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New insight into social relationships in dairy cows and how time of birth, parity, and relatedness affect spatial interactions later in life

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ABSTRACT

Social interactions between cows play a fundamental role in the daily activities of dairy cattle. Real-time location systems provide on a continuous and automated basis information about the position of individual cows inside barns, offering a valuable opportunity to monitor dyadic social contacts. Understanding dyadic social interactions could be applied to enhance the stability of the social structure promoting animal welfare and to model disease transmission in dairy cattle. This study aimed to identify the effect of different cow characteristics on the likelihood of the formation and persistence of social contacts in dairy cattle. The individual position of the lactating cows was automatically collected once per second for 2 wk, using an ultra-wideband system on a Swedish commercial farm consisting of almost 200 dairy cows inside a freestall barn. Social networks were constructed using the position data of 149 cows with available information on all characteristics during the study period. Social contacts were considered as a binary variable indicating whether a cow pair was within 2.5 m of each other for at least 10 min per day. The role of cow characteristics in social networks was studied by applying separable temporal exponential random graph models. Our results revealed that cows of the same parity interacted more consistently, as well as those born within 7 d of each other or closely related by pedigree. The repeatability of the topological parameters indicated a consistent short-term stability of the individual animal roles within the social network structure. Additional research is required to elucidate the underlying mechanisms governing the long-term evolution of social contacts among dairy cattle and to investigate the relationship between these networks and the transmission of diseases in the dairy cattle population.

Key words: animal behavior, animal welfare, precision livestock farming, social network analyses

INTRODUCTION

Like many mammal species, cattle live in structured groups with a well-established social hierarchy. Cows form preferential social relationships within stable social groups (Gygax et al., 2010). Social interactions between cows play a major role in animal welfare and production (Bouissou et al., 2001). Previous studies have described how cow interactions were more likely to involve individuals with similar attributes (e.g., individuals of the same breed, lactation stage, gregariousness, or parity; Boyland et al., 2016; Churakov et al., 2021). Disturbances in social relationships, such as regrouping animals according to age or production stage, or insufficient space allowance (Bouissou et al., 2001; Rocha et al., 2020) may cause stress and trigger aggressive and abnormal behavior, and thus have longterm effects on animal health and, consequently, animal production. Moreover, social interactions also drive important mechanisms by which transmission of different pathogens between individuals can occur (Kappeler et al., 2015). Therefore, the study of social networks may provide insights into animal behavior and disease transmission, thereby contributing to the improvement of animal welfare and production (Croft et al., 2008).

Previous literature published regarding the study of social interactions in cattle is predominantly based on observational studies. Some studies reported that older cows established more positive social interactions (Pinheiro Machado et al., 2020), and that calves developed long-lasting social relationships with peers (Raussi et al., 2010). Nevertheless, observational studies based on human assessments and decisions are generally limited by the number of animals included and the duration of the study, which hinders continuous monitoring of the animals. Additionally, human observations of animal behavior are time consuming and prone to interpreta-

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tion biases, leading to variability in data quality dependent on the experience of the observer.

Precision livestock farming (**PLF**) technologies would potentially solve these limitations by allowing the automated collection of a wide range of different information and eliminating the subjectivity and biases associated with human observations, ensuring the generation of more consistent data. Ultra-wideband (**UWB**) technology is one of the most accurate indoor positioning real-time location systems (**RTLS**; Gygax et al., 2010; Pascacio et al., 2021; Ren et al., 2021a). The UWB-based RTLS offer a valuable opportunity to monitor the spatial interactions occurring on dairy farms and have consequently been applied to the study of social contacts between dairy cows (Rocha et al., 2020; Hansson et al., 2023).

Social network analysis (SNA) has been suggested as a tool for understanding the social networks constructed, based on dyadic spatial interactions (Wey et al., 2008). Social network analysis facilitates the analysis of the social network structure at individual and group level (Croft et al., 2008). Moreover, the exponential random graph models (ERGM) described by Robins and Pattison (2010) are statistical approaches that allow modeling of social network structure and study dependencies in cross-sectional graphs. Furthermore, the separable temporal ERGM (STERGM) allow the modeling of dynamic social networks and the study of the formation (newly established social contacts absent the previous day) and persistence (maintenance of contacts already established on the previous day) of the social contacts using conditional logistic regressions (Krivitsky and Handcock, 2014).

Previous studies have highlighted specific factors that may influence social networks in cattle. The presence of relatives in the herd may lead to the development of stronger bonds between conspecifics (Reinhardt and Reinhardt, 1981; Ramseyer et al., 2009), for instance. In addition, shared youth experience and dry periods may have an effect on the formation of preferential relationships in dairy cows (Færevik et al., 2006; Raussi et al., 2010; Gutmann et al., 2015). These results were obtained through direct observation of animal behavior, which limited the number of individuals monitored. Over the last decade, some studies implemented PLF technologies to monitor dyadic interactions in larger populations of dairy cattle on a continuous basis (Gygax et al., 2010; Chopra et al., 2020; Hansson et al., 2023). These studies outlined the benefits of utilizing PLF to monitor social contacts in dairy cattle, providing results on the role of parity and DIM in the number of social contacts established (Boyland et al., 2016; Hansson et al., 2023). However, dyadic contacts in cattle exhibit complexity as these interactions vary among individuals and across multiple days (Chen et al., 2014; Rocha et al., 2020), which reinforces the importance of adopting specific approaches, such as STERGM, to study the temporal aspects of the social networks of dairy cows.

The aim of the present study was to identify the effect of different cow characteristics on the likelihood of establishing new social contacts and their persistence through time, with particular emphasis on contacts established between cows that were born or dried off at the same time, or cows related by pedigree. Moreover, the study aimed to investigate the degree of stability of the social role of dairy cows. We hypothesize that cows with similar characteristics, such as being in the same parity and born within 7 d of each other, are more likely to form contacts, and these contacts will persist for longer periods compared with cows with different characteristics. We anticipate that social role of dairy cows may change gradually over time, while maintaining a certain level of stability.

