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8 **Author(s):** Laura Ozella[a,b*], Joss Langford[b,c], Laetitia Gauvin[a], Emily Price[b], Ciro Cattuto[a,d], Darren P.
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The effect of age, environment and management on social contact patterns in sheep

Laura Ozella[a,b*], Joss Langford[b,c], Laetitia Gauvin[a], Emily Price[b], Ciro Cattuto[a,d], Darren P. Croft[b]

[a] *ISI Foundation, Turin, Italy.*

[b] *Centre for Research in Animal Behaviour, University of Exeter, Exeter, UK*

[c] *Activinsights Ltd., Cambridgeshire, UK*

[d] *Department of Computer Science, University of Turin, Turin, Italy*

*Corresponding author. E-mail: laura.ozella@isi.it

Abstract

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

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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

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

2. Methods
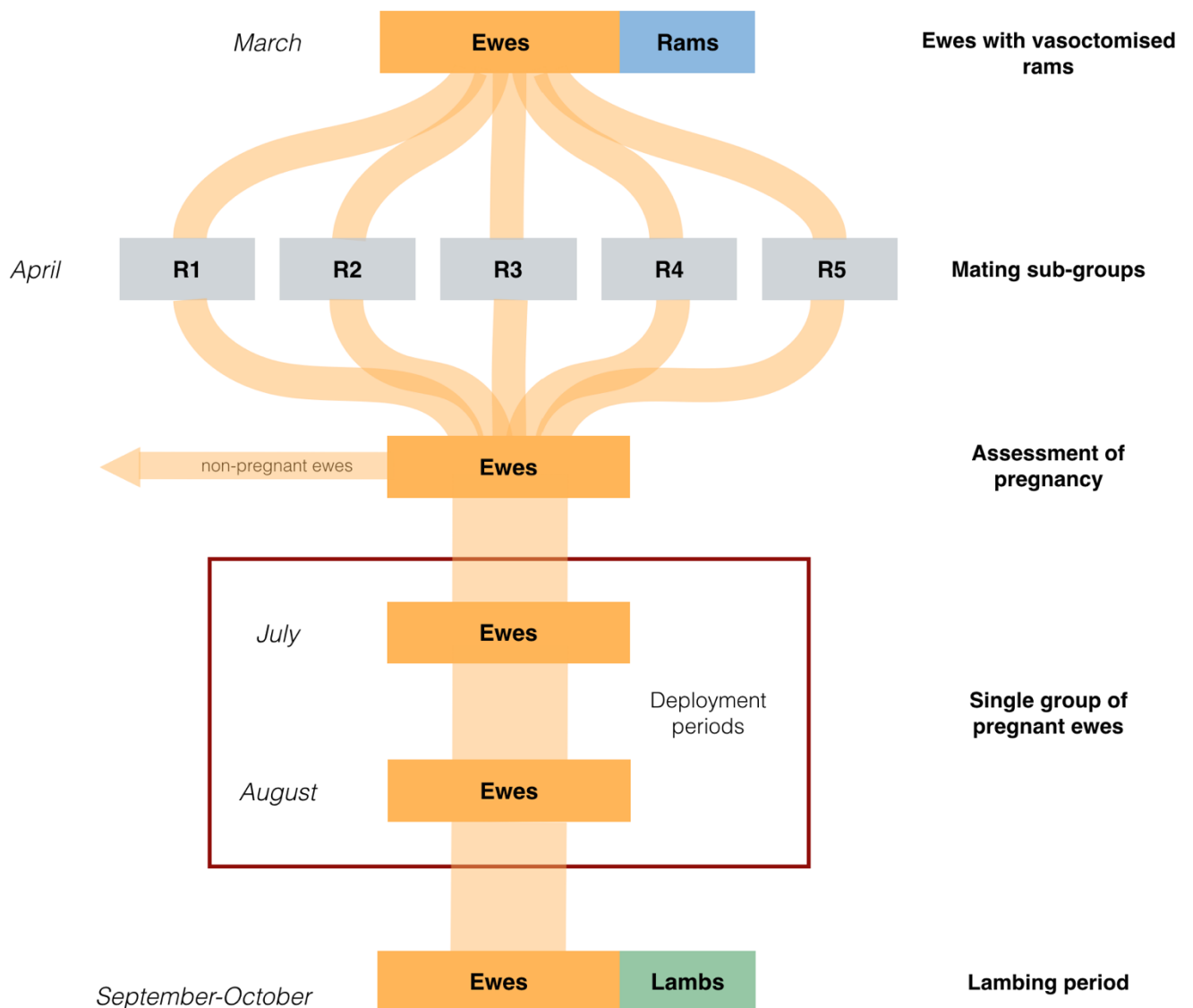
2.1 *Data collection*

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

time of the study ewes were aged from 2 years to 9 years old, and all ewes were weighed before the start of

the deployments. The complete pedigree of the flock is known (for both maternal and paternal pedigree)

and the pedigree was used to compute the pairwise coefficient of relatedness among all individuals. The

coefficient ranged between 0 (no relatives) and 0.5 (mother–daughter or full siblings).

