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1 **Spatial positioning of individuals in a group of feral horses: a case study using drone technology**

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17

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29

30 **Keywords:** Drone; Horse; Nearest neighbor; Repulsion and Attraction; Spatial position; Social

31 relationship

32 **1. Introduction**

33 From ants to elephants, some organisms form groups and others live largely in solitude. Social living may
34 improve foraging efficiency if individuals share information about food availability and location.
35 Furthermore, forming a group has other benefits that depend on the needs of each species. For example, it
36 might serve to reduce predation risk, reduce energy consumption related to air or water resistance, or
37 improve reproduction efficiency (Barak and Yom-Tov 1989; Herskin and Steffensen 1998; Weimerskirch
38 et al. 2001; Cameron et al. 2009).

39 One theory predicts that individuals at the periphery of a group are at higher risk of predation
40 than individuals in central positions (Hamilton 1971). Some researchers have argued that food gains, as
41 well as predation risk, are often higher at the peripheries. Thus, animals must at some level consider the
42 tradeoff between predation risk and foraging benefits when choosing their spatial position within a group
43 (Morrell and Romey 2008). As a result, risk of predation and degree of feeding competition, for example,
44 can vary with respect to spatial position (Hirsch 2007).

45 Previous studies investigating spatial positioning in animals have focused on groups of
46 numerous species, including schools of fish, flocks of birds, and groups of mammals (Rhine et al. 1985;
47 van Schaik and van Noordwijk 1987; Janson 1990; Hirsch 2011; Ryder et al. 2012; Teichroeb et al.
48 2015). Important social dynamics within animal groups that potentially affect individual spatial position
49 often include dominance, friendships, and kin relationships. For example, movement of individual social
50 mammals is strongly influenced by their social relationships such that the dominant or older individuals
51 are more likely to become the leader in the leader-follower relationship (King et al. 2011; Sueur and
52 Deneubourg 2011; Andrieu et al. 2016; Tokuyama and Furuichi 2017). In addition to social relationships,
53 physical relationships between individuals within a space (i.e., distance, proximity, and orientation) need
54 to be taken into account when considering animal movement because they might be a mediating factor
55 between the relationships and movements. Researchers have investigated proximity among conspecifics
56 within groups and found that shorter inter-individual distance indicates closer relationships in Japanese
57 macaques (Furuichi 1983) and that proximity correlated with the reproductive states of female rhesus
58 monkeys (Czaja et al. 1975). Similar aspects have been observed in horses. Crowell-Davis et al. (1986)
59 showed that the sex difference between foals and their nearest neighbors changes as the foals develop

60 (Crowell-Davis et al. 1986). Kimura (1988) found that the partners who frequently accompany the nearest
61 neighbor were not the same as those who participate in mutual grooming among females (Kimura 1998).
62 Using spatial-positioning data, Bourjade et al. (2015) and Briard et al. (2015) reported that there might be
63 no leaders on collective departure in domestic horses and the influence of a stallion on the group behavior
64 is not strong (Bourjade et al. 2015; Briard et al. 2015).

65 To obtain data on spatial positions, researchers recently have started using bio-logging
66 technologies in which GPS devices are mounted on animals or video recordings are taken from relatively
67 high above ground and are analyzed using image processing (Lukeman et al. 2010a; Rosenthal et al.
68 2015; Farine et al. 2017). These studies have shown rules with respect to the distance and angle between
69 individuals within a group, suggesting strong preference and anisotropy of the direction for neighboring
70 individuals (Ballerini et al. 2008a; Lukeman et al. 2010a; Katz et al. 2011; Pettit et al. 2013; Rosenthal et
71 al. 2015). Researchers have further suggested that the spatial area surrounding a single individual in a
72 group can be divided into three zones: attraction (two individuals move toward each other when they are
73 too far apart), orientation (two individuals tend to face the same direction), and repulsion (two individuals
74 avoid each other when they are too close) (Couzin et al. 2002).

75 In the case of large mammals in the wild however, attaching GPS devices to all group members
76 or recording video that covers the locations of all group members from high enough above the ground is
77 difficult (e.g., if video recordings are made from human eye height, recording orientation and the masking
78 of individuals by other animal makes high accuracy analysis of individual spatial positions difficult).
79 Although studies have investigated spatial relationships in mammals including horses, they have been
80 primarily conducted with captive animals that were confined to a relatively small area or they relied on
81 visual judgements of the distance between individuals, which are often categorical (e.g., less than 1 m or
82 greater than 5 m) (Krueger et al. 2014; Briard et al. 2015). Recently, researchers succeeded in obtaining
83 location data from wild baboons by mounting GPS devices on them (Strandburg-Peshkin et al. 2015;
84 Farine et al. 2017), but the data were not collected from all group members, which exemplifies the
85 difficulty of attaching GPS devices to wild mammals. To obtain data from GPS devices, animals must
86 first be captured and they must weigh enough to carry the device. Thus, the question remains: are there
87 any differences in spatial positions across and within taxonomic groups? Are the rules (e.g., existence of

