1   **Title**: Lateral position preference in grazing feral horses

2   **Short running title**: Spatial lateralisation in feral horses

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17

27 **Abstract**

28 Behavioural lateralisation is an effective way for animals to manage daily tasks by

29 specializing behaviour to either side of the body. Many types of lateralisation are linked

30 to the function of each brain hemisphere. Lateralisation of monitoring behaviour in

31 mother-infant relationships occurs in a wide range of mammals, where infants

32 frequently use their left eye to monitor their mother. However, few studies have focused

33 on this type of spatial relationships among adults in daily life, such as during foraging.

34 The present study focused on monitoring adult feral horse behaviour using quantitative

35 analysis of spatial relationships, using drone technology. We found that horses form a

36 localised spatial relationship to their nearest neighbour. Specifically, the nearest

37 neighbour was located to the left rear of a target individual significantly more frequently

38 than to the right rear. Furthermore, the nearest neighbour was less frequently located

39 behind a target individual. We propose that this relationship is caused by a left-eye

40 preference, because information via the left eye predominantly proceeds to the right

41 hemisphere, which is dominant for social processing.

42

43 Key words: Laterality, spatial positioning, horses, drone

1. Introduction

Many animals demonstrate various types of laterality. There is functional and

morphological asymmetry between the left and the right brain hemispheres (Bisazza,

Rogers, & Vallortigara 1998; Halpern, 2005; LeMay, 1976; Levy, 1977; Lindell, 2013),

and this asymmetry corresponds to several types of behavioural laterality. Many studies

have supported the right hemisphere theory, where the right hemisphere is superior for

social processing (Brancucci, Lucci, Mazzatenta, & Tommasi, 2009; Jackson, 1915;

Okubo, Ishikawa, & Kobayashi, 2013). This superiority is considered to be related to the

dominance of the left eye in the perception of social stimuli (Brancucci et al., 2009).

Specifically, monitoring conspecifics using the left eye/right hemisphere provides

advantages including better facial expression detection, increased frequency of positive

interactions that strengthen inter-individual relationships, more aggression during

agonistic behaviour, and quicker reactions to movement by conspecifics and predators

(Austin & Rogers, 2012, 2014; Karenina, Giljov, Ingram, Rowntree, & Malashichev,

2017; Nagy, Ákos, Biro, & Vicsek, 2010). Most previous reports focusing on the laterality

of social interactions have investigated interactions in a counter-directed position, where

61 individuals face each other, and findings include the left-cradling bias in mother-infant

62 relationships in humans and great apes (Giljov, Karenina, & Malashichev, 2018; Harris,

63 2010; Sieratzki & Woll, 1996). In species that have a relatively large binocular field of

64 view, mothers hold their infants on the left side of the body in a counter-directed position,

65 so that both are in an optimal position to monitor each other because both can use optimal

66 information flow. The left-cradling bias in mother-infant relationships has recently been

67 expanded to a diverse range of mammals, especially in species moving in codirected

68 positions, where individuals are side-by-side on parallel paths. For example, offspring of

69 the feral horse, Pacific walrus, Siberian tundra reindeer, saiga antelope, muskox, eastern

70 grey kangaroo, red kangaroo, sheep, orca, and beluga whale are more often on the right

71 side of their mothers than on the left (Giljov et al., 2018; Karenina, Giljov, Glazov, &

72 Malashichev, 2013; Karenina et al., 2017; Karenina, Giljov, Ivkovich, Burdin, &

73 Malashichev, 2013; Versace, Morgante, Pulina, & Vallortigara, 2007). Researchers

74 consider that infants take the initiative in positioning in situations such as rest or slow

75 movement, and prefer to view their mothers using the left eye. This consistency in

76 laterality among mammals implies an ancient evolutionary origin of this bias. However,

77 it remains unknown whether the bias is limited to mother-infant relationships. If using the

78 left eye field of view works well in mother-infant relationships, we might expect that this

79 type of position bias also occurs between adults that live in groups, because adults also

80 need to adjust their distance and positioning relative to other individuals to maintain

81 group cohesion. To investigate whether lateral bias exists in spatial positioning among

82 adult animals, we analysed data from adult feral horses. Feral horses usually form long-

83 term stable groups (Berger, 1977) and do not frequently face each other in foraging

84 situations, although mutual grooming and mutual swatting of flies are performed in

85 counter-directed positions (i.e., two individuals facing opposite directions) (Feist,

86 Mccullough, & Dean, 1976; Heleski, Shelle, Nielsen, & Zanella, 2002). Horses are a good

87 species for studying behavioural lateralisation because they have a relatively small field

88 of binocular vision, estimated at 80°, and their left and right eyes have largely independent

89 views of their left and right sides, respectively (Harman, Moore, Hoskins, & Keller, 1999).

