

Title: Lateral position preference in grazing feral horses

Short running title: Spatial lateralisation in feral horses

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26

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.

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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

individuals face each other, and findings include the left-cradling bias in mother-infant relationships in humans and great apes (Giljov, Karenina, & Malashichev, 2018; Harris, 2010; Sieratzki & Woll, 1996). In species that have a relatively large binocular field of view, mothers hold their infants on the left side of the body in a counter-directed position, so that both are in an optimal position to monitor each other because both can use optimal information flow. The left-cradling bias in mother-infant relationships has recently been expanded to a diverse range of mammals, especially in species moving in codirected positions, where individuals are side-by-side on parallel paths. For example, offspring of the feral horse, Pacific walrus, Siberian tundra reindeer, saiga antelope, muskox, eastern grey kangaroo, red kangaroo, sheep, orca, and beluga whale are more often on the right side of their mothers than on the left (Giljov et al., 2018; Karenina, Giljov, Glazov, & Malashichev, 2013; Karenina et al., 2017; Karenina, Giljov, Ivkovich, Burdin, & Malashichev, 2013; Versace, Morgante, Pulina, & Vallortigara, 2007). Researchers consider that infants take the initiative in positioning in situations such as rest or slow movement, and prefer to view their mothers using the left eye. This consistency in laterality among mammals implies an ancient evolutionary origin of this bias. However,

it remains unknown whether the bias is limited to mother-infant relationships. If using the left eye field of view works well in mother-infant relationships, we might expect that this type of position bias also occurs between adults that live in groups, because adults also need to adjust their distance and positioning relative to other individuals to maintain group cohesion. To investigate whether lateral bias exists in spatial positioning among adult animals, we analysed data from adult feral horses. Feral horses usually form long-term stable groups (Berger, 1977) and do not frequently face each other in foraging situations, although mutual grooming and mutual swatting of flies are performed in counter-directed positions (i.e., two individuals facing opposite directions) (Feist, Mccullough, & Dean, 1976; Heleski, Shelle, Nielsen, & Zanella, 2002). Horses are a good species for studying behavioural lateralisation because they have a relatively small field of binocular vision, estimated at 80°, and their left and right eyes have largely independent views of their left and right sides, respectively (Harman, Moore, Hoskins, & Keller, 1999). Several studies have reported laterality in behaviours including agonistic and affiliative behaviours in counter-directed positions, vigilance to auditory stimuli, and relative spatial positioning in mother-infant relationships in horses in co-directed positions (i.e., two

individuals facing the same direction) (Austin & Rogers, 2012, 2014; Farmer, Krueger, & Byrne, 2010; Farmer, Krüger, Byrne, & Marr, 2018; Karenina et al., 2017; Karenina, Giljov, & Malashichev, 2018). According to previous studies, horses frequently use their left eyes during these behaviours, similar to other species. Specifically, horses have a left-eye preference for monitoring novel stimuli, and a left-body preference for threatening and attacking within harem bands and for positive social interactions in mother-infant relationships (Austin & Rogers, 2014; Karenina et al., 2017; Larose, Richard-Yris, Hausberger, & Rogers, 2006). Thus, functional lateralisation is not limited to infancy but continues throughout adulthood. We therefore hypothesised that this left-eye bias in monitoring conspecifics also occurs in adult–adult spatial positioning, although we did not have a detailed specific hypothesis as to which way such a lateral bias might appear in spatial positioning; as such, our study was exploratory in nature. The present study aimed to address the question of whether previously observed lateral preferences are reflected in the positioning of adult horses while grazing, and if so, which side is preferred.

2. Materials and methods

In the present study, we analysed images taken from drones, which allowed us to test whether there was any lateral bias in spatial positioning in adult horses during foraging, with a focus on the position of a target horse and its nearest neighbouring individual.