MATERIALS AND METHODS

Ethical Considerations

The authors declare that according to the Swedish Animal Welfare Act, no ethical approval is needed for this type of study, thus the research was not submitted to an Animal Ethics Committee.

Animals and Housing

The present study was performed on a Swedish commercial farm that houses around 210 dairy cows, in a noninsulated freestall barn. The cows were grouped into 2 different milking groups, according to the nutritional requirements of the animals (Figure 1). Group 1 primarily consisted of early- to mid-lactation cows, and group 2 of mid- to late-lactation cows. Henceforth, these groups will be referred to as the early-lactation group and the late-lactation group, respectively. Cows were routinely switched between groups at approximately 170 DIM upon confirmation of pregnancy or when designated for slaughter. After birth, calves were moved from the cow within 24 h, and placed in individual pens for the first 2 wk. Subsequently, they were regrouped in groups of 7 until 12 wk and then in constant groups of 10 until they were expected to calve, at which time they were moved to the calving boxes. Dry cows were kept in a different barn for at least 6 wk until 2 wk before the expected calving date when they were moved to the calving boxes. The freestall barn covered approximately 1,984 m². As can be seen in Figure 1, we defined 2 functional areas within the barn: the resting area (942 m²) consisting of the cubicles and the inner alleys and the feeding area (1,042 m²) composed of the alleys beside the feeding tables and outer alleys. The functional areas were defined to account for variations in spatial interactions and the possibility of cows having different partners in different areas (Reinhardt and Reinhardt, 1981). Calves and dry cows were housed separately in different buildings. The dairy cows were milked twice a day in a milking parlor from GEA (2 \times 12 GEA Euro class 800 with Dematron 75, GEA Farm Technologies, Bönen, Germany). Milking events took place around 0430 and 1630 h and lasted around 1.5 h for each group and event. The early-lactation group contained between 96 and 100 lactating cows during the study period, and the late-lactation group contained between 87 and 94 cows. The cows were fed ad libitum at an open feed bunk (12 times a day with a total mixed ration) and had approximately 0.57 m of feed space per cow in the early-lactation group, and 0.62 m in the late-lactation group. There were 102 and 103 cubicles in the early- and late-lactation group, respectively, with rubber mattresses and sawdust as bedding material. The cow to cubicle ratio was at maximum 0.98 in the early-lactation group and 0.91 in the latelactation group during the study period.

Data Collection

The position data of the lactating cows were automatically collected with an RTLS (CowView, GEA Farm Technologies, Bönen, Germany), with a 1-s fixed rate. The cows were equipped with a tag mounted on the collar that sent UWB signals to the receivers, installed in the ceiling throughout the barn. The positions of the cows within the barn were estimated by triangulation with an accuracy of 0.78 m (Hansson et al., 2023). The accuracy was determined by calculating the mean error distance based on measurements from 13 fixed tags strategically distributed throughout the barn. Positioning data were downloaded directly from GEA's server from October 16 to 29, 2020; no RTLS outages were reported during this period. The present study excluded (6 cows in the early-, and 2 in the latelactation group) tags with more than 70% of missing data during a 24-h period, following Ren et al. (2021b).

The missing position information was interpolated using modified Akima interpolation (Akima, 1970), except for missing position data at the beginning and the end of a day, which were filled in using the first posterior and anterior nonmissing positions, respectively. The interpolation method selection was based on the interpolation accuracies reported by Ren et al. (2022).

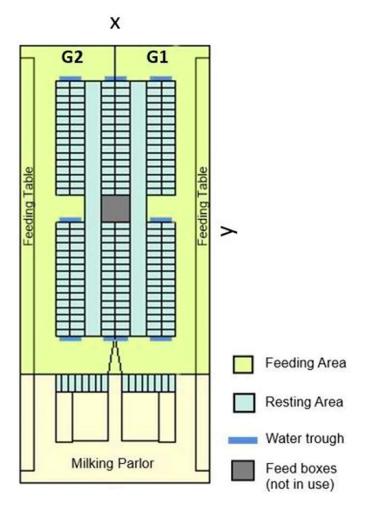


Figure 1. Schematic map of the freestall barn under study (74 \times 33 m), where y and x represent the direction of the y- and x-axis. The farm is divided into 2 milking groups: early- (G1) and late-lactation (G2) groups. The cubicles are in the central parts of the barn and the feeding tables along both sides. The beige area is outside the boundaries of the cows in the milking group, except for transport between the pen area and the milking parlor.

The interpolation procedure was performed using Matlab (2020) to accurately capture the distance between pairs of cows throughout the days.

Individual cow information data, regarding age, breed, pedigree, pregnancy diagnosis, and claw trimming records, were extracted from the Swedish official milk recording scheme, whereas information about parity, calving date, and tag ID was provided by the farm. Each cow included in this study was assigned to one of 3 lactation stages: early (7–49 DIM), mid (50–179 DIM), or late (≥180 DIM) lactation, according to the average DIM during the study period. Cows with breed proportion above 75% were defined as purebred Holstein or Red Dairy Cattle, according to the dominant breed. Cows with breed proportion below 75% were

defined as crossbreds. Cows were defined as pregnant one day after the last successful insemination, based on a later confirmed pregnancy in the pregnancy diagnosis records.

Regarding claw health, regular claw trimmings were conducted every 6 to 8 wk on the selected farm. For this study, animals with at least one record of a claw disorder, reported in the 2 claw trimming records before (August 12, 2020, and September 28, 2020) and after (November 24, 2020, and January 5, 2021) the study period, were considered to be "with claw health remark." Therefore, claw health was defined as claws with or without remarks. Claw remarks were based on both minor and major claw disorder lesions, such as digital dermatitis, double sole, heel horn erosion, interdigital hyperplasia, sole hemorrhage, verrucose dermatitis, white line abscess, and white line separation. Further information regarding the characteristics of the animals included in this study can be found in Hansson et al. (2023).