90 Several studies have reported laterality in behaviours including agonistic and affiliative

91 behaviours in counter-directed positions, vigilance to auditory stimuli, and relative spatial

92 positioning in mother-infant relationships in horses in co-directed positions (i.e., two

93   individuals facing the same direction) (Austin & Rogers, 2012, 2014; Farmer, Krueger,

94   & Byrne, 2010; Farmer, Krüger, Byrne, & Marr, 2018; Karenina et al., 2017; Karenina,

95   Giljov, & Malashichev, 2018). According to previous studies, horses frequently use their

96   left eyes during these behaviours, similar to other species. Specifically, horses have a left-

97   eye preference for monitoring novel stimuli, and a left-body preference for threatening

98   and attacking within harem bands and for positive social interactions in mother-infant

99   relationships (Austin & Rogers, 2014; Karenina et al., 2017; Larose, Richard-Yris,

100   Hausberger, & Rogers, 2006). Thus, functional lateralisation is not limited to infancy but

101   continues throughout adulthood. We therefore hypothesised that this left-eye bias in

102   monitoring conspecifics also occurs in adult–adult spatial positioning, although we did

103   not have a detailed specific hypothesis as to which way such a lateral bias might appear

104   in spatial positioning; as such, our study was exploratory in nature. The present study

105   aimed to address the question of whether previously observed lateral preferences are

106   reflected in the positioning of adult horses while grazing, and if so, which side is preferred.

107

108   **2. Materials and methods**

109 In the present study, we analysed images taken from drones, which allowed us to test

110 whether there was any lateral bias in spatial positioning in adult horses during foraging,

111 with a focus on the position of a target horse and its nearest neighbouring individual.

112 The study was conducted in Serra D'Arga, an 825 m high mountain located in

113 northern Portugal (8°42′N, 41°48′E). The horses' habitat included a grass field, rocky

114 ground, a forest, and shrub areas (Ringhofer et al., 2017) (Appendix 1). Over 250

115 identified feral horses, categorised as Garrano horses, lived in the site. They roamed freely

116 over the mountain living on the natural grazing and water resources. There were no

117 artificial barriers to impede their movement, they did not have daily human contact, and

118 they were not fed by humans. Horses form long-term stable harems and unstable bachelor

119 groups, and we focused on two harems in June 2016, May–July 2017, and May–July 2018.

120 We chose the two groups because it was relatively easy to find these groups compared

121 with other groups. Both were one-male harems. We followed 10 individuals in 2016, 19

122 individuals in 2017, and 11 individuals in 2018. Kameoka, in Kyoto 17, was one year old,

123 and was an immature male and, not the stallion (Appendix 2). In 2017, Kyoto and Hyogo

124 were constantly together and kept a close distance between one another; there were

125   therefore cases in which the nearest neighbour of an individual was a horse from the other

126   group. Eight horses were less than 1 year old and these individuals were excluded from

127   the analysis due to their high dependency on their mothers, because the aim of the present

128   study was to analyse adult individuals. For the same reason, data from the mothers of

129   these foals were also excluded from the analysis. Although seven foals died before 1 year

130   of age, one foal survived beyond 1 year and the individual was included in the analysis

131   from this point on. In sum, 5 individuals in 2016, 11 individuals in 2017, and 7 individuals

132   in 2018 contributed to the data.

133   The recordings involved 4–13 (average 6.7) video clips per day and these were

134   taken between 9:00 and 18:00. Video clips were taken for approximately 15 min every 30

135   min, from 25–80 m above the ground (the heights were decided on a case-by-case basis

136   to be able to include all target group individuals in one image) using unmanned aerial

137   vehicles (drones). Still images were obtained by taking images from the video clips after

138   1 min from the beginning of the clips (i.e., there was 30 min between two consecutive

139   still images). The distortion of the camera lens was corrected using the lens filter function

140   in Photoshop CC (Adobe Systems incorporated) (Inoue et al., 2018). The drone took off

141   10–50 m away from the horses. The drones used for collecting data were the Phantom 3

142   Advanced, Phantom 3 Professional, and Mavic Pro (DJI, China). Behavioural observation

143   was performed by SI during flights to estimate group states. We defined the states as

144   foraging, traveling, and resting, and only analysed data during foraging because horses

145   change their spatial positioning formation depending on their state (Inoue et al., 2018).