The study was conducted in Serra D'Arga, an 825 m high mountain located in northern Portugal (8°42'N, 41°48'E). The horses' habitat included a grass field, rocky ground, a forest, and shrub areas (Ringhofer et al., 2017) (Appendix 1). Over 250 identified feral horses, categorised as Garrano horses, lived in the site. They roamed freely over the mountain living on the natural grazing and water resources. There were no artificial barriers to impede their movement, they did not have daily human contact, and they were not fed by humans. Horses form long-term stable harems and unstable bachelor groups, and we focused on two harems in June 2016, May–July 2017, and May–July 2018.

We chose the two groups because it was relatively easy to find these groups compared with other groups. Both were one-male harems. We followed 10 individuals in 2016, 19 individuals in 2017, and 11 individuals in 2018. Kameoka, in Kyoto 17, was one year old, and was an immature male and, not the stallion (Appendix 2). In 2017, Kyoto and Hyogo were constantly together and kept a close distance between one another; there were

therefore cases in which the nearest neighbour of an individual was a horse from the other group. Eight horses were less than 1 year old and these individuals were excluded from the analysis due to their high dependency on their mothers, because the aim of the present study was to analyse adult individuals. For the same reason, data from the mothers of these foals were also excluded from the analysis. Although seven foals died before 1 year of age, one foal survived beyond 1 year and the individual was included in the analysis from this point on. In sum, 5 individuals in 2016, 11 individuals in 2017, and 7 individuals in 2018 contributed to the data.

The recordings involved 4–13 (average 6.7) video clips per day and these were taken between 9:00 and 18:00. Video clips were taken for approximately 15 min every 30 min, from 25–80 m above the ground (the heights were decided on a case-by-case basis to be able to include all target group individuals in one image) using unmanned aerial vehicles (drones). Still images were obtained by taking images from the video clips after 1 min from the beginning of the clips (i.e., there was 30 min between two consecutive still images). The distortion of the camera lens was corrected using the lens filter function in Photoshop CC (Adobe Systems incorporated) (Inoue et al., 2018). The drone took off

10–50 m away from the horses. The drones used for collecting data were the Phantom 3 Advanced, Phantom 3 Professional, and Mavic Pro (DJI, China). Behavioural observation was performed by SI during flights to estimate group states. We defined the states as foraging, traveling, and resting, and only analysed data during foraging because horses change their spatial positioning formation depending on their state (Inoue et al., 2018). After excluding images of horses in the resting or traveling states, 184 images were analysed. All harem group members were recorded and clearly visible in each of the 184 images (Appendix 1).

We measured an individual's coordinates as a central point between the head and the base of the tail and defined an individual's direction as a vector from the base of the tail to the base of the neck; the magnitude of the vector was defined as the body length. Mean body length of adult horses was used as a unit of distance, because it is relatively stable and fixed (Appendix 1). Using individuals' coordinates in each image, nearest neighbours were determined for each individual. When the distance to the nearest neighbour was more than two body lengths, data were excluded from the analysis according to previous studies (Karenina et al., 2017; Inoue et al., 2018). To analyse spatial

relationships among adults only, we excluded mothers and foals from the analysis. Although it is known that proximity between individuals is related to their social bonds, our analysis did not rely on just a few pairs (Appendix 3) (Kimura, 1998; Schneider & Krueger, 2012; Wolter, Stefanski, & Krueger, 2018). A total of 308 points were analysed to quantify relative positioning.

Circular variance was calculated to analyse the degree of variance in body direction of individuals (CV_d):

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

where N is the number of vectors $\vec{v}_{di}$, and $\vec{v}_{di}$ indicates a unit vector of the direction of individual i (Appendix 4). If all individuals face the same direction, $CV_d = 0$, whereas if they face completely random directions, $CV_d = 1$. Circular variance among individuals' positions (CV_p) was calculated from the same formula:

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

where $\vec{v}_{pi}$ indicates a unit vector from the central point of an individual to the central point of their nearest neighbour i (Appendix 4). A Rayleigh test was used to investigate 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

individual needed to be fixed to one of the two individuals; and (2) the overall result (described in the Results section) showed that the position of the nearest neighbour was biased to the left-rear compared with the right-rear, and so we were interested to see if the same trend could be seen in a pair-by-pair comparison, or if a certain pair contributed to the overall results. Circular analyses and all statistical analyses were performed using “Circular” package (Pocernich & Agostinelli, 2017), R 3.3.2 and RStudio (V1.1.447, Rstudio, Inc.).

