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27 **The effect of age, environment and management on social contact patterns in sheep**

28

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39

40 **Abstract**

41 Social structures of group-living farm animals can have important implications for animal welfare and
42 productivity. Understanding which factors can have an effect on social behaviour is thus important
43 in order to develop the best management strategies in livestock industries. Here, we studied the
44 social network structure of a flock of 84 Poll Dorset ewes and collecting dyadic associations data
45 through the use of proximity sensors during two study periods. First, we analysed the social structure
46 of ewes at a group-level, by analysing the community structure, and at individual-level, by
47 determining whether the ewes showed social differentiation in their association patterns. Second,
48 we measured for the contribution of genetic relatedness, age, weight, reproductive status and
49 previous management sub grouping on social associations to test for homophily effects. Lastly, we
50 evaluated whether social clustering was influenced by the stocking density of individuals in a field,
51 and by weather parameters, through the use of two climatic indices, the Temperature-Humidity
52 Index (THI) and the Wind Chill Index (WCI). Our results showed that the pairwise associations

53 between ewes are not-random and highly heterogeneous, both in total time spent in contact and in
54 contacts duration. There was no evidence that ewes were subdivided into social communities, and
55 at individual level, they showed markedly differentiated social relationships, demonstrating
56 preferences in social ties. However, the factors that influenced the preferred social interactions
57 between individuals changed over time. In the first study period ewes tended to maintain the social
58 bonds formed in previous management sub grouping, most likely due to a social familiarization
59 resulting from repeated interactions with the same individuals. In the second study period similarity
60 in age influenced the strength of associations among ewes. We found no significant influence of
61 reproductive status, weight (as an indicator of body size) and genetic relatedness on proximity
62 associations in either study period. Moreover, our results showed the tendency of the ewes to form
63 social clusters varied in relation to animals' density, and Wind Chill Index (WCI). The identification of
64 conditions that modify the social behaviour of sheep is critically important in order to implement
65 management and productivity strategies and our results highlight how flock social structure can
66 change depending on environmental and social contexts.

67

68 **Keywords**

69 Contact patterns, sheep, proximity sensors, social behaviour, assortment, environmental conditions.

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72 **1. Introduction**

73 Gregarious animals form social relationships with group members, and there is growing evidence that social
74 behaviours are positively correlated with the survival and reproductive success of individuals (Silk, 2007). In
75 production settings, management practices can modify the social interactions of group-living farm animals,
76 depending on group composition and available space (Keeling, 2001). Nevertheless, the social behaviour of
77 farm animals is plastic and dynamic, and allows animals to adapt to varying environmental and social
78 conditions within a confined group (Estevez et al., 2007). In recent years the livestock production industry

79 has intensified efforts to improve animal health and well-being due to increasing ethical issues and public
80 concern about animal welfare. Animal welfare is influenced by the social environment and by the opportunity
81 to express certain social behaviours despite the limitations due to bounded space and management practices
82 (Sevi et al., 2001).

83 Domestic sheep display an intensely gregarious social behaviour, and develop stable social relationships with
84 other members of the flock (Veissier et al., 1998; Fisher and Matthews, 2001). Adult sheep are able to
85 recognise their group members, and under free ranging conditions, they avoid unfamiliar animals (Lawrence
86 and Wood-Gush, 1988; Keller et al., 2011). Sociality of sheep is influenced by a variety of factors including
87 breeding period (Norton et al., 2012), age of animals (Lawrence, 1990; Doyle et al., 2016), and environmental
88 and management factors such as group size (Michelena et al., 2008; Jørgensen et al., 2009), shelter type
89 (Broster et al., 2010), weather conditions (Champion et al., 1994; Doyle et al., 2016), and individual
90 characteristics such as temperament or personality (Michelena et al., 2008; Doyle et al., 2016). One
91 increasingly popular method to assess the contact patterns between animals is the use of proximity sensors
92 (Krause et al., 2013), which allow for automated collection of contact data 24h a day. To date, proximity
93 sensors have been used on domestic sheep to assess the interactions between ewes and lambs in relation to
94 the shelter type (Broster et al., 2010), to evaluate the relationship between social cohesion of ewes and their
95 feeding motivation (Freire et al., 2012), and association patterns (Doyle et al., 2016).

96

97 Here, we studied the social relationships between pedigree, performance-recorded Poll Dorset ewes,
98 collecting dyadic associations data through the use of proximity sensors on a commercial farm, during two
99 sampling periods. The main aim of our study was to evaluate which factors could affect the social bonds in a
100 flock of adult female sheep (ewes) and whether these factors changed over time. First, we described the
101 social network of ewes, and we analysed the social structure of ewes at a group-level, by analysing the
102 community structure, and at individual-level, by determining whether the ewes showed social differentiation
103 in their relationships. Second, we tested the influence of relatedness, age, weight, reproductive status, and
104 previous management sub grouping on total time in proximity between pairs of ewes for each sampling

105 period. Specifically, we hypothesised that: i. related ewes will be more likely to interact than unrelated ewes
106 due to the inclusive fitness benefits of interacting with kin (Griffin and West, 2002; West et al., 2002); ii. that
107 individuals of similar age will be more familiar with each other and thus more likely to interact; iii. that
108 individuals of similar weight (i.e., body mass) will interact more with each other given that body mass is an
109 important determinant of social rank in ungulates (McElligott et al., 2001; Holand et al., 2004); iv. individuals
110 would assort based on lambing date (i.e., reproductive status) due to the potential anti-predator benefits
111 that lactating ewes may gain by associating together (Beauchamp, 2003; Rieucou and Martin, 2008); v.
112 individuals belonging to the same mating group will be more familiar with each other and maintain the social
113 bonds formed in the sub-group (Keller et al., 2011). Lastly, we evaluated the effect of environmental
114 conditions on patterns of social contact. In particular, we assessed if two climatic indices, namely the THI
115 (Temperature-Humidity Index) and WCI (Wind Chill Index), and the density of the animals are related with
116 the clustering coefficient of the network.

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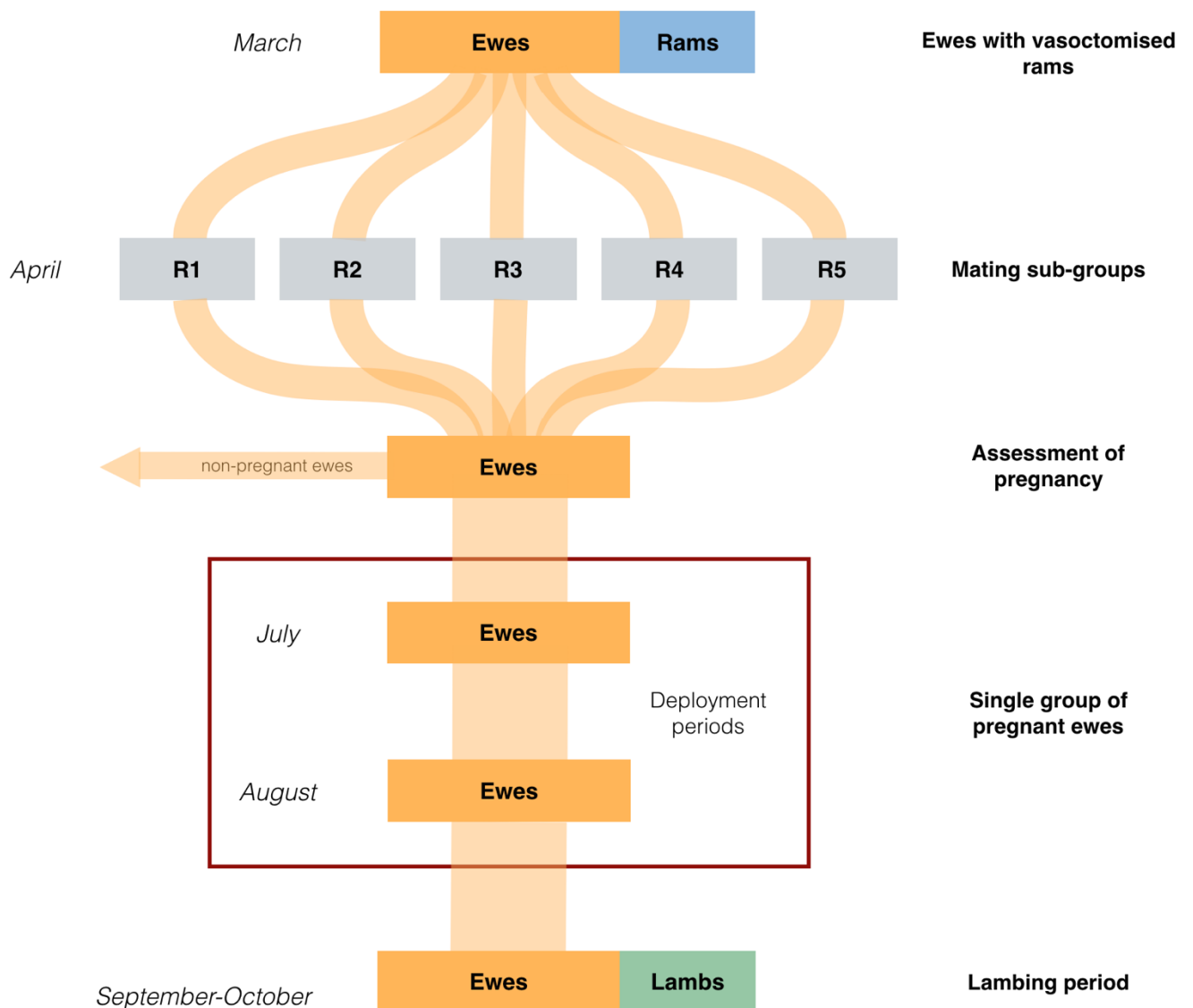
118 **2. Methods**