146   After excluding images of horses in the resting or traveling states, 184 images were

147   analysed. All harem group members were recorded and clearly visible in each of the 184

148   images (Appendix 1).

149   We measured an individual's coordinates as a central point between the head

150   and the base of the tail and defined an individual's direction as a vector from the base of

151   the tail to the base of the neck; the magnitude of the vector was defined as the body length.

152   Mean body length of adult horses was used as a unit of distance, because it is relatively

153   stable and fixed (Appendix 1). Using individuals' coordinates in each image, nearest

154   neighbours were determined for each individual. When the distance to the nearest

155   neighbour was more than two body lengths, data were excluded from the analysis

156   according to previous studies (Karenina et al., 2017; Inoue et al., 2018). To analyse spatial

157   relationships among adults only, we excluded mothers and foals from the analysis.

158   Although it is known that proximity between individuals is related to their social bonds,

159   our analysis did not rely on just a few pairs (Appendix 3) (Kimura, 1998; Schneider &

160   Krueger, 2012; Wolter, Stefanski, & Krueger, 2018). A total of 308 points were analysed

161   to quantify relative positioning.

162   Circular variance was calculated to analyse the degree of variance in body

163   direction of individuals (CV_d):

164    $$CV_d = 1 - \frac{1}{N} \sum_i |\vec{v}_{di}|$$

165   where N is the number of vectors $\vec{v}_{di}$, and $\vec{v}_{di}$ indicates a unit vector of the direction of

166   individual i (Appendix 4). If all individuals face the same direction, $CV_d = 0$, whereas if

167   they face completely random directions, $CV_d = 1$. Circular variance among individuals'

168   positions (CVp) was calculated from the same formula:

169    $$CV_p = 1 - \frac{1}{N} \sum_i |\vec{v}_{pi}|$$

170   where $\vec{v}_{pi}$ indicates a unit vector from the central point of an individual to the central

171   point of their nearest neighbour i (Appendix 4). A Rayleigh test was used to investigate

172   whether the population of circular data from which a sample was drawn differed from

173   randomness, by comparing the sum of random vectors and the sum of observed vectors

174   (Wilkie, 1983).

175   To further analyse the spatial positions of nearest neighbours, we created a two-

176   body-length-diameter circular area surrounding a target individual and divided it into 24

177   zones with an angle of 15° per zone. The front direction of a target individual was set as

178   0° (or 360°), and the angle was defined in a counterclockwise direction. Each zone had a

179   15° range (0°–15°, 15°–30°, etc.; the left of a target individual was 90°, the back 180°,

180   and the right 270°). G-tests and residual analyses were run to examine the frequency at

181   which the nearest neighbour was located in each of these 24 zones compared with the

182   expected value. To investigate whether the overall trend came from just a few pairs, we

183   computed the laterality index (LI) in all observed pairs as follows: $LI = L / (L + R)$, where

184   L indicates the frequency of the nearest neighbour being located on the left side of the

185   target individual and R indicates the frequency for the right side. We computed the LI of

186   the rear individual in reference to the front individual because (1) if we calculated the LI

187   of a pair of individuals, A and B, by counting both the sides (left or right) of A in reference

188   to B and of B in reference to A, then the LI would always be zero, so the reference

189   individual needed to be fixed to one of the two individuals; and (2) the overall result

190   (described in the Results section) showed that the position of the nearest neighbour was

191   biased to the left-rear compared with the right-rear, and so we were interested to see if the

192   same trend could be seen in a pair-by-pair comparison, or if a certain pair contributed to

193   the overall results. Circular analyses and all statistical analyses were performed using

194   "Circular" package (Pocernich & Agostinelli, 2017), R 3.3.2 and RStudio (V1.1.447,

195   Rstudio, Inc.).

196

197   **3. Results**

198   For nearest neighbours within two body lengths, circular variance among directions was

199   0.52, which means that the distribution differed from uniform distribution, but that the

200   horses faced the same direction $(p < 0.01$, Rayleigh test; Appendix 5). Excluding mothers

201   and foals, density maps of nearest neighbours showed clear trends of locations that

202   significantly differed from uniform distribution (Figure 1; $n = 308$, $p < 0.01$, Rayleigh

203   test). Nearest neighbours were significantly more likely to be located in the left rear area

204   than in the right rear area $(n = 130$, $p = 0.021$, binomial test), but a trend for increased

205 frequency in the right front area compared with the left front area was not significant (n

206 $= 178$, $p = 0.30$, binomial test). These data came from a total of 45 pairs, and among these