3. Results

For nearest neighbours within two body lengths, circular variance among directions was 0.52, which means that the distribution differed from uniform distribution, but that the horses faced the same direction ($p < 0.01$, Rayleigh test; Appendix 5). Excluding mothers and foals, density maps of nearest neighbours showed clear trends of locations that significantly differed from uniform distribution (Figure 1; $n = 308$, $p < 0.01$, Rayleigh test). Nearest neighbours were significantly more likely to be located in the left rear area than in the right rear area ($n = 130$, $p = 0.021$, binomial test), but a trend for increased

frequency in the right front area compared with the left front area was not significant ($n = 178, p = 0.30$, binomial test). These data came from a total of 45 pairs, and among these pairs, 26 pairs showed bias to the left rear compared with right rear (i.e., $LI > 0.5$), 12 pairs showed bias to the right rear ($LI < 0.5$), and the remaining 7 pairs did not show side bias ($LI = 0.5$; Appendix 3). When the surrounding area of an individual was divided into 15° zones, there was non-uniform frequency in the zone of the nearest neighbour (G-test, $G = 40.641, df = 23, p = 0.01$). Residual analyses showed that the frequency of the nearest neighbour in the 180° – 195° zones was significantly lower than in other zones, while the frequency of the nearest neighbour in the 120° – 135° zones was significantly higher (Table 1, Figure 2). Circular variance of vectors of an individual and its nearest neighbour were 0.10 in the right front area and 0.086 in the left rear area (Figure 2).

4. Discussion

Our results were threefold. Firstly, the nearest neighbour was located to the left rear of a target individual significantly more frequently than to the right rear. Secondly, 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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292 **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.

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297 **Competing interests**

298 We declare no competing interests.

299

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

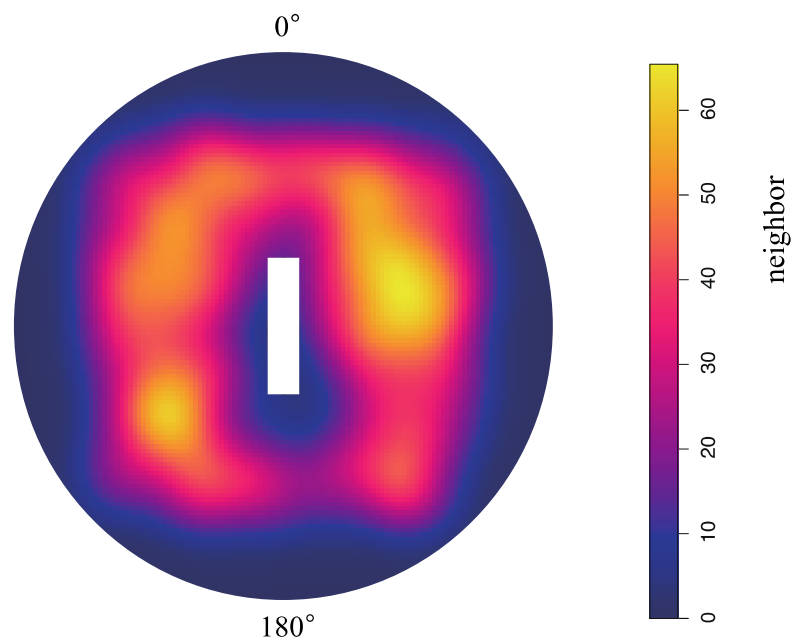
Zone (Degree)	Frequency	P-value
0-15	13	0.96
15-30	17	0.23
30-45	13	0.96
45-60	17	0.23
60-75	11	0.60
75-90	14	0.74
90-105	11	0.60
105-120	12	0.81
120-135	22	0.0090 *
135-150	9	0.27
150-165	11	0.60
165-180	11	0.60
180-195	3	0.0050 *
195-210	6	0.051
210-225	6	0.051
225-240	10	0.42
240-255	13	0.96
255-270	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 $p < 0.05$

