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1 **A preliminary comparison between proximity and interaction-based methods to**
2 **construct equine (*Equus caballus*) social networks**

3

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8

9 **Highlights**

- 10 • Social networks based on proximity were similar to affiliative interaction networks
- 11 • Global Positioning System units enabled equine proximity networks to be constructed
- 12 • Utilising wearable technology proved a more cost-effective means of data collection
- 13 • It is unclear if considering activity level is useful for building social networks

14 **Abstract**

15 Evidence suggests that keeping horses in groups may be beneficial, as increased opportunities
16 for social interaction have been linked to improved welfare and trainability. Considering social
17 structure within these groups is also recommended, so attempts may be made to minimise inter-
18 horse aggression and subsequent injury risk, thus encouraging more owners to adopt this
19 management practice. Manual observation of dyadic interactions is often considered the most
20 reliable way to determine group structure. However, alternative methods, such as the use of
21 inter-individual proximity, may be more practical but first requires validation in the species of
22 interest to ensure reliability.

23 Four interaction-based methods, which considered (1) 'All observed', (2) 'Affiliative', (3)
24 'Allogrooming' and (4) 'Agonistic' equine interactions, were used to construct social networks
25 for three small domestic horse groups following 20hrs of observation. Horses also wore Global
26 Positioning System (GPS) units, so distance between group members could be calculated every
27 10-minute, with this information used to create proximity networks for each group. Mantel
28 tests were run in Socprog2.9 to determine if networks based on observed interactions are
29 structurally similar to those based on inter-individual proximity. Accelerometers were also

30 used to monitor horse activity, to investigate the effect that filtering proximity data by activity
31 level has on its agreement with interaction-based methods.

32 Mantel tests identified that proximity networks were similar to networks based on affiliative
33 interactions between horses, with positive but non-significant agreement seen in all three
34 groups ('Group A': $Z=0.85438$, $n=4$, $P=0.05$; 'Group B': $Z=0.61582$, $n=3$, $P=0.475$; 'Group
35 C': $Z=0.88925$, $n=4$, $P=0.05$) Proximity was not seen to be significantly associated with any
36 other methods.

37 These findings suggest that GPS-derived proximity may be a viable alternative to manually
38 collected data when affiliative interactions are of interest. Although, more work is warranted
39 to establish how generalisable these results are in larger groups, and how variables, such as
40 field size, group composition and resource provision, influence method agreement. Ultimately,
41 this study has assessed agreement between existing social network techniques, whilst also
42 considering the costs associated with each, the results of which are of use to inform both equine
43 management and future studies.

44

45 **Keywords:** Accelerometry; Equine; Global Positioning Systems; Social network analysis

46

47 **Introduction**

48 Horses (*Equus caballus*) are highly gregarious, with social behaviours playing an important
49 role within herds. Despite this, modern equine management limits opportunities for social
50 contact due to the extensive use of single box housing (Ruet et al., 2019), regardless of the fact
51 that this management style has been linked to increased stress (Visser, et al., 2008; Yarnell, et
52 al., 2015) reactivity (Lesimple, et al., 2011) and increased stereotypies in horses (Normando,
53 et al., 2011). This is largely due to concerns that group housing increases aggressive encounters
54 and injury risk (Hartmann et al., 2015). Consequently, work to improve understanding of social
55 structure within domestic horse groups may help to overcome this by enabling more informed
56 companion selection and the identification of factors that increase the frequency of aggressive
57 encounters. Monitoring group structure may also provide a novel method to assess both welfare
58 (Boissy et al., 2007; Koene and Ipema, 2013), stress (Proudfoot & Habing, 2015), and better
59 understand the influence of social status on parameters such as foraging efficacy and weight
60 maintenance (Giles, et al., 2020).

61 Social network analysis (SNA) is a widely used technique to summarise social structure within
62 a group (Davis, et al., 2018;). It typically involves either the manual observation and recording

63 of all dyadic interactions that occur within the group ('interaction-based' approach) or
64 monitoring spatial association between individuals within the group ('proximity-based'
65 approach) (Croft, et al., 2008). Whilst interaction-based methods are widely considered to be
66 the most reliable representation of true social structure (Whitehead, 2008), the practical
67 application of this method is limited by the need to manually monitor the group, which may
68 not be possible outside of daylight hours or for wide roaming species (Marchant-Forde, 2015).
69 Consequently, proximity-based methods may be more readily applied to equid groups,
70 particularly as data may be collected remotely, causing minimal disruption to the animals, with
71 the addition of devices such as proximity collars (Boyland et al., 2013) or global positioning
72 system (GPS) units (Hampson et al., 2010; Sato et al., 2017). As this method may be considered
73 more convenient and is potentially less sensitive to observer influence and subjectivity, some
74 may consider it a more practical substitute for interaction-based techniques. Whether or not
75 these two methods can be used interchangeably continues to be a contentious topic amongst
76 animal researchers (Castles et al., 2014; Davis et al., 2018; Farine et al., 2016). It appears that,
77 whilst there may be potential for proximity to act as a valid proxy for social interactions,
78 research is needed to assess under what conditions, and with which species, this is a reliable
79 alternative (Farine, 2015b). Proximity may be a good predictor of interaction context in the
80 horse as affiliative social equine behaviours, such as mutual grooming or resting together,
81 require individuals to be close to one another for a prolonged period of time (Wolter, et al.,
82 2018). In feral horse groups, some agreement between the frequency of mutual grooming and
83 spatial proximity was reported (Wolter et al., 2018), suggesting that social networks
84 constructed using these different methods may be comparable. However, it is unclear if the
85 same would be seen within domestic groups, particularly as differences in the social behaviour
86 and group spacing has been observed between horses kept under naturalistic and domestic
87 conditions (Christensen, et al., 2002).

88 The identification of affiliative relationships within equine proximity networks may be
89 enhanced if activity levels during dyadic interactions are considered (Farine, 2015; Muller, et
90 al., 2018). This could be achieved with the application of wearable accelerometers (Bailey et
91 al., 2018; Burla et al., 2014) and may help to determine if close proximity is due to a chance
92 passing or a high intensity agonistic interaction, rather than a decision to remain stationary near
93 another individual for an extended period of time (Farine, 2015).

94 The work of Castles et al. (2014) and Farine (2015) clearly highlights that work to compare
95 different methods of social networks construction is warranted, particularly when these

96 networks are focussed on domestically housed horse groups. Therefore, we addressed the
 97 following questions: (1) Are equine social networks based on inter-individual proximity
 98 comparable with those based on context-specific interactions? (2) Does filtering proximity data
 99 by activity level improve agreement with interaction-based networks? We also consider the
 100 reliability and associated cost of each method to fully realise their potential for real-life
 101 application.

102

103 **Methodology**

104 **Animals and Housing**

105 During May, June and July 2019, three independent groups of mature horses, referred to as
 106 ‘Group A’ ($n=4$; mean age 20 ± 4.55 [SD] years), ‘Group B’ ($n=3$; mean age 17.67 ± 7.09 [SD]
 107 years) and ‘Group C’ ($n=4$; mean age 16 ± 7.17 [SD] years) were studied (*table 1*). All groups
 108 were considered stable, having been together for a minimum of three years, and at the time of
 109 the study were living out in their respective fields at either ‘Location 1’ ($50^{\circ}48'48''N$,
 110 $0^{\circ}57'35''W$; Field size: $2325.66m^2$) (‘Group A’ (during May/ early June) and ‘Group C’ (late
 111 June/ July)) or ‘Location 2’ ($50^{\circ}49'07''N$, $0^{\circ}58'59''W$; Field size: $3108.25m^2$) (‘Group B’
 112 during May 2019) for 24 hrs per day, seven days per week. These fields were considered to
 113 contain adequate grass for all individuals without need for additional forage, with all horses
 114 receiving only one small concentrate feed in the evening around 19:00h. Some shelter was
 115 provided by a row of mixed-species trees that bordered the fields on the East and West side in
 116 ‘Location 1’ and the North side in ‘Location 2’. No additional resources were provided other
 117 than a water trough, which was a permanent fixture in each field.