During the deployment in August daily meteorological data were recorded via a weather station (Davis

Vantage Pro2 Plus). In particular, 24 h mean temperature (°C), 24 h mean relative humidity (%), 24 h mean

wind speed (m/s) were recorded. From these measures we calculated two climatic indices, the THI

(Temperature-Humidity Index) (Thom, 1959) and the WCI (Wind Chill Index) (Tucker et al., 2007). The

Temperature Humidity Index (THI) is a measure that accounts for the combined effects of environmental

temperature and relative humidity to assess the risk of heat stress (Segnalini et al., 2011):

$$THI = 0.8 \times T + [RH \times (T - 14.4)] + 46.4$$

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

Cold stress was most often quantified by means of the Wind Chill Index (WCI) (Tucker et al., 2007), that

relates ambient temperature and wind speed:

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

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

2.2 Proximity sensors

The proximity sensing platform has been designed by the SocioPatterns collaboration consortium

(http://www.sociopatterns.org). The hardware is open-source and based on the design developed by the

OpenBeacon project (http://www.openbeacon.org). The proximity sensors used in this study have been

previously deployed in social network studies on animals (Wilson-Aggarwal et al., 2019). The devices measure

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.

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

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

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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

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

2.5 *Impact of the Environment on Social Network*

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

3. Results

### 3.1 Pattern of social association

3.1.1 Contact data and network analysis

In July a total of 146,861 contacts between ewes were recorded over 15 days; in August a total of 95,618 contacts were recorded over 14 days. Aggregated contact networks were formed by 84 nodes and 3471 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.
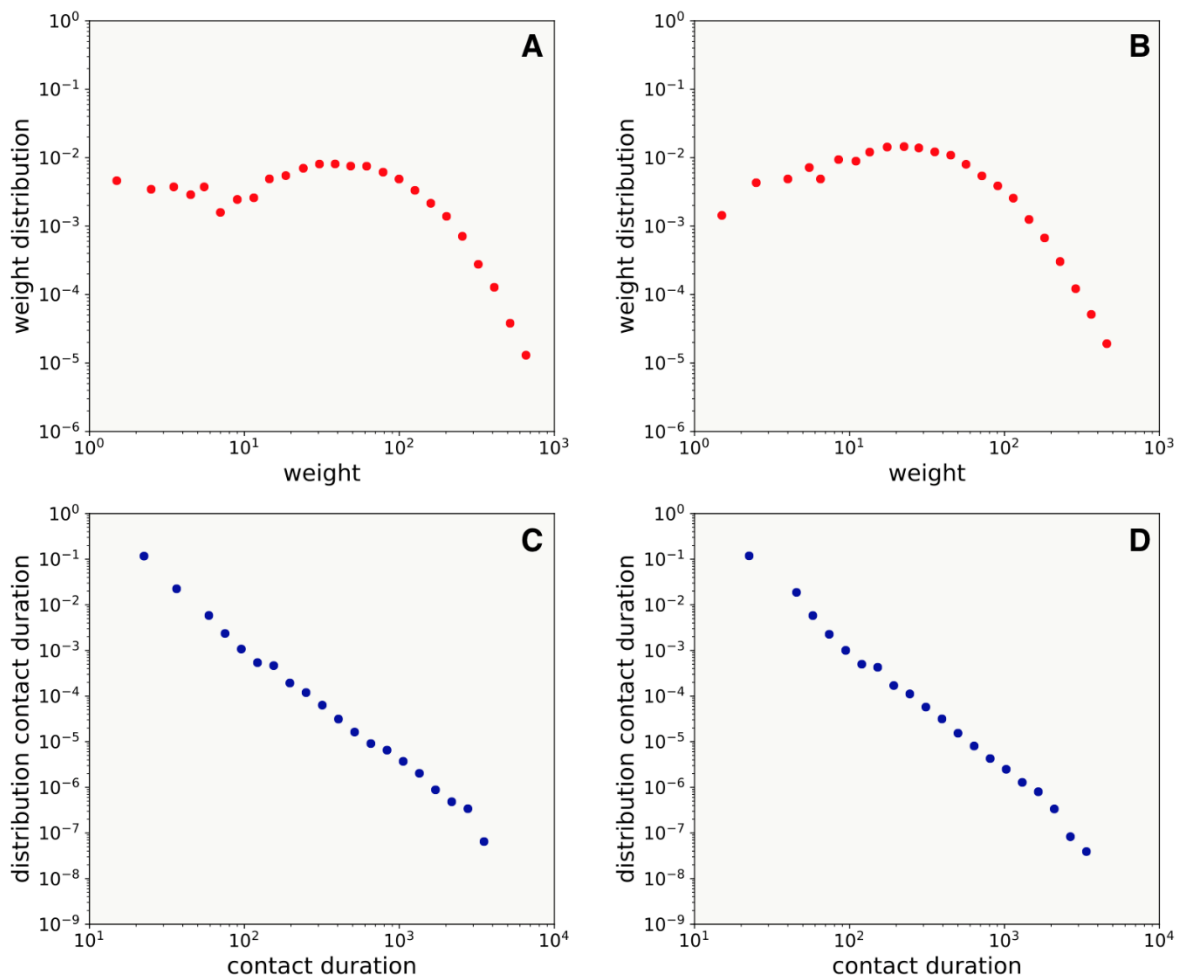
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253   Figure 2. Distributions of the weights of the aggregated contact networks in July (panel A) and August (panel B);