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120 **2.1 Data collection**

121 The study was carried out on a commercial sheep farm in Devon, UK. Generally, most sheep are short-day
122 seasonal breeders, and the breeding season starts in autumn or winter, whereas, Poll Dorset have strong
123 aseasonal capabilities and they can breed at any time during the year. The breeding techniques on study
124 farm are common to Poll Dorset breeders, and the breeding cycle starts in mid-March, as shown in the flow-
125 chart of flock breeding management (Figure 1) with vasectomised rams being introduced to a single, massed
126 group of ewes for 4 weeks to help stimulate oestrus. In mid-April the ewes are separated into mating sub-
127 groups with one fertile ram per sub-group (indicated as R1 to R5) for 5 weeks (two oestrus cycles). The mating
128 subgroups of ewes were 25, 25, 24, 24 and 21 in size, from R1 to R5 respectively. Subsequently, the ewes are
129 aggregated into a single flock (119 ewes) for 7 weeks and assessed for pregnancy by ultra-sound scanning.
130 Non-pregnant ewes (35 ewes) are removed to a separate group and the flock of ewes were 84 in size during

131 the further phases of management. The sheep were kept outdoors on permanent grass leys with no
 132 supplementary feeding. The field enclosure size for the groups ranged between 1.15 and 2.13 ha. In this
 133 study, data collection from the group of pregnant ewes took place in summer 2018, during two sampling
 134 periods of 15 consecutive days in July, and 14 consecutive days in August. The flock moved between fields
 135 during the study and the area of each field was recorded to examine the effect of flock density on contact
 136 patterns. Lambing followed in September through to early October, and lambing dates were recorded.



137
 138 Figure 1. Flow-chart of flock management. Data collection periods took place in July and August.

139
 140 During each study period, proximity sensors were deployed on 84 ewes to record patterns of social contact
 141 between individuals. Sensors were fixed to a freely-rotating neck collar with a total weight of ~100g. At the

142 time of the study ewes were aged from 2 years to 9 years old, and all ewes were weighed before the start of
143 the deployments. The complete pedigree of the flock is known (for both maternal and paternal pedigree)
144 and the pedigree was used to compute the pairwise coefficient of relatedness among all individuals. The
145 coefficient ranged between 0 (no relatives) and 0.5 (mother–daughter or full siblings).

146

147 During the deployment in August daily meteorological data were recorded via a weather station (Davis
148 Vantage Pro2 Plus). In particular, 24 h mean temperature (°C), 24 h mean relative humidity (%), 24 h mean
149 wind speed (m/s) were recorded. From these measures we calculated two climatic indices, the THI
150 (Temperature-Humidity Index) (Thom, 1959) and the WCI (Wind Chill Index) (Tucker et al., 2007). The
151 Temperature Humidity Index (THI) is a measure that accounts for the combined effects of environmental
152 temperature and relative humidity to assess the risk of heat stress (Segnalini et al., 2011):

$$153 \quad \text{THI} = 0.8 \times T + [\text{RH} \times (T - 14.4)] + 46.4$$

154 where T is air temperature in °C and RH is the relative humidity in decimal form.

155 Cold stress was most often quantified by means of the Wind Chill Index (WCI) (Tucker et al., 2007), that
156 relates ambient temperature and wind speed:

$$157 \quad \text{WCI} = 13.12 + 0.62 \times T - 13.17 \times [\text{WS}]^{0.16} + 0.40 \times T \times [\text{WS}]^{0.16}$$

158 where T is air temperature in °C and WS is wind speed in km/h.

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162 **2.2 Proximity sensors**

163 The proximity sensing platform has been designed by the SocioPatterns collaboration consortium
164 (<http://www.sociopatterns.org>). The hardware is open-source and based on the design developed by the
165 OpenBeacon project (<http://www.openbeacon.org>). The proximity sensors used in this study have been
166 previously deployed in social network studies on animals (Wilson-Aggarwal et al., 2019). The devices measure
167 3 cm in diameter and weight 2.7 g, are powered by a lithium coin battery (3 g CR2032), leading to a final

168 weight < 6 g. Sensors in close proximity exchange with one another a maximum of about 1 power packet per
169 second, and the exchange of low-power radio-packets is used as a proxy for the spatial proximity of the
170 animals wearing the sensors (Cattuto et al., 2010). In particular, close proximity is measured by the
171 attenuation, defined as the difference between the received and transmitted power. In this study we set the
172 attenuation threshold at - 75 dBm to detect proximity events between devices situated within 1-1.5 m of one
173 another. This distance between ewes allows detection of a close-contact situation, during which social
174 interactions between animals might occur. We defined that a contact occurs between two animals during a
175 time slice duration of 20 seconds if the proximity devices exchanged at least 1 radio packet during that
176 interval and the median attenuation of received packets exceeds the attenuation threshold. The output from
177 each proximity sensor provides a record of the date and time of the start of every contact with any of the
178 other proximity sensors, each of which has its own individual identification number, and the duration of each
179 contact.

180

181

182 ***2.3 Pattern of social association***

183 ***2.3.1 Contact data and network analysis***

184 We computed the number of contact events recorded for each ewe and the statistical distribution of the
185 duration of contact events. We also generated aggregated contact networks for the two experimental time
186 periods (July and August). We considered ewes as nodes of the network, while the edges represented the
187 presence of at least one recorded contact event between two individuals during the aggregation time
188 window. Given a contact network, we defined the weight w_{ij} of an edge between nodes i and j the cumulative
189 duration of the contact events recorded between two individuals. Network edges are undirected and the
190 weights on the edges are symmetric ($w_{ij} = w_{ji}$). We studied the statistical distributions of weights of the
191 contact networks.

192

193 ***2.3.2 Modular structure of aggregated networks***

194 We used the Newman’s modularity clustering algorithm (Newman, 2006), which is an eigenvector-based
195 method that uses permutation to find optimal community division (Newman, 2006; Whitehead, 2008). We
196 computed the modularity coefficient Q for each aggregated network, that measures the strength of division
197 of a network into modules communities.

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201 **2.3.3 Social differentiation**

202 To assess whether associations between ewes were more heterogeneous than we would expect given a null
203 hypothesis that all animals associate uniformly, we computed the statistic of social differentiation using the
204 following equation (Whitehead, 2008):

$$205 \quad S = \frac{\sqrt{\text{Variance}(w_{ij}) - \text{Mean}(w_{ij})}}{\text{Mean}(w_{ij})}$$

206 Where w_{ij} of an edge between nodes i and j is the cumulative time in contact between two individuals.

207 We compared the observed social differentiation value for each deployment, with a suite of values generated
208 by 10,000 null networks. Each null network was made by randomizing the nodes of the temporal network
209 obtained from the output of sensors and then by computing null aggregated networks.

210

211

212 **2.4 Pattern of social assortment**

213 We tested the influence of genetic relatedness, age, weight, reproductive status, and mating group on total
214 time in proximity between pairs of ewes for each deployment. We used multiple regression with matrices
215 (MRM) implemented in the R (R Development core team 2014) package *ecodist* (Goslee and Urban, 2007).
216 MRM involves a multiple regression of a response matrix on any number of explanatory matrices, and it tests
217 the significance of explanatory variables by permutation.

