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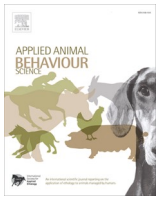

Association networks and social temporal dynamics in ewes and lambs

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ABSTRACT

Sheep are highly social domesticated animals that evolved to live in large and structured groups. As in other group-living species, individuals differ in the level of association they have with others, and these associations often result in lasting and stable social bonds. However, there are substantial gaps in our knowledge of the temporal social dynamics in sheep, and how their social bonds vary in relation to environmental changes. Here, we aimed to assess the social relationships between ewes and lambs, collecting dyadic associations data of 41 ewes and 55 lambs through the use of proximity loggers on a commercial farm. We computed association indices between each pair of animals to estimate the proportion of time any two individuals associated. We first generated an aggregated network of the whole 13-day observation period, and we compared the values of association indices between different types of dyads (i.e., lamb-mother, lamb-ewe non-mother, lambs littermates, lambs non-littermates, ewe-ewe). We generated aggregated contact networks on a daily scale to compare the ego-networks of individuals obtained in successive time windows to determine how stable social associations were over time. As would be expected, the highest values of association indices were found in dyads formed by dams and lambs (0.17 ± 0.11) and by lambs of the same litter (0.32 ± 0.09). Both single-born and twin-born lambs showed high association values with their dams (single-born: 0.24 ± 0.11; twin-born: 0.1 ± 0.05), although twin-born lambs had stronger associations with their littermates compared with those with their mothers (p-value < 0.001). At a temporal level, the flock exhibited periods of high network stability at the beginning and at the end of the study period. However, periods of social instability occurred one-two days after management interventions, such as changes in field size. These transitory periods of social instability were driven by changes in the association patterns of ewes and single born lambs. In contrast, the ego-networks of twin-born lambs remained relatively stable, supported by strong association levels between twins. Thus, the social instability of the social network was not a global one, but some parts of the network remained stable while others underwent important changes. Our study represents a first step to track social associations within an ewe-lamb group using proximity tags and advances our understanding of the social organisation of sheep. We highlight the importance of detecting social network instability as a consequence of different types of perturbations in order to identify the presence of social rearrangements.

1. Introduction

Gregarious and social animals often exhibit non-random interactions among socially connected individuals that form part of a complex social structure (Sosa, 2016). Individuals of group-living species differ in the level of interaction they have with others, and these interactions often result in lasting and stable social bonds (Verspeek et al., 2019). Farm animal species are generally gregarious (Estevez et al., 2007) and the social environment is fundamental for their welfare. However, the husbandry practices of the modern commercial farms typically do not take the social relationships into consideration, despite a growing body of evidence demonstrating important positive effects of the maintenance

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of social bonds. In wild animals, it is well known that the maintenance of a small number of strong and enduring social bonds can have a significant impact on individual fitness (McFarland et al., 2017). For example, well-connected individuals may benefit from greater longevity (Silk et al., 2010) and enhancing offspring survival (Silk et al., 2009) in baboons, and increased reproductive success in feral horses (Cameron et al., 2009). Long-term relationships that allow the maintenance of stable groups often are constituted by relatives (e.g., Archie et al., 2006; Silk, 2007). In mammals, the mother-offspring bond may influence the development of their offspring' social relationships (Fairbanks, 1996). It is well known that offspring develop a strong bond with their primary caregiver, usually the mother (Broad et al., 2006). This figure provides protection and thus a secure base from which to explore the environment and develop other social relationships (Curley and Keverne, 2005; Nowak and Boivin, 2015).

Stable associations of non-relatives are observed less frequently, although stable non-kin groups may offer individual and group benefits (e.g., feral horses: Cameron et al., 2009; semiferal ponies: Stanley et al., 2018). Social behaviour evolves when the benefits of close relationships overcome the costs (Krause and Ruxton, 2002). There are a number of potential benefits from living in groups, which include the protection from predators, and the cooperation in foraging and mating opportunities (Silk, 2007). On the other hand, sociality can be costly for competition for limited resources and reproductive opportunities and for increasing probability of disease transmission (Kutsukake, 2009). In sheep, for example, the tendency to form social groups is influenced by the forage availability (Dumont and Boissy, 2000).

Factors that disrupt social stability may result in individual-level costs due to a breakdown of social structure. Demographic processes naturally bring changes in social relationships due to birth and deaths in the population (Shizuka and Johnson, 2019). However, social structure can also vary over short timescales (e.g., days, weeks), due to individuals adjusting their social interactions in response to changes in the environment (e.g., the availability of resources) (Henzi et al., 2009; Sick et al., 2014). Although social relationships naturally change over time, transitory states of instability can be driven by extrinsic factors such as unsuccessful predator attacks or human intervention, that cause group members to become temporarily separated (Maldonado-Chaparro et al., 2018). Such social instability could induce a physiological stress response, especially if stability is not restored (Henzi et al., 2009). However, little is known about how temporary instability in social relationships affect group dynamics in animal societies, and whether these effects can influence the functionality of the entire group (Maldonado-Chaparro et al., 2018).

Sheep represent a common type of domesticated animals with a marked sociality that usually live in structured groups (Nowak et al., 2008). In farm settings, sheep are usually maintained in single-sex groups of similar age or size, the main exceptions being the ewe-lamb groups at lambing and ewe-ram groups at mating. Previous research has demonstrated that sheep develop stable social relationships with other members of the flock (Fisher and Matthews, 2001). In single-sex groups social bonds are influenced by individual characteristics such as temperament and personality (Michelena et al., 2008; Doyle et al., 2016), age (Doyle et al., 2016; Ozella et al., 2020), and social familiarisation (Ozella et al., 2020). As in other ungulates species, in sheep a strong bond develops between the mother and her own young shortly after birth (Nowak et al., 2008). The ewe-lamb bond promotes nutritional sustenance through milk and the development of social bonds with other members of the flock (Hinch et al., 1987; Napolitano et al., 2008). Aside from interacting with their mother, lambs are also able to discriminate between other members of their flock mainly through vocal communication (Sebe et al., 2004). In the field, twin lambs often remain in close physical proximity, even when they are not near their mother (Walser et al., 1981; Walser and Williams, 1986), although the closeness of sibling bonds varies across breeds (Arnold and Pahl, 1974). In conjunction the gradual decline of milk yield from the mother, subgroups of lambs are formed, and within these groups, preferential associations between familiar unrelated young animals may be established (Nowak et al., 2008). Nevertheless, our understanding of temporal stability of sheep social associations remains limited, as well as how this stability can be influenced by changes in the environment. As the sheep industry becomes more aware of the impact the social environment can have on welfare and production, understanding the social dynamics and which factors can affect social stability within a flock is of paramount importance in farm animal management.