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

morning and in the early noon, and decline after 3 pm, and a peak of number contact occurred at 12 pm and

markedly decreased at 1 pm, for both study periods (see Supplementary Material, Figure S2). The number of

contacts decreased during the night for both deployments.
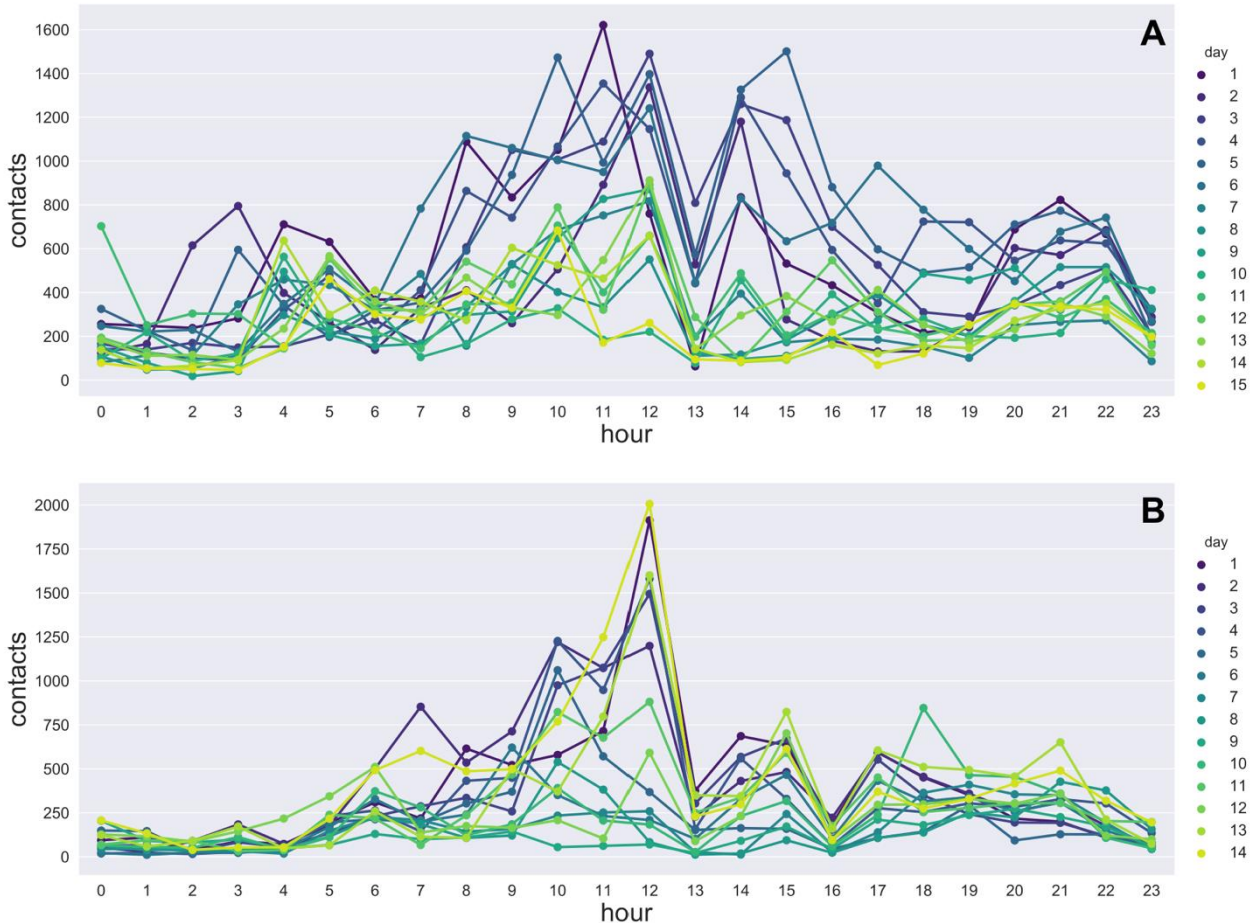
Figure 3. Timeline of hourly contact activities by day of experiment in July (A) and August (B).