218 In this study, the matrix of associations (total time spent in proximity by each pair of ewes) is the response
219 variable, while explanatory variables are represented as distance matrices measuring the extent of similarity

220 between dyads. We included a relatedness matrix and other variables of interest into dissimilarity matrices.
221 For age and weight, we computed the absolute difference in age and weight for each dyad. For reproductive
222 status we computed the absolute difference of lambing dates for each dyad. We coded similarity of mating
223 group as 1 if the ewes belonged to the same mating group, and 0 if they belonged to another group. All p-
224 values for MRM analyses were calculated based on 10,000 permutations. In order to evaluate and select
225 which variables should be included in MRM, we used a backward selection procedure (Crawley, 1993) with
226 least significant variables being removed sequentially, until a minimum adequate model (MAM) was reached
227 in which all variables were retained at p-value ≤ 0.05 .

228

229 ***2.5 Impact of the Environment on Social Network***

230 In order to analyse how the ewes are associated with each other to form clusters, and how this varies over
231 time depending on environmental conditions, we computed the daily average clustering coefficient.
232 Clustering coefficient ranges from 0 to 1, and it is higher in a group of animals containing tight and closed
233 social units. Then, we quantified the influence of environmental parameters (i.e., climatic indices and
234 density of ewes in the field) on daily clustering coefficient for the August deployment using a General
235 Linear Model with THI, WCI and field size included as explanatory variables. Table S4 (see Supplementary
236 Material) shows the environmental data (total space area, ewes per ha) and weather parameters (24 h
237 mean temperature, 24 h mean relative humidity, 24 h mean wind speed) in the August deployment.

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239 **3. Results**

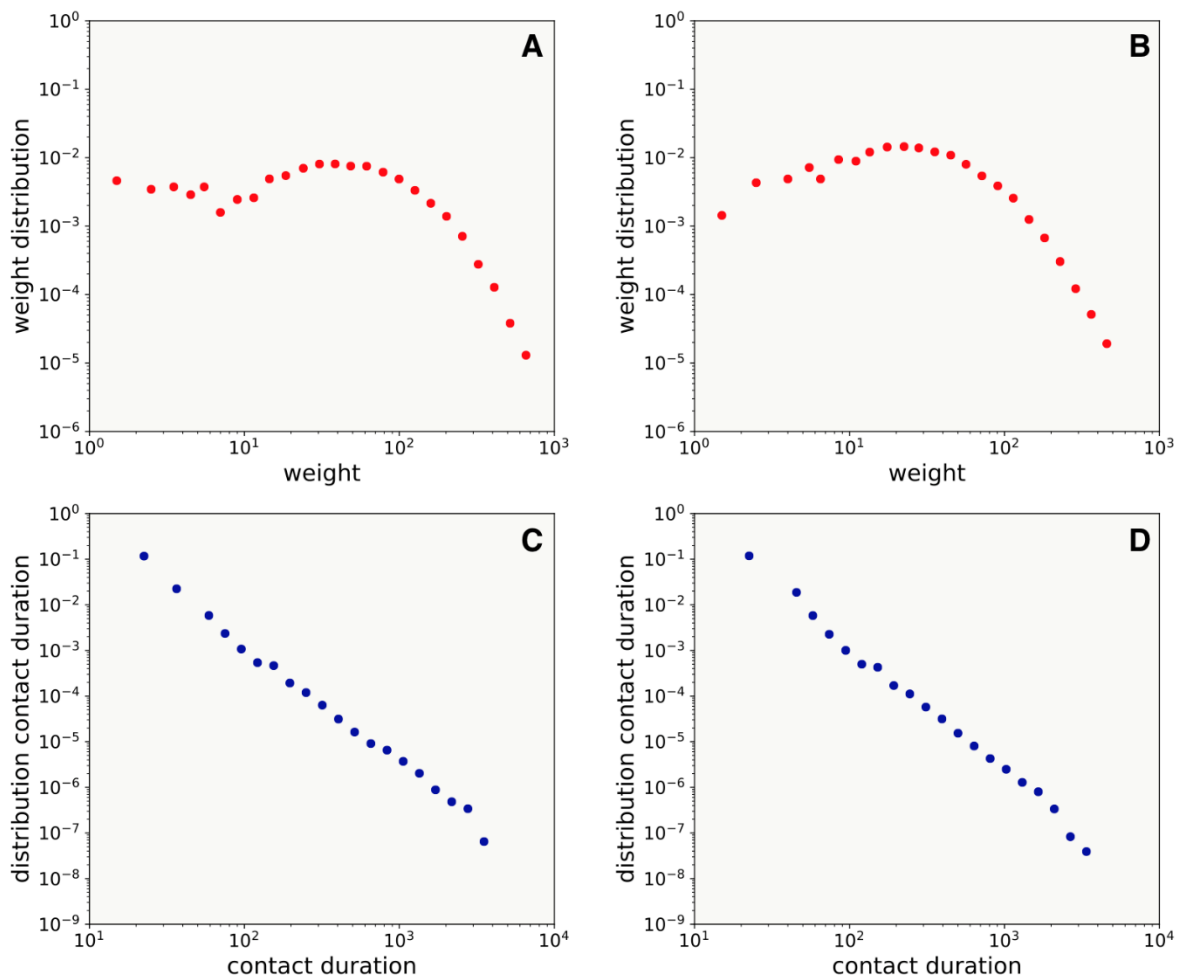
240

241 ***3.1 Pattern of social association***

242 ***3.1.1 Contact data and network analysis***

243 In July a total of 146,861 contacts between ewes were recorded over 15 days; in August a total of 95,618
244 contacts were recorded over 14 days. Aggregated contact networks were formed by 84 nodes and 3471
245 edges for July and 3483 edges for August. The distribution of the weights was heterogeneous as shown in

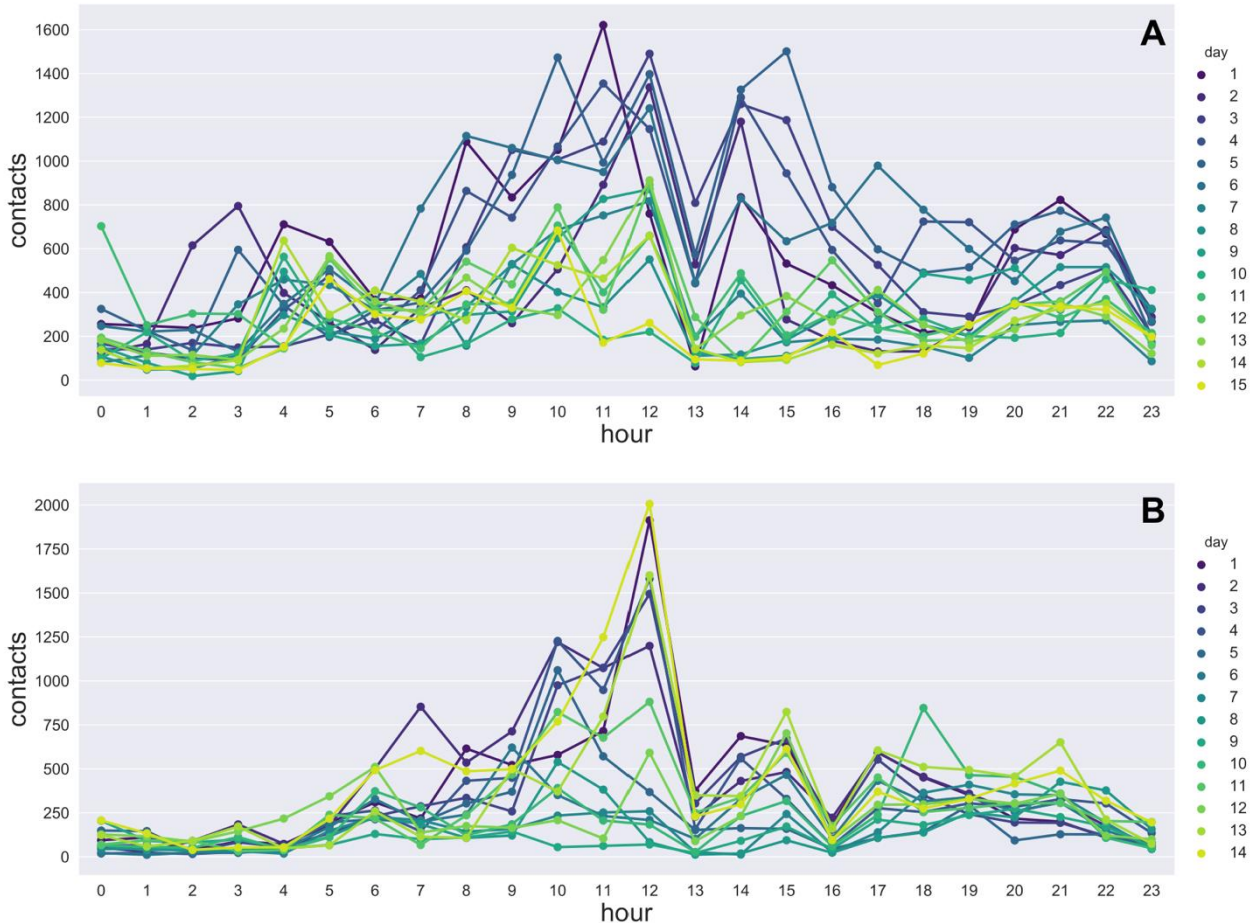
246 Figure 2, both for July aggregated network (panel A), and August aggregated network (panel B). Moreover,
 247 Figure 2 shows the probability of distribution of ewe-to-ewe contact durations; there were comparable
 248 distributions for July (panel C) and August (panel D). The contact duration distribution shows a highly
 249 heterogeneous distribution and decay as a power law: most of the contacts were short, and there were few
 250 long-lasting contacts. The mean contact duration measured over all contact events was 48 seconds for July
 251 and 45 seconds for August and with 1.4% of contact exceeding 5 minutes in July, and 1.1% in August.