207 pairs, 26 pairs showed bias to the left rear compared with right rear (i.e., LI > 0.5), 12

208 pairs showed bias to the right rear (LI < 0.5), and the remaining 7 pairs did not show side

209 bias (LI $= 0.5$; Appendix 3). When the surrounding area of an individual was divided into

210 15° zones, there was non-uniform frequency in the zone of the nearest neighbour (G-test,

211 $G = 40.641$, $df = 23$, $p = 0.01$). Residual analyses showed that the frequency of the nearest

212 neighbour in the 180°–195° zones was significantly lower than in other zones, while the

213 frequency of the nearest neighbour in the 120°–135° zones was significantly higher

214 (Table 1, Figure 2). Circular variance of vectors of an individual and its nearest neighbour

215 were 0.10 in the right front area and 0.086 in the left rear area (Figure 2).

216

217 **4. Discussion**

218   Our results were threefold. Firstly, the nearest neighbour was located to the left

219 rear of a target individual significantly more frequently than to the right rear. Secondly,

220 the nearest neighbour tended to be located to the right front of a target individual more

221   frequently than to the left front, although this trend was not significant. Thirdly, the

222   nearest neighbour was less frequently located behind a target individual, which is

223   consistent with a previous study (Inoue et al., 2018).

224   The following two scenarios can be postulated to interpret these three findings.

225   The first scenario assumes that the rear individual has the initiative in positioning behind

226   the front individual when the rear individual approaches the front individual. Given that

227   the nearest neighbour is located more often in left-rear of a target individual, this first

228   scenario would indicate that the rear individual has a preference to use its right eye to

229   monitor the front individual at its right front.

230   In contrast, the second possible scenario assumes that the front individual has

231   the initiative in positioning when it is approached by an individual from behind. When an

232   individual approaches another individual from behind, the front animal changes its

233   direction to avoid a situation where the other individual is located in its blind spot (i.e.,

234   behind the target individual). The front individual then turns its body to see the rear

235   individual using its left eye, resulting in the nearest neighbour (the rear individual) being

236   located in the left rear more than in the right rear position.

237   We consider the second scenario to be more plausible, because laterality would

238   be expected to appear more strongly when monocular vision is used than when binocular

239   vision can be used. When a rear individual approaches a front individual, the rear

240   individual can use binocular vision to see the front individual. However, when a front

241   individual attempts to see a rear individual, the front individual can use only monocular

242   vision (either the left eye or the right eye) by turning left or right. Because information

243   via the left eye, which predominantly proceeds to the right brain hemisphere, is dominant

244   in perceiving social stimuli, the front individual may then tend to turn its body to see the

245   rear individual using its left eye. This may explain why the nearest neighbour was less

246   frequently located behind the target individual, and was more frequently located in the

247   left rear than in the right rear.

248   A further interpretation is that, when individual A is the nearest neighbour of a

249   target individual B, then individual B is also likely to be the nearest neighbour of

250   individual A. Therefore, if the nearest neighbour of a target individual is more frequently

251   located in the left rear of the individual, then the nearest neighbour of the latter individual

252   would be located in the right front, assuming that the two individuals' head directions are

253 similar. This is consistent with our results, where the nearest neighbour tended to be

254 located in the right front rather than the left front. However, the head direction of the rear

255 individual is not always the same as that of the front individual and can vary (the rear

256 individual could approach the front individual from the right or left, because the rear

257 individual can use both eyes to monitor the front individual). Therefore, any trend in the

258 nearest neighbour's location would be expected to be weak due to variation in head

259 direction of the rear individual. This is also consistent with our finding that there was no

260 significant lateralisation of the nearest neighbour in the front of individuals.

261   To verify our results and interpretation, a sequential analysis of the change in

262 head direction of a front individual when it is approached from behind, toward the blind

263 spot, is warranted. Recordings of movements of a target and its nearest neighbour would

264 reveal which of these two has the initiative to decide positioning, and whether the

265 individual with the initiative has a preference to see conspecifics using its left or right eye.

266 The very short battery life of drones (approximately 15–20 min) is the most prominent

267 challenge to conducting a sequential analysis, and we could therefore not conduct such a

268 study. We expect that future advancement in technology will solve this challenge.