88 attraction-repulsion areas or anisotropy of nearest neighbors) for spatial positioning of individual fish
89 within schools or birds within flocks also applicable to wild mammals? Quantitative data on spatial
90 positioning is imperative for understanding the processes and rules that generate variation in the patterns
91 exhibited across and within taxa. To address this question, we conducted the present case study using
92 drones—unmanned aerial vehicles that are remotely controlled by an operator— to focus on large and
93 feral mammals. Although researchers have already used drones to examine some species of wild and
94 domestic animals (Vermeulen et al. 2013;Chrétien et al. 2016; Goolsby et al. 2016; Torney et al. 2016;
95 Jung 2017), most of these studies focused on detecting and monitoring them from the perspective of
96 conservation and management, and few have focused on animal behavior (Ozogány and Vicsek 2014).

97 Using drones enables the recording of all members of a group from the sky, which is optimal
98 for analyzing spatial positions, as long as no obstacles come between the drone and subject animals. Feral
99 horses meet the first requirement of this methodology because they usually live in relatively monotonous
100 plains that are covered with grasses and herbs, as opposed to complex three-dimensional spaces that
101 include tall trees or thick bushes that can block a drone’s line of sight. Horses usually form long-term
102 stable harems comprising multiple members (Berger 1977; Klimov 1988), which are comparable to some
103 primate species that also form stable groups with fixed members (Nishida 1968; Harcourt 1978; Kano
104 1982; Linklater and Cameron 2009).

105 In the present study, we investigated several characteristics related to spatial position in a group
106 of feral horses as a case study for clarifying the nature of spatial positions within a mammal group. We
107 investigated characteristics that have been commonly investigated in the case of fish schools and bird
108 flocks, including the relative positions of each individual in the group, inter-individual distances, and the
109 distances and angles to the nearest neighbors (Lukeman et al. 2010a; Strandburg-Peshkin et al. 2013;
110 Rosenthal et al. 2015). Additionally, we tested for correlation between social networks measured by
111 grooming frequency (which has previously been used as an indicator of friendship association) and spatial
112 position, as a study by Kimura (1998) suggested a possibility that these two might differ. Our focus was
113 on analyzing stationary spatial positions because fast and relatively long-distance movement of individual
114 feral horses makes positional analysis difficult for a number of reasons (e.g., short battery life and the
115 drone’s own movement). We focused on stationary spatial positions during foraging, a situation in which

116 horses do not engage in fast or long-distance movement. The present study had two primary aims: (1) to
117 describe the basic characteristics of stationary spatial positions within a group of horses and (2) to clarify
118 how social networks in a group influence spatial position.

119

120 **2. Material and Methods**

121 *2.1 Study site and animals*

122 The study was conducted in June 2016 at Serra D'Arga, an 825 m high mountain located in northern
123 Portugal (8°42'N, 41°48'E), which was established as a new research site in 2016 (see Ringhofer et al.
124 2017 for details) (Figure 1). This region has a Mediterranean climate, and the horse habitat includes a
125 grass field, rocky ground, a forest, and shrub areas. More than 200 feral Garrano horses live in this region
126 (Ringhofer et al. 2017). The focal group comprised one adult male (Uzumasa), seven adult females (Uji,
127 Katsura, Gion, Fushimi, Kishiwada, Ayabe, and Akashi), and two foals born in the spring of 2016. One
128 adult female (Akashi) was in the process of transferring from another group; this female moved back and
129 forth between the two groups throughout the observation period. All members of the group were
130 identifiable by their appearance. Analysis was conducted during the period when this individual was
131 present in the group.

132 The target group had two foals. The orientation and distance of foals depended on those of
133 their mothers. We excluded data from these two foals as our goal was to analyze the positions and
134 relationships of independent adult horses. A separate analysis including the foals is provided as
135 Supplementary Material.

136 The field observations complied with the guidelines for animal studies in the wild issued by
137 the Wildlife Research Center of Kyoto University, Japan.