252
 253 Figure 2. Distributions of the weights of the aggregated contact networks in July (panel A) and August (panel B);
 254 distributions of contact durations measured over July (panel C), and August (panel D) experimental periods.

255
 256 Figure 3 shows the temporal patterns of the hourly number of contacts over July (A) and August (B)
 257 experimental periods. In July, the number of contacts were significantly higher during the first six days of
 258 deployments (see Supplementary Material, Figure S1, panel A). Overall, contacts were numerous in the late

259 morning and in the early noon, and decline after 3 pm, and a peak of number contact occurred at 12 pm and
 260 markedly decreased at 1 pm, for both study periods (see Supplementary Material, Figure S2). The number of
 261 contacts decreased during the night for both deployments.



262
 263 Figure 3. Timeline of hourly contact activities by day of experiment in July (A) and August (B).

264

265

266 **1.1.1 Modular structure of aggregated networks**

267 In July the modularity coefficient Q was 0.06, and in August was 0.08. The Q coefficient range from 0 (random
 268 associations) to 1 (no association between closed units or communities), and, as suggested by Newman
 269 (2004), non-zero values indicate deviations from randomness, and Q values ≥ 0.3 usually indicate good
 270 clusters divisions.

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1.1.2 Social differentiation

The social differentiation measured in July and August deployment were 0.84 and 0.93, and the median values of social differentiation of null networks were 0.71 and 0.73. There was significant social differentiation in both deployments (p -values < 0.001).

1.2 Pattern of social assortment

Results from the multiple regression matrices showed that ewes did not significantly associate together with respect to genetic relatedness, reproductive status, and weight in either deployment. In the July deployment ewes tended to spend more time with ewes belonging to the same mating group (regression coefficient = 7.18, p -value = 0.033), where as in the August deployment ewes tended to associate with others of a similar age (regression coefficient = -3.10, p -value = 0.026).

1.3 Impact of the Environment on Social Network

The results showed that ewes tended to cluster together when the WCI increased, and when field sizes were smaller in the August deployment (i.e., when the density of ewes increased) (Table 1).

Table 1. General Linear Model results predicting the effects of Wind Chill Index, Temperature Humidity index and field areas on daily clustering coefficient.

| <i>Variable</i> | <i>Estimate</i> | <i>Standard error</i> | <i>t-value</i> | <i>p-value</i> |
|-----------------|-----------------|-----------------------|----------------|----------------|
| WCI | 0.101 | 0.041 | 2.469 | 0.033 |
| THI | -0.055 | 0.029 | -1.838 | 0.096 |
| area | -0.198 | 0.079 | -2.486 | 0.032 |

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297 **2. Discussion**

298 Overall, our results showed that the dyadic associations between ewes are not-random, and the individuals
299 had differentiated social relationships based on characteristic similarity. Nevertheless, the attributes that
300 influence the social interactions between individuals change over time. Furthermore, environmental and
301 microclimate parameters were identified as predictors for the tendency of ewes to associate to each other
302 to form clusters.

303 We found a difference in the total number of proximity events between deployments. Despite the higher
304 number of proximity events were registered in July, the distributions of total time spent in contact by two
305 ewes and of contact durations are very similar for both deployments. Though, within each study period, our
306 analysis revealed large heterogeneities in the social contact behaviour between ewes. Even though some
307 ewes formed strong social bonds, most individuals showed weak associations. Individual heterogeneity in
308 social relationships, both in number and in strength of associations, has been previously reported in several
309 species, including farm animals (Gygax et al., 2009; Norton et al., 2012; Boyland et al., 2016). The timeline of
310 hourly number of contacts showed some peaks in both deployments, suggesting coordinate behaviours
311 among ewes. Moreover, the density of animals positively affects the number of proximity events among
312 ewes. High densities have been reported to increase social conflict and aggressive behaviours in farm animals
313 (Estevez et al., 2007; Rodenburg and Koene, 2007), and in particular, aggression in ewes is sensitive to
314 changes in space allowance (Jørgensen et al., 2009).

315 Our analysis revealed no evidence of community structure at any study period, indicating the absence of
316 distinct social groups within the flock. Previous works have found that the existence of sub-groups within an
317 established flock, with larger groups tending to split into sub-groups (Kawai, 1989; Michelena et al., 2008),
318 and this varies with different breeds (Arnold et al., 1981). Nevertheless, Kawai (1989) showed that the size

319 and the composition of sub-groups was not stable, and individuals did not have significant subgrouping
320 partners.

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322 At an individual level, the ewes showed highly differentiated social relationships and preferred association
323 with the same individuals more often than would be expected if associations occurred at random. Social
324 interactions among animals rarely are random, and individuals tend to associate with others that share their
325 characteristics such as age, social rank, reproductive status, genetic relatedness and behavioural
326 specialization (e.g. Vander Wal et al. 2015; Sosa, 2016; Machado et al., 2019). In our study, we found that
327 ewes were associated with individuals with whom they shared similar attributes (i.e. homophily), however,
328 these attributes were different depending on deployment, demonstrating that the social structure of the
329 flock changed over time.

330 In July, ewes maintained the social bonds formed in the subgroups for breeding. Social recognition of
331 individuals plays an important role in development of social familiarization in sheep (Keller et al., 2011).
332 Previous studies provided evidence that adult sheep can discriminate between familiar and unfamiliar
333 conspecifics through the visual channel (Kendrick et al., 2001; Ferreira et al., 2004), and through olfactory
334 and auditory signals (Keller et al., 2011). In our study, social familiarity, resulting from repeated interactions
335 between ewes, may be an important factor influencing associations among individuals in this species.

336 The strength of associations in August's social network was significantly affected by the tendency of the ewes
337 to associate with individuals of similar age. Age homophily has previously been reported in many species,
338 including primates (Carter et al., 2015; Sosa, 2016), dolphins (Lusseau and Newman, 2004), and marmots
339 (Wey and Blumstein, 2010). Our results agreed with those obtained in previous studies on domestic sheep:
340 Lawrence (1990) showed that juvenile ewes spend more time in contact with each other, and in a more
341 recent study, Doyle et al. (2016) found that similarity in age is associated with strong social bonds in adult
342 ewes. Our findings indicate that the ties that were formed among sheep in the early stages of ontogenetic
343 development have been maintained over time, and in our study these relationships were reasserted after
344 five weeks of separation.

345 We found no significant influence of reproductive status, weight (as an indicator of body size) and genetic

346 relatedness on strength of associations in both deployments. Reproductive status is an important factor
347 influencing association patterns between females in Grevy's zebra (Sundaresan et al., 2007), and feral horses
348 (Heitor and Vicente, 2010; Bouskila et al., 2015). The association of individuals with similar reproductive
349 status may reflect a tendency of females for the protection of the offspring by improving the vigilance tactics
350 as a mean of reducing predation risk (Heitor and Vicente, 2010). We suggest that a change in ecological
351 pressures associated with domestication, such as the reduction of predatory pressure, may have reduced the
352 need of ewes to associate assortatively by reproductive status.

353 Our results showed that dyadic associations were not more likely to occur among ewes of similar body size,
354 in agreement with those obtained by Doyle et al. (2016) in a domestic flock. In ungulates, body size is
355 commonly correlated with social rank (e.g., McElligott et al., 2001), and, although we did not directly measure
356 the social rank, our results also agreed with those obtained by Vander Wal et al. (2015) that found no effect
357 of social status on proximal associations in bighorn ewes.