118

119 **Table 1** - Overview of sample population

Study I.D.	Group	Height (cm)	Breed	Age (yrs)	Sex
1	A	149.86	New Forest	25	M
2	A	137.16	New Forest X	14	G
3	A	139.70	Welsh Sec C X	20	M
4	A	157.48	TB X	21	M
5	B	139.70	New Forest	10	G
6	B	162.56	TB X	19	M
7	B	132.08	New Forest	24	G
8	C	142.24	New Forest	20	M
9	C	139.70	Appaloosa X	9	G

10	C	132.08	Connemara	24	M
11	C	144.78	Cob X	11	M

120

121 **Observation protocol**

122 On randomly assigned days during this time period, groups were observed for 2 hr periods,
 123 during which time all dyadic interactions, the time at which they occurred, and the individuals
 124 involved were recorded using a continuous behaviour sampling method, supported by a study
 125 specific ethogram (table 2). All observations were completed by one observer, who was
 126 familiar with equine behaviour and positioned a minimum of 2m outside of the field fence line.
 127 Prior to the study onset, this observer was tested for reliability against another also familiar
 128 with equine behaviour.

129 Horse observations (2hrs) took place in either the morning (between 9:00 and 13:00) or the
 130 afternoon (between 13:00 and 17:00) until a total of 20h had been collected for each group.
 131 Times were randomised to prevent any effects of diurnal rhythm. Horses were not ridden or
 132 removed from the field at any point on observation days.

133

134 **Table 2** - Ethogram of equine interactions, adapted from Cozzi, et al. (2010); Jørgensen, et al. (2009); Jørgensen,
 135 Liestøl, and Bøe (2011); McDonnell and Poulin (2002) and Pierard et al. (2019).

	Interaction	Description
Affiliative Interactions	Allogrooming	Seen between two individuals, positioned with bodies laterally parallel to one another (usually head-to-shoulder or head-to-tail) to enable gentle nipping, nuzzling or rubbing each other's neck, mane, rump or tail. This action will be maintained for ≥ 10 s
	Play	Play directed at one or multiple other individuals, which may or may not be reciprocated. Includes movements such as rapid biting, grasping and pulling at the others body, mane, tail or limbs, where body position is maintained for ≥ 10 s. May also include a 'play fight' involving movements such as rearing, circling, kneeling and chasing. Play will be distinguished from true fighting by the fact that during play, individuals appear to alternate offensive and defensive roles, and stop short of injury.
	Head rest	One horse rests it's chin or entire head on the neck, body or rump of another individual. Maintained for longer than 10s.
	Groom-attempt	Two individuals position their bodies laterally parallel to one another (as described above, see ' <i>Allogrooming</i> ') and may also begin gentle nipping, nuzzling or rubbing each other's neck, mane, rump or tail, although this is not maintained for ≥ 10 s.
	Follow	Moving immediately behind another horse (within three body-lengths) that had just initiated locomotion, for at least 10s without initiating physical contact.
	Approach	Moving towards another individual to be within two body-lengths of another horse that does not immediately move away and remaining there for at least 10 s without initiating physical contact.

	Touch	Contact made by one individual with any area on the body of another, does not provoke an observable response from the receiver. If an aggressive response from either individual is observed immediately following this action, 'touch' will instead be replaced by this agonistic interaction.
Agonistic Interactions	Bite	Opening and rapid closing of the jaws to make contact at any location on the body, head or limbs of another individual.
	Kick	One or both hind legs lift off the ground and rapidly extend backwards toward another horse, with apparent intent to make contact (which may or may not occur).
	Strike	With ears laid back, and one forelimb is moved outward to make contact, or in an apparent attempt to make contact, with the body or limbs of the other individual. Often accompanied by high pitched vocalisation.
	Push	Pressing of the head, neck, shoulder, chest or body against another horse, causing it to move, or reposition one or more limbs to retain balance.
	Threat to bite	Bite intention movement with ears back and neck extended, jaws are open but do not make physical contact with other individual.
	Threat to kick	Individual behaves as if they may kick, by swinging rump or backing up, and by raising or stamping a hind leg toward another individual, but they will stop short without extending a limb backwards.
	Chase	One horse pursuing another at a fast pace. The chaser typically pins the ears, lowers the head, exposes the teeth and bites at the rump and tail of the pursued horse.
	Displacement	Approach of one individual causes another/ multiple other individuals to move away so that inter-individual distance is maintained or increased, without physical contact being made (facial expression may convey aggression).
	Drive	Initially appears to be a displacement, but the initiator will continue to pursue the receiver at a fast-walk pace, often with head lowered towards the ground and ears back.
Neutral Interactions	Mutual Nasal Sniff	Two or more individuals engaged in simultaneous olfactory investigation of one another positioned with noses in close proximity.
	Body Sniff	One individual will perform an olfactory investigation of another individual, which may or may not be reciprocated. Using their nose to investigate any part of the body, limbs or head.

136 **Monitoring Equipment**

137 Prior to every observation period, a ‘field safe’ headcollar (Nylon headcollar with Velcro®,
138 Rhinegold, UK) to horses with a Holux GPS unit (Holux RCV-3000, measuring: 6.3 x 4.1 x
139 1.8 cm, weight: 49.9 g) contained within a small ‘Ziplock’ bag attached with electrical tape to
140 the ventral side (Sato et al., 2017) (*fig. 1*). GPS loggers were set to
141 log and store position, in degrees of latitude and longitude, every 10
142 minutes. This sampling interval was used to ensure the independence
143 of samples when calculating spatial proximity, as results from Wells
144 and Feh (unpublished, quoted by Feh (1988)) found that horses show
145 a mean latency of changing spatial distribution of group members
146 every 8 min.

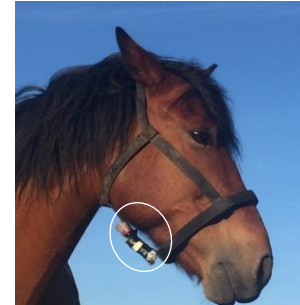


Figure 1- Global Positioning System (GPS) device contained within ‘Ziplock’ bag and attached to field-safe headcollar (Author’s own, 2019)

147 For half the observation time (10/20hrs) horses wore fly rugs (Zebra
148 Print Fly Combo Rug, Rhinegold, UK) with the neck removed to
149 attach a non-commercial version of the Orscana sensor (Arioneo,
150 Paris, France) measuring: 5.0x1.5cm, weight: 17g, housed within a
151 7 x 7cm nylon mesh pocket, located at the hollow area below the left
152 hip (*fig. 2*) (Arioneo, 2019) containing an internal accelerometer and
153 gyroscope set to log movement data every minute. To determine if
154 wearing rugs containing an accelerometer influenced the frequency
155 or type of interactions recorded, the total number of interactions initiated was calculated for
156 each horse in both the ‘Rug’ and ‘No Rug’ condition and Wilcoxon Signed Rank tests were
157 run to identify significant differences between them.