138

139 *2.2 Data collection*

140 Photos of the target group were taken every 30 min using an unmanned aerial vehicle (drone, Phantom3
141 Advanced, DJI, China) (Figure 2). The vehicle was a quadcopter with a video camera (1080p resolution)
142 that was operated remotely with the camera angle set perpendicular to the ground. The drone took off
143 approximately 10–50 m from the horses and flew at an altitude of 25–80 m. Advance test flights

144 confirmed that as long as the drone stayed at least 10 m away from the horses, they did not run away,
145 panic, or show any other behavioral responses to the drone. Because horses did not move rapidly, position
146 data from two consecutive scans would not be independent if the scan interval was too short. Therefore,
147 we set the scan interval at 30 min to avoid this potential for correlated horse positions.

148 While photos were taken, the positions of each individual were recorded from the ground by
149 observers who could identify individuals. When horses were located in the shadows of trees, we stopped
150 taking photos, and began again after 30 min. Three to thirteen images were acquired per day, and a total
151 of 102 images were acquired during our 13-day observation. Observation lasted 4–10 h per day, for a
152 total of 88.5 h over the course of the study.

153

154 *2.3 Behavioral data collection*

155 We also recorded aggressive behavior and grooming events using all-occurrence sampling (Altmann
156 1974). These recordings took place regardless of whether or not the drone was flown. Grooming and
157 aggressive behaviors performed against or by foals were not analyzed. Similar to a previous study with
158 horses (Heitor et al. 2006), aggressive behaviors included biting, chasing, kicking, and striking were
159 considered indicators of social rank within the group. We then calculated the frequency of aggressive
160 events per hour and per individual.

161

162 *2.4 Image categorization*

163 We excluded images from further analysis if they did not contain all individuals. Additionally,
164 individuals from other groups were occasionally present with the target group, and such cases were also
165 excluded from analysis. Group activities were divided into three categories: (1) travel (the entire group
166 walked/ran toward a certain direction, often in a line), (2) rest (more than half the group rested
167 motionlessly, usually packed in a small space), and (3) forage (group members foraged freely). We
168 determined the category of activity based on observations before and after taking the drone photos, and
169 then excluded instances of travel and rest from the analysis. This resulted in 61 foraging images (60% of
170 the total number of images) for further analysis.

171

172 *2.5 Correction of camera distortion*

173 The distortion of the camera lens was corrected using the lens filter function in Photoshop CC (Adobe
174 Systems incorporated) selecting the FC300 camera property for DJI Phantom 3, which was provided by
175 Photoshop CC as a preset value. We confirmed the accuracy of the correction by taking a photo of a
176 checkerboard grid with a known absolute size and applying the lens-distortion correction. We then
177 calculated the error by comparing the length of the grid in the photo with its actual length. Before we
178 corrected the distortion using Photoshop CC, the maximum error was 12% and around the periphery of
179 the photo. After correction, it was 3% or less. This was acceptable, and we thus based our analysis on the
180 distortion-corrected images.

181

182 *2.6 Calculation of distance and direction*

183 We used three measures to characterize the spatial positions of individuals within the group: inter-
184 individual distance, nearest neighbor distance, and the distance between each individual and the center of
185 the group. This latter value was calculated based on the x-y pixel coordinates of each individual's
186 location in a 3200×4000 pixels photo, with the top left of an image being the origin (0, 0). The group
187 center was defined as the average of all individual coordinates. We defined an individual's location as the
188 midpoint between the tip of the head and the base of the tail. Average body length (BL) of all individuals
189 was used as the unit of length for further analysis in measuring the distance between individuals. This was
190 because the drone's ground height varied, and the scale of the images was thus different in each
191 photograph (i.e., the length of a pixel represented a different absolute length in the real environment)
192 because no standard object of known size could be placed in the photos. The assumption here is that
193 because all members were present in all photos that we analyzed, the average body length of all
194 individuals should remain constant across photos. Body length was the distance between the base of the
195 tail and the base of the neck. The reason for not using the tip of the head was that head orientation varied
196 depending on the posture of the horses. When horses were grazing in the field, they lowered their head. In
197 contrast, the distance from the base of the neck to the base of the tail was relatively constant and always
198 straight, as viewed from above via the drone.

199 To characterize the direction of individual horses, we used individual vectors. We calculated
200 vectors from the base of the tail to the tip of the head. Although several previous studies have adopted one
201 body length (≤ 1.5 m) as the category that best estimates the strength of the interaction between two
202 horses, we defined “proximity” as two individuals being within 2 BL of each other. This was because our
203 method measures the distance between the center point of one individual to that of another, not the edge
204 of one individual to the edge of another, as was the case in previous studies (Waring 1983; Heitor and
205 Oom 2006). Our study remains comparable to these previous studies because 2 BLs using our method is
206 effectively equivalent to 1 BL in the Waring (1983) and Heitor and Oom (2006) studies (the distance
207 from the central point of the body and its outer surface is roughly 0.5 BL, which is then multiplied by two
208 individuals), with the proviso that the two measures are not actually identical because the animals are not
209 circular in shape. Next, to investigate how the orientation of an individual to its nearest neighbor depends
210 on position (front and rear, viewed from the target individual), we calculated the inner product between
211 the unit vector of an individual (from the tail base to the head) and that of its nearest neighbor. Higher
212 inner product values indicate greater orientation alignment.