From the total of 194 lactating dairy cows housed in this farm during the studied period, the approximate ratio of square meters per animal in the barn was 10 m² (early-lactation group), and 11 m² (late-lactation group), and around 5 m² per cow and area (feeding and resting areas). Only cows present during the entire study period in one of the groups (83 in the early-, and 80 in the late-lactation group) and with information for all the traits (73 cows in the early-, and 76 in the late-lactation group) were included in the analysis. Animals with missing information for age (2 cows in the late-lactation group), claw health (one cow in the early-lactation group and 2 cows in the late-lactation group) and pedigree relatedness (9 cows in the earlylactation group) were not considered in the study. The data collected from the 149 dairy cows considered in the analyses are summarized in Table 1. The average age of the 149 lactating cows was approximately 4 yr and ranged from 2 to 9 yr. Specifically, the average age of the animals in the early-lactation group was slightly lower (3.78 yr), compared with the late-lactation group (4.05 yr).

The pedigree information concerning the 149 cows comprised 8,594 animals, with an average number of generations of 17.74 and a pedigree completeness index of 0.74. The average number of generations was calculated as the mean of the maximum number of generations traced per individual, whereas the pedigree completeness index, which represents the proportion of known ancestors in each ascending generation, was estimated following MacCluer et al. (1983). Among the 149 cows, there were 12 animals with a relationship coefficient over 0.5 and 40 animals with a relationship coefficient ranging between 0.25 and 0.50.

Table 1. Summary of data collected from the 149 cows considered in the analysis by lactation group for each characteristic

Characteristic	Early-lactation group	Late-lactation group
Parity		
1	20	21
2	19	27
3+	34	28
Lactation stage		
Early (7–49 DIM)	17	0
Mid (50–179 DIM)	52	16
Late (>180 DIM)	4	60
Breed		
Holstein	21	19
Red Dairy Cattle	19	22
Crossbred	33	35
Pregnancy status		
Pregnant	31	60
Open	42	16
Claw health		
$Remark^1$	19	24
No remark	54	52

¹Remark for major or minor lesions. The numbers in the table indicate the number of cows considered in this study, which includes 73 and 76 cows in the early- and late-lactation groups, respectively.

Estimating Social Contacts of Lactating Cows Using RTLS Data

The position data automatically collected with the UWB RTLS with a 1-s fixed rate were used to estimate the distance among the 149 lactating cows selected for the present study. The cubicles of the resting area had a median width of 120.5 cm. Thereby, the maximum distance between the UWB tags when 2 cows lie in consecutive cubicles would be approximately 2.5 m. Collar-based positioning data do not capture the entire space occupied by individuals' bodies. Therefore, spatial interactions within different distances can occur in the feeding area, such as shorter distances when cows stand face to face, whereas longer distances may be observed when a cow stands behind or follows another cow, for example. Thus, we quantified the time spent by each lactating cow together with the rest of the herd per functional area, using the position data and considering a distance radius threshold of 2.5 m, to include several types of proximity interactions (Rocha et al., 2020; Hansson et al., 2023). The study of Chopra et al. (2020) defined proximity interactions between cows when the individuals were 3 m apart. Similarly, in the study conducted by Boyland et al. (2016), proximity interactions within 1.5 to 2.0 m had a significant positive relationship with social grooming. However, a previous study conducted by our research group (Hansson et al., 2023) found no qualitative change in the results when varying the distance threshold to either 1.5 or 3.0 m. Therefore, this study assumed that a social contact existed between a pair of cows when they were within a distance of 2.5 m. The duration of the contacts was calculated independently for each lactation group, and the 2 functional areas in the barn using Matlab (2020; Figure 1). We aggregated all dyadic contacts between cow pairs for each day (i.e., 24 h) of the 14 d considered in this study. As we calculated the contact time per cow, we found slight differences within each pair; the minimum time reported per pair of animals and area was considered in subsequent analyses. Moreover, the position data were also used to estimate the time the animals spent within the functional areas per day (Figure 1). Following that, we computed the proportion of time each animal spent per day in the feeding area by dividing it by the total time reported by the RTLS; this ratio is hereafter referred to as the time in area. Therefore, the higher and the lower the value of the time in area, the longer the time spent in the feeding and resting area, respectively.

To avoid considering stochastic short contacts, cows crossing each other with no intention of interacting due to the limited space of the barn, we defined a 600-s time threshold (10 min) per day to consider that a contact between lactating cows occurred. Therefore, contact matrices, known as adjacency matrices in graph theory terminology, were constructed for each lactation group, functional area, and day, considering only contacts longer than 10 min. Data from the adjacency matrices computed per day were coded in a binary format, where 1's denote the occurrence of a contact (presence of an edge linking a specific pair of nodes), and 0's indicate that no contact longer than 10 min was reported during the day (absence of an edge linking the nodes). Moreover, Hansson et al. (2023) reported that increasing the time threshold could influence the significance of the results. Hence, the present study explored 2 additional time thresholds for the feeding area (20 and 30 min) and 3 for the resting area (20, 30, and 60 min).

Statistical Analysis

R statistical software version 4.2.0 (R Core Team, 2022) was used for data preprocessing and statistical analyses. The source code used is publicly available at https://github.com/CSI-DT/SNA. First, variance inflation factors (VIF) were estimated to test for multicollinearity among the cow's characteristics considered in this study (age, breed, claw health, DIM, lactation stage, parity, pregnancy status, and time spent in each area). This was done using the car package (Fox and Weisberg, 2018) by incorporating the 8 aforementioned variables as fixed effects in a linear model, along with the inclusion of the animal effect as a random effect using the nlme package (Pinheiro et al., 2022). Repeated measurements were not considered in this step. The VIF values confirmed that the implementation of age

and parity, and DIM and lactation stage together could inflate the regression coefficient variance due to their multicollinearity (Supplemental Table S1; https://pub.epsilon.slu.se/31159/; Marina et al., 2023). After excluding age and DIM from the model, the VIF values were approximately 1, indicating no multicollinearity issues among the characteristics included in the second model. Therefore, as determined by the collinearity analysis, age and DIM were excluded from the subsequent analyses.