269   In sum, we found that spatial positioning of nearest neighbours is lateralised

270   among adult feral horses during foraging. Previous studies reported that the left eye and

271   right hemisphere are frequently used during agonistic and affiliative behaviours in horses

272   and other species (Austin & Rogers, 2012, 2014; Deckel, 1995; Farmer et al., 2018;

273   Garbanati et al., 1983). In addition, offspring of various mammal species tend to monitor

274   their mother using their left eye (Karenina et al., 2017). Our study illustrates that spatial

275   positioning bias is not restricted to mother-infant relationships, but can also be seen

276   between adults. However, we did not investigate developmental change with aging in the

277   present study and further research is needed to understand how this bias might change

278   with age. In addition, our research site was characterised by the presence of wolves, which

279   are predators of horses, and a future direction to be studied would thus include the

280   possibility that horses might use different eyes to detect conspecifics and predators.

281   Further quantitative studies using drones to investigate relationships between spatial

282   positioning and social variables, including sex and social rank, will provide new insight

283   into the effect of social relationships on spatial distributions, from local aspect to global

284   views; that is, from nearest neighbours to the whole group. In conclusion, technological

285   developments have allowed us to investigate the spatial relationships of terrestrial animals

286   in detail, and future advances may reveal the underlying mechanisms of these

287   relationships, which could lead to a better understanding of the evolutionary foundations

288   of human behaviour (Torney et al., 2018; Westley, Berdahl, Torney, & Biro, 2018)

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Author contributions

293   S.I. configured the study and collected and analysed data. M.R. and R.M. identified horses

294   and their groups. All authors contributed to the manuscript and approved the final version.

295

296

Competing interests

298   We declare no competing interests.

299

Ethical Statement

301   The field observations complied with guidelines for animal studies in the wild issued by

302   the Wildlife Research Center of Kyoto University, Japan.

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305

306 **Table 1** Residual analyses following a G-test for the frequency of nearest neighbours
307 within each zone.
308

| Zone (Degree)	Frequency	P-value
0-15	13	0.96
15-30	17	0.23
30-45	13	0.96
45-60	17	0.23
60-75	11	0.60
75-90	14	0.74
90-105	11	0.60
105-120	12	0.81
120-135	22	0.0090 *
135-150	9	0.27
150-165	11	0.60
165-180	11	0.60
180-195	3	0.0050 *
195-210	6	0.051
210-225	6	0.051
225-240	10	0.42
240-255	13	0.96
255-270	16	0.37
270-285	17	0.23
285-300	19	0.079
300-315	18	0.14
315-330	16	0.37
330-345	8	0.17
345-360	15	0.54