Here, we studied the social relationships between pedigree, performance-recorded Poll Dorset ewes and lambs, collecting dyadic associations data through the use of proximity loggers on a commercial farm. The primary aim of this study is to assess the social associations of ewes and lambs (both twin-born lambs and single-born lambs) and how stable these associations are over time. We predicted that data collected by the proximity loggers would be useful to detect the social system of this species, including the stability and instability of the social network. Specifically, we computed association indices between each pair of animals to estimate the proportion of time any two individuals spent associated and we generated association networks in which nodes corresponded to individuals and the edges (i.e., connections) between two nodes were weighted with the association index between those individuals. We first generated an aggregated network of the whole experimental time period, and we compared the values of association indices between different types of dyads. In addition, we generated aggregated contact networks on a daily scale, and we compared the ego-networks (i.e., the network of a focal node, called "ego" and the nodes to whom ego is directly connected to) of individuals obtained in successive time windows to determine how stable were the associations between animals over time.

2. Material and methods

2.1. Data collection

The study was carried out on a commercial sheep farm of Poll Dorset breed in Devon, UK. Generally, most sheep are short-day seasonal breeders, whereas Poll Dorset have strong aseasonal capabilities and they can breed at any time during the year. The breeding techniques on the study farm are common to Poll Dorset breeders. The breeding cycle was described in detail in a previous work that occurred on the same farm (Ozella et al., 2020). Briefly, the breeding cycle starts in mid-March, with vasectomised rams being introduced to a single, massed group of ewes for up to 4 weeks to help stimulate oestrus. In mid-April the ewes are separated into mating sub-groups with one fertile ram per sub-group. Subsequently, the ewes are aggregated into a single flock for 7 weeks and assessed for pregnancy by ultrasound scanning. Lambing followed in September through to early October, and lambing dates were recorded.

In this study, data collection took place in October 2019 for 13 consecutive days during the lambing period from a group of ewes and lambs. During the study period proximity sensors were deployed on a flock composed by 114 individuals. However, a total of 96 sensors were included in the data analysis since we excluded the sensors that had anomalies, and the sensors that did not register contacts for the entire duration of the study. Thus, we analysed the patterns of social contact of 41 ewes and 55 lambs (28 twin-born and 27 single-born lambs). The age of lambs ranged between 7 and 28 days at the beginning of the study period.

Sensors were fixed to a freely rotating neck collar with a total weight of ~100 g for the ewes and were fixed to an expandable harness with a total weight of ~100 g for the lambs. The sheep were kept outdoors on permanent grass leys with no supplementary feeding. At the beginning of the study period, the field enclosure size for the flock was approximately 1.7 acres. The field size was progressively increased during the course of the deployment to facilitate strip grazing: new field sections

were opened on the fourth and the eighth day of deployment, reaching an approximate field enclosure size of 3.3 and 4.9 acres respectively (see supplementary material).

2.2. Proximity sensors

The proximity sensing platform was designed by the SocioPatterns collaboration (http://www.sociopatterns.org). The data were collected and processed using a proximity-sensing system previously deployed for animal studies (Wilson-Aggarwal et al., 2019; Ozella et al., 2020; Fielding et al., 2021). The system is based on wearable proximity loggers that exchange low-power radio packets (Cattuto et al., 2010), and use packet exchange and receive radio signal strength as a proxy for physical proximity. The devices measure 3 cm in diameter and weigh 2.7 g, are powered by a lithium coin battery (3 g CR2032), leading to a final weight < 6 g. Close-range proximity is defined in terms of signal strength attenuation, defined as the difference between the received and transmitted signal strength. In this study, we set the attenuation threshold to a level (- 75 dBm) corresponding to a physical distance of about 1–1.5 m; this distance allowed the detection of a close-contact situation between sheep, during which social interactions might occur (Ozella et al., 2020). A "contact event" was identified when the devices exchanged at least one radio packet during a time interval of 20 s. After a contact is established, it is considered ongoing as long as the devices continue to exchange at least one radio packet for every subsequent 20 s interval. Conversely, a contact was considered broken if a 20 s interval elapses with no exchange of radio packets. Each device has a unique identification (ID) number that is used to link the information on the contacts established by the individual carrying the device. For the present study, the system was operated in a distributed fashion: contact data was stored in the local memory of individual devices. After collecting the devices at the end of the study, data from individual devices were downloaded and the time-resolved proximity networks recorded by individual devices were combined to build a global, time-resolved proximity graph.

2.3. Social differentiation

We calculated social differentiation as the measure of the variation in relationships among members of the flock under study, i.e., how much variation there is in dyadic probability of association (Whitehead, 2008).

We computed the social differentiation using the following equation (Whitehead, 2008):

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

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

2.4. Association index

To estimate the proportion of time any two individuals, *a* and *b*, spent associated, an association index was calculated for each dyad (pair of individuals). Multiple methods have been proposed for assessing dyadic social association indices (e.g., Whitehead and Dufault, 1999; Wey et al., 2008). We calculated pairwise social associations using the following formula:

$$AI = \frac{x_{ab}}{x_{ab} + x_a + x_b}$$

Where x_{ab} is the number of sampling periods when a and *b* are observed in association, x_a is the number of sampling periods when only *a* was observed, and x_b is the number of sampling periods when only *b* was observed. Our sampling periods are 20-second consecutive windows, in accordance with the temporal resolution of the proximity sensing system. The index ranges from 0 (the two individuals were never observed together) to 1 (the individuals were always observed together). The higher the value of the index, the greater the level of association between that pair of individuals.