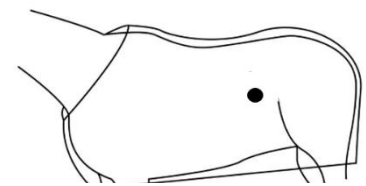


Figure 2 - Location of the Orscana sensor under horse rug (Arioneo, 2017).

158 All internal clocks were synchronised prior to data collection. Prior to each data collection
159 period, 20 minutes habituation time for observer and equipment was allowed. At the end of
160 each data collection period data were downloaded for subsequent analysis.

161

162 **Equipment Tests**

163 **GPS device**

164 Two Holux RCV-3000 GPS units were placed on the ground at a distance of 2m. The inter-
165 device distance was increased at ten-minute intervals so that 2m, 5m, 10m and 15m were
166 captured. Inter-device distances were calculated from the given degrees of latitude and

167 longitude using a variation of Haversine's distance formula, where 'x' and 'y' represents
168 longitude and latitude respectively for both 'device 1' and '2':

169

$$1.2742 \times 10^7 A \sin \sqrt{\sin \left(\frac{(y_2 \frac{\pi}{180}) - (y_1 \frac{\pi}{180})}{2} \right)^2 + \left(\cos \left(y_2 \frac{\pi}{180} \right) \cos \left(y_1 \frac{\pi}{180} \right) \sin \left(\frac{x_2 \frac{\pi}{180} - x_1 \frac{\pi}{180}}{2} \right) \right)^2}$$

171

172 Average deviation from the true distance (reference measure) was 0.081 ± 0.783 [SD]m, thus
173 the devices were considered suitable for use as this is well within the range reported for models
174 used in similar studies (Sato et al., 2017). This conclusion was further supported with the
175 construction of a Bland-Altman plot where 78/80 data points (97.5%) fall within the calculated
176 limits of agreement.

177 *Accelerometer*

178 To determine if the accelerometers differentiated between varying activity levels, and to
179 identify values that constitute 'high activity' for use in later analysis, two horses were fitted
180 with a sensor, and spent 10 minutes in each of the following conditions:

- 181 • **'Standing'**- horses stood tied up outside of their usual stables.
- 182 • **'Grazing'**- horses were loose in their usual field and observed so that ten minutes
183 involving no interactions with conspecifics or extended periods of locomotion
- 184 • **'Walking'** – horses were led in hand on a grass surface in walk
- 185 • **'Trotting'**- horses were led in hand on a grass surface in trot

186 Differences in median accelerometry output between each condition were tested for statistical
187 significance using Friedman Tests. This test identified significant differences ($\chi^2=30.00$; DF=3;
188 $P<0.001$) in the accelerometry output values between four activity conditions (Standing;
189 Grazing; Walking; Trotting). Post-hoc Wilcoxon tests found that all four conditions were
190 significantly different (W=0.00; DF=1; $P=0.006$), even when a Bonferroni correction factor
191 was applied, reducing the critical P-value to 0.008, therefore the accelerometer could reliably
192 differentiate between these activity levels.

193

194 **Social Network Construction**

195 Six social networks, four based on observation of specific interactions and two based on GPS-
196 derived proximity, were created for each group, using the methods outlined in *table 3*. In

197 methods 1-4 the strength of connection between dyads was calculated as a proportion of the
198 total number of interactions observed for the whole group (Castles et al., 2014), as was the
199 frequency of close proximity in methods 5 and 6, which was given as a percentage of the total
200 number of GPS fixes. This allowed for the underlying structure of each network to be compared,
201 even if the total number of associations sampled initially differed between methods.

Table 3- Methods of network construction

Method	Name	Type	Description & Edge Definition
1	All interactions	Observation of Interactions	Network will be constructed based on all dyadic interactions manually observed between individuals. Edge Definition: frequency of interaction between individuals, given as a percentage of the total number of all interactions observed within the group.
2	Affiliative interactions only	Observation of Interactions	Network will be constructed based on all affiliative (as defined in study ethogram) dyadic interactions manually observed between individuals. Edge Definition: frequency of affiliative interaction between individuals, given as a percentage of the total number of all interactions observed within the group.
3	Allogrooming Frequency	Observation of Interactions	Network will be constructed based on the number of dyadic allogrooming interactions (as defined in study ethogram) manually observed between individuals. Edge Definition: frequency of allogrooming observed between individuals, given as a percentage of the total number of all allogrooming interactions observed within the group.
4	Agonistic interactions only	Observation of Interactions	Network will be constructed based on all agonistic (as defined in study ethogram) dyadic interactions manually observed between individuals. Edge definition: frequency of agonistic interaction between individuals, given as a percentage of the total number of all interactions observed within the group.
5	5m proximity	GPS-derived Proximity	Based on GPS data sampling location every 10 minutes, with inter-individual distance calculated using Haversine's distance formula. All individuals positioned within 5m of each other at the time of each sample will be recorded. Edge Definition: frequency that individuals are $\leq 5m$ from each other, given as a percentage of the total number of GPS samples logged.
6	Low activity proximity	GPS-derived Proximity	As above (method 5) but only individuals that are positioned within 5m of each other <u>and</u> performing low levels of activity (accelerometry values ≤ 1000) at the time of interaction will be defined as associating. All incidence of close proximity that occur at higher activity levels will not be recorded or used to construct this network. Edge Definition: frequency that individuals are $\leq 5m$ from each other whilst showing low levels of activity, given as a percentage of the total number of GPS samples logged.

203 **Statistical Analysis**

204 *Network Comparison*

205 Mantel Z-tests were run with 1000 permutations in Socprog2.9 (compiled version) to compare
206 association matrices derived using the different methods, providing a two-sided p-value and
207 matrix correlation coefficient (Z) based on the correlation between non-diagonal elements of
208 the test matrices (Whitehead, 2008). Proximity networks were first tested against ‘all
209 interaction’ networks, before interactions was further categorised (*table 4*) to reflect either
210 affiliative, agonistic or allogrooming interaction, and again tested against the original proximity
211 network. The alpha value for this study was set at $P \leq 0.05$.

212

213 **Table 4** - Classification of interactions by type

Affiliative	Play; Head rest; Groom attempt; Follow; Approach; Touch
Agonistic	Bite; Kick; Strike; Push; Threat to bite; Threat to kick; Chase; Displacement; Drive
Neutral	Mutual Nasal Sniff; Body Sniff
Allogrooming	Allogrooming

214

215 *Incorporating Accelerometry*

216 Once these results had been obtained, further work was undertaken to determine if filtering
217 proximity data, so that only associations which occurred whilst horses were showing low levels
218 of activity (defined as accelerometry values ≥ 1000) were used to construct a new proximity
219 network, improved agreement with interaction-based methods. The equipment tests conducted
220 to assess accelerometer suitability formed the basis for the choice of activity threshold (see S1).
221 An output value of ≥ 1000 was considered to be a reasonable cut off point, as this was seen to
222 remove all activities where accelerometry output equated to walking or higher-level activities.
223 This would enable the GPS data to be filtered so that only incidence of close proximity that
224 occur whilst both individuals are stationary would remain. As accelerometers and rugs were
225 only worn for 10 hours (50% of total observation time), new networks were created, utilising
226 the same methods described previously (*table 3*), based only on days where this equipment was
227 present. The proximity-based networks developed were tested against ‘All Interaction’,
228 ‘Affiliative Interaction’, and ‘Agonistic Interaction’, again with Mantel tests in Socprog2.9.