311 **Figure**

312

313 **Figure 1**



314

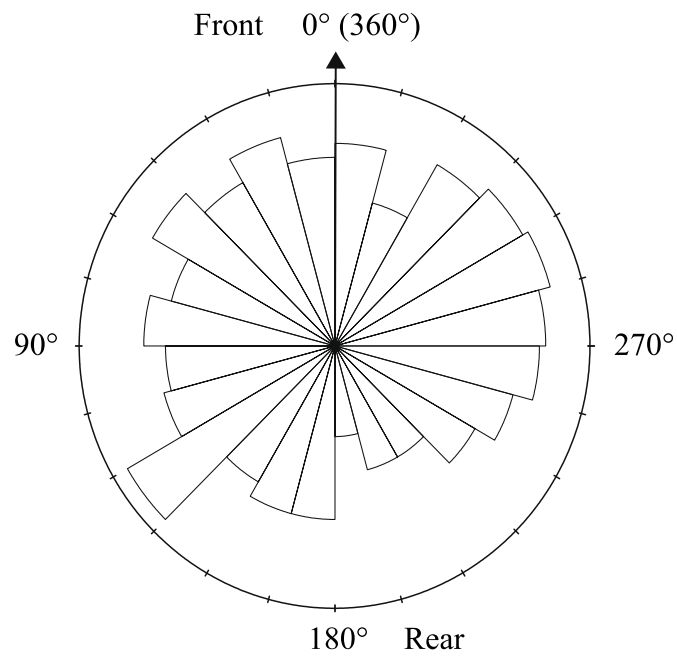
315 Heat map showing the density of nearest neighbours within two body lengths (BL) around

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

325 **References**

- 326 Angelo Bisazza, L. J. Rogers. and G. Vallortigara. (1998). The Origins of Cerebral
327 Asymmetry: A Review of Evidence of Behavioural and Brain Lateralization in
328 Fishes, Reptiles and Amphibians, 22(3), 411–426. [https://doi.org/10.1016/S0149-](https://doi.org/10.1016/S0149-7634(97)00050-X)
329 7634(97)00050-X
- 330 Austin, N. P., & Rogers, L. J. (2012). Limb preferences and lateralization of aggression,
331 reactivity and vigilance in feral horses, *Equus caballus*. *Animal Behaviour*, 83(1),
332 239–247. <https://doi.org/10.1016/j.anbehav.2011.10.033>
- 333 Austin, N. P., & Rogers, L. J. (2014). Lateralization of agonistic and vigilance
334 responses in Przewalski horses (*Equus przewalskii*). *Applied Animal Behaviour*
335 *Science*, 151, 43–50. <https://doi.org/10.1016/j.applanim.2013.11.011>
- 336 Berger, J. (1977). Organizational systems and dominance in feral horses in the Grand
337 Canyon. *Behavioral Ecology and Sociobiology*, 2(2), 131–146.
338 <https://doi.org/10.1007/BF00361898>
- 339 Brancucci, A., Lucci, G., Mazzatenta, A., & Tommasi, L. (2009). Asymmetries of the
340 human social brain in the visual, auditory and chemical modalities. *Philosophical*
341 *Transactions of the Royal Society B: Biological Sciences*, 364(1519), 895–914.

342 <https://doi.org/10.1098/rstb.2008.0279>

343 Deckel, A. W. (1995). Laterality of Aggressive Responses in *Anolis*, 200, 194–200.

344 Farmer, K., Krueger, K., & Byrne, R. W. (2010). Visual laterality in the domestic horse

345 (*Equus caballus*) interacting with humans. *Animal Cognition*, 13(2), 229–238.