358 The influence of relatedness on social relationships in gregarious animals is very varied. Relatedness has an
359 effect on the strength of social bonds in macaques (Widdig et al., 2001; Schülke et al., 2013), and marmots
360 (Wey and Blumstein, 2010), and in these species, kinship is an important factor to maintain social cohesion.
361 However, in other species, association strength of individuals is not correlated to their genetic relatedness
362 (bighorn sheep: Vander Wal et al., 2015; feral horses: Cameron et al., 2009, Bouskila et al., 2015; racoon:
363 Hirsch et al., 2013), and contact patterns between animals are influenced by other factors. We did not find
364 any effect of relatedness on contact patterns in the current study.

365 Our findings showed daily variation in clustering of ewes during the August's data collection period, in
366 relation to environmental factors and microclimatic condition. As we expected, changes in clustering of
367 individuals occurred in relation to animals' density. Very few studies have examined the relationship between
368 climatic parameters and contact networks in sheep. Influences of daily temperatures and rainfall was found
369 in time spent in contact among ewes (Doyle at al., 2016), and it was observed that clustering under the
370 shaded areas of the shelter increased during the hottest part of the day (Broster and Doyle, 2013). However,
371 the weather parameters do not act separately and interact in a very complex way. To account for this,
372 weather factors have been combined into singles measures, called climatic indices, previously used to assess

373 the thermal stress in farm animals and its consequences on production traits (Van laer et al., 2014). Our
374 results showed that the tendency of the ewes to form clusters varied in relation to the Wind Chill Index. We
375 suppose that the clustering behaviour reflected the strategy of ewes to coalesce around a scarce resource
376 (i.e. the windward field hedge) in case of thermal discomfort. Specifically, our results are related to the
377 oceanic climate of Devon in south-west England, and we cannot generalize our findings for different climatic
378 zones. In particular our deployment took place during the summer, the daily mean temperatures ranged
379 from 12°C to 19°C and the relative humidity ranged from 70% to 95%.

380 In conclusion, our study has shown that monitoring of social behaviour of sheep through the use of proximity
381 sensors is a valuable tool for advancing our understanding of social system of this species, which has the
382 potential to enhance management practices in production settings. Our results indicate that the social bonds
383 between ewes were dynamic and evolved over time, and factors influencing proximity events were social
384 familiarity and similarity in age. Moreover, clustering behaviour was influenced by microclimatic and
385 environmental conditions. We speculate that the social structure of the flock can change with environmental
386 and social conditions, and the identification of circumstances that modify the social behaviour of sheep is
387 critically important in order to implement management and productivity strategies. However, the proximity
388 sensors do not provide information about the behavioural context of the contacts. An exciting area for future
389 research is to combine proximity sensors with other sensors such as accelerometers to infer not just who is
390 interacting but also the nature of the interaction. Finally, we suggest that studying the social organization
391 over the annual productivity cycle will lead to better understanding of the factors shaping domestic sheep
392 social structure.

393

394 **Declarations of interest**

395 The authors declare there was no conflict of interest. All data was collected under ethics approval from the
396 University of Exeter (application number: eCLESPsy000541).

397

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403

404

405 **3. References**

406 - Arnold, G.W., Wallace, S.R., Rea, W.A., 1981. Associations between individuals and home-range
407 behaviour in natural flocks of three breeds of domestic sheep. *Appl. Anim. Ethol.*, 7(3), 239-257.
408 [https://doi.org/10.1016/0304-3762\(81\)90081-X](https://doi.org/10.1016/0304-3762(81)90081-X).

409 - Beauchamp, G., 2003. Group-size effects on vigilance: a search for mechanisms. *Behav. Processes*
410 63(3), 111-121. doi:10.1016/S0376-6357(03)00002-0.

411 - Bouskila, A., Lourie, E., Sommer, S., de Vries, H., Hermans, Z.M., van Dierendonck, M., 2015. Similarity
412 in sex and reproductive state, but not relatedness, influence the strength of association in the social
413 network of feral horses in the Blauwe Kamer Nature Reserve. *Isr. J. of Ecol. Evol.*, 61(2), 106-113.
414 <http://dx.doi.org/10.1080/15659801.2016.1149921>.

415 - Boyland, N.K., Mlynski, D.T., James, R., Brent, L.J., Croft, D.P., 2016. The social network structure of
416 a dynamic group of dairy cows: From individual to group level patterns. *Appl. Anim. Behav. Sci.*, 174,
417 1-10. <https://doi.org/10.1016/j.applanim.2015.11.016>.

418 - Broster, J.C., Dehaan, R.L., Swain, D.L., Friend, M.A., 2010. Ewe and lamb contact at lambing is
419 influenced by both shelter type and birth number. *Animals*, 4(5), 796-803.
420 doi:10.1017/S1751731110000030.

421 - Broster, J., Doyle, R., 2013. Measuring resource use in sheep with proximity logger technology. In
422 New Zealand spatially enabled livestock management symposium (p. 13).

- 423 - Cameron, E.Z., Setsaas, T.H., Linklater, W.L., 2009. Social bonds between unrelated females increase
424 reproductive success in feral horses. *Proc. Natl. Acad. Sci. U.S.A.*, 106(33), 13850-13853.
425 doi:10.1073/pnas.0900639106.
- 426 - Carter, A.J., Lee, A.E., Marshall, H.H., Ticó, M.T., Cowlshaw, G., 2015. Phenotypic assortment in wild
427 primate networks: implications for the dissemination of information. *Royal Soc. Open Sci.*, 2(5),
428 140444. <https://doi.org/10.1098/rsos.140444>.
- 429 - Cattuto, C., Van den Broeck, W., Barrat, A., Colizza, V., Pinton, J.F., Vespignani, A., 2010. Dynamics of
430 person-to-person interactions from distributed RFID sensor networks. *PloS one*, 5(7), e11596.
- 431 - Champion, R.A., Rutter, S.M., Penning, P.D., Rook, A.J., 1994. Temporal variation in grazing behaviour
432 of sheep and the reliability of sampling periods. *Appl. Anim. Behav. Sci.*, 42(2), 99-108.
433 [https://doi.org/10.1016/0168-1591\(94\)90150-3](https://doi.org/10.1016/0168-1591(94)90150-3).
- 434 - Crawley, M.J. 1993. *GLIM for ecologists*. 1993 Oxford. UK: Blackwell Scientific Publications.
- 435 - Doyle, R.E., Broster, J.C., Barnes, K., Browne, W.J., 2016. Temperament, age and weather predict
436 social interaction in the sheep flock. *Behav. Processes*, 131, 53-58.
437 doi:10.1016/j.beproc.2016.08.004.
- 438 - Estevez, I., Andersen, I. L., Nævdal, E., 2007. Group size, density and social dynamics in farm animals.
439 *Appl. Anim. Behav. Sci.*, 103(3-4), 185-204. doi:10.1016/j.applanim.2006.05.025.
- 440 - Ferreira, G., Keller, M., Saint-Dizier, H., Perrin, G., Lévy, F., 2004. Transfer between views of
441 conspecific faces at different ages or in different orientations by sheep. *Behav. Processes*, 67(3), 491-
442 499. doi:10.1016/j.beproc.2004.08.005.
- 443 - Fisher, A., Matthews, L., 2001. The social behaviour of sheep. In: *Social behaviour in farm animals*
444 (pp. 211-245). CAB International, Wallingford, UK.
- 445 - Freire, R., Swain, D.L., Friend, M.A., 2012. Spatial distribution patterns of sheep following
446 manipulation of feeding motivation and food availability. *Animals*, 6(5), 846-851.
447 doi:10.1017/S1751731111002126.
- 448 - Goslee, S.C., Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data.
449 *J. Stat. Softw.*, 22(7), 1-19.