229

230 **Cost-benefit Analysis of Social Network Construction Methods**

231 The initial cost (£) of all specialist equipment required to undertake the different methods of
232 social network construction, and the time (*hrs*) required to achieve this, was calculated. This
233 was based on the requirements of a single observer to collect and analyse 10hrs of data for a
234 group of four horses in a 2325.66m² field.

235

236 **Ethical Statement**

237 The study and all procedures were approved by the Sparsholt Research Ethics and Standards
238 Group prior to data collection.

239 **Results**

240 In total, 999 interactions were observed across the three horse groups ('Group A'= 220; 'Group
241 B'=339; 'Group C'=440), 497 of which were categorised as 'affiliative' ('Group A'=116;
242 'Group B'=173; 'Group C'=208), 453 as 'agonistic' ('Group A'=90; 'Group B'=142; 'Group
243 C'=221), and 28 as an 'allogrooming' interaction ('Group A'=11; 'Group B'=6; 'Group
244 C'=11). Inter-observer reliability was tested using Fleiss Kappa and considered 'Very good',
245 ($\kappa=0.82888$, $Z=6.0165$, $P<0.001$). Mantel tests compared proximity-based networks against
246 networks constructed using 'all interactions' showing a positive relationship in each of the
247 three groups (Group A: $Z=0.88478$, $P=0.121$; Group B: $Z=0.72875$, $P=0.533$; Group C:
248 $Z=0.69174$, $P=0.233$) although all lacked significance. When the same proximity network was
249 tested against only affiliative interactions, positive but non-significant associations were seen
250 in 'Group A' ($Z=0.85438$, $P=0.05$), 'Group B' ($Z=0.61582$, $P=0.475$) and 'Group C'
251 ($Z=0.88925$, $P=0.05$). Agreement between proximity and allogrooming networks was seen to
252 differ between the groups, with positive but non-significant agreement seen in 'Group B'
253 ($Z=0.92447$, $P=0.324$) and 'Group C' ($Z=0.52606$, $P=0.573$), and a non-significant negative
254 association in 'Group A' ($Z=-0.61721$, $P=0.216$). Agonistic networks were positively
255 associated with proximity in 'Group A' ($Z=0.51863$, $P=0.466$), 'Group B' ($Z=0.33103$,
256 $P=0.845$) and had a negative relationship in 'Group C' ($Z=-0.26442$, $P=0.612$) although none
257 of these reached significance.

258

259 **Considering Activity Level**

260 As only 50% of the data collected were used to create new activity networks, the relationship
 261 between proximity and the interaction-based methods differed from that previously reported.
 262 Allogrooming networks were not included as the low number of allogrooming events observed
 263 meant that there were insufficient data for network construction when half of the original data
 264 were excluded. When an ‘activity filter’ was applied to remove all associations that occurred
 265 when accelerometer values were ≥ 1000 , only 3, 6 and 2 of the original associations were
 266 removed for ‘Group A’, ‘Group B’ and ‘Group C’ respectively, and consequently there was no
 267 changes in the agreement seen between proximity and any of the methods (*Table 5*).

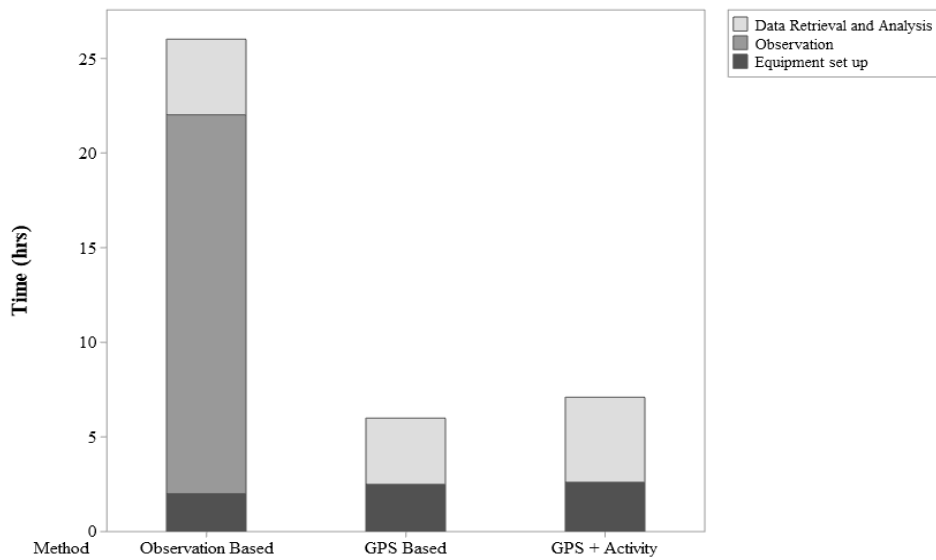
268 **Table 5** - Mantel test results when ‘All interactions’, ‘Affiliative’ and ‘Agonistic’ networks were compared with
 269 proximity both before and after an activity filter is applied.

		Original Proximity	Proximity with ‘activity filter’ applied
Group A (n=4)	All Interactions	0.08544 (P=0.680)	0.08544 (P=0.706)
	Affiliative Interactions	0.30935 (P=0.504)	0.30935 (P=0.423)
	Agonistic Interactions	-0.32640 (P=0.602)	-0.32640 (P=0.673)
Group B (n=3)	All Interactions	-0.18898 (P=0.793)	-0.18898 (P=0.808)
	Affiliative Interactions	-0.43637 (P=0.838)	-0.43637 (P=0.836)
	Agonistic Interactions	0.99795 (P=0.166)	0.99795 (P=0.168)
Group C (n=4)	All Interactions	0.66621 (P=0.227)	0.66621 (P=0.236)
	Affiliative Interactions	0.82125 (P=0.146)	0.82125 (P=0.119)
	Agonistic Interactions	-0.09611 (P=0.833)	-0.09611 (P=0.862)

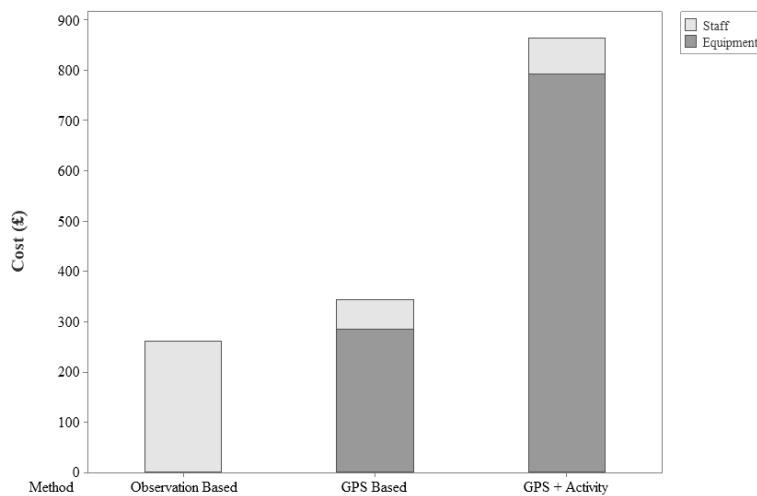
270
 271 Wilcoxon signed rank tests identified a significant difference in the occurrence of ‘All
 272 interactions’ (W=65.00; n=11; DF=1; P=0.005) and ‘Agonistic Interactions’ (W=50.00; n=11;
 273 DF=1; P=0.025) between ‘No Rug’ and ‘Rug’ conditions (see S2).