213

214 *2.7 Random test*

215 Under complete spatial randomness, individual positions in local areas follow a Poisson distribution and
216 the average distance to the nearest neighbor follows a Weibull distribution (Fortin et al. 2002). To
217 measure the randomness of individual positions, we used the following index:

$$218 \quad q = \frac{d\sqrt{n}}{\pi r^2}$$

219 where r is the average distance to the nearest neighbor for all individuals in an image, n is the number of
220 individuals, and d represents the distance between the group center and the furthest individuals. If q
221 equals 0.5, horse positions are random, if it is close to 0, positions are in a limited smaller area, and if it is
222 close to 1, positions have some non-random regularity (Skellam 1952; Pollard 1971).

223

224 *2.8 Social network analysis*

225 To estimate the strength of association between two individuals, we used measures of grooming and
226 proximity frequency. Mutual grooming and proximity are generally used to estimate the positive
227 relationship between individuals (Briard et al. 2015). We calculated simple ratio indices (SRI) for each
228 measure that were defined as follows:

$$229 \quad SRI = \frac{x}{x + y_a + y_b}$$

230 where x represents the frequency of grooming or the proximity between individuals a and b , y_a is the
231 frequency of grooming or the proximity between individual a and other individuals, and y_b is the same as
232 y_a , but for individual b (Cairns and Schwager 1987). Additionally, we calculated a distance index (DI)
233 from the average distance between each pair of individuals:

$$234 \quad DI = \frac{-D_{ab} + 0.5(D_a + D_b)}{0.5(D_a + D_b)}$$

235 where D_{ab} represents the average distance between individuals a and b , and D_a and D_b represent the
236 maximum distance between individuals a and b and other individuals, respectively. In this way, we
237 obtained three weighted (from 0 to 1) indices of interactions (grooming, proximity, and distance). We
238 then measured eigenvector centrality to clarify the influence of each individual in these networks with
239 Ucinet 6.0 software (Borgatti et al. 2002).

240

241 *2.9 Statistical analysis*

242 Statistical tests were performed with R 3.3.2 (R Development Core Team 2016). With respect to the
243 distribution of the distance between individuals, we first determined whether the distribution followed a
244 Weibull distribution based on the reasoning described above. However, visual inspection of the data
245 indicated a gamma distribution; thus, we tested whether it followed a gamma distribution. With respect to
246 the social network, we used Ucinet 6.0 to conduct Quadratic Assignment Procedure (QAP) tests to assess
247 the influence of grooming on proximity and distance. We used 5000 permutations in the QAP tests.

248

249 **3 Results**

250 *3.1 Aggressive behavior*

251 At this research site, the frequency of aggressive behaviors was very low. We observed only 10
252 aggressive behaviors over the course of the study, and average frequency per individual per hour was
253 0.03. This was significantly lower (Kruskal-Wallis test, $\chi^2 = 28.718$, $df = 3$, $p < 0.01$) than what was
254 reported in previous studies of feral horses at other sites (Heitor and Vicente 2008; Keiper 1988; Weeks
255 et al. 2000; the frequencies of aggressive behaviors were 2.43, 5.9, and 0.4, respectively). Therefore,
256 social rank could not be determined statistically.

257

258 *3.2 Relative locations of individuals*

259 Analyzing the distance of each individual from the central point revealed that the mean distance was
260 significantly greater for the male (Uzu) than for five of the seven females (Figure 3; Steel test, $n = 61$,
261 Uzu-Uji: $t = 5.48$, $p < 0.01$, -Kis: $t = 4.19$, $p < 0.05$, -Kat: $t = 4.26$, $p < 0.05$, -Aya: $t = 1.89$, $p = 0.95$, -
262 Gio: $t = 4.44$, $p < 0.05$, -Fus: $t = 2.65$, $p = 0.61$, -Aka: $t = 4.65$, $p < 0.01$). We did not find any significant
263 differences in female positioning regarding the center vs. the periphery (ANOVA, $n = 61$, $df = 6$, $F = 2.03$,
264 $p = 0.06$).