Second, correlations between the time in area and the total interaction time per animal were estimated by considering both functional areas and lactation groups independently. The total interaction time per animal was estimated by summing the total contact time with other animals within the herd, considering both functional areas and lactation groups independently. A strong correlation between total interaction time and time in area will highlight the importance of including this variable in subsequent models. In the early-lactation group, the correlation was 0.60 in both areas. In contrast, the correlations for the late-lactation group were 0.65 for the feeding area, and 0.56 for the resting area. These values indicated a clear association between the time in area and the total interaction time reported each day for each cow, in both the feeding and the resting area. Therefore, the inclusion of this covariate in subsequent analyses is mandatory as the longer the time the animals spend in each functional area, the greater the likelihood of random interactions. Hansson et al. (2023) described differences between the time in area spent according to parity and lactation stage. The inclusion of this covariable corrected this effect, allowing the right assumptions to be drawn about the other effects included in the models.

Social Network Analyses

The adjacency matrices were used to construct the social networks using the sna package (Butts, 2020). Social networks were constructed with nodes representing individual cows, and the (spatial) interactions between any 2 cows were represented as the presence (1) or absence (0) of an edge linking the nodes. Social networks were visualized as sociograms using the igraph package (Csárdi and Nepusz, 2006).

Subsequently, we calculated the topological network parameters per area, lactation group, and day, using the sna package (Butts, 2020). Topological network parameters offer valuable insights into the social roles of dairy cows within the herd. The topological network parameters considered in this study included betweenness centrality, closeness centrality, degree, and eigenvector centrality scores. The betweenness central-

ity parameter quantifies the number of shortest paths between 2 nodes that pass through a specific node, with respect to the total number of shortest paths. Hereafter, the betweenness was normalized by dividing the total number of pairs of nodes, excluding the node itself. The betweenness coefficient reflects the contribution of an individual node to the network's connectivity (Wandelt et al., 2019). The closeness centrality parameter estimates the average shortest path length of a node. This parameter represents how closely connected a particular node is to the rest of the nodes of the network (Martínez-López et al., 2009). Eigenvector centrality scores are the elements of the eigenvector corresponding to the dominant eigenvalue of the adjacency matrix, with the scores standardized to be nonnegative and with a maximum value of 1. The eigenvector centrality parameter summarizes in a unique value the number of interactions and their quality. High values indicate that a particular node is connected to several nodes which themselves have high scores (Newman, 2018). Last, the node degree represents the total number of interactions (edges) related to a particular node.

The repeatability and heritability of the topological network parameters were estimated per functional area and lactation group, through the application a general mixed linear model (Equation 1) using the brms package (Bürkner, 2017):

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_{a}\mathbf{a} + \mathbf{Z}_{k}\mathbf{u} + \boldsymbol{\epsilon}, \tag{1}$$

where y is a vector of topological parameters across individuals, X is a design matrix relating the values of y to the fixed effect parameters given in the vector β , which included the cow's characteristics that revealed no signs of multicollinearity, a is a vector describing the additive genetic effects, \mathbf{Z}_{a} is an incidence matrix relating each of the additive genetic effects to an individual's phenotype. The other random effects are given by **u** each with corresponding incidence matrix \mathbf{Z}_k , and ε is a vector of residual effects. The random variables are assumed to be normally distributed. Specifically, a is normally distributed with $(0, \mathbf{A}\sigma_a^2)$, where σ_a^2 is the genetic variance and \mathbf{A} is the additive relationship matrix derived from the pedigree, and **u** is normally distributed with $(0, \sigma_k^2)$, where σ_k^2 is the permanent environmental variance. Repeatability was calculated as the sum of the individual and the permanent environmental variances divided by the phenotypic variance, whereas heritability was estimated as the proportion of the genetic variance in relation to the phenotypic variance. Repeatability indicates the proportion of the total phenotypic variation in multiple measurements of a characteristic that is attributed to variation within individuals and heritability represents the proportion of the phenotypic variation of a characteristic attributed to genetic factors (Boake, 1989; Falconer and Mackay, 1996; Lynch and Walsh, 1998). On one hand, high or moderate repeatabilities will suggest a consistent role of animals in the social network over time. On the other hand, high or moderate heritabilities will indicate that selective breeding based on these parameters could be used to improve or manipulate social behavior in dairy cattle populations.

We applied the STERGM, described by Krivitsky and Handcock (2014), to explore how cow characteristics influence the evolution of social networks over the 14 d considered in this study. The model was fitted separately for each functional area and lactation group using the conditional maximum likelihood estimation procedure (Krivitsky and Handcock, 2014). This models the probability of a new contact occurring given that there was no contact the previous day (referred to as formation) and the probability of a contact given that there was a contact the previous day (persistence). The STERGM assumes that the contact probability, given the state from the previous day, is independent of states at earlier days. In this model, the probability of a contact between individual i and j is independent of another contact between individual i and k, where $j \neq k$, because only exogenous parameters, external characteristics that are not part of the social network structure, were fitted in the model.