- 450 - Griffin, A.S., West, S.A., 2002. Kin selection: fact and fiction. *Trends Ecol. Evol.*, 17(1), 15-21.
451 [https://doi.org/10.1016/S0169-5347\(01\)02355-2](https://doi.org/10.1016/S0169-5347(01)02355-2).
- 452 - Gygas, L., Neisen, G., Wechsler, B., 2010. Socio-Spatial Relationships in Dairy Cows. *Ethology*, 116(1),
453 10-23. doi:10.1111/j.1439-0310.2009.01708.x.
- 454 - Heitor, F., Vicente, L., 2010. Affiliative relationships among Sorraia mares: influence of age,
455 dominance, kinship and reproductive state. *J. Ethol.*, 28(1), 133-140. doi:10.1007/s10164-009-0165-
456 9.
- 457 - Hirsch, B.T., Prange, S., Hauver, S.A., Gehrt, S.D., 2013. Genetic relatedness does not predict racoon
458 social network structure. *Animal Behav.*, 85(2), 463-470.
459 <http://dx.doi.org/10.1016/j.anbehav.2012.12.011>.
- 460 - Holand, Ø., Gjøstein, H., Losvar, A., Kumpula, J., Smith, M.E., Røed, K.H., Nieminen, M., Weladji, R.B.,
461 2004. Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *J.*
462 *Zool.*, 263(4), 365-372. doi:10.1017/S0952836904005382.
- 463 - Jørgensen, G.H.M., Andersen, I. L., Berg, S., Bøe, K.E., 2009. Feeding, resting and social behaviour in
464 ewes housed in two different group sizes. *Appl. Anim. Behav. Sci.*, 116(2-4), 198-203.
465 doi:10.1016/j.applanim.2008.08.014.
- 466 - Kawai, K., 1989. The flexible grouping and behavioral character of a flock of Suffolk ewes (*Ovis aries*).
467 *J Ethol.*, 7(1), 41-51. <https://doi.org/10.1007/BF02350581>.
- 468 - Keeling, J.L., 2001. Social behavior in farm animals. CABI.
- 469 - Keller, M., Cornilleau, F., Archer, E., Lévy, F., 2011. Development of social familiarity in ewes. *Physiol.*
470 *Behav.*, 104(3), 392-397. doi: 10.1016/j.physbeh.2011.04.030.
- 471 - Kendrick, K.M., da Costa, A.P., Leigh, A.E., Hinton, M.R., Peirce, J.W., 2001. Sheep don't forget a face.
472 *Nature*, 414(6860), 165.
- 473 - Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., Rutz, C., 2013. Reality mining of animal
474 social systems. *Trends Ecol. Evol.*, 28(9), 541-551. doi: 10.1016/j.tree.2013.06.002
- 475 - Lawrence, A.B., Wood-Gush, D.G.M., 1988. Home-range behaviour and social organization of Scottish
476 blackface sheep. *J. Appl. Ecol.*, 25(1), 25-40. doi: 10.2307/2403607.

- 477 - Lawrence, A.B., 1990. Mother-daughter and peer relationships of Scottish hill sheep. *Animal Behav.*,
478 39(3), 481-486. [https://doi.org/10.1016/S0003-3472\(05\)80412-9](https://doi.org/10.1016/S0003-3472(05)80412-9).
- 479 - Lusseau, D., Newman, M.E., 2004. Identifying the role that animals play in their social networks. *Proc*
480 *Biol Sci.*, 271(suppl_6), S477-S481. doi:10.1098/rsbl.2004.0225.
- 481 - Machado, A.M.S., Cantor, M., Costa, A.P.B., Righetti, B.P.H., Bezamat, C., Valle-Pereira, J.V.S., P. C.
482 Simões-Lopes P.C., Castilho P.V., Daura-Jorge, F.G., 2019. Homophily around specialized foraging
483 underlies dolphin social preferences. *Biol. Lett.*, 15(4), 20180909.
484 <http://dx.doi.org/10.1098/rsbl.2018.0909>.
- 485 - McElligott, A.G., Gammell, M.P., Harty, H.C., Paini, D.R., Murphy, D.T., Walsh, J.T., Hayden, T.J., 2001.
486 Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating
487 success?. *Behav. Ecol. Sociobiol.*, 49(4), 266-272. doi:10.1007/s002650000293.
- 488 - Michelena, P., Sibbald, A. M., Erhard, H.W., McLeod, J.E., 2008. Effects of group size and personality
489 on social foraging: the distribution of sheep across patches. *Behav. Ecol.*, 20(1), 145-152.
490 doi:10.1093/beheco/arn126.
- 491 - Newman, M.E., 2004. Analysis of weighted networks. *Phys. Rev. E*, 70(5), 056131.
492 doi:10.1103/PhysRevE.70.056131.
- 493 - Newman, M.E., 2006. Modularity and community structure in networks. *Proc. Natl. Acad. Sci. U.S.A.*,
494 103(23), 8577-8582. doi:10.1073/pnas.0601602103.
- 495 - Norton, E., Benaben, S., Mbotha, D., Schley, D., 2012. Seasonal variations in physical contact amongst
496 domestic sheep and the implications for disease transmission. *Livest. Sci.*, 145(1-3), 34-43.
497 doi:10.1016/j.livsci.2011.12.017.
- 498 - OpenBeacon. <http://www.openbeacon.org>. (Accessed 4 July 2019).
- 499 - R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for
500 Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>>.
- 501 - Rieucou, G., Martin, J.G., 2008. Many eyes or many ewes: vigilance tactics in female bighorn sheep
502 *Ovis canadensis* vary according to reproductive status. *Oikos*, 117(4), 501-506. doi:
503 10.1111/j.2007.0030-1299.16274.x

- 504 - Rodenburg, T.B., Koene, P., 2007. The impact of group size on damaging behaviours, aggression, fear
505 and stress in farm animals. *Appl. Anim. Behav. Sci.*, 103(3-4), 205-214.
506 <https://doi.org/10.1016/j.applanim.2006.05.024>
- 507 - Schülke, O., Wenzel, S., Ostner, J., 2013. Paternal relatedness predicts the strength of social bonds
508 among female rhesus macaques. *PLoS One*, 8(3), e59789. doi:10.1371/journal.pone.0059789.
- 509 - Sevi, A., Taibi, L., Albenzio, M., Muscio, A., Dell'Aquila, S., Napolitano, F., 2001. Behavioral, adrenal,
510 immune, and productive responses of lactating ewes to regrouping and relocation. *J. Animal Sci.*,
511 79(6), 1457-1465. <https://doi.org/10.2527/2001.7961457x>.
- 512 - SocioPatterns. <http://www.sociopatterns.org/>. (Accessed 4 July 2019).
- 513 - Sundaresan, S.R., Fischhoff, I.R., Dushoff, J., Rubenstein, D.I., 2007. Network metrics reveal
514 differences in social organization between two fission–fusion species, Grevy’s zebra and onager.
515 *Oecologia*, 151(1), 140-149. doi:10.1007/s00442-006-0553-6.
- 516 - Segnalini, M., Nardone, A., Bernabucci, U., Vitali, A., Ronchi, B., Lacetera, N., 2011. Dynamics of the
517 temperature-humidity index in the Mediterranean basin. *Int. J. Biometeorol.*, 55(2), 253-263.
518 doi:10.1007/s00484-010-0331-3.
- 519 - Silk, J.B., 2007. The adaptive value of sociality in mammalian groups. *Philos. Trans. Royal Soc. B*
520 362(1480), 539-559. doi: 10.1098/rstb.2006.1994.
- 521 - Sosa, S., 2016. The influence of gender, age, matriline and hierarchical rank on individual social
522 position, role and interactional patterns in *Macaca sylvanus* at ‘La Forêt des singes’: A multilevel
523 social network approach. *Front. Psychol.*, 7, 529. doi:10.3389/fpsyg.2016.00529.
- 524 - Thom, E.C., 1959. The discomfort index. *Weatherwise*, 12(2), 57-61.
525 <https://doi.org/10.1080/00431672.1959.9926960>
- 526 - Tucker, C.B., Rogers, A.R., Verkerk, G.A., Kendall, P.E., Webster, J.R., Matthews, L.R., 2007. Effects of
527 shelter and body condition on the behaviour and physiology of dairy cattle in winter. *Appl. Anim.*
528 *Behav. Sci.*, 105(1-3), 1-13. <https://doi.org/10.1016/j.applanim.2006.06.009>.
- 529 - Van laer, E., Moons, C.P.H., Sonck, B., Tuytens, F.A.M., 2014. Importance of outdoor shelter for cattle
530 in temperate climates. *Livest. Sci.* 159 (1), 87–101. <http://dx.doi.org/10.1016/j.livsci.2013.11.003>.