265

266 *3.3 Distribution of distance between individuals*

267 The distribution of inter-individual distances could indicate whether horse positions are random or related
268 to aggregation or diffusion. The histogram of all inter-individual distances followed a gamma distribution
269 (shape = 2.24, rate = 0.172; -S test, $n = 1708$, $D = 0.06$, $p = 0.11$) (Fig. 4), while that for nearest-neighbor
270 distances did not follow a gamma distribution (shape = 1.83, rate = 0.31; K-S test, $n = 488$, $D = 0.1394$, p
271 < 0.01) or a Weibull distribution (shape = 1.18, scale = 6.38; K-S test, $n = 488$, $D = 0.14$, $p < 0.01$) (Fig.
272 4). The peak of the nearest-neighbor histogram was shifted left compared with that of the all-pair
273 histogram. We excluded the male from q-value calculation because he was located in the periphery.
274 Figure 5 shows the q-value histogram. The peak was around 0.5, but the cases less than 0.5 outnumbered
275 those greater than 0.5.

276

277 *3.4 Positioning and orientation of the nearest neighbor*

278 Rather than being uniform, the density plot for the nearest-neighbor data was biased depending on the
279 angle (K-S test, $n = 444$, $D = 1$, $p < 0.01$). Figure 6 shows a density plot of nearest neighbors within 5 BL
280 that is magnified from a density plot within 10 BL. The plot shows that the nearest neighbor tended to be
281 located toward the sides of a horse more frequently than toward the back or front (Fig. 6).

282 Next, the ratio of inner products larger than 0 to those less than 0 was smaller when the
283 nearest neighbor was located behind a horse than when it was located in front (prop test, $n = 132$, $\chi^2 =$
284 1.56 , $df = 1$, $p = 0.10$). Thus, when the nearest neighbor was behind a horse, the target individual was less
285 frequently orientated in a similar direction. Further, the minimum and average values for the rear (mean:
286 0.62 , minimum: -0.64) were higher than those for the front (mean: 0.44 , minimum: -0.99), whereas the
287 maximum values were the same (both were 1).

288

289 *3.5 Social network analysis*

290 Three social networks were drawn from the three quantified social interactions: grooming, proximity (< 2
291 BL; see Methods), and inter-individual distance (Fig. 7). The proximity and inter-individual distance
292 networks trended towards a correlation, although it was not statistically significant (QAP test, $r = 0.30$, p
293 $= 0.09$). This result was expected because removing auto-correlation between the two networks was not
294 possible. We found a significant correlation between the grooming and inter-individual distance networks
295 (QAP test, $r = 0.51$, $p < 0.01$), but not between the grooming and proximity networks (QAP test, $r =$
296 -0.14 , $p = 0.27$).

297 For each network, we next calculated the eigenvector centrality, which indicates power in a
298 network. Individuals with high eigenvector centralities were different in each of the three networks.
299 Regarding the inter-individual distance network, no individual had high power in terms of eigenvector
300 centrality.

301

302 **4. Discussion**

303 In the present study, we were able to characterize aspects of individual spatial positioning within a group
304 of feral horses as a test case using a drone. We found a sex difference in spatial positioning in which a
305 male was located toward the periphery of the group more frequently than females, at least during the

306 breeding and birth season (our observation period). Distribution of inter-individual distances showed a
307 regularity in that it fit with a gamma distribution. Additionally, spatial distributions were not random
308 within the area, as indicated by the q-value that tended to be less than 0.5. Nearest neighbors were located
309 toward the sides of horses more often than toward the rear. Finally, grooming frequency and the spatial
310 cohesion did not correlate with each other.

311 Our finding indicating that the distance from the central point to an individual did not differ
312 among females contradicts a previous study which showed that subordinate horses were more likely to be
313 located in the periphery of a group comprising a gelding and several females (Ingólfssdóttir and
314 Sigurjónsdóttir 2008). The richness of food resources in our study site might have resulted in less
315 competition among individuals. Center/periphery positioning is thought to affect foraging efficiency less
316 when is food is depleted more slowly, which was the case for grass and herbs that covered this field site
317 (Morrell and Romey 2008; Hirsch 2007). This could also explain the low frequency of aggressive
318 behavior during our observation period. The tendency for the male to be located at the periphery could be
319 related to a seasonal behavioral pattern. Thus, the male might have been attempting to defend females in
320 the group from other males by staying in the periphery. This possibility is supported by previous research
321 demonstrating that females choose males that protect them from harassment (Rubenstein 1994; Linklater
322 et al. 1999). Notably, more than 20 other groups, including bachelor groups, were located in the same
323 field (Ringhofer et al. 2017). To better understand the social and ecological factors influencing the
324 positioning of horses, future studies collecting location data in non-breeding seasons will be necessary.