346 <https://doi.org/10.1007/s10071-009-0260-x>

347 Farmer, K., Krüger, K., Byrne, R. W., & Marr, I. (2018). Sensory laterality in affiliative

348 interactions in domestic horses and ponies (*Equus caballus*). *Animal Cognition*,

349 21(5), 631–637. <https://doi.org/10.1007/s10071-018-1196-9>

350 Feist, D., McCullough, R., & Dean, J. (1976). Behavior patterns and communication in

351 feral horses population, with the exception of completion of a range boundary

352 fence. *Ethology*, 371(4), 337–371. [https://doi.org/10.1111/j.1439-](https://doi.org/10.1111/j.1439-0310.1976.tb00947.x)

353 [0310.1976.tb00947.x](https://doi.org/10.1111/j.1439-0310.1976.tb00947.x)

354 Garbanati, J. A., Sherman, G. F., Rosen G. D., Hofmann M., Yutzey, D. A., Denenberg,

355 V. H. (1983). Handling in infancy, brain laterality and muricide in rats.

356 *Behavioural Brain Research*, 7, 351–359.

357 Giljov, A., Karenina, K., & Malashichev, Y. (2018). Facing each other: Mammal

358 mothers and infants prefer the position favouring right hemisphere processing.
359 *Biology Letters*, 14(1). <https://doi.org/10.1098/rsbl.2017.0707>

360 Halpern, M. E. (2005). Lateralization of the Vertebrate Brain: Taking the Side of Model
361 Systems. *Journal of Neuroscience*, 25(45), 10351–10357.
362 <https://doi.org/10.1063/1.4810907>

363 Harman, A. M., Moore, S., Hoskins, R., & Keller, P. (1999). Horse vision and an
364 explanation for the visual behaviour originally explained by the “ramp retina.”
365 *Equine Veterinary Journal*, 31(5), 384–390. [https://doi.org/10.1111/j.2042-](https://doi.org/10.1111/j.2042-3306.1999.tb03837.x)
366 [3306.1999.tb03837.x](https://doi.org/10.1111/j.2042-3306.1999.tb03837.x)

367 Harris, L. J. (2010). Side biases for holding and carrying infants: Reports from the past
368 and possible lessons for today. *Laterality* (Vol. 15).
369 <https://doi.org/10.1080/13576500802584371>

370 Heleski, C. R., Shelle, A. C., Nielsen, B. D., & Zanella, A. J. (2002). Influence of
371 housing on weanling horse behavior and subsequent welfare, 78.

372 Jackson H. (1915). On the nature of the duality of the brain. *Brain*, 38(1–2), 80–86.
373 <https://doi.org/10.1093/brain/38.1-2.80>

374 Karenina, K., Giljov, A., Glazov, D., & Malashichev, Y. (2013). Social laterality in
375 wild beluga whale infants: Comparisons between locations, escort conditions, and
376 ages. *Behavioral Ecology and Sociobiology*, 67(7), 1195–1204.
377 <https://doi.org/10.1007/s00265-013-1545-2>

378 Karenina, K., Giljov, A., Ingram, J., Rowntree, V. J., & Malashichev, Y. (2017).
379 Lateralization of mother-infant interactions in a diverse range of mammal species.
380 *Nature Ecology and Evolution*, 1(2). <https://doi.org/10.1038/s41559-016-0030>

381 Karenina, K., Giljov, A., Ivkovich, T., Burdin, A., & Malashichev, Y. (2013).
382 Lateralization of spatial relationships between wild mother and infant orcas,
383 *Orcinus orca*. *Animal Behaviour*, 86(6), 1225–1231.
384 <https://doi.org/10.1016/j.anbehav.2013.09.025>

385 Karenina, K., Giljov, A., & Malashichev, Y. (2018). Lateralization of mother-infant
386 interactions in wild horses. *Behavioural Processes*, 148(November 2017), 49–55.
387 <https://doi.org/10.1016/j.beproc.2018.01.010>

388 Kimura, R. (1998). Mutual grooming and preferred associate relationships in a band of
389 free-ranging horses. *Applied Animal Behaviour Science*, 59(4), 265–276.

390 Larose, C., Richard-Yris, M. A., Hausberger, M., & Rogers, L. J. (2006). Laterality of
391 horses associated with emotionality in novel situations. *Laterality*, 11(4), 355-367.