The fitted STERGM can be described as follows. Let $Y_{ij,t}$ be equal to 1, if there exists an edge between nodes i and j at time t, and 0, if there is no edge between nodes i and j at time t. The fitted STERGM consists of 2 fitted logistic regressions with $Y_{ij,t}$ as response, by splitting the data set into 2 for $Y_{ij,t} = 0$ and $Y_{ij,t} = 1$, one for the formation part of the model, and one for the persistence part of the model, respectively (Equation 2).

$$\begin{split} & \log \mathrm{itP} \left(Y_{ij,t+1} = 1 | Y_{ij,t} = y_{ij,t} \right) = \mu_{edges} + \beta_{breed_k} x_{nf,breed_k} \\ & + \gamma_{breed} x_{nm,breed} + \beta_{claw\,health_l} x_{nf,claw\,health_l} \\ & + \gamma_{claw\,health} x_{nm,claw\,health} + \beta_{lactation\,stage_p} x_{nf,lactation\,stage_p} \\ & + \gamma_{lactation\,stage} x_{nm,lactation\,stage} + \beta_{\mathrm{parity}_q} x_{nf,\mathrm{parity}_q} \\ & + \gamma_{parity} x_{nm,\mathrm{parity}} + \beta_{pregnancy\,status} x_{nf,pregnancy\,status} \\ & + \gamma_{pregnancy\,status} x_{nm,\mathrm{pregnancy\,status}} + \gamma_{AGEcont} x_{nm,AGEcont} \\ & + \gamma_{DIMcont} x_{nm,DIMcont} + \beta_{REL} x_{edge,REL} + \beta_{time\,in\,area} x_{time\,in\,area}, \end{split}$$

where $y_{ij,t} = 0$ for the formation part of the model, and $y_{ij,t} = 1$ for the persistence part of the model. Hence, the formation model fits the probability of a connection

(edge) existing between individuals i and j, given that there was no connection between them at the previous time point, and the persistence model fits the same probability, given that there was a connection at the previous time point. Each model included an intercept term μ_{edges} , several node factor effects denoted by β , and node match effects denoted by γ . Hence, β_{breed_k} was the node factor effect for breed k with corresponding covariate $x_{nf,breed_k}$ with value equal to the number of cows of breed k (i.e., 0, 1, or 2), connected to edge ij, whereas γ_{breed} was the node match effect for breed, with corresponding covariate $x_{nm,breed}$ equal to 1, if the 2 cows i and j were the same breed, and 0 otherwise. The node factor and node match for claw health, lactation stage, parity, and pregnancy status were defined similarly.

In addition, with the aim to assess the effect of establishing social contacts between cows of having shared early life experiences, or experiences in the last drying period together, or sharing a filial relationship, 3 additional variables were considered for each lactation group separately: (1) contemporary age (Age_{cont}) represented 2 cows born within 7 d, fitted as $\gamma_{AGEcont}$, where $x_{nm,AGEcont}$ was equal to 1 if 2 cows were contemporary, and 0 otherwise; (2) equivalently, 2 cows calved within 7 d were defined as contemporary DIM (DIM_{cont}) fitted in the model as $\gamma_{DIMcont}$, and (3) the relationship matrix (**REL**) fitted in the model as an edge covariable effect (β_{REL}) , which represents the relationship coefficients computed from the pedigree information. Hence, for individuals i and j, the value of $x_{edge,REL}$ is given by the element in row i and column j of the additive relationship matrix. Further, the time in area was fitted as a regression parameter $\beta_{time\ in\ area}$, where $x_{time\ in\ area}$ was the proportion of the time spent in the feeding area. It corrects the probability of an existing edge by the time spent in the area. Since the fitted STERGM are 2 conditional logistic regressions, the estimated effects shall be interpreted as conditional log-odds ratios. A more detailed description of the STERGM approach can be found in Supplemental Material S1 (https://pub .epsilon.slu.se/31159/; Marina et al., 2023).

Finally, the STERGM analyses were repeated, considering 2 additional time thresholds for the feeding area (20 and 30 min), and 3 for the resting area (20, 30, and 60 min) to assess the effect of the time threshold on the role of the characteristics included in this study on social contacts.

RESULTS

Before presenting the effect of different cow characteristics on the likelihood of establishing new social contacts and their persistence through time, we present results describing the topological network parameters and the temporal development of the social networks.

Social Network Parameters

Sociograms illustrate the cumulative number of contacts among individuals over the study period, considering both lactation groups and functional areas (Figure 2 and Supplemental Figure S1; https://pub.epsilon .slu.se/31159/; Marina et al., 2023). The sociograms revealed that the feeding area had a longer average cumulative number of contacts for both lactation groups (early: 2.82 d; late: 2.25 d) compared with the resting area (early: 2.12 d; late: 2.15 d). A graphical representation of the evolution of the social networks throughout the 14 d can be found for the early-lactating group in Supplemental Figure S2 (feeding area) and Supplemental Figure S3 (resting area; https://pub.epsilon.slu.se/ 31159/; Marina et al., 2023). The corresponding plots for the late-lactating group are found in Supplemental Figures S4 and S5 (https://pub.epsilon.slu.se/31159/; Marina et al., 2023).

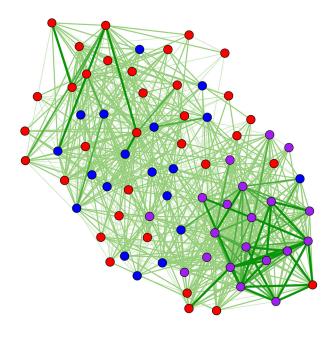
Table 2 presents the global average of the estimated topological parameter values for each cow across the 14-d study period, along with their corresponding repeatabilities and heritabilities. The topological parameters showed moderate values of repeatability, ranging from 0.21 (closeness) to 0.42 (eigenvector). The eigenvector centrality parameter presented the highest repeatability in both functional areas and lactation groups, indicating that this is the most stable measure over time. In general, the repeatability values of the topological parameters were higher in the late-lactation group, compared with the early-lactation group. In contrast, the heritabilities of the topological parameters showed low to moderate values, and varied between lactation groups. The heritabilities ranged from 0.07 (betweenness) to 0.10 (eigenvector) in the early-lactation group, and ranged from 0.16 (closeness) to 0.20 (eigenvector) in the late-lactation group. Hence, the eigenvector centrality parameter was consistent both over time and between close relatives.