Although there are multiple levels of relatedness within the flock, for this study we have taken into account following type of dyads: lamb-mother, lamb-ewe (non-mother), lambs littermates, lambs non-littermates, ewe-ewe (see supplementary material), and we computed the association index for these dyads. Moreover, we considered a familiar group as composed by ewes and their offspring (twin-born lamb or single-born lambs).

2.5. Association networks

Time-aggregated, weighted networks were generated based on the proximity data: the nodes of the network are individuals, an edge between two individuals indicates that at least one contact involving those individuals was recorded during the temporal aggregation window. The weight w_{ij} of an edge between nodes *i* and *j* is defined as the association index between those individuals. Network edges are undirected and the weights on the edges are regarded as symmetric ($w_{ij} = w_{ji}$). The degree of a node *i* in the network corresponds to the number of distinct individuals with whom individual *i* has been in contact. We first generated an aggregated network of the full experimental time period (13 days). For the aggregated network we computed the density. The network density describes the portion of the potential connections in a network that are actual connections. A potential connection is a connection that could potentially exist between two nodes, regardless of whether it does. The value of the density ranges from 0 to 1, with the lower limit corresponding to networks with no relationships and the upper limit representing networks with all possible relationships. The closer the value is to 1, the denser is the network and the more cohesive are the nodes in the network.

In addition to the whole observation interval, we generated aggregated networks at the daily scale, by aggregating data collected each day between 12 am and 12 am of the next day. A daily scale has a direct relevance to farms as management of the flock occurs on a daily basis. We aimed to understand whether the associations between animals are stable and representative of the social structure or fluctuate over different timescales. We thus built aggregated networks in which nodes represent individuals and weighted links give the association indices computed on a daily scale and we obtained a series of successive snapshots corresponding to association networks in successive time windows.

2.6. Individual social stability

To determine the stability of associations between animals over time, we calculated the similarities between each couple of daily association networks obtained in successive time windows (12 am and 12 am of the next day). We quantify social stability at the level of the individual by calculating the Local Cosine Similarity (LCS) (Singhal, 2001) on individual ego-networks (i.e., the network of a focal node, called "ego" and the nodes to whom ego is directly connected to). The LCS of a node *i* is given by the cosine similarity between the vectors of weights involving *i* in each network. We considered two different time periods t_1 and t_2, we denote $w_{ij,\,t1}$ and $w_{ij,\,t2}$ the weight of the link between individual *i* and *j* in the network aggregated over t_1 and t_2 respectively. The local cosine similarity of *i* in the network between t_1 and t_2 is:

$$LCS \quad (i) = \frac{\sum_j w_{ij}^{(t1)} w_{ij}^{(t2)}}{\sqrt{\sum_j \left(w_{ij}^{(t1)}\right)^2} \sqrt{\sum_j \left(w_{ij}^{(t2)}\right)^2}}$$

The local cosine similarity is given as a value between 0 (*i* had

association in t_1 with totally different subjects with respect to $t_{2)}$ and 1 (*i* had the same association in both time periods with exactly the same individuals). Overall, an individual whose ego-network changes strongly between t_1 and t_2 will have a lower cosine similarity, whereas individuals whose ego-network is similar in both days will be associated with a higher cosine similarity. The cosine similarity values between days therefore follow the evolution of the stability or instability of the considered ego-network over time and we used the average value over all individuals as a global measure of the network's stability between two days.

2.7. Statistical analysis

We compared the observed social differentiation value, with a suite of values generated by 1000 null networks using the z-test, p-values < 0.05 was considered as statistically significant. Each null network was made by randomising the nodes of the temporal network obtained from the output of sensors and then by computing null aggregated networks.

One-way permutation test and Two-sample permutation test were used to compare the indices of association between dyads, p-values < 0.05 was considered as statistically significant.

3. Results

3.1. Social differentiation

We obtained an observed social differentiation value measured at the group level and for different types of dyads; we compared the observed values with a distribution of values generated by the null networks. Overall, there was significant social differentiation in the flock (Table 1): animals associated with some individuals more and other individuals less than would be expected by chance alone (i.e., a random-mixing model). We found that the observed values of social differentiation of ewe-ewe relationships were lower than the distribution of values generated by the null networks, showing a lower variation in dyadic association than would be expected by chance. On the contrary, the social differentiation measured for single-born lambs and twin-born lambs with other lambs (excluding the interactions between littermates) were higher than the distribution of values generated by the null networks, showing a higher variation in dyadic association than would be expected by chance.

Table 1
Social differentiation measured at group level and for different types of dyads: observed values; median of the distribution of values generated by the 1000 null networks; 95% confidence interval of the distribution of values generated by the 1000 null networks; p-values obtained from the comparison between the observed values and the distribution of values obtained by the null model.

	Observed	Median of null distribution	95% confidence interval of null distribution	p-value
Group level	5.31	1.01	0.99–1.03	< 0.001
Ewe-ewe	0.90	1.05	0.96–1.15	0.002
Single-born lambs with other lambs	0.92	0.68	0.66–0.70	< 0.001
Twin-born lambs with other lambs (excluding littermates)	4.51	0.70	0.68–0.72	< 0.001
Ewe-lamb (excluding mothers-lambs)	1.24	0.82	0.80–0.85	< 0.001

3.2. Association indices over the whole study period

We computed the association indices over the entire experimental period (13 days), and we obtained an aggregated network formed by 96 nodes (41 ewes and 55 lambs) and 4429 edges. The mean degree (i.e., number of connections with other individuals) was 92.7 (range 73–95) (see Supplementary material), and the network density (i.e., ratio of the number of edges to the number of possible edges) was 0.97. This value of density, close to 1, demonstrates that this is a dense network and that the individuals are highly connected with each other. The average social association index of the group was 0.005, however, the values were strongly influenced by the type of dyad (see supplementary material).