274 **Cost-benefit Analysis of Methods**

275 The financial and time costs associated with three different methods of data collection were
 276 recorded and displayed (*fig. 3 & 4*) to enable comparison between the three techniques.
 277 Researcher time (referred to as staffing costs in *fig. 4*) was priced at £10 per hour in accordance
 278 with other work of this nature.



279
 280 **Figure 3** - Time required to collect 10hrs of data for a group of four horses using three different methods.



281 **Figure 4** - Equipment and staffing costs (paid at a rate of £10/hour) required to collect and analyse 10hrs of data
 282 for a group of four horses in a 2325.66m² field, compared across three methods.

283 **Table 6** - cost of equipment, shown for each specific item, required to collect 10hrs of data for a group of four
 284 horses using three different methods.

Method	Equipment	Cost (£)		
		Single unit	4x units	Total

Observation Based	No specialised equipment required	0	0	0
GPS Based	Headcollars (Rhinegold Field-safe headcollar)	6.95	27.8	
	GPS Device (Holux RCV-3000)	64	256	283.8
GPS + Activity	Fly Rugs (Rhinegold Zebra-print Combo)	35.95	143.8	
	Headcollars (Rhinegold Field-safe headcollar)	6.95	27.8	
	GPS Device (Holux RCV-3000)	64	256	791.6
	Accelerometer (Orscana sensor*)	91	364	

*note that the Orscana sensor used is not currently available to purchase, so this price has been estimated based on the cost of a commercially available earlier version.

285

286 **Discussion**

287 **Agreement with Proximity Networks**

288 This study assessed the viability of proximity as a proxy for interactions in small horse groups
289 through Mantel test comparison of their resulting social networks.

290

291 *All interactions*

292 Agreement between ‘proximity’ and ‘all interaction’ networks was consistent across the three
293 groups, with all demonstrating a positive, although not significant, relationship. This trend for
294 positive agreement may be considered logical, as fundamentally individuals must be in close
295 proximity for an interaction to occur (Croft et al., 2016). Although, this information alone does
296 not give any indication of the relationship shared by these individuals, and could just as likely
297 be the result of frequent agonistic interactions, as the existence of a positive social bond. The
298 causal nature of these association is also unclear, as without further investigation it is not
299 possible to determine if individuals are actively choosing to spend time near conspecifics whom
300 they prefer interacting with, or if they are interacting more frequently simply because they are
301 nearby. Whilst no artificial resources were provided, it was not possible to remove what may
302 be referred to as ‘natural resources’ (shade, distribution of grass species, etc.) which may have
303 somewhat biased space usage and, consequently, dyadic interaction frequency.

304 Overall, the relationship between proximity and ‘all interactions’ lacked significance, although
305 it is worth noting that the small sample size may have reduced the likelihood of mantel tests

306 returning significant results, particularly in ‘Group B’ where only three subjects were present,
307 highlighting a need for more work to determine the extent to which this is likely to have an
308 effect. However, the use of small groups in this study was intentional, as this was believed to
309 most closely reflect how most modern domestic horses are housed.

310

311 *Affiliative Interactions*

312 Proximity was seen to agree most closely with affiliative networks. This would suggest that
313 horses do exhibit a preference to spend time near individuals with whom they share more
314 positive exchanges, thereby aligning with the results of Wolter et al. (2018), who suggest that
315 this may evidence the existence of positive social bond between individuals. This supports the
316 use of GPS derived data, not only in studies to map physical contact, but also in those that
317 consider the nature of relationships within a group. Although, this conclusion was only reached
318 based on results from two of the three groups in this study, so caution must be exercised when
319 these methods are used interchangeably in groups of less than four horses, and that further work
320 is conducted to determine the effect of group size and composition.

321

322 *Allogrooming Interactions*

323 A decision was made to construct separate allogrooming networks, rather than only considering
324 these interactions within the affiliative network, as allogrooming is frequently used as a
325 measure for social network construction in Equidae (Stanley et al., 2018), and there is some
326 evidence to suggest that this may be particularly relevant for the analysis of social bonds
327 alongside interindividual proximity in horses (Wolter et al., 2018). Networks based on close
328 proximity were not seen to be significantly associated with networks based on allogrooming
329 frequency. These findings are in contrast to those of Wolter et al. (2018) and Koene and Ipema
330 (2013), although, this may be attributed to the fact that mare/ foal relationships existed in the
331 latter study, or because both of these examples used ‘nearest neighbour’ as a measure of
332 proximity measure, rather than the frequency that individuals were within a set distance as was
333 used here. It is worth considering that Stanley et al. (2018) reported that incidence of mutual
334 grooming was too infrequently observed in horses to allow reliable networks to be built at all
335 times of the year. As allogrooming frequency is known to fluctuate between seasons, and
336 altered by factors such as parasite load and coat growth (Wolter et al., 2018) this could in itself
337 be considered an unreliable method for long term network construction. This, in addition to the

338 fact that only low levels of allogrooming were observed in this study, could explain the
339 differences seen between allogrooming and proximity network. Additionally, allogrooming
340 relationships within the groups were observed to be asymmetric, with the same individuals
341 always initiating allogrooming bouts. This was noted in a previous study of cattle, where
342 allogrooming behaviour was not completely reciprocal (Val-Laillet, et al., 2009). These authors
343 argue that the asymmetric nature of allogrooming relationships raises the question of whether
344 affiliative bonds can be inferred from on undirected networks, whilst Dunbar and Shultz (2010)
345 also theorise that allogrooming and spatial proximity might represent different aspects of
346 bonding.

347

348 *Agonistic Interactions*

349 Agonistic interactions were found to be inconsistent in their relationship with proximity across
350 the groups with none reaching significance. Additionally, there was no agreement between the
351 affiliative and agonistic networks, thereby indicating that the two social behaviours followed
352 different patterns within the groups. This aligns with previous studies in cattle (Foris et al.,
353 2019; Val-Laillet et al., 2009) and horses (Pierard et al., 2019) where authors suggest that that
354 separate analyses of the two interaction types may not provide a complete picture of group
355 social structure.

356

357 **Filtering by Activity Level**

358 No change in method agreement with proximity was seen when this activity filter was applied.
359 This result was largely attributed to the fact that horses in this sample rarely performed activity
360 at levels above the pre-designated threshold, highlighting the difficulties in selecting a
361 threshold that is appropriate for the sample group whilst also being sufficiently high to meet
362 research aims. A limitation of the present study was that equipment tests only investigated the
363 accelerometers ability to differentiate between simple equine gaits, but failed to account for
364 other movements and social interactions that are of primary interest in this study. Consequently,
365 it is recommended that further work investigates the inclusion of accelerometry in social
366 network construction and interpretation, but is preceded by a more comprehensive study to first
367 assess accelerometer ability to quantify equine activity. However, the use of an accelerometer
368 at all in SNA may be questionable as setting a threshold would rule out all high activity
369 interactions, included those that are 'play based', which may have wider implications for

370 welfare in domestic individuals (Hausberger, et al., 2012). Furthermore, comparison between
371 the ‘rug’ and ‘no rug’ conditions suggested that the presence of the accelerometer and fly
372 rugs may have had some impact on group interactions. The Orscana device was chosen for
373 use as it has been specifically designed and marketed for use in the target species, and thus its
374 ability to withstand impact from the horses (e.g. whilst rolling) had been verified to some
375 extent. Other devices that do not require a rug to be worn do exist, and may be preferable for
376 use when social interactions are of interest, although further work to investigate their
377 reliability and robustness when used on horses in the field, and determine their ideal
378 placement for use in social network studies, would be beneficial (Thompson et al., 2017).