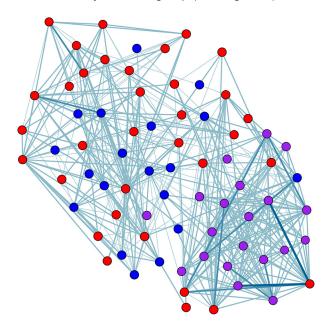
Social Network Formation and Persistence Analyses

The following results show to what extent familiar cows are more likely to establish new contacts, and to what extent these contacts will persist more compared with cows with different characteristics. Figure 3 depicts the results of social network formation and persistence analyses defined in Equation 2. The individual coefficients are log-odds ratios estimated by STERGM. In the formation model, positive coefficients indicate

Early lactation group (Feeding Area)

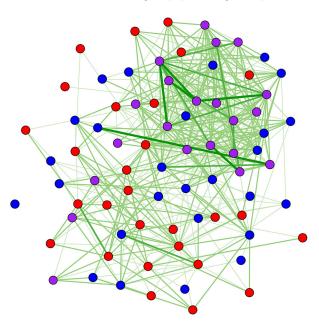
Early lactation group (Resting Area)





Late lactation group (Feeding Area)

Late lactation group (Resting Area)



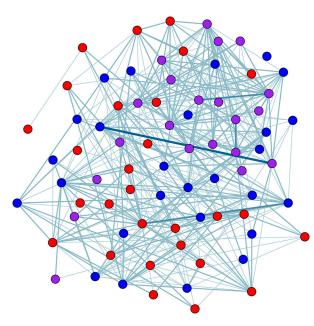


Figure 2. The sociograms represent the cumulative number of contacts during the 14 d of the study for the feeding (green edges) and resting (blue edges) areas for the early- and late-lactation groups. The thickness and darkness of the edges represent the cumulative contacts over the studied days. Only cumulative contacts over 7 d are shown in this figure. The colors of the nodes represent the parity number: red (1), blue (2), and purple (3+).

an increased likelihood of contact formation in the network than expected by chance, whereas negative coefficients suggest a decreased likelihood. In the persistence

model, positive coefficients indicate a higher probability of contact persistence, whereas negative coefficients indicate a lower probability of contact persistence.

Table 2. Descriptive statistics, repeatability, and heritability of the topological network parameters over the 14 d of the study

ıty	Late-lactation group	Feed Rest	0.11 0.16 0.09 0.15	
Heritability	Early-lactation group	Rest	0.08 0.09	0.09 0.07
		Feed	0.07	0.08
eatabil	Late-lactation group	Feed Rest	0.33	0.40 0.42
		Feed	0.26	0.23
	Early-lactation group	Rest	0.25 0.37	0.38
		Feed	0.31 0.24	0.24 0.34
Mean (SD)	Late-lactation group	Rest	26.1 (14.32) 0.59 (0.03)	$23.29 (6.25) \\ 0.11 (0.03)$
		Feed	25.49 (14.66) 0.60 (0.04)	$24.47 (7.17) \\ 0.11 (0.03)$
	Early-lactation group	Rest^3	25.48 (14.76) 0.59 (0.04)	$\begin{array}{c} 22.10 \ (6.21) \\ 0.11 \ (0.03) \end{array}$
		Feed ²	21.32 (10.94) 0.63 (0.04)	$29.43 (6.80) \\ 0.11 (0.03)$
		.em	etweenness ⁴ loseness ⁵	egree" igenvector ⁷

The study included 73 and 76 cows in the early- and late-lactation groups, respectively.

²Feed: refers to the feeding area.

³Rest: refers to the resting area.

Betweenness centrality quantifies the number of shortest paths between 2 nodes that pass through a specific node.

 5 Closeness centrality estimates the average shortest path length of a node. 6 Degree represents the total number of social contacts related to a particular node.

Eigenvector centrality represents the scores of the eigenvector corresponding to the dominant eigenvalue of the adjacency matrix.

Contemporary age (Age_{cont}) showed a strong effect on the formation and persistence of social contacts in both functional areas and lactation groups. The estimated Age_{cont} coefficients ranged from 0.14 to 0.80 (P-values ranged from <0.001 to 0.44). Hence, animals born within 7 d of each other had 15% to 123% higher odds of either establishing new contacts or maintaining existing contacts, depending on the functional area and lactation group, compared with animals born more than 7 d apart.

The results showed that closely related individuals had a higher probability of forming new contacts than distantly related individuals, since the REL edge covariate showed a positive effect on the social contact formation in both functional areas and lactation groups (P-values ranged from 0.001 to 0.02). The estimates ranged from 0.78 to 1.20, indicating that formation odds increased from 1% to 2% per percentage unit of the relationship index. These results implied that, for instance, full sibs would have higher odds of establishing new social contacts, from 30% to 58% (depending on the functional area and lactation group), compared with half-sibs. The DIM_{cont} formation and persistence coefficients, however, were unremarkable (P-values ranged from 0.04 to 0.89).

The formation and persistence coefficients for parity match were positive in both functional areas and lactation groups, ranging from 0.13 to 0.51 (P < 0.001). This consistent outcome throughout the areas and lactation groups implied that cows from the same parity were more likely to have contact among themselves (odds increased from 14% to 67%), whether or not they were in contact the previous day, compared with cows from different parities. First parity cows showed greater contact persistence odds throughout the days, from 11% to 38%, compared with cows with a higher number of parities (P-values ranged from <0.001 to 0.01). Pregnancy status showed an effect on the contact formation in both functional areas and lactation groups (P-values varied from 0.001 up to 0.02), suggesting that pregnant cows were more likely to establish new contacts in the feeding area than open cows. Nevertheless, the sign of these estimated effects was not consistent between lactation groups in the resting area. Claw health showed a positive effect in the late-lactation group (P-value < 0.001) concerning contact formation coefficients, suggesting that animals without remarks were more likely to establish new social contacts in the resting area.