- 531 - Vander Wal, E., Gagné-Delorme, A., Festa-Bianchet, M., Pelletier, F., 2015. Dyadic associations and
532 individual sociality in bighorn ewes. *Behav. Ecol.*, 27(2), 560-566. doi:10.1093/beheco/arv193.
- 533 - Veissier, I., Boissy, A., Nowak, R., Orgeur, P., Poindron, P., 1998. Ontogeny of social awareness in
534 domestic herbivores. *Appl. Anim. Behav. Sci.*, 57(3-4), 233-245. [https://doi.org/10.1016/S0168-1591\(98\)00099-9](https://doi.org/10.1016/S0168-1591(98)00099-9).
- 535
- 536 - Whitehead, H., 2008. *Analyzing animal societies: quantitative methods for vertebrate social analysis*.
537 University of Chicago Press.
- 538 - Wey, T.W., Blumstein, D.T., 2010. Social cohesion in yellow-bellied marmots is established through
539 age and kin structuring. *Animal Behav.*, 79(6), 1343-1352. doi:10.1016/j.anbehav.2010.03.008.
- 540 - West, S.A., Pen, I., Griffin, A.S., 2002. Cooperation and competition between relatives. *Science*,
541 296(5565), 72-75. doi:10.1126/science.1065507.
- 542 - Widdig, A., Nürnberg, P., Krawczak, M., Streich, W.J., Bercovitch, F.B., 2001. Paternal relatedness and
543 age proximity regulate social relationships among adult female rhesus macaques. *Proc. Natl. Acad. Sci. U.S.A.*, 98(24), 13769-13773. <https://doi.org/10.1073/pnas.241210198>.
- 544
- 545 - Wilson-Aggarwal, J.K., Ozella, L., Tizzoni, M., Cattuto, C., Swan, G. J., Moundai, T., Silk, M., Zingesser
546 J.A., McDonald, R.A., 2019. High-resolution contact networks of free-ranging domestic dogs *Canis familiaris* and implications for transmission of infection. *PLoS neglected tropical diseases*, 13(7),
547 e0007565. <https://doi.org/10.1371/journal.pntd.0007565>.
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558 **Supplementary material**

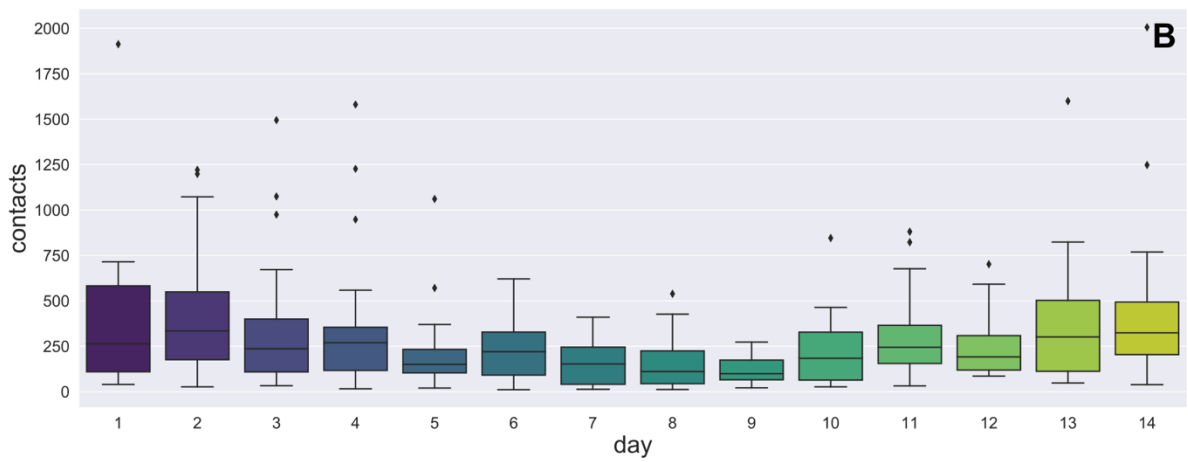
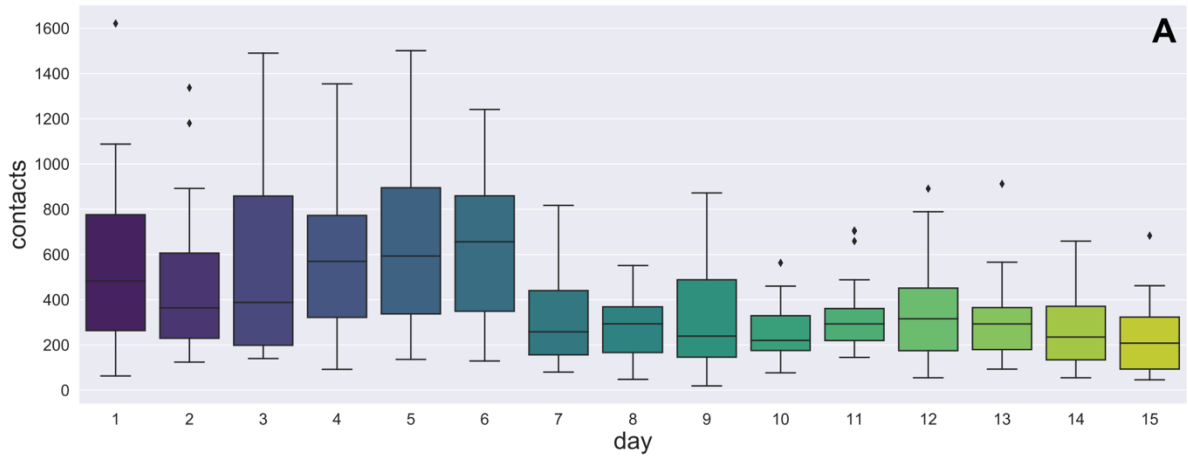
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560 **Contact data**

561 We computed the number of contacts among ewes for each day grouped by hour, for both deployments.
562 Figure S1 shows the distribution of the number of contacts for each day of deployment for July study period
563 (panel A) and August study period (panel B). Given the non-independent nature of the contact data, all the
564 statistical analyses were carry out using permutation tests (10,000 permutations were used). The number of
565 contacts in each sampling day were compared using the Kruskal– Wallis test, followed by the Pairwise post
566 hoc permutation test, implemented in the R (R Development core team 2014) package *coin*. The number of
567 contacts differed significantly between sampling days for both deployments (July: $X^2 = 72.277$, p-value <
568 0.001; August: $X^2 = 41.374$, p-value < 0.001). Table S1 and S2 show the p-values obtained by Pairwise post
569 hoc permutation test for July and August respectively. Figure S2 shows the sum of contacts grouped by hour
570 for July (panel A) and August (panel B) study periods.

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574 Figure S1. Distribution of the number of contacts for each day of deployment for July study period (A) and
 575 August study period (B). The box and whisker plots illustrate the interquartile range, and the black lines
 576 indicate the median. The error bars extend from the box to the highest and lowest values.

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586 Table S1. P-values obtained by the Pairwise post hoc permutation test for comparison of number of contacts

587 among sampling days in July. P-values < 0.05 are in bold.

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| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|----|------------------|--------------|--------------|------------------|------------------|------------------|-------|-------|-------|-------|--------------|-------|-------|-------|
| 2 | 0.239 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 3 | 0.543 | 0.522 | - | - | - | - | - | - | - | - | - | - | - | - |
| 4 | 0.725 | 0.181 | 0.496 | - | - | - | - | - | - | - | - | - | - | - |
| 5 | 0.489 | 0.050 | 0.208 | 0.563 | - | - | - | - | - | - | - | - | - | - |
| 6 | 0.364 | 0.045 | 0.239 | 0.529 | 0.836 | - | - | - | - | - | - | - | - | - |
| 7 | 0.006 | 0.107 | 0.055 | 0.006 | <0.001 | <0.001 | - | - | - | - | - | - | - | - |
| 8 | 0.003 | 0.062 | 0.044 | 0.001 | <0.001 | <0.001 | 0.942 | - | - | - | - | - | - | - |
| 9 | 0.006 | 0.086 | 0.037 | 0.005 | <0.001 | <0.001 | 0.852 | 0.860 | - | - | - | - | - | - |
| 10 | <0.001 | 0.015 | 0.018 | <0.001 | <0.001 | <0.001 | 0.563 | 0.457 | 0.725 | - | - | - | - | - |
| 11 | 0.012 | 0.375 | 0.261 | 0.008 | 0.001 | <0.001 | 0.337 | 0.386 | 0.312 | 0.050 | - | - | - | - |
| 12 | 0.027 | 0.256 | 0.148 | 0.007 | 0.001 | 0.001 | 0.642 | 0.536 | 0.509 | 0.256 | 0.869 | - | - | - |
| 13 | 0.009 | 0.143 | 0.085 | 0.004 | <0.001 | <0.001 | 0.757 | 0.733 | 0.702 | 0.204 | 0.563 | 0.725 | - | - |
| 14 | 0.001 | 0.038 | 0.011 | 0.001 | <0.001 | <0.001 | 0.509 | 0.757 | 0.687 | 0.934 | 0.117 | 0.327 | 0.409 | - |
| 15 | <0.001 | 0.004 | 0.002 | <0.001 | <0.001 | <0.001 | 0.129 | 0.173 | 0.256 | 0.375 | 0.022 | 0.059 | 0.063 | 0.348 |

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595 Table S2. P-values obtained by the Pairwise post hoc permutation test for comparison of number of contacts

596 among sampling days in August. P-values < 0.05 are in bold.