379

380 **Cost/ benefit Analysis**

381 Whilst a researcher’s primary concern should ultimately be producing reliable results, it is
382 inevitable that financial and time costs associated with different techniques are going to
383 influence their choice of methodology. The ideal method would be quick, cheap and easy to
384 use without limiting their ability to provide results that align with the study aims (Holt and
385 Elliott, 2002). The GPS units were straightforward to use and greatly reduced the time needed
386 to collect data, whilst also appearing well tolerated by the sample horses. This technique has
387 the added advantage of enabling data to be obtained remotely following device attachment,
388 facilitating the collection of data outside of daylight hours, even when horses are out of sight,
389 or where group behaviour may be altered by human presence. More data may also be collected
390 over a longer time period, which is likely to increase confidence in the resulting network
391 (Feczko et al., 2015; Henzi et al., 2009). Although, caution must be taken to ensure that this
392 does not lead to networks becoming too dense, as several researchers report this may mean
393 closer dyadic interactions are missed, thus making the network less representative in species,
394 like horses (Stanley et al., 2018), who typically form close relationships (Castles et al., 2014;
395 Farine, 2015; Faust, 2006).

396 Whilst the equipment required for ‘GPS’ and ‘GPS & Activity’ based methods did mean that
397 total costs were considerably higher than the observation-based methods, it must be
398 remembered that this equipment represents a ‘one-time only’ purchase, and as its use greatly
399 decreased researcher time (and subsequent staffing costs), it would likely lead to lower costs
400 in studies running for a greater length of time.

401 Despite these advantages, an obvious drawback of this GPS-based method is the inability for
402 the directionality of interactions to be identified, which greatly limits the amount of information
403 gathered via this technique (Pinter-Wollman et al., 2014). The use of directed ties would likely
404 have been beneficial in the current study to provide a more comprehensive overview of the
405 interactions taking place, and may have provided additional insight into why some methods do
406 not agree, for example, if close proximity between a pair is due to relentless agonistic advances
407 (apparent ‘bullying’) from one individual, rather than a mutual ‘decision’ to be near one another
408 (Schino and Aureli, 2017).

409

410 **Subjectivity in interaction classification**

411 The categorisation of interactions as either ‘affiliative’, ‘agnostic’ or ‘neutral’ is likely to have
412 been highly influential in this studies outcome (Fureix, et al., 2012), and whilst every effort
413 was made to base this decision on empirical evidence, the subjectivity surrounding this
414 warrants acknowledgement. An observation was made that when ‘displacement’ interactions
415 were observed, the receiving horse would rarely move further than a few meters away, with
416 many then returning a few minutes later to again be near the individual who initiated the
417 interaction. Whilst this is a purely anecdotal observation, existing work reports that threats
418 involving no physical contact were seen to represent more than 80% of total aggressive
419 interactions within domestic groups (Jørgensen, et al., 2009), with displacement behaviours
420 most commonly seen, and considered these necessary to maintain herd structure (Ladewig,
421 2018; Sigurjonsdottir, et al., 2012). This may suggest that some agonistic interactions are a
422 ‘normal’ part of co-existing in a stable herd, the presence of which may not necessarily mean
423 that the individuals involved have a more ‘negative’ relationship. Thus, the inclusion of these
424 interactions in the agonistic network may limit its agreement with proximity. Additionally,
425 Sigurjónsdóttir and Haraldsson (2019) chose to discount ‘kick’ and ‘threat to kick’ interactions,
426 as VanDierendonck et al. (2009) argues that these may be defensive in nature, rather than
427 having agonistic intent and, therefore, may provide an unrepresentative overview of agonistic
428 relationships.

429 **Selecting Distance Thresholds for Association**

430 Association thresholds for Equidae within existing literature often equate to ‘one horse body
431 length’ (approx. 1.5 m) (Kimura, 1998; Proops et al., 2012), or ‘two body lengths’
432 (Sigurjónsdóttir et al., 2003), with Jørgensen et al. (2009) observing that horses had their
433 nearest neighbour within 2m for more than 60% of the time. More recently, work by
434 Hildebrandt et al. (2021) suggests that, in large horse groups, 3m may be the most appropriate
435 distance threshold. Consequently, the
436 use of 5m thresholds in the present study
437 may be considered slightly larger than is
438 ideal for equine studies, however,
439 results of a pilot study suggested that
440 smaller distances may not be suitable
441 for use with GPS-based sampling, as the
442 location of GPS units on the head may
443 mean the distance reported between
444 animals is overestimated in relation to
445 their physical distance, as demonstrated



Figure 5 - The distance between two horses given by GPS-units positioned on the head (yellow arrow) and their observed physical distance (blue arrow).

446 in *fig. 5*. This represents a potential limitation of the GPS-based methods if the use of smaller
447 thresholds is desired. However, as the ‘ideal’ distance for use with domestic horses is currently
448 unknown, the extent to which this poses an issue is not yet fully understood. A study that uses
449 data manipulation to trial different thresholds in domestic horse herds, similar to that of Davis
450 et al. (2018), could further elucidate the impact that changing this element has on the resulting
451 social network, and its subsequent agreement with interaction rates.

452

453 **Conclusions**

454 The main drivers of this study were the lack of knowledge surrounding group structure in
455 domestically kept horse herds, and the inconsistencies reported in existing literature regarding
456 the methods used to investigate this. Whilst the use of GPS-derived proximity has many
457 practical benefits, and enables several of the limitations surrounding manual observation to be
458 overcome, this study suggests that it may only be a viable alternative when the aim is to monitor
459 affiliative interactions, although more work is recommended to further substantiate these
460 conclusions, and investigate the wider impact of management factors on inter-method
461 agreement. It should also be noted that, whilst the use of GPS-derived proximity is associated

462 with lower staffing and time costs, this approach does require additional equipment to be
463 purchased, although it may be possible to write off these initial costs over the duration of its
464 use. It is worth considering that the use of GPS-derived data alone does not enable directed
465 networks to be created, and could therefore be considered a less informative method,
466 potentially making it inappropriate to meet some research aims. The ability to easily and
467 reliably assess equine social structure is undoubtedly of value, to promote and optimise
468 management practices that better align with the ethology of this species, ultimately improving
469 their health, welfare and potentially performance. This study should be considered a useful
470 resource to guide future research, as it has acknowledged the cost and limitations surrounding
471 available methods alongside their reliability, to fully realise their potential for real-life
472 application.