As we expected, the higher values of association indices were found in dyads formed by dams and lambs (mean±SD: 0.167 ± 0.111) and by lambs of the same litter (mean±SD: 0.318 ± 0.09), thus, in order to understand what the strongest association are among these categories, we compared the indices of association between littermates, twin-born lambs with their mothers, and single-born lambs with their mothers. We found a significant difference between the categories (one-way permutation test: maxT = 5.66; p-value < 0.001). Pairwise permutation tests revealed that the association of dams and twin-born lambs was significantly lower compared to those among littermates (p-value < 0.001) and compared to the association between dams and single-born lambs (p-value < 0.001). This result suggests that the twin-born lambs had a greater association with their siblings compared to the association with their mothers. Moreover, the association among littermates was significantly greater than the association between dams and single-born lambs (p-value = 0.03) (Fig. 1).

In addition, we aimed to learn whether the gender of lambs could influence the strength of social associations with the dams and with the littermates. We found that the association between dams and male lambs was significantly greater than the association with female lambs (Two-sample permutation test: Z = 0–2.28; p-value = 0.02) (Fig. 2, left panel). However, the gender of littermates did not influence the strength of dyadic social association between littermates (One-way permutation test: maxT = 0.75; p-value = 0.73) (Fig. 2, right panel).

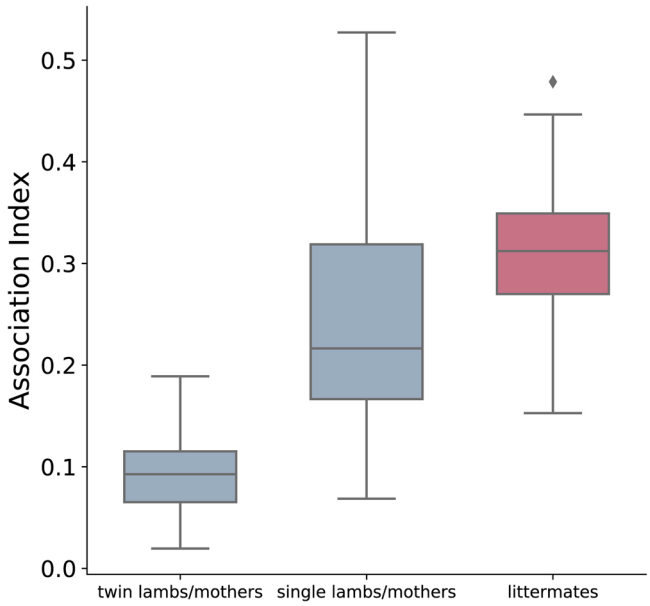

Fig. 1. Dyadic social association indices of sheep of different categories: mothers/twin-born lambs, mothers/single-born lambs and littermates. In each box the line marks the median and the extremities of the box correspond to the 25 and 75 percentiles, the whiskers give the 5 and 95 percentiles of each distribution. The lamb-lamb association indices are shown in purple; the lamb-mother association indices are shown in grey.

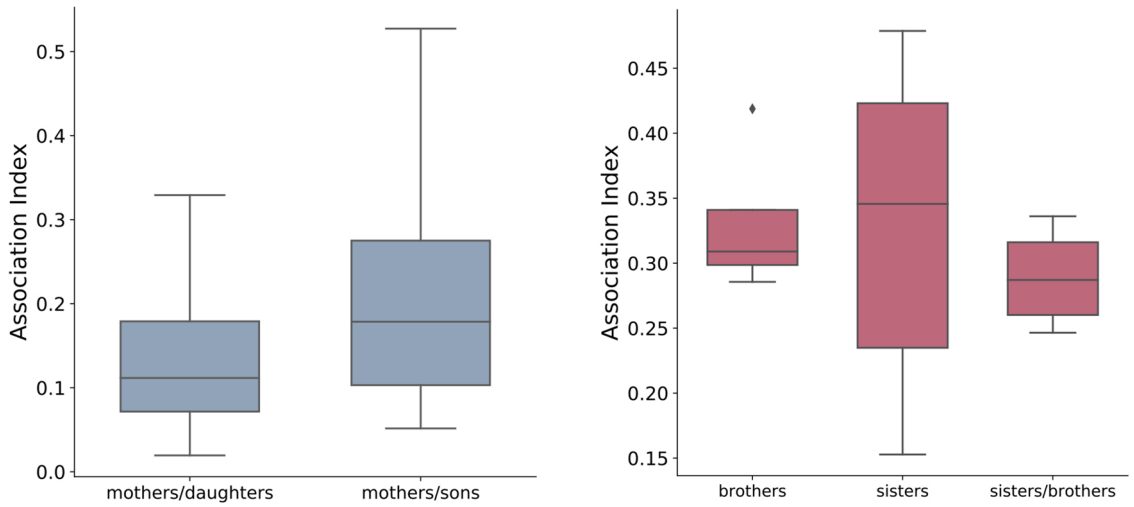

Fig. 2. Dyadic social association indices of sheep of different categories considering the gender of lambs: mothers/daughters and mothers/sons (left panel); brothers, sisters and brothers/sisters (right panel). In each box the line marks the median and the extremities of the box correspond to the 25 and 75 percentiles, the whiskers give the 5 and 95 percentiles of each distribution. The lamb-lamb association indices are shown in purple; the lamb-mother association indices are shown in grey.