392 LeMay, M. (1976). Morphological Cerebral Asymmetries of Modern Man, Fossil Man,
393 and Nonhuman Primate. *Annals of the New York Academy of Sciences*, 280(1
394 Origins and E), 349–366. <https://doi.org/10.1111/j.1749-6632.1976.tb25499.x>

395 Levy, J. (1977). the Mammalian Brain and the Adaptive Advantage of Cerebral
396 Asymmetry. *Annals of the New York Academy of Sciences*, 299(1), 264–272.
397 <https://doi.org/10.1111/j.1749-6632.1977.tb41913.x>

398 Lindell, A. K. (2013). Continuities in Emotion Lateralization in Human and Non-
399 Human Primates. *Frontiers in Human Neuroscience*, 7(August), 1–9.
400 <https://doi.org/10.1016/j.neuron.2014.08.058>

401 Nagy, M., Ákos, Z., Biro, D., & Vicsek, T. (2010). Hierarchical group dynamics in
402 pigeon flocks. *Nature*, 464(7290), 890–893. <https://doi.org/10.1038/nature08891>

403 Okubo, M., Ishikawa, K., & Kobayashi, A. (2013). No trust on the left side: Hemifacial
404 asymmetries for trustworthiness and emotional expressions. *Brain and Cognition*,
405 82(2), 181–186. <https://doi.org/10.1016/j.bandc.2013.04.004>

406 Pocernich, M., & Agostinelli, M. C. (2017). Package ‘circular.’

407 Ringhofer, M., Inoue, S., Mendonça, R. S., Pereira, C., Matsuzawa, T., Hirata, S., &

408 Yamamoto, S. (2017). Comparison of the social systems of primates and feral

409 horses: data from a newly established horse research site on Serra D’Arga,

410 northern Portugal. *Primates*, 58(4), 479–484. [https://doi.org/10.1007/s10329-017-](https://doi.org/10.1007/s10329-017-0614-y)

411 0614-y

412 Schneider, G., & Krueger, K. (2012). Third-party interventions keep social partners

413 from exchanging affiliative interactions with others. *Animal behaviour*, 83(2), 377-

414 387.

415 Sieratzki J.S., & Woll B. (1996). Why do mothers carry babies on their left. *Advances in*

416 *Child Development and Behavior*, 1746–1748.

417 <https://doi.org/10.1103/PhysRevLett.87.133603>

418 Inoue S., Yamamoto S., Ringhofer M., Mendonça R. S., Pereira C. & Hirata S. (2018).

419 Spatial positioning of individuals in a group of feral horses : a case study using

420 drone technology, e.