Sensitivity Analysis and Results Validation

The sensitivity of the results depending on the definition of a contact was evaluated by estimating the STERGM coefficients considering different time

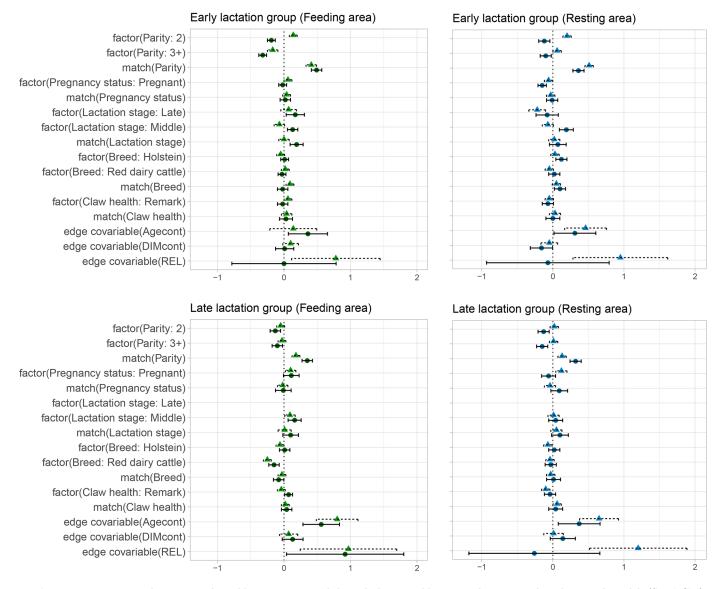


Figure 3. Formation and persistence log-odds ratios estimated through the separable temporal exponential random graph models (STERGM). Formation estimates are depicted by light green and blue triangles for the feeding and resting areas, respectively. Persistence estimates are represented by dark green and blue circles for the feeding and resting areas, respectively. Error bars represent the estimates 95% confidence intervals. The model included the following terms: (1) factor: sum of the node values for all existing edges in the network; (2) match: number of edges in which the value between the nodes (i, j) is the equivalent; (3) covariable: sum of the node value for all existing edges in the network; (4) edge covariable: value for each edge appearing in the network. Age_{cont} represents pairs of animals born within 7 d of each other. DIM_{cont} corresponds to pairs of animals calved within 7 d of each other. REL stands for the relationship matrix based on pedigree records.

thresholds for the feeding area (20 and 30 min) and for the resting area (20, 30, and 60 min). As seen in Supplemental Table S2 (https://pub.epsilon.slu.se/31159/; Marina et al., 2023), a higher time threshold used in the social networks slightly modified the results obtained. Features that revealed moderate to high relevance in the logistic model maintained their impact on social networks, regardless of the time threshold (e.g., parity and Age_{cont}). In general, parity formation and persistence coefficients revealed strong positive match effects in all scenarios (*P*-values ranged from

<0.001-0.04), except for the early-lactation group in the resting area considering a time threshold of 60 min (P-value = 0.07). Age_{cont} formation coefficients remained significant as the applied time thresholds increased (P-values ranged from <0.001 to 0.04, respectively), with the same exception (P-value = 0.09). In addition, the results highlighted some features whose role in the STERGM results varied as the time threshold increased (e.g., breed and pregnancy); the results for these characteristics were generally inconsistent when comparing lactation groups.

DISCUSSION

The present study used RTLS technology to explore the role of different individual characteristics in the formation and persistence of social networks in dairy cows. Social networks provide information about individual and group social behaviors, allowing the study of the behavior at both levels (Croft et al., 2008). Our results revealed that cows of the same parity interacted more consistently, as well as those born within 7 d of each other or closely related by pedigree. In practice, housing familiar cows together may contribute to the stability of the social structure and hence promote dairy cow welfare (Gutmann et al., 2015). In addition, the present work simultaneously addressed the level of stability of the social role of dairy cows by estimating the repeatability of the topological parameters on a daily basis.

Social Network Analyses

Our results are consistent with previous studies describing a greater tendency to establish preferential relationships between individuals with similar attributes (Boyland et al., 2016; Churakov et al., 2021). The propensity of similar entities to have contact with each other is defined as homophily in SNA. In addition, Churakov et al. (2021) described how older cows tend to lay down more frequently in cubicles close to the milking area while younger cows occupy less busy areas, which could also favor the homophily related to parity found in this work. Furthermore, Supplemental Figure S1 (https://pub.epsilon.slu.se/31159/; Marina et al., 2023) illustrates the contacts that have been observed recurrently during the 14 d of the study, most of which involved cows of the same age. Our results also indicated homophily in both contact formation and persistence between cows born within 7 d of each other. Most of the pairs of animals born 7 d apart were composed of animals in the same parity (61 out of 62), which implies that the homophily effect outweighed the parity effect, as only one pair of animals belonged to different parities. Previous studies also described how calves that have been together since birth or shared early stages of life, develop stronger social bonds among themselves (Sato et al., 1987; Færevik et al., 2006; Raussi et al., 2010). Early social relationships between calves are beneficial and should be maintained as long as possible in cattle husbandry (Raussi et al., 2010). Additionally, the pedigree relationship index revealed a positive contact formation, in agreement with previous studies that describe how familiarity between individuals can lead to the development of stronger bonds between conspecifics (Reinhardt and Reinhardt, 1981; Ramsever et al., 2009; Bolt et al., 2017).