3.3. Temporal variation of association indices

3.3.1. Group level

We analysed the dynamics of the network aggregated at daily timescales (from 12 am to 12 am of the next day), to detect periods of stability or instability across all individuals. In Fig. 3 we show the LCS values at the group level (averaged over all individuals). The colour-coded matrix shows the dynamics of the social network at the group level at a daily scale. Two periods of network stability, with values of LCS closer to 1, clearly appear as blocks of darker colour (Fig. 4, panel A): the block 1 (days 1–5: the average of the average LCS values, excluding the diagonal was 0.88, SD = 0.01) and the block 2 (days 11–13: average of values was 0.87, SD = 0.02). Such large values of the average cosine similarity between different days imply that the individuals keep stable ego-networks, and therefore highlight periods of network stability.

On the other hand, at some days the average cosine similarity was lower, and we identified blocks of lighter colour (Fig. 4, panel B): block 3 (day 6: mean = 0.81, SD = 0.03) and block 4 (days 9–10: mean = 0.75, SD = 0.02). These lower values indicate that the networks differed between days suggesting potential periods of network instability. Even if these values are not close to 0, they imply some rearrangement of the ego-networks because they were lower compared to those observed during the periods with higher network stability.

The size of the field in which the flock was housed was progressively increased during the deployment due to management practices (strip

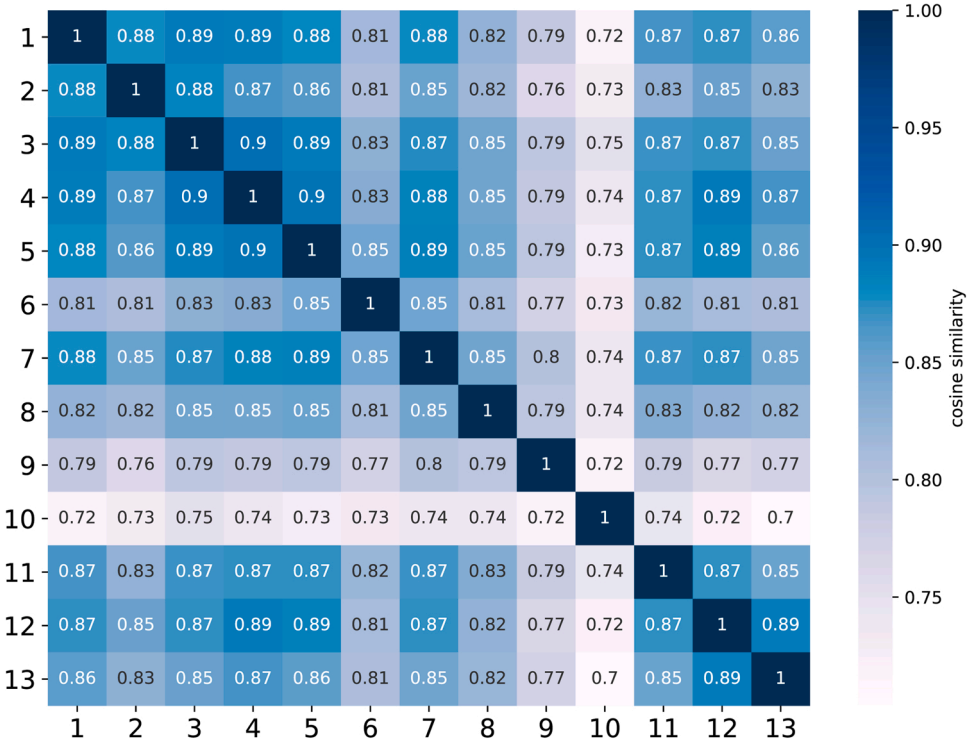

Fig. 3. Cosine Similarities between daily networks. Colour coded matrix of average local cosine similarity values measured between daily network snapshot for every individual and for every pair of days.

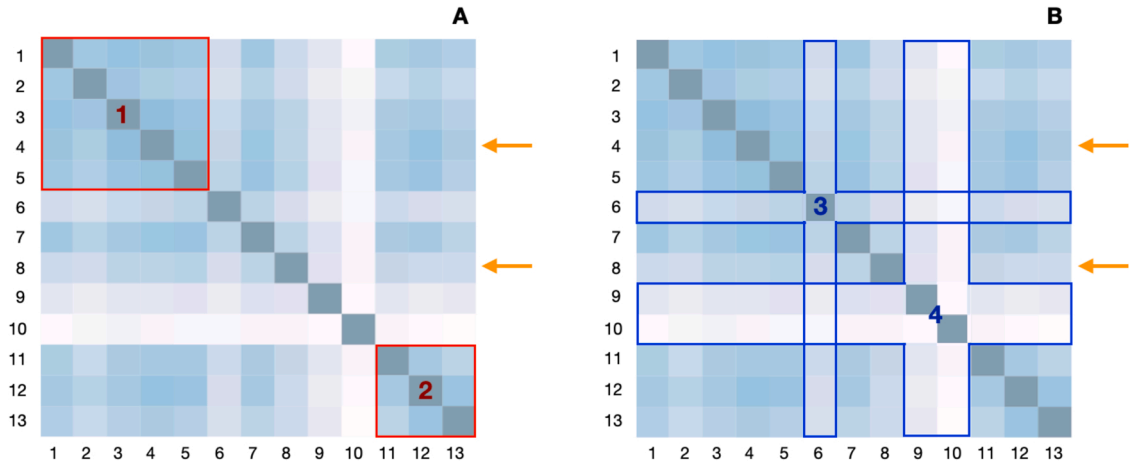

Fig. 4. Cosine Similarities between daily networks. Panel A: colour coded matrix of average local cosine similarity with highlighted periods of network stability in red (blocks 1 and 2). Panel B: colour coded matrix of average local cosine similarity with highlighted periods of network instability in blue (blocks 3 and 4). Orange arrows indicate the days field size was changed.

grazing): new field sections were opened on the fourth and the eighth day of deployment, indicated with orange arrows in Fig. 4. The network instability periods occurred one-two days after the management changes, however, the flock network stability shown during the first five days of the study, reverted during the last three days, despite the increase of available space.

3.3.2. *Twin and single-born lambs' and ewes' ego-networks*

We studied the LCS for twin-born lambs, single-born lambs and ewes' ego-networks in order to investigate if the periods of stability and instability of the global network depended on the type of ego-networks.