1.1.1 Modular structure of aggregated networks

In July the modularity coefficient Q was 0.06, and in August was 0.08. The Q coefficient range from 0 (random

associations) to 1 (no association between closed units or communities), and, as suggested by Newman

(2004), non-zero values indicate deviations from randomness, and Q values $\geq$ 0.3 usually indicate good

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.

Variable	Estimate	Standard error	t-value	p-value
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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2. Discussion

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

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

Our analysis revealed no evidence of community structure at any study period, indicating the absence of distinct social groups within the flock. Previous works have found that the existence of sub-groups within an established flock, whit larger groups tending to split into sub-groups (Kawai, 1989; Michelena et al., 2008), 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.

321

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

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

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

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

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

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Supplementary material

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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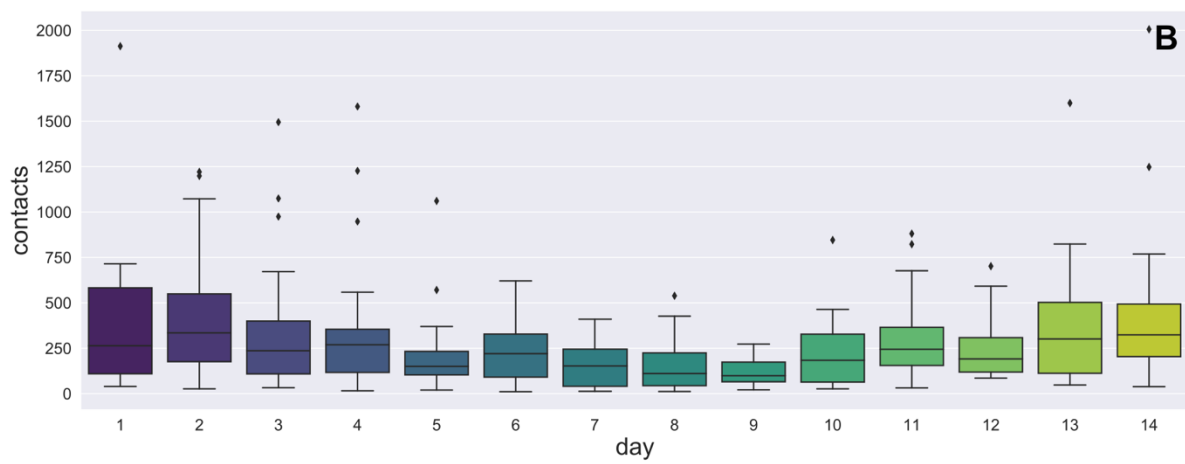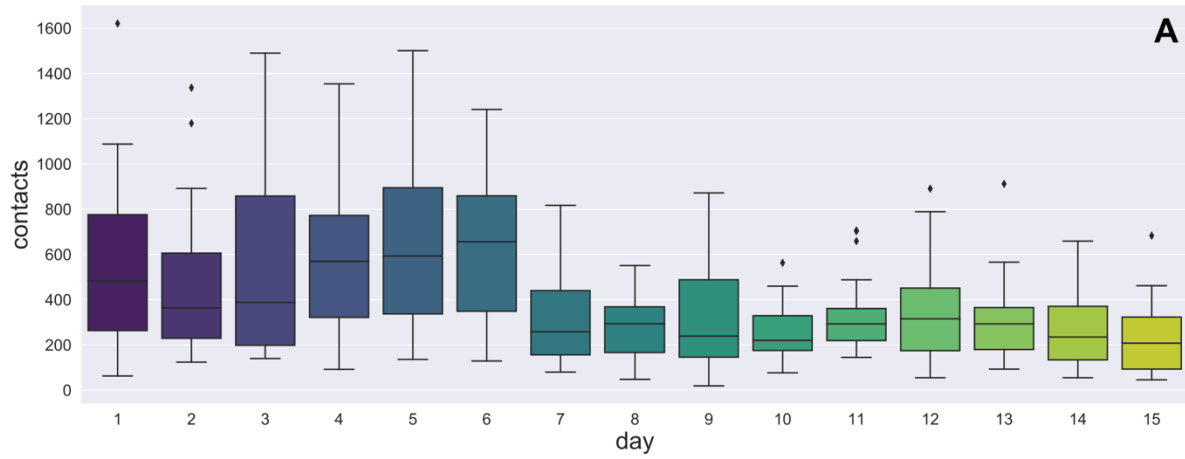
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574 Figure S1. Distribution of the number of contacts for each day of deployment for July study period (A) and