325 Our result regarding the distance to the nearest neighbor suggests that horses have a repulsion
326 area with a 3-BL radius. The distribution of distances to the nearest neighbor did not follow a Weibull
327 distribution. According to a Weibull distribution, which reflects a random distribution of points (Fortin et
328 al. 2002), the distance between two points can be as close as possible to 0. Thus, a repulsion area creates a
329 non-Weibull (non-random) distribution. The result of the q-value analysis also supports the idea that
330 individual horses were not located at random positions. The low frequency of q-values greater than 0.6
331 further suggests the possibility that individuals are attracted to each other within groups of horses. Thus,
332 our results indicate that horses might have both areas of repulsion and attraction, similar to findings in
333 flocks of birds and schools of fish, although the horses might also sometimes follow a random

334 distribution as indicated by the ~30% of cases in which the q-value was around 0.5. However, we must
335 keep in mind that our result is not direct evidence of repulsion and attraction areas, as we relied on
336 photographic data of stationary positions, rather than measuring movements. Further studies with
337 movement or velocity data are thus warranted.

338 The nearest neighbors of the horses were located on the sides more frequently than to the rear.
339 Horses are able to see 350 degrees around themselves, but they have a blind spot directly behind them
340 (Rees 1993). Therefore, horses may express fear of animals or objects grouping to their rear, which
341 renders them invisible. Our results regarding the orientation of the nearest neighbors support this
342 hypothesis. The average and minimum values of the inner product for the rear were higher than those for
343 the front. This result indicates that individuals located behind others did not completely reverse their
344 orientations to the individuals in front of them. This may be because horses tend to avoid putting animals
345 in their blind spot or because they try to avoid being in the blind spots of other animals. Anisotropic
346 positioning of the nearest neighbor has been reported in starlings and surf scoters (Ballerini et al. 2008;
347 Lukeman et al. 2010; Pettit et al. 2013). But a direct comparison of our findings with horses and the
348 previous study with starlings should be approached with caution because horses live in 2D space and
349 starlings live in 3D space. On the other hand, a comparison between horses and surf scoters (Lukeman et
350 al. 2010) would be more feasible because scoters in the cited study lived in 2D space (floated on the sea
351 surface). Thus both horses and scoters lived in 2D space and can more easily be compared. Although our
352 study had a similar research question to that by Lukeman et al. (2010), our results were somewhat
353 different. In particular, the nearest neighbors of scoters were usually located to the front or rear, and most
354 were within 2 BL. Preference for positioning with respect to the nearest neighbor seems to depend on the
355 species, as well as on factors such as environment, the number of individuals in a group, and density of
356 individuals.

357 Kimura (1998) reported that a partner with highest grooming frequency differed from the
358 most frequent nearest neighbor in free-ranging horses. Our results from social network analysis showed
359 mixed trends. The social networks measured by grooming frequency and proximity had a positive
360 correlation, while the social network measured by distance (i.e., used as a quantitative measure) did not
361 correlate with grooming networks. Individuals with high eigenvector centrality were different in each of

362 the three networks. Grooming, proximity, and inter-individual distance might to some extent indicate
363 different and independent social relationships between individuals. Observing one type of social
364 interaction is clearly insufficient for describing horse society, and different types of indices can illustrate
365 different aspects of horse society.

366 One limitation of our study is the short observation period. However, some factors favor
367 short-term data acquisition for investigating social relationships in horses. First, addition of individuals
368 due to the birth of new foals changes the positioning of individuals within a group. In the present study,
369 we excluded the foals that were dependent on their mothers from the analysis (see Supplementary
370 Material for the inclusion of foals in the analysis). However, horse foals grow rapidly. Thus, these foals
371 must be included in the analysis at some point when their spatial positioning becomes independent.
372 Second, immigration/emigration of individuals between groups is common (Linklater and Cameron 2009;
373 see Ringhofer et al. 2017 for the data from the present study site), and the addition/loss of individuals will
374 also affect spatial positioning within a group. Along with the passage of time after the addition of
375 individuals, the relationships between individuals within a group can change. By the time the
376 relationships have stabilized again, another immigration/emigration might occur. Therefore, the
377 relationships of individual horses in our study area are constantly changing. Even if we collect long-term
378 data, we would need to segment the data into short-term periods based on these reasons. With that said,
379 long-term data on multiple groups of horses are necessary to verify our results, and we plan to conduct
380 further research on related topics in the future.