Fig. 5 shows that the patterns of the social dynamic between days of single-born lambs (mean = 0.76, SD = 0.08) and ewes (mean = 0.82, SD = 0.06) were similar to those observed at the group level, with periods of stability at the beginning and at the end of the study period with two days of instability at day 9 and 10, and to a lesser extent at day 6. However, the matrix of the twin-born lambs (mean = 0.90, SD = 0.02) did not show evident periods of instability. This implies that the instability of the network was not a global one but that some parts of the network remained stable while others underwent important changes.

Moreover, we aimed to investigate if the ego-networks stability of twin-born lambs was due to the association with their dams or the association among littermates, so we computed the local cosine similarity of their ego-networks after removing associations with their family members. Fig. 6 shows the local cosine similarity values between daily networks for twin-born lambs' ego-networks excluding the association with their littermate (Panel A: mean = 0.70, SD = 0.06), excluding the association with their dam (Panel B: mean = 0.92, SD = 0.02), and excluding the association both with their littermate and with their dam (Panel C: mean = 0.32, SD = 0.05). The colour-coded matrices A and B show lower level of LCS at day 9, 10 and to a lesser extent at day 6, showing periods of network instability, while matrix C shows lower values of LCS without period of instability. The higher average LCS values of matrix B confirms the strong and stable associations among litter mates and a high network stability during the first three days of the study period. Thus, confirming that, also at the temporal level, the association among littermates is stronger than the association with their dams, and the temporal stability of the twin-born lambs' ego-networks (observed in Fig. 5) was due to the association with their littermates.

To better understand the network dynamics, we studied the temporal evolution of the ego-networks, and we computed the local cosine similarity values between one day and the next (Fig. 7). The twin-born lambs had an average high cosine similarity (mean = 0.79, SD = 0.02) over the entire study period, showing a strong stability of their ego-networks, thus confirming the patterns observed in cosine similarity matrices. The stability of twin-born ego-networks was therefore not influenced by management interventions.

On the other hand, both single-born lambs and ewes showed, in a synchronised way, stable ego-networks at the beginning of the study period, before undergoing a strong rearrangement at days 9 and 10, followed by a return to the previous structure detected during the first days of the period of the study (Fig. 7, left panel).

In addition, we studied the temporal evolution of ego-networks for the three categories excluding the associations with family members, and we computed the LCS values between one day and the next (Fig. 7, right panel). Ewes exhibited an average higher cosine similarity over the entire study period compared those obtained from twin-born lambs and single-born lambs, showing a greater and stable association with flock

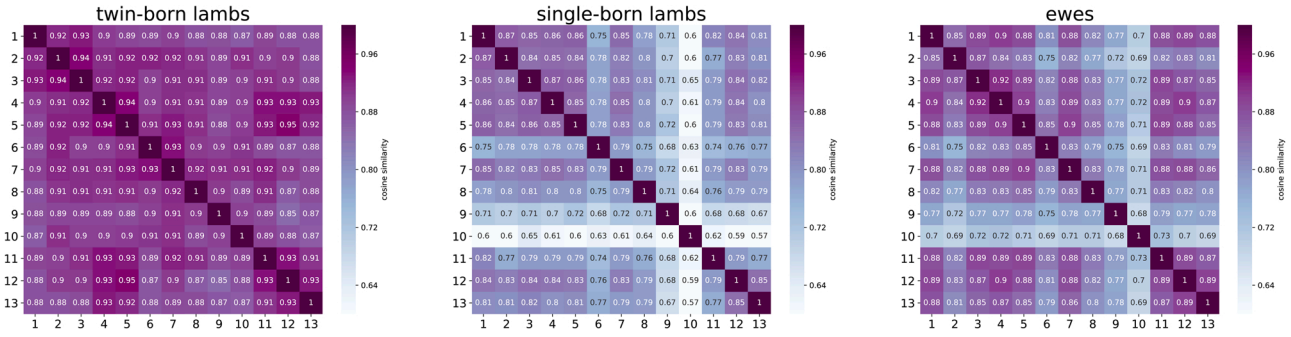

Fig. 5. Cosine Similarities between daily networks in different types of ego-networks: twin-born lambs, single-born lambs and ewes. Colour coded matrices show the average local cosine similarity values between every couple of days.

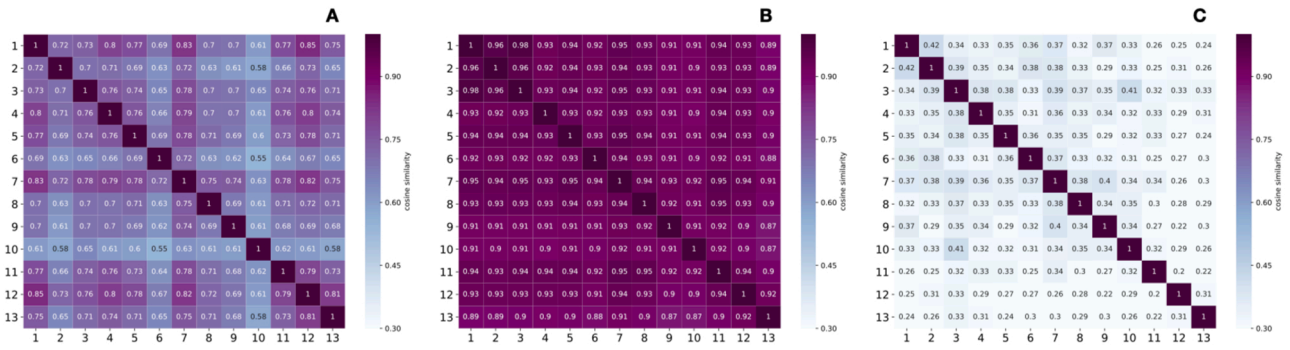

Fig. 6. Cosine Similarities between daily ego-networks of twin-born lambs excluding the associations with components of the same family group. Panel A: excluding the association with their litter mate; Panel B: excluding the association with their mother; Panel C: excluding the association both with their litter mate and with their mother. Colour coded matrices show the average local cosine similarity values between every couple of days.