473

474

475

References

- 476 Bailey, D.W., Trotter, M.G., Knight, C.W., Thomas, M.G., 2018. Use of GPS tracking collars and
477 accelerometers for rangeland livestock production research. *Transl. Anim. Sci.* 2, 81–88.
478 <https://doi.org/10.1093/tas/txx006>
- 479 Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman,
480 B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., Aubert, A., 2007. Assessment of positive
481 emotions in animals to improve their welfare. *Physiol. Behav.*
482 <https://doi.org/10.1016/j.physbeh.2007.02.003>
- 483 Bourjade, M., Moulinot, M., Henry, S., Richard-Yris, M.A., Hausberger, M., 2008. Could adults be
484 used to improve social skills of young horses, *Equus caballus*? *Dev. Psychobiol.* 50, 408–417.
485 <https://doi.org/10.1002/dev.20301>
- 486 Boyland, N.K., James, R., Mlynski, D.T., Madden, J.R., Croft, D.P., 2013. Spatial proximity loggers
487 for recording animal social networks: Consequences of inter-logger variation in performance.
488 *Behav. Ecol. Sociobiol.* 67, 1877–1890. <https://doi.org/10.1007/s00265-013-1622-6>
- 489 Burla, J.B., Ostertag, A., Schulze Westerath, H., Hillmann, E., 2014. Gait determination and activity
490 measurement in horses using an accelerometer. *Comput. Electron. Agric.* 102, 127–133.
491 <https://doi.org/10.1016/j.compag.2014.01.001>
- 492 Cameron, E.Z., Setsaas, T.H., Linklater, W.L., 2009. Social bonds between unrelated females increase
493 reproductive success in feral horses. *Proc. Natl. Acad. Sci.* 106, 13850–13853.
494 <https://doi.org/10.1073/pnas.0900639106>
- 495 Castles, M., Heinsohn, R., Marshall, H.H., Lee, A.E.G., Cowlshaw, G., Carter, A.J., 2014. Social
496 networks created with different techniques are not comparable. *Anim. Behav.*
497 <https://doi.org/10.1016/j.anbehav.2014.07.023>
- 498 Christensen, J.W., Rundgren, M., Olsson, K., 2006. Training methods for horses: Habituation to a
499 frightening stimulus. *Equine Vet. J.* 38, 439–443. <https://doi.org/10.2746/042516406778400574>
- 500 Croft, D.P., Darden, S.K., Wey, T.W., 2016. Current directions in animal social networks. *Curr. Opin.*
501 *Behav. Sci.* <https://doi.org/10.1016/j.cobeha.2016.09.001>
- 502 Davis, G.H., Crofoot, M.C., Farine, D.R., 2018. Estimating the robustness and uncertainty of animal
503 social networks using different observational methods. *Anim. Behav.* 141, 29–44.
504 <https://doi.org/10.1016/j.anbehav.2018.04.012>

- 505 Farine, D.R., 2015. Proximity as a proxy for interactions: Issues of scale in social network analysis.
506 *Anim. Behav.* 104, e1–e5. <https://doi.org/10.1016/j.anbehav.2014.11.019>
- 507 Farine, D.R., Strandburg-Peshkin, A., Berger-Wolf, T., Ziebart, B., Brugere, I., Li, J., Crofoot, M.C.,
508 2016. Both Nearest Neighbours and Long-term Affiliates Predict Individual Locations During
509 Collective Movement in Wild Baboons. *Sci. Rep.* 6, 27704. <https://doi.org/10.1038/srep27704>
- 510 Faust, K., 2006. Comparing Social Networks: Size, Density, and Local Structure. *Metod. Zv.* 3, 185–
511 216.
- 512 Feczko, E., Mitchell, T.A.J., Walum, H., Brooks, J.M., Heitz, T.R., Young, L.J., Parr, L.A., 2015.
513 Establishing the reliability of rhesus macaque social network assessment from video observations.
514 *Anim. Behav.* 107, 115–123. <https://doi.org/10.1016/j.anbehav.2015.05.014>
- 515 Feh, C., 1988. Social behaviour and relationships of Prezewalski horses in Dutch semi-reserves. *Appl.*
516 *Anim. Behav. Sci.* 21, 71–87. [https://doi.org/10.1016/0168-1591\(88\)90101-3](https://doi.org/10.1016/0168-1591(88)90101-3)
- 517 Foris, B., Zebunke, M., Langbein, J., Melzer, N., 2019. Comprehensive analysis of affiliative and
518 agonistic social networks in lactating dairy cattle groups. *Appl. Anim. Behav. Sci.* 210, 60–67.
519 <https://doi.org/10.1016/J.APPLANIM.2018.10.016>
- 520 Fureix, C., Bourjade, M., Henry, S., Sankey, C., Hausberger, M., 2012. Exploring aggression regulation
521 in managed groups of horses *Equus caballus*. *Appl. Anim. Behav. Sci.* 138, 216–228.
522 <https://doi.org/10.1016/j.applanim.2012.02.009>
- 523 Godde, S., Humbert, L., Côté, S.D., Réale, D., Whitehead, H., 2013. Correcting for the impact of
524 gregariousness in social network analyses. *Anim. Behav.* 85, 553–558.
525 <https://doi.org/10.1016/j.anbehav.2012.12.010>
- 526 Hampson, B.A., Morton, J.M., Mills, P.C., Trotter, M.G., Lamb, D.W., Pollitt, C.C., 2010. Monitoring
527 distances travelled by horses using GPS tracking collars. *Aust. Vet. J.* 88, 176–181.
528 <https://doi.org/10.1111/j.1751-0813.2010.00564.x>
- 529 Haney Jr., T.A., Mercer, J.A., 2011. :Exploring Animal Social Networks. *Int. J. Exerc. Sci.* 4, 133–140.
530 <https://doi.org/10.1086/598282>
- 531 Hartmann, E., Bøe, K.E., Christensen, J.W., Hyypä, S., Jansson, H., Jørgensen, G.H.M., Ladewig, J.,
532 Mejdell, C.M., Norling, Y., Rundgren, M., Särkijärvi, S., Søndergaard, E., Keeling, L.J., 2015. A
533 Nordic survey of management practices and owners' attitudes towards keeping horses in groups.
534 *J. Anim. Sci.* 93, 4564–4574. <https://doi.org/10.2527/jas.2015-9233>
- 535 Hausberger, M., Fureix, C., Bourjade, M., Wessel-Robert, S., Richard-Yris, M.A., 2012. On the
536 significance of adult play: What does social play tell us about adult horse welfare?
537 *Naturwissenschaften* 99, 291–302. <https://doi.org/10.1007/s00114-012-0902-8>
- 538 Henzi, S.P., Lusseau, D., Weingrill, T., Van Schaik, C.P., Barrett, L., 2009. Cyclicity in the structure
539 of female baboon social networks. *Behav. Ecol. Sociobiol.* 63, 1015–1021.
- 540 Hildebrandt, F., Büttner, K., Salau, J., Krieter, J., Czycholl, I., 2021. Proximity between horses in large
541 groups in an open stable system – Analysis of spatial and temporal proximity definitions. *Appl.*
542 *Anim. Behav. Sci.* 242, 105418. <https://doi.org/10.1016/j.applanim.2021.105418>
- 543 Holt, G., Elliott, D., 2002. Cost benefit analysis: a summary of the methodology. *Bottom Line* 15, 154–
544 158. <https://doi.org/10.1108/08880450210450915>
- 545 Jørgensen, G.H.M., Borsheim, L., Mejdell, C.M., Søndergaard, E., Bøe, K.E., 2009. Grouping horses
546 according to gender-Effects on aggression, spacing and injuries. *Appl. Anim. Behav. Sci.* 120,
547 94–99. <https://doi.org/10.1016/j.applanim.2009.05.005>
- 548 Kimura, R., 1998. Mutual grooming and preferred associate relationships in a band of free-ranging
549 horses. *Appl. Anim. Behav. Sci.* 59, 265–276. [https://doi.org/10.1016/S0168-1591\(97\)00129-9](https://doi.org/10.1016/S0168-1591(97)00129-9)
- 550 Koene, P., Ipema, B., 2013. Social networks and welfare in future animal management. *Animals* 4, 93–
551 118. <https://doi.org/10.3390/ani4010093>
- 552 Ladewig, J., 2018. Body language: Its importance for communication with horses. *J. Vet. Behav.*
553 <https://doi.org/10.1016/j.jveb.2018.06.042>
- 554 Lesimple, C., Fureix, C., LeScolan, N., Richard-Yris, M.-A., Hausberger, M., 2011. Housing conditions
555 and breed are associated with emotionality and cognitive abilities in riding school horses. *Appl.*
556 *Anim. Behav. Sci.* 129, 92–99. <https://doi.org/10.1016/j.applanim.2010.11.005>