381 In terms of using a drone, the advantages include higher accuracy and more objective data
382 than can be recorded with human eyes at head height. Our method will be applicable to studies with many
383 other species such as cows, elephants, and other ungulates that have been already monitored by the drone
384 technology (Vermeulen et al. 2013;Chrétien et al. 2016; Goolsby et al. 2016; Torney et al. 2016; Jung
385 2017). At the same time however, the use of drones has several environmental limitations. First, flying a
386 drone is impossible if the wind is too strong (approximately > 10 m/s for the drone we used in our study)
387 (DJI 2015). In fact, we experienced a situation in which our drone became uncontrollable and flew away
388 in a sudden strong wind. Second, drones are best when applied to diurnal animals living in open areas.
389 Recording forest-living animals via drone is difficult and hindered by trees. In addition, using drones to

390 record nocturnal animals is still difficult, although using an infrared camera is a potential option. Third,
391 the battery-life of quadcopter-type drones (like the one used in our study) is only about 15 min, which is
392 very short. Fixed-wing drones have a longer battery-life, but they are not capable of hovering, and thus
393 recording animals that stay put in a given area is impossible with fixed-wing drones. Quadcopter drones
394 are capable hovering but their short battery-life is certainly a limitation. Therefore, we have to take into
395 consideration the short-battery life when we use drones for scientific studies. Indeed, this limitation was
396 one of the factors that forced us to limit our analysis to analyze stationary situations. Fourth, quadcopter
397 drones also make noise, thus it is not suitable for nervous animals that might react to the noise. Using
398 drones thus has advantages and disadvantages, and our study has provided an example of what can be
399 achieved when using them in animal studies. Our study has thus opened up new possibilities for studying
400 animal behavior in the wild.

401

402 Figure 1. Serra D'Arga and horses.



403

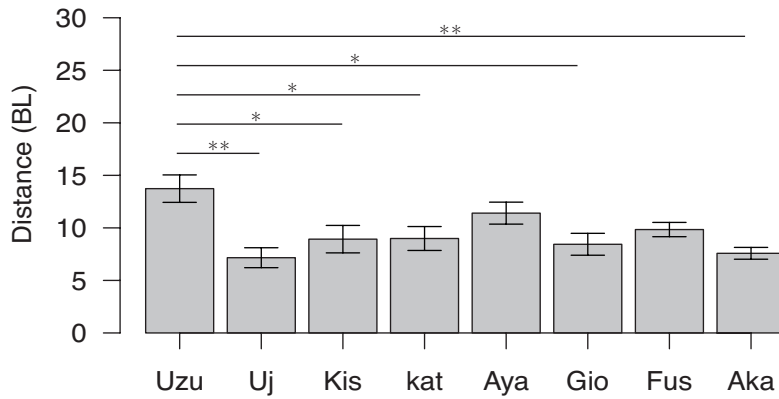
404

405 Figure 2. Drone picture of the Kyoto group.

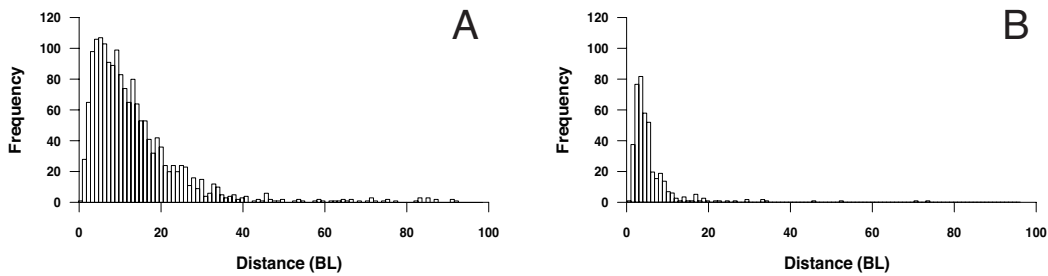


406

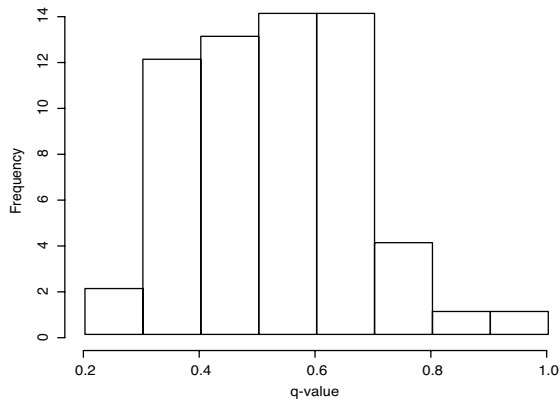
407 Figure 3. Average distance (+SE) between each individual and the central point of the group. Uzu is the
 408 only male in this group.



409
 410 Figure 4. Histograms of inter-individuals distance. Bin size is 1 body length (BL). (A) Histogram of the
 411 distances between all pairs. The peak of this histogram was around 4 BL. (B) Histogram of the distance to
 412 nearest neighbor. The peak of this histogram was 3 BL.