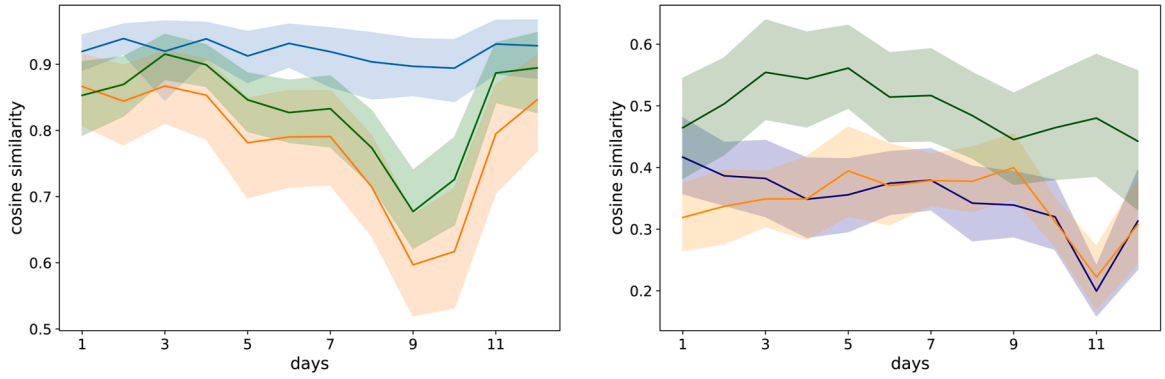

Fig. 7. Temporal evolution of ego-networks computed between one day and the next (LCS(i) (t, t + 1) for each day t). Left panel: ewes, single-born lambs and twin-born lambs; Right panel: ewes (excluding the association with offspring), single-born lambs (excluding the association with dams) and twin-born lambs (excluding the associations with littermates and dams). The lines give for each group the average of cosine similarity value over time, shaded areas show the 95% confidence interval. Ewes: green lines; Twin-born lambs: blue lines; Single-born lambs: orange lines.

members not belonging to their family group. Both twin-born and single-born lambs presented, in a synchronised way, a rearrangement of their ego-networks on day 11.

4. Discussion

We have gathered high-resolution proximity data on the contacts between Poll Dorset ewes and lambs to study social associations within the flock housed in a commercial farm. We aimed to study the social associations within the flock over the whole study period and at temporal level, by comparing the ego-networks of the animals aggregated at daily timescales, to detect periods of social stability or instability. Firstly, we found significant social differentiation in the relationships within the flock; individuals associated more or less with some individuals than would be expected if social association occurred at random. Nevertheless, the social differentiation varied between ewes and lambs; lambs associated with other lambs (excluding the littermates) non-uniformly, often forming preferential relationships with some while avoiding other individuals. On the contrary, ewe-ewe associations displayed a low variation in social differentiation, by showing a tendency to interact more uniformly than we would expect by chance. We suppose that during the lambing period, the ewes are more engaged in the care and the feeding of the lambs and their sociality with other adult individuals change, and they do not develop preferential relationships with other ewes. In our previous study, carried out on the same sheep farm, we observed a high social differentiation in ewe-ewe relationships and thus marked social preferences (Ozella et al., 2020) in a group of pregnant ewes, i.e., during a different stage in the production cycle. This agrees with a study by Norton et al. (2012), that revealed a strong variation of physical contacts within a flock depending on the breeding cycle. In particular, a clear reduction in between-ewe contact was observed amongst individuals with lambs, which is consistent with reports that mothering ewes avoid other sheep.

As expected, higher values of association indices were found in dyads formed by dams and lambs, compared to the values observed for dyads formed by lambs and non-mother ewes, when we generated an aggregated network of the full experimental time period. Mother-young relationships are well studied in sheep and previous studies emphasised that a close and exclusive attachment or bond between the ewe and her lambs is fundamental to the survival of the lamb (e.g., Nowak et al., 2000; Dwyer and Lawrence, 2005; Moraes et al., 2016). The strong mother-young bond is established between new-born and their dams after parturition (Nowak, 1996). The primary function of the dam-lamb relationship is to provide a source of nutrition and protection from predators and other conspecifics (Nowak et al., 2000). Moreover, this relationship is essential for lamb postnatal activity and for the development of social behaviour with siblings and peers (Moberg and Wood, 1985; Ligout and Porter, 2004). The pairs of dam-lambs stay in close contact for 90–100 days (Galeana et al., 2007), and at 60 days of age the average distance at pasture is about 5 m (Napolitano et al., 2008). While the ewe-lamb bond has been extensively studied, only a few studies have focused on gender differences of lambs in relation with the dam-lamb relationship (e.g., Warren and Mysterud, 1995; May et al., 2008; Freitas-de-Melo and Ungerfeld, 2020). Male lambs generally have a higher level of locomotor activity, which may result in a greater distance from their mother (Warren and Mysterud, 1995). Certain individual traits of male lambs may affect their locomotor activity, such as the fearlessness (Vandenheede and Bouissou, 1993) and a higher body weight compared

to the female lambs (Freitas-de-Melo and Ungerfeld, 2020). Nevertheless, we observed that association between dams and male lambs was significantly greater than the association with female lambs. May et al. (2008) did not observe any difference in ewe-lamb distance or locomotor activity in gender, although female lambs synchronised their behaviour more with their mother than males resulting in closer ewe–lamb distances. Our results are in agreement with those of Freitas-de-Melo and Ungerfeld (2020) who found that the responses of ewes that are separated from male lambs were greater than of those that were separated from female lambs, suggesting a stronger attachment between ewes and male lambs. On the other hand, this study demonstrated the presence of the asymmetric ties between lambs and dams, since male lambs were in a more advanced stage of independence from their mothers compared to the female lambs (Freitas-de-Melo and Ungerfeld, 2020). In our study, we could not determine the symmetry or the asymmetry of the bonds, given the undirected network obtained from the proximity sensors used.