421 Torney, C. J., Lamont, M., Debell, L., Angohiatok, R. J., Leclerc, L. M., & Berdahl, A.

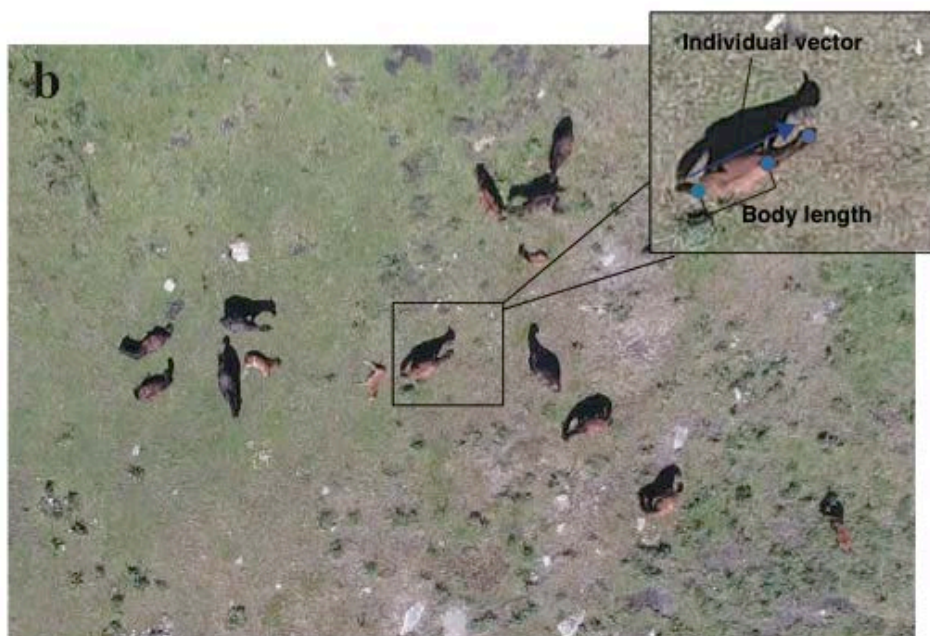
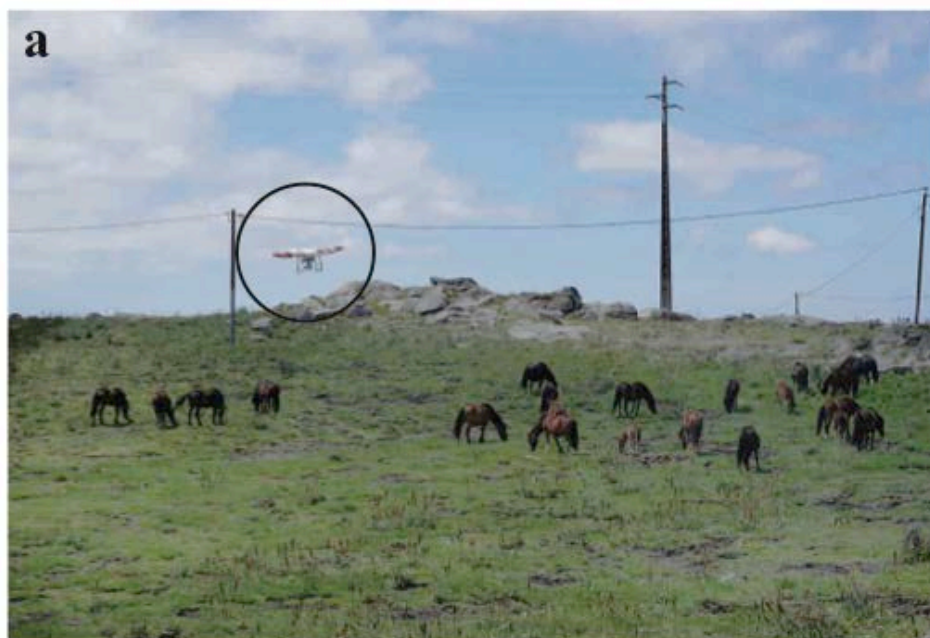
422 M. (2018). Inferring the rules of social interaction in migrating caribou.
423 *Philosophical Transactions of the Royal Society B: Biological Sciences*,
424 373(1746). <https://doi.org/10.1098/rstb.2017.0385>

425 Versace, E., Morgante, M., Pulina, G., & Vallortigara, G. (2007). Behavioural
426 lateralization in sheep (*Ovis aries*). *Behavioural Brain Research*, 184(1), 72–80.
427 <https://doi.org/10.1016/j.bbr.2007.06.016>

428 Wolter, R., Stefanski, V., & Krueger, K. (2018). Parameters for the Analysis of Social
429 Bonds in Horses. *Animals*, 8(11), 191.

430 Westley, P. A. H., Berdahl, A. M., Torney, C. J., & Biro, D. (2018). Collective
431 movement in ecology: From emerging technologies to conservation and
432 management. *Philosophical Transactions of the Royal Society B: Biological*
433 *Sciences*, 373(1746). <https://doi.org/10.1098/rstb.2017.0004>

434 Wilkie, D. (1983). Rayleigh test for randomness of circular data. In *Applied statistics*.
435
436



(b) An example of images that were taken by the drone and used for analysis. An individual's vector was defined as a vector from the base of the tail to the base of the neck. Body length of an individual was defined as the magnitude of the individual's vector, because this region was relatively inflexible and stable. Mean body length of all adult individuals in one image was used as the unit of measurement for distance. Because the absolute height of the drone was not consistent, we needed to use relative distance to measure distances. We only used images that contained all group members. Therefore, mean body length was always constant and was used as the unit of measurement for distance.