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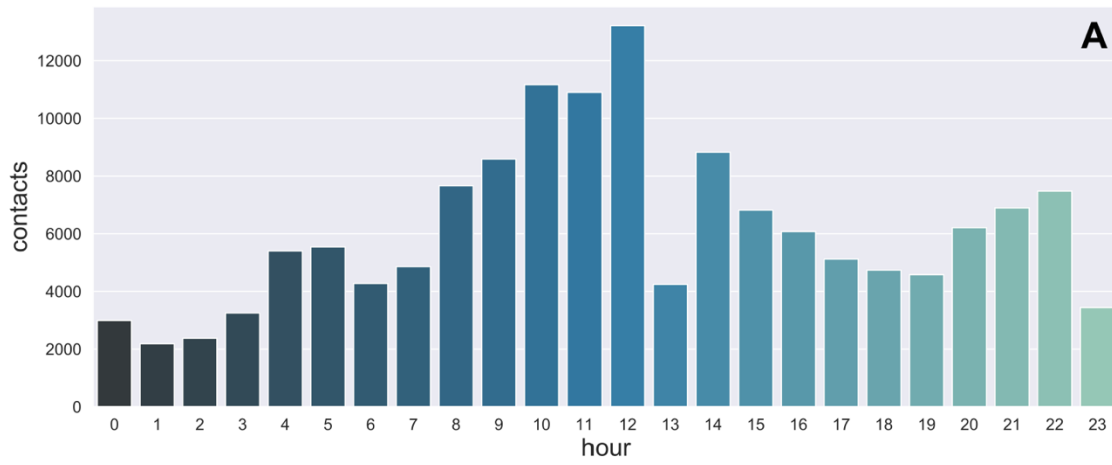
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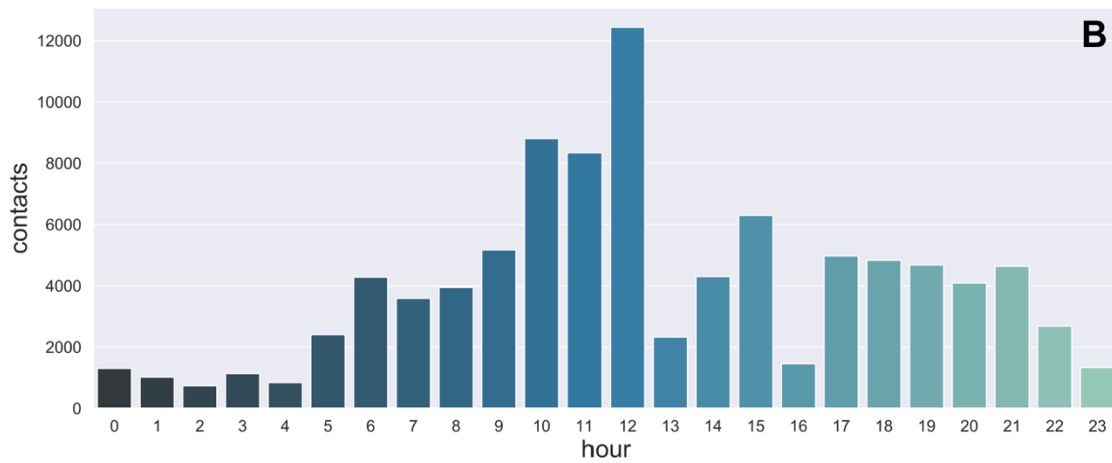
Figure S2. Sum of contacts grouped by hour for July (A) and August (B) study periods.

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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.

	July (R^2=0.013)		August (R^2=0.012)	
Variable	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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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).

628

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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