We found that both single-born and twin-born lambs showed higher association values with their dams, compared to the values observed for dyads formed by lambs and non-mother ewes. However, twin-born lambs had stronger associations with their littermates compared with those with their mothers. Previous studies showed that twin-born lambs interact preferentially with their littermates rather than other agemates (e.g., Walser and Williams, 1986; Nowak, 2008). Ligout and Porter (2004) assessed the influence of mothers on the development of their lambs' discriminative social interactions. They demonstrated that lambs reared with their mother displayed a clear preference for their twin compared to a familiar unrelated agemate, whereas artificially reared lambs did not. This study suggests that the presence of the mother somehow influences the development of a selective bond between littermate lambs, and the recognition of unrelated agemates appears to develop more rapidly when lambs are raised in the absence of their mother. We found that the gender of twins did not influence the strength of their social association, although close associations between same-sex twins, compared to mix-sex twins, were most commonly observed in previous studies (Nowak, 2008). However, our findings cannot be generalised due the limited number of twins involved in our study (14 pairs).

At a temporal level, we analysed the association networks dynamics using the cosine similarity between the daily ego-networks. Cosine similarity is a very versatile measure and can be used to compare networks over different timescales and it allows to visualise periods of global network stability, and to identify moments of instability (Gelardi et al., 2019). When we computed the cosine similarity values at the group level (averaged over all individuals), we found periods of high network stability at the beginning and at the end of the study period and some days during which some social network rearrangements took place. We hypothesise that social changes of the flock were influenced by management changes, indeed, the size of the field in which the flock was housed was progressively increased during the study period due to the strip grazing protocol: the network instability periods occurred approximately one-two days after the management changes. These network rearrangements occurred after some delay probably because the sheep clustered on the new grass for one-two days before spreading out once it has been eaten. After this delay, they have maximised their inter-individual distances when the space availability increases due to their tendency to explore new environments (Caroprese et al., 2009; Averós et al., 2014). However, the social instability proved to be transitory, the high cosine similarity values, shown during the first five days of the study, were reverted during the last three days, by demonstrating a high level of selectivity in the network structure.

The network instability detected at group level was the result of the average cosine similarity computed at individual level. However, when the average cosine similarity was low, the distribution of the individual cosine similarity was broad, with some individuals maintaining their ego-network (i.e., larger values of the cosine similarity) while others changed dramatically (i.e., lower values of the cosine similarity). This implies that the instability of the network was not a global one, but some parts of the network remained stable, while others underwent important changes. The individual cosine similarities allow to identify individuals with more or less stable ego-networks, as well as interesting patterns of synchronisation of ego-networks temporal evolution (Gelardi et al., 2019). We observed that the twin-born lambs presented a strong social stability over the entire study period, while both single-born lambs and ewes showed periods of social instability, similar to those observed at the group level. In particular, single-born lambs and ewes showed stable ego-networks at the beginning and at the end of the study period, and they went through a strong rearrangement on days 9 and 10. Stable twin-born lambs' ego-networks are underpinned by robust association levels between twins. This result confirmed the strong relationship between littermates already observed at aggregated level, and the temporal stability of their bond despite the environmental perturbations. Moreover, the associations among littermates were stronger and more stable than the associations with their dams. More than 70% of the activities between twin lambs are synchronised (Bechet et al., 1989) during which they keep very short distances between each other. This proximity is maintained even when they are not near to their mother (Walters et al., 1981). On the other hand, we found periods of social rearrangements, when we excluded the associations among twins, demonstrating that management changes can affect the stability of the dam-lamb relationships.

In addition, we investigated how the stability of the network was influenced by the associations with the family members (i.e., mothers and littermates). Overall, we found low values of cosine similarity suggesting that animals tend to not maintain stable associations with individuals other than their own mothers and littermates. However, ewes exhibited greater and stable associations with other flock members, compared to those obtained from twin-born and single born lambs, and these associations were not influenced by the modification of the field area size. On the contrary, the relationships between lambs and the other members of the flock undergo a rearrangement after the management changes. Interestingly, there seems to be a lag of one day between the social instability observed among family members and non-family members, suggesting that the social bonds that first have undergone the management modifications are those between individuals belonging to the same family group.

The study has a number of limitations to be considered before findings can be generalised. Overall, it was performed based on data collected during a limited period of time (13 days) and only on one commercial farm. Further studies on a larger and more representative sample would be desirable (i.e., different breeds and more farms), and the study design should take into account a longer period of data collection, as well as additional dimensions of relatedness (for example half-siblings, aunts, grandmothers).

In conclusion, our study represents a first step to track social associations within an ewe-lamb group which we hope will provide the basis for more detailed and expansive studies. The proximity sensors used in this study allowed us to collect valuable data for advancing our understanding of the social system of this species and to identify possible causes of social network instability. Moreover, calculating cosine similarity proved to be a sensitive and versatile method to understand changes in individual social relationships. In particular, we found that behind the stability or instability at the group level, there is a complex mixture of stable and unstable ego-networks. This implies that some animals maintain their social relationships independently to management modification, while others went through social changes. Identifying the conditions that influence the social stability within a flock and at individual level is critically important to implement management and productivity strategies in commercial farms, such as changes in the composition of animal groups, reduction of flock density, and identification of optimal size of field.

Future research exploring patterns of social dynamics across other

breeds and flocks would be particularly valuable to assess how generalisable our findings are. Moreover, the detection of network instability as a consequence of different types of perturbations, for example the regrouping and the relocation of the animals, could allow us to better understand the social dynamics of the flock and eventually the presence of social stress. Finally future research could include the use of other sensors, such as accelerometers which could provide information about the behavioural context of the social dynamics.

Declaration of Competing Interest

The authors declare there was no conflict of interest. Data available upon request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2021.105515.

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