* indicates $p < 0.05$

309

310

311   **Figure**

312

313   **Figure 1**
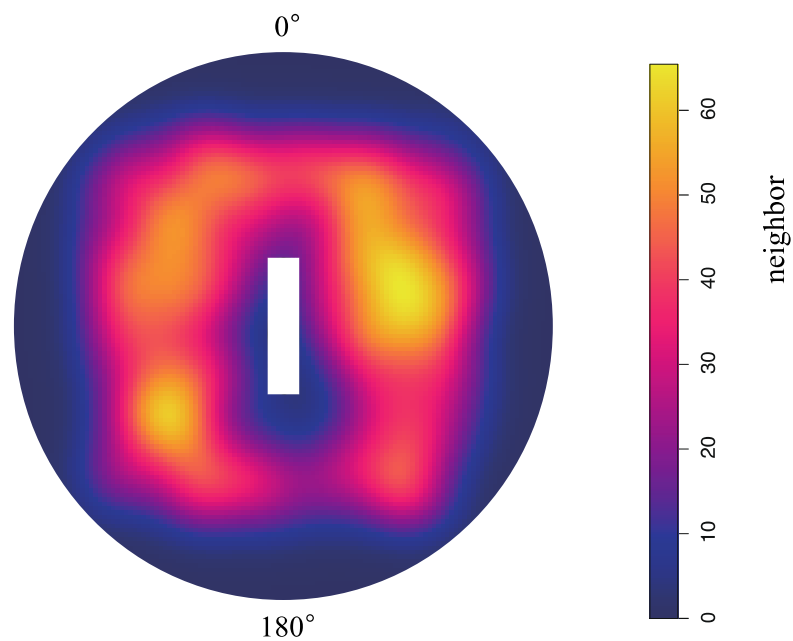
314

315   Heat map showing the density of nearest neighbours within two body lengths (BL) around
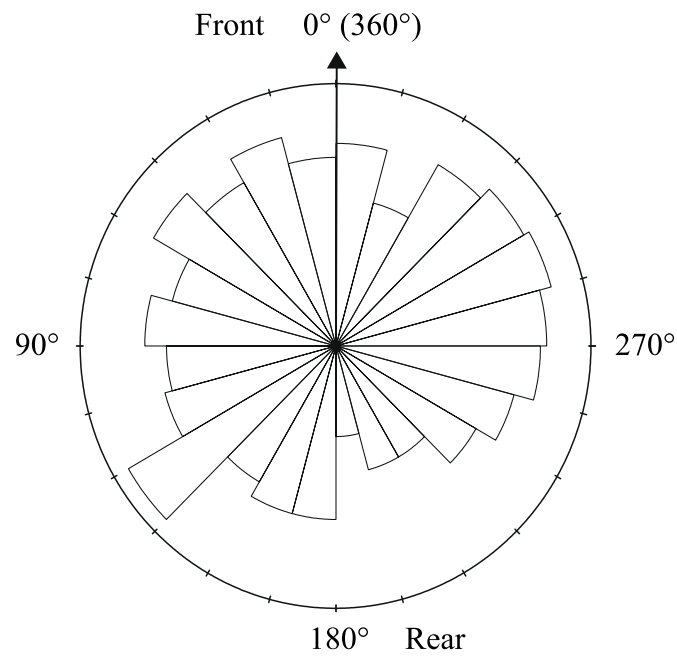
316   an individual. In total, 308 points were used to create this map and bin sizes were $\Delta x = \Delta y$

317    $= 0.67$ BL; there were 17 points per square unit.

318

319 **Figure 2**

320

321 Rose diagram of the positioning of nearest neighbours ($n = 308$). Each bar's height

322 represents the frequency of nearest neighbours in each zone. Circular variance was

323 higher in the right and front zones compared with the left and rear zones.

324

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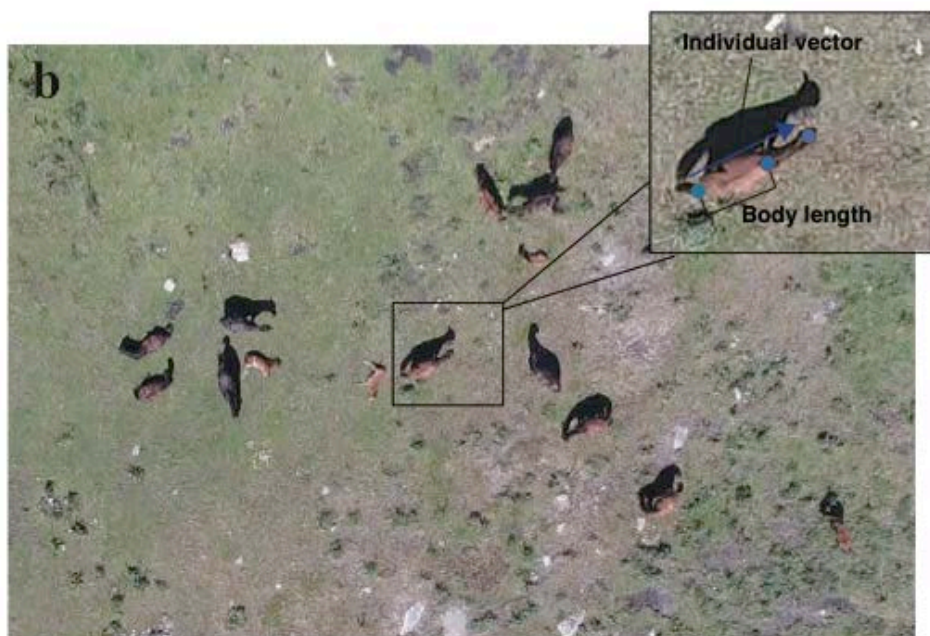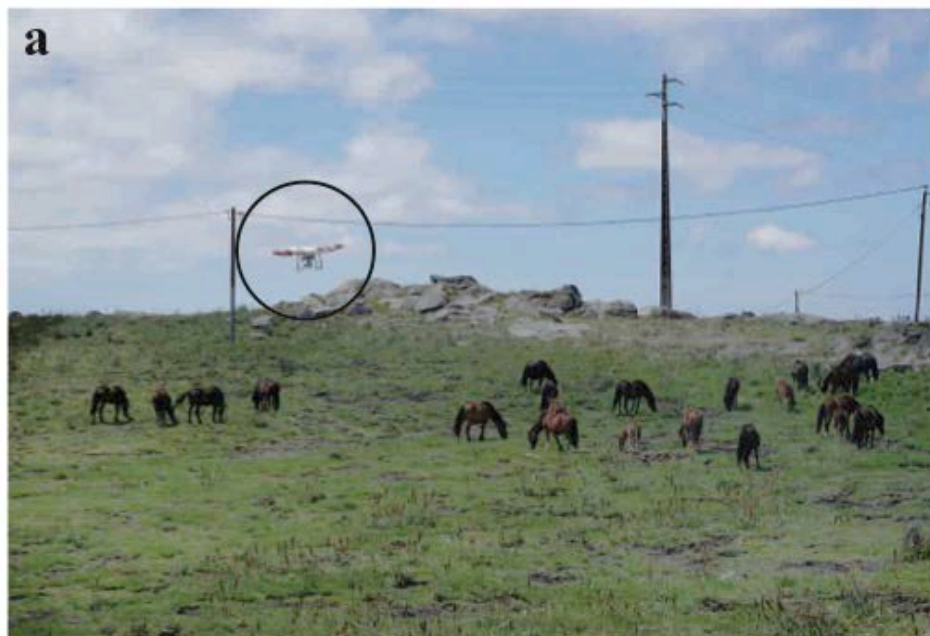424   *373*(1746). https://doi.org/10.1098/rstb.2017.0385