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| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|----|------------------|------------------|--------------|--------------|--------------|--------------|--------------|--------------|------------------|--------------|-------|-------|-------|
| 2 | 0.741 | - | - | - | - | - | - | - | - | - | - | - | - |
| 3 | 0.522 | 0.386 | - | - | - | - | - | - | - | - | - | - | - |
| 4 | 0.409 | 0.261 | 0.901 | - | - | - | - | - | - | - | - | - | - |
| 5 | 0.041 | 0.011 | 0.167 | 0.227 | - | - | - | - | - | - | - | - | - |
| 6 | 0.107 | 0.041 | 0.397 | 0.502 | 0.457 | - | - | - | - | - | - | - | - |
| 7 | 0.011 | 0.002 | 0.046 | 0.071 | 0.536 | 0.288 | - | - | - | - | - | - | - |
| 8 | 0.005 | 0.002 | 0.021 | 0.046 | 0.235 | 0.180 | 0.710 | - | - | - | - | - | - |
| 9 | <0.001 | <0.001 | 0.004 | 0.010 | 0.146 | 0.036 | 0.543 | 0.844 | - | - | - | - | - |
| 10 | 0.076 | 0.033 | 0.219 | 0.409 | 0.741 | 0.975 | 0.248 | 0.186 | 0.079 | - | - | - | - |
| 11 | 0.584 | 0.317 | 0.885 | 0.869 | 0.069 | 0.353 | 0.023 | 0.014 | 0.001 | 0.208 | - | - | - |
| 12 | 0.279 | 0.096 | 0.749 | 0.642 | 0.317 | 0.804 | 0.151 | 0.029 | 0.001 | 0.433 | 0.522 | - | - |
| 13 | 0.820 | 0.584 | 0.657 | 0.433 | 0.072 | 0.096 | 0.010 | 0.007 | 0.002 | 0.090 | 0.628 | 0.369 | - |
| 14 | 0.710 | 0.958 | 0.312 | 0.212 | 0.006 | 0.034 | 0.001 | 0.001 | <0.001 | 0.019 | 0.248 | 0.077 | 0.710 |

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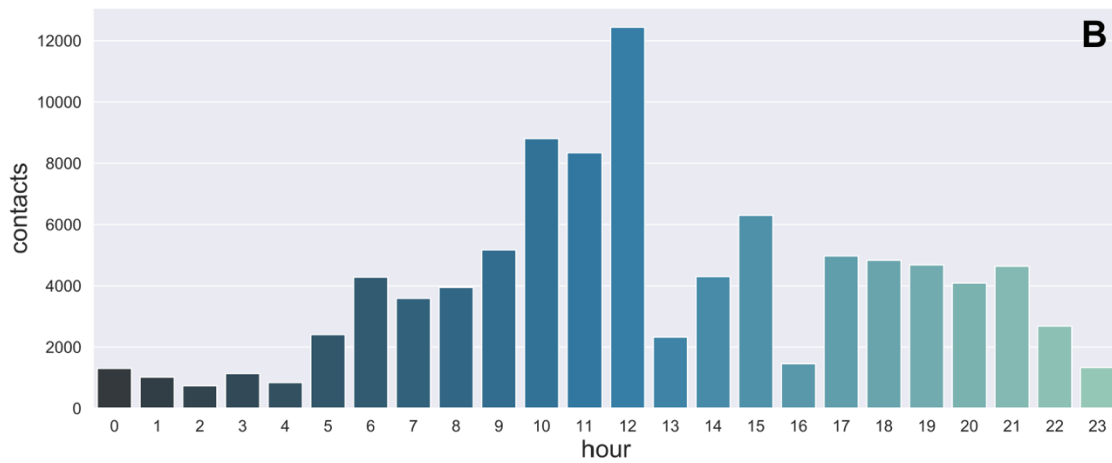
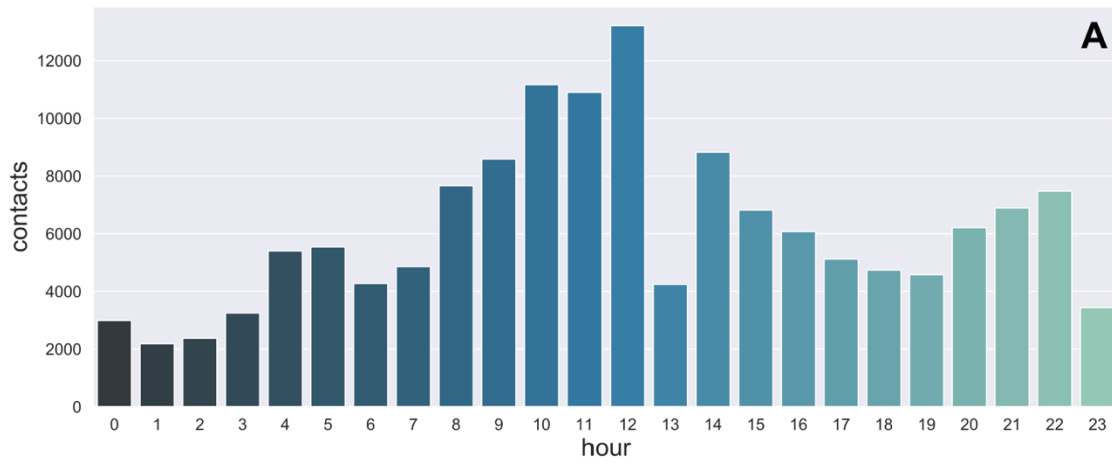
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608 Figure S2. Sum of contacts grouped by hour for July (A) and August (B) study periods.

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618 **Pattern of social assortment**

619 Table S3 shows the results from multiple regression with matrices (MRM) with all variables included.

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621 Table S3. Effects of all variables on the total time in proximity between ewes for July and August deployments.

| Variable | July (R ² =0.013) | | August (R ² =0.012) | |
|---------------------|---------------------------------|---------|-----------------------------------|---------|
| | Regression coefficient | p-value | Regression coefficient | p-value |
| Relatedness | 25.21 | 0.34 | 11.77 | 0.48 |
| Age | -3.50 | 0.12 | -3.35 | 0.01 |
| Weight | -0.28 | 0.59 | 0.36 | 0.26 |
| Reproductive status | -1.09 | 0.15 | 0.28 | 0.28 |
| Mating group | 6.29 | 0.08 | 0.30 | 0.91 |

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624 **Environmental and weather parameters**

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626 Table S4. Environmental and weather parameters in the August deployment: total space area (ha); Ewes
627 per ha; 24 h mean temperature (°C); 24 h mean relative humidity (%); 24 h mean wind speed (km/h).

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| Date | Total area (ha) | Ewes per ha | Mean temperature (°C) | Mean humidity (%) | Mean wind speed (km/h) |
|----------|-----------------|-------------|-----------------------|-------------------|------------------------|
| 04/08/18 | 2.47 | 34 | 19.6 | 81.3 | 4.97 |
| 05/08/18 | 2.47 | 34 | 19.7 | 70.4 | 5.13 |
| 06/08/18 | 2.47 | 34 | 17.8 | 81.4 | 2.82 |
| 07/08/18 | 2.47 | 34 | 15.5 | 82.8 | 4.18 |
| 08/08/18 | 2.47 | 34 | 14.3 | 84.7 | 2.91 |
| 09/08/18 | 2.47 | 34 | 14.0 | 79.7 | 3.8 |
| 10/08/18 | 2.47 | 34 | 12.8 | 84.4 | 6.37 |
| 11/08/18 | 2.47 | 34 | 12.5 | 93.4 | 7.05 |
| 12/08/18 | 2.47 | 34 | 15.9 | 95.6 | 8.79 |

| | | | | | |
|----------|------|----|------|------|------|
| 13/08/18 | 1.92 | 43 | 16.6 | 88.2 | 5.5 |
| 14/08/18 | 1.92 | 43 | 16.7 | 88.7 | 4.96 |
| 15/08/18 | 1.92 | 43 | 17.1 | 86.7 | 6.86 |
| 16/08/18 | 1.92 | 43 | 15.3 | 85.2 | 6.89 |
| 17/08/18 | 1.92 | 43 | 14.1 | 85.7 | 3.3 |

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