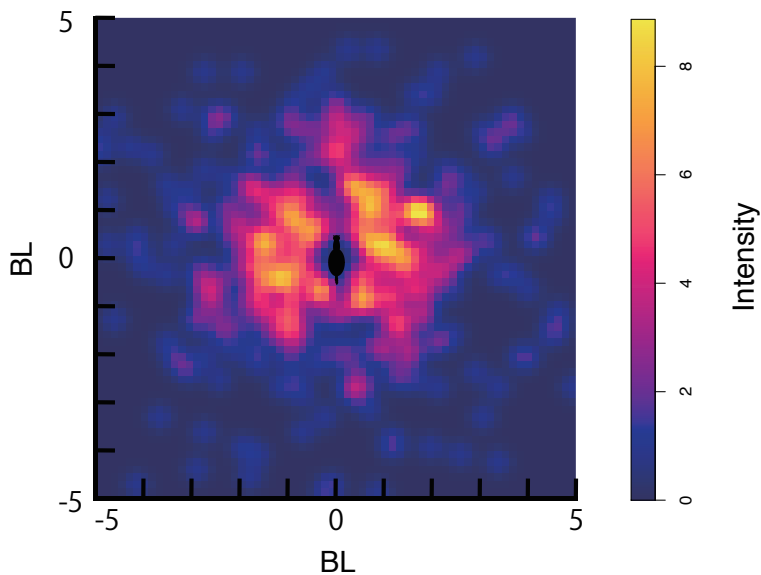
413
 414
 415
 416
 417
 418 Figure 5. q-value histogram.



419

420 Figure 6. Density plot of nearest neighbor positions within 5 body lengths (BL).

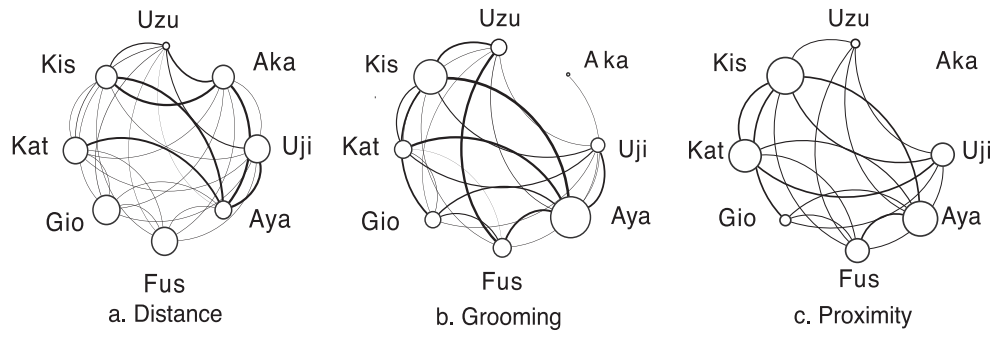
421 We drew the density plot of the nearest neighbor based on pooled data from all individuals with the R
 422 package “spatstat” (Baddely and Turner, 2007), with bin sizes of $\Delta x = \Delta y = 0.5$ BL, and smoothing
 423 with a Gaussian Blur = 0.4. If the nearest neighbors were located more than 10 BL away, these cases
 424 were excluded from analysis because 91% of the data regarding the distance to the nearest neighbor fell
 425 within 10 BL.



426

427 Figure 7. Horse social networks (a: distance, b: grooming and c: proximity).

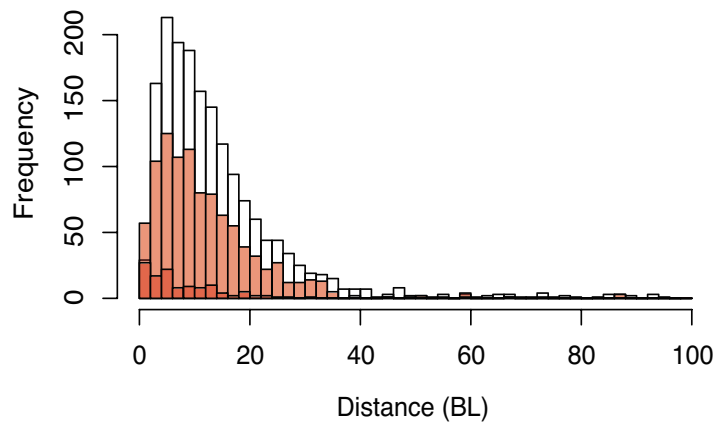
428



430

431 **Supplemental Figure 1**

432 Distribution of distances between foals and other individuals (Orange) compared with distances between
433 all individuals including foals (white), and distances between foals and their mothers (Red). The result
434 shows that the distances between foals and other individuals tended to be shorter than those between all
435 individuals. Additionally, the distribution of peak distances between foals and their mothers was shifted
436 to left compared with other distributions.



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