 2011). In horses herding, males initiate the movement from behind, and the movement subsequently spreads as the females interact with each other, as the herding progresses. We initially thought that herding is a movement of harem groups in which females are forced by the male to move; however, we found that the strong influence of the male occurs only at the beginning of the movement. This might be due to the social relationships within a harem group of horses. Conspecific individuals maintain long-term stable relationships with one another within the harem, different from the social relationships observed in other animal species in previous studies of animal movements; the female–male and female–female relationships are also different. Females were observed to have stable relationships, regardless of their genetic relatedness (Stanley et al. 2018), and were also observed to keep these relationships even after the death of the harem male (Rubenstein 1994). Therefore, strong bonds between the females might cause an attraction towards one another during herding, resulting in two different phases of interactions. The influence of strong social bond on attraction towards one another during the movement was also suggested in the studies with baboons, which also form stable social groups; baboons preferred to initiate movement together with other group members with a bias towards social affiliates (King et al. 2011; Farine et al. 2016). To the best of our knowledge, this study is the first to suggest possible herding mechanisms involved in maintaining group cohesiveness.

Our study suggests that individual-level interactions might be related to group cohesiveness and determine group-level phenomena. Few empirical studies have suggested that individual differences in interaction determine spatial organization in a group (Farine et al. 2017; Jolles et al. 2017; Strandburg-Peshkin et al. 2017). As we used small data sets observed only during herding in the breeding season, further work is required to understand male–female and female–female interactions during the movement of horse groups in detail, using the novel techniques from this

study to gather more data about various types of movement in different seasons and with the use of agent-based modeling to analyze the data. This will demonstrate how individual-level mechanisms are related to group-level behavioral coordination for maintaining group cohesiveness. There are still a few studies that have investigated the movements of socially stable animal groups at high temporal and spatial resolution (desert baboons: King et al. 2011; olive baboons: Strandburg-Peshikin et al. 2015, 2017; Farine et al. 2016, 2017), and our result differs from the results of these studies in that the movement initiation of individuals during herding showed two phases of interaction. Empirical studies analyzing the interactions between individuals and groups of animal species with various social systems will enable a better understanding of how animals maintain groups and provide insight into the evolution of social organization in animals.

Data accessibility All supplementary data are available on Dryad.

Compliance with ethical standards

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.

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

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