Appendix 2

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

Fushimi	Female	Gion	Female	Kakogawa	Female	Gion	Female
Gion	Female	Katsura	Female	Maiko	Female	Himeji	Female
Katsura	Female	Kishiwada	Female	Miki	Female	Kakogawa	Female
		Kameoka					
Kishiwada	Female	(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

Appendix 3

Ratio of lateral positioning of the nearest neighbor located in the rear area in all observed pairs. LI indicates the Laterality Index, computed as $LI = L / (L + R)$, where L is the frequency of the nearest neighbor in the left rear area of the target individual, and R is the frequency of the nearest neighbor in the right rear area.

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

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

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

Uzumasa	Kishiwada	0	1	0.00
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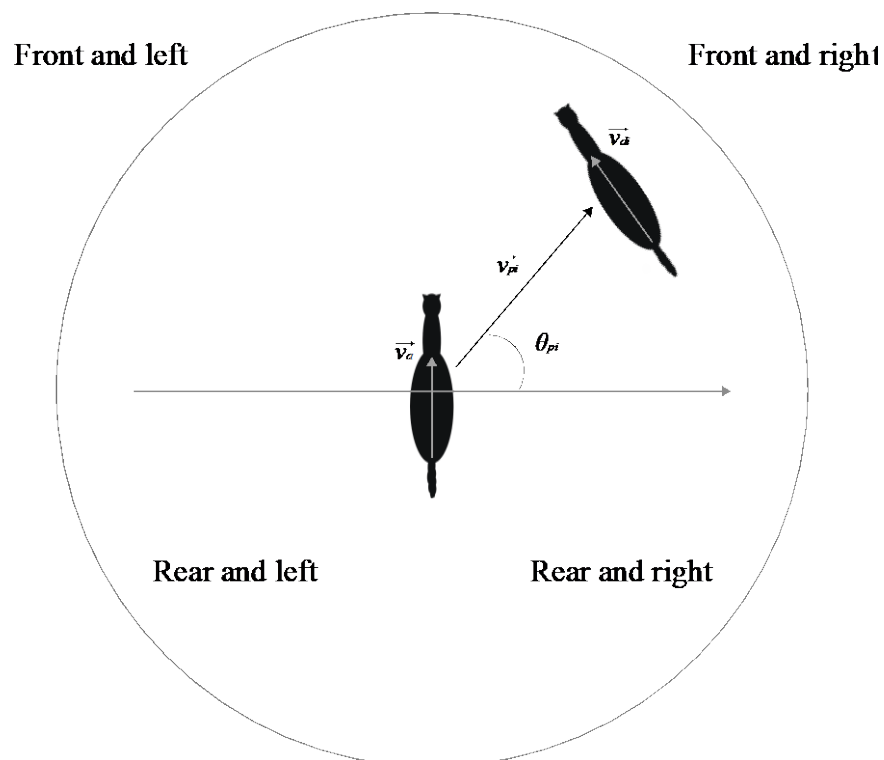
2018

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

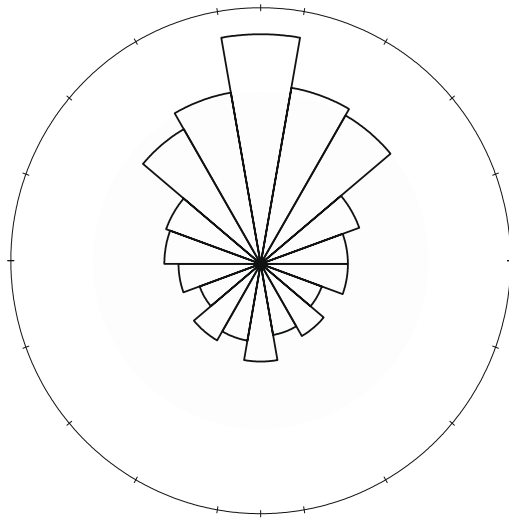
465 Relationships among vectors used in the analysis of circular variance, and definitions of

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