557 Marchant-Forde, J.N., 2015. The Science of Animal Behavior and Welfare: Challenges, Opportunities,
558 and Global Perspective. *Front. Vet. Sci.* 2, 16. <https://doi.org/10.3389/fvets.2015.00016>

559 Morrison, R., Sutton, D.G.M., Ramsay, C., Hunter-Blair, N., Carnwath, J., Horsfield, E., Yam, P.S.,
560 2015. Validity and practical utility of accelerometry for the measurement of in-hand physical
561 activity in horses. *BMC Vet. Res.* 11, 233. <https://doi.org/10.1186/s12917-015-0550-2>

562 Muller, Z., Cantor, M., Cuthill, I.C., Harris, S., 2018. Giraffe social preferences are context dependent.
563 *Anim. Behav.* 146, 37–49. <https://doi.org/10.1016/j.anbehav.2018.10.006>

564 Normando, S., Meers, L., Samuels, W.E., Faustini, M., Ödberg, F.O., 2011. Variables affecting the
565 prevalence of behavioural problems in horses. Can riding style and other management factors be
566 significant? *Appl. Anim. Behav. Sci.* 133, 186–198.
567 <https://doi.org/10.1016/j.applanim.2011.06.012>

568 Pierard, M., McGreevy, P., Geers, R., 2019. Effect of density and relative aggressiveness on agonistic
569 and affiliative interactions in a newly formed group of horses. *J. Vet. Behav.* 29, 61–69.
570 <https://doi.org/10.1016/j.jveb.2018.03.008>

571 Pinter-Wollman, N., Hobson, E.A., Smith, J.E., Edelman, A.J., Shizuka, D., De Silva, S., Waters, J.S.,
572 Prager, S.D., Sasaki, T., Wittenmyer, G., Fewell, J., McDonald, D.B., 2014. The dynamics of
573 animal social networks: Analytical, conceptual, and theoretical advances. *Behav. Ecol.*
574 <https://doi.org/10.1093/beheco/art047>

575 Proops, L., Burden, F., Osthaus, B., 2012. Social relations in a mixed group of mules, ponies and
576 donkeys reflect differences in equid type. *Behav. Processes* 90, 337–342.
577 <https://doi.org/10.1016/j.beproc.2012.03.012>

578 Proudfoot, K., Habing, G., 2015. Social stress as a cause of diseases in farm animals: Current knowledge
579 and future directions. *Vet. J.* <https://doi.org/10.1016/j.tvjl.2015.05.024>

580 Ruet, A., Lemarchand, J., Parias, C., Mach, N., Moisan, M.-P., Foury, A., Briant, C., Lansade, L., 2019.
581 Housing Horses in Individual Boxes Is a Challenge with Regard to Welfare. *Animals* 9, 621.
582 <https://doi.org/10.3390/ani9090621>

583 Sato, F., Tanabe, T., Murase, H., Tominari, M., Kawai, M., 2017. Application of a wearable GPS unit
584 for examining interindividual distances in a herd of Thoroughbred dams and their foals. *J. Equine
585 Sci.* 28, 13–17. <https://doi.org/10.1294/jes.28.13>

586 Schino, G., Aureli, F., 2017. Reciprocity in group-living animals: Partner control versus partner choice.
587 *Biol. Rev.* 92, 665–672. <https://doi.org/10.1111/brv.12248>

588 Schneider, G., Krueger, K., 2012. Third-party interventions keep social partners from exchanging
589 affiliative interactions with others. *Anim. Behav.* 83, 377–387.
590 <https://doi.org/10.1016/J.ANBEHAV.2011.11.007>

591 Shultz, S., Dunbar, R., 2010. Bondedness and sociality. *Behaviour* 147, 775–803.
592 <https://doi.org/10.1163/000579510X501151>

593 Sigurjónsdóttir, H., Haraldsson, H., 2019. Significance of Group Composition for the Welfare of
594 Pastured Horses. *Animals* 9, 14. <https://doi.org/10.3390/ani9010014>

595 Sigurjónsdóttir, H., Thorhallsdóttir, A.G., Hafthorsdóttir, H.M., Granquist, S.M., 2012. The behaviour
596 of stallions in a semiferal herd in Iceland: Time budgets, home ranges, and interactions. *Int. J.
597 Zool.* 2012, 1–7. <https://doi.org/10.1155/2012/162982>

598 Sigurjónsdóttir, H., Van Dierendonck, M.C., Snorrason, S., Thórhallsdóttir, A.G., 2003. Social
599 relationships in a group of horses without a mature stallion. *Behaviour* 140, 783–804.
600 <https://doi.org/10.1163/156853903322370670>

601 Stanley, C.R., Mettke-Hofmann, C., Hager, R., Shultz, S., 2018. Social stability in semiferal ponies:
602 networks show interannual stability alongside seasonal flexibility. *Anim. Behav.* 136, 175–184.
603 <https://doi.org/10.1016/j.anbehav.2017.04.013>

604 Thompson, C.J., Luck, L., Keshwani, J., Pitla, S., 2017. Effect of sensor placement on acceleration data
605 to monitor equine activity. *J. Equine Vet. Sci.* 52, 65. <https://doi.org/10.1016/j.jevs.2017.03.070>

606 Val-Laillet, D., Guesdon, V., von Keyserlingk, M.A.G., de Passillé, A.M., Rushen, J., 2009.
607 Allogrooming in cattle: Relationships between social preferences, feeding displacements and
608 social dominance. *Appl. Anim. Behav. Sci.* 116, 141–149.

609 <https://doi.org/10.1016/j.applanim.2008.08.005>
610 VanDierendonck, M.C., de Vries, H., Schilder, M.B.H., Colenbrander, B., Thorhallsdóttir, A.G.,
611 Sigurjónsdóttir, H., 2009. Interventions in social behaviour in a herd of mares and geldings. *Appl.*
612 *Anim. Behav. Sci.* 116, 67–73. <https://doi.org/10.1016/j.applanim.2008.07.003>
613 Visser, E.K., Ellis, A.D., Van Reenen, C.G., 2008. The effect of two different housing conditions on
614 the welfare of young horses stabled for the first time. *Appl. Anim. Behav. Sci.* 114, 521–533.
615 <https://doi.org/10.1016/j.applanim.2008.03.003>
616 Whitehead, Hal, 2008. Precision and power in the analysis of social structure using associations. *Anim.*
617 *Behav.* 75, 1093–1099. <https://doi.org/10.1016/j.anbehav.2007.08.022>
618 Whitehead, Hal., 2008. SOCPROG programs: analyzing animal social structures. *Behav. Biol.*
619 *Sociobiol.* 63, 765–778.
620 Wolter, R., Stefanski, V., Krueger, K., 2018a. Parameters for the Analysis of Social Bonds in Horses.
621 *Animals* 8, 191. <https://doi.org/10.3390/ani8110191>
622 Yarnell, K., Hall, C., Royle, C., Walker, S.L., 2015. Domesticated horses differ in their behavioural and
623 physiological responses to isolated and group housing. *Physiol. Behav.* 143, 51–57.
624 <https://doi.org/10.1016/j.physbeh.2015.02.040>
625
626