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435

436

437   **Appendix 1**

438

439   (a) Feral horses and the drone (circled in the figure) soon after take-off in Serra D'Arga.

440   (b) An example of images that were taken by the drone and used for analysis. An

441   individual's vector was defined as a vector from the base of the tail to the base of the

442   neck. Body length of an individual was defined as the magnitude of the individual's

443   vector, because this region was relatively inflexible and stable. Mean body length of all

444   adult individuals in one image was used as the unit of measurement for distance.

445   Because the absolute height of the drone was not consistent, we needed to use relative

446   distance to measure distances. We only used images that contained all group members.

447   Therefore, mean body length was always constant and was used as the unit of

448   measurement for distance.

449
450   **Appendix 2**
451

Kyoto 2016		Kyoto 2017		Hyogo 2017		Hyogo 2018	
Name	Sex	Name	Sex	Name	Sex	Name	Sex
Uzumasa	Male	Uzumasa	Male	Kobe	Male	Kobe	Male
Akashi	Female	Ayabe	Female	Akashi	Female	Akashi	Female
Ayabe	Female	Fushimi	Female	Himeji	Female	Fushimi	Female

Name	Sex	Name	Sex	Name	Sex	Name	Sex
Fushimi	Female	Gion	Female	Kakogawa	Female	Gion	Female
Gion	Female	Katsura	Female	Maiko	Female	Himeji	Female
Katsura	Female	Kishiwada	Female	Miki	Female	Kakogawa	Female
Kishiwada	Female	Kameoka (Katsura's son)	Male	Tarumi	Female	Maiko	Female
Uji	Female	Foal of Fushimi	Male	Uji	Female	Miki	Female
Foal of Katsura (Kameoka)	Male	Foal of Katsura	Male	Foal of Himeji	Female	Uji	Female
Foal of Uji	Female			Foal of Maiko	Female	Foal of Akashi	Male
						Foal of Uji	Male

452

453

454 **Appendix 3**

455

456 Ratio of lateral positioning of the nearest neighbor located in the rear area in all observed pairs.

457 LI indicates the Laterality Index, computed as $LI = L / (L + R)$, where L is the frequency of the

458 nearest neighbor in the left rear area of the target individual, and R is the frequency of the nearest

459 neighbor in the right rear area.

460

2016					Tarumi	Uji	0	3	0.00
Name	**Name**	**L**	**R**	**LI**	Uji	Miki	1	0	1.00
Ayabe	Fushimi	2	0	1.00	Uzumasa	Gion	1	0	1.00

Name	Name	L	R	LI
Ayabe	Gion	2	0	1.00
Fushimi	Ayabe	1	0	1.00
Gion	Fushimi	1	0	1.00
Kishiwada	Gion	1	0	1.00

2017

Name	Name	L	R	LI
Akashi	Kakogawa	1	0	1.00
Akashi	Miki	6	1	0.86
Akashi	Uji	5	2	0.71
Ayabe	Kameoka	1	0	1.00
Ayabe	Kishiwada	4	2	0.67
Gion	Kameoka	2	0	1.00
Gion	Kishiwada	1	1	0.50
Gion	Uji	2	2	0.50
Kakogawa	Kobe	1	0	1.00
Kakogawa	Miki	1	0	1.00
Kakogawa	Uji	2	4	0.33
Kameoka	Kishiwada	0	2	0.00
Kameoka	Miki	2	0	1.00
Kameoka	Uzumasa	1	0	1.00
Kobe	Tarumi	0	1	0.00
Miki	Kobe	1	1	0.50
Tarumi	Miki	0	1	0.00

Name	Name	L	R	LI
Uzumasa	Kishiwada	0	1	0.00

2018

Name	Name	L	R	LI
Fushimi	Gion	3	1	0.75
Fushimi	Himeji	2	0	1.00
Fushimi	Kakogawa	2	2	0.50
Fushimi	Maiko	2	1	0.67
Fushimi	Miki	4	2	0.67
Gion	Himeji	2	1	0.67
Gion	Kakogawa	1	2	0.33
Gion	Kobe	1	1	0.50
Gion	Miki	3	1	0.75
Himeji	Maiko	0	3	0.00
Himeji	Miki	3	7	0.30
Kakogawa	Maiko	3	1	0.75
Kobe	Himeji	2	0	1.00
Kobe	Kakogawa	0	1	0.00
Kobe	Maiko	2	2	0.50
Kobe	Miki	1	1	0.50
Maiko	Gion	0	1	0.00
Maiko	Miki	4	3	0.57
Miki	Kakogawa	2	3	0.40

461

462

463 **Appendix 4**
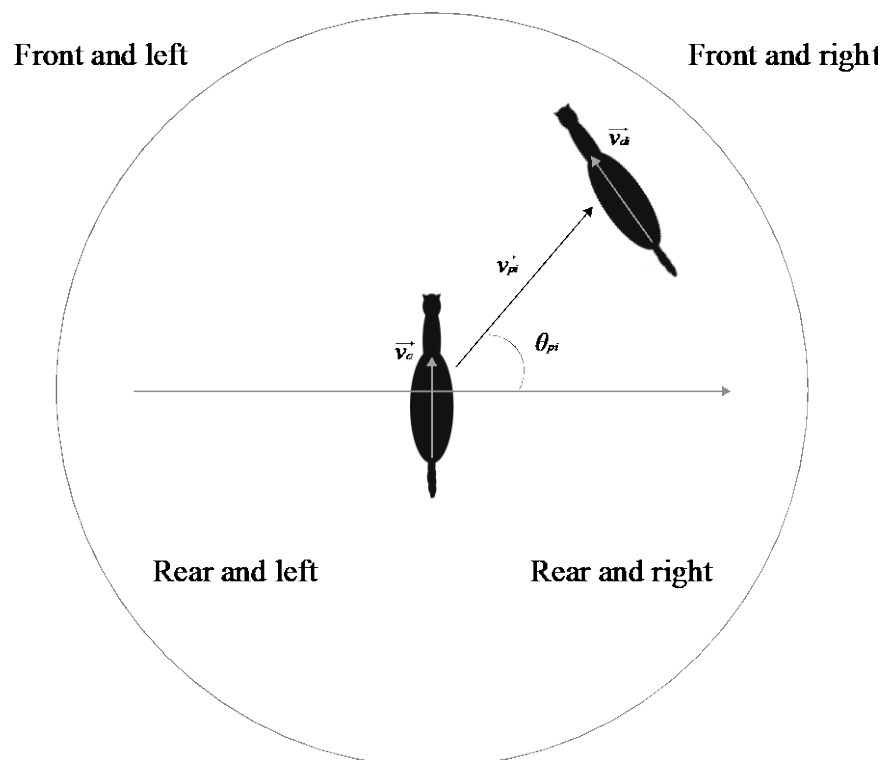
464

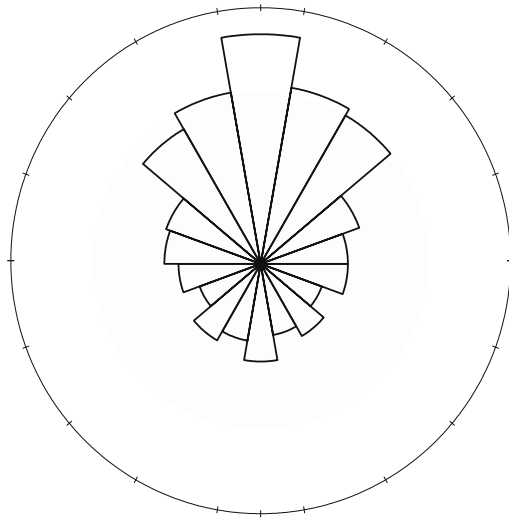465 Relationships among vectors used in the analysis of circular variance, and definitions of

466 each zone in the rear area of the target individual. We defined quadrants as the front and

467 right, rear and right, rear and left, and front and left areas.

468
469 **Appendix 5**

470

471   The histogram of the directions of nearest neighbours within two body lengths, with 0

472   being the same direction as the target individual.

473

474

475