Furthermore, the present work analyzed other factors that did not show consistent results between the lactation groups or functional areas, such as the breed, claw health, contemporary DIM, lactation stage, and pregnancy status. Previous studies related health status to changes in lying behavior (Barker et al., 2018; Tucker et al., 2021). The most critical disorders in dairy cattle are lameness, which can result in longer lying times, and mastitis, which could reduce lying times and feed intake (Barker et al., 2018; Tucker et al., 2021). Nevertheless, Hansson et al. (2023) found no differences in time spent in the resting area between cows with and without claw remarks. They also reported no discrepancies in the time spent in the different functional areas when comparing the SCC information (Hansson et al., 2023). Therefore, this information was not included in the present work. Discrepancies between coefficients found in the functional areas could be explained by the fact that cows might have different partners in different areas (Reinhardt and Reinhardt, 1981).

Stability of Topological Parameters

The spatial information provided by the RTLS technology allowed us to construct social networks, enabling us to characterize the animals by different topological statistics (Krause et al., 2009). Topological statistics permit the evaluation of individuals by their role in the overall position within social networks (Rocha et al., 2020). The estimated topological parameters are well known in graph analyses (Sosa et al., 2021), and have proven useful for describing social network characteristics in dairy cattle (Bolt et al., 2017; Mekonnen et al., 2019; Burke et al., 2022). The lower degree and closeness average, and the higher betweenness average in the resting area than in the feeding area, indicated that the social networks in the resting area were composed of more central nodes (i.e., a group of animals with a more relevant role in the network; Golbeck, 2013). These results suggest that contacts in the feeding area may be more stochastic because cows are more active in the feeding area compared with the resting area, where they lie down for longer time periods, which could explain observed patterns. In contrast, the resting area may provide opportunities for animals to selectively choose their companionship, leading to potentially more deliberate social contacts in that context.

The moderate repeatability values found in this study agree with previous studies in dairy cattle that compared social networks, revealing that around 50% of the interactions between the cows were stable when comparing weeks (Boyland et al., 2016; Bolt et al., 2017). The present work studied the repeatability of the topological parameters at daily level, which varied

slightly between the functional areas and the lactation groups. Rocha et al. (2020) described the sociality of a cow as a stable individual trait but dependent on the functional area where the contacts occurred. This could explain the differences in repeatability values between functional areas considered in this study (Table 2). In addition, differences between lactation groups could be explained by the early-lactation group being composed of recently calved cows undergoing physiological changes, and a higher number of nonpregnant cows that come into heat, which may affect their social behavior, and thus slightly reduce the repeatability of the topological parameters. Regarding the heritabilities of the topological parameters, similar ranges were described in previous studies in pigs (Agha et al., 2022a,b). The eigenvector centrality parameter exhibited notable repeatability and heritability values for the studied topological parameters. Cows connected to many other cows with many connections will have a high eigenvector centrality. So, cows with the highest eigenvector centrality score will be the ones influencing other cows the most directly or indirectly throughout the social network. Hence, transmission (of e.g., infectious disease) will spread quickly through the network if initiated by a cow with high eigenvector centrality. The heritability of the topological parameters of the social network suggests a possible susceptibility of genetic variation influenced by current breeding programs focused on dairy production. Considering the close relationship of social behavior with animal welfare, breeding programs should thoroughly evaluate the magnitude and direction of genetic correlations between topological parameters of social networks and characteristics considered in selection programs. The differences in heritability values found between lactation groups might be due to the limited number of animals included in this study. Additional studies in larger populations are required to accurately estimate the heritability of these parameters and their genomic correlation with the traits relevant to the dairy industry.

The ample repeatability of the topological parameters suggests robust stability of the individual roles within the social network structure and, therefore, a potential for short-term prediction of social network structure and individual social behavior. This would enable the detection of changes in social behavior, including those resulting from diseases, facilitating early identification and intervention measures. Daily social interactions are an essential feature of cattle behavior and have a fundamental effect on animal welfare. Disruptions to social relationships, such as age-based regrouping or insufficient space allowance, may cause stress and trigger aggressive and abnormal behavior (Grant and Albright, 2001; von Keyserlingk et al.,

2008), leading to long-term health effects. In addition, close proximity, grooming, and social bonding among dairy cattle facilitate the transmission of diseases that depend on direct animal contact (e.g., some mastitiscausing bacteria) (Kappeler et al., 2015). Hence, social networks may play a significant role in determining contact patterns and potential routes of disease transmission in dairy cattle. For a thorough understanding of the spatial interactions occurring in the barn, further studies are needed that focus on the combined analysis of the social networks of both functional areas, which could be investigated using the multilayer approach implemented in the multinet R package (Magnani et al., 2021).

Study Limitations and Perspectives on Social Network Analyses in Dairy Cattle

The social networks considered in this study were constructed using the RTLS and applying the time and the distance thresholds of 10 min and 2.5 m. Hence, binary social networks were analyzed. Different approaches, such as the simple ratio index applied by Formica et al. (2021), could be considered in the analyses to weigh the level of social contact between cows, instead of using binary social networks. However, the different time thresholds tested in this study and the different time thresholds and distances studied by Hansson et al. (2023) (1.5 m and 3.0 m) show that the results are not sensitive to the chosen thresholds.

Our study builds upon the research conducted by Hansson et al. (2023), which is based on a different subpopulation from the same farm and time period. While Hansson et al. (2023) focused on identifying cow characteristics associated with the number of contacts per cow, our study used SNA to model the interaction data. This allowed us to estimate the stability of the topographical parameters of the social networks on a daily basis and determine how cow characteristics influence the formation and persistence of proximity interactions.

Proximity does not imply direct social interaction between individuals (Albery et al., 2021). In fact, the spatial interactions detected in this study could be influenced by the spatial constraints of freestall barns and individual differences in resource use. Nevertheless, Boyland et al. (2016) described a positive correlation between dairy cow proximity contacts and affiliative social interactions, such as social grooming, but not agonistic interactions. Hence, the observed results might be based mainly on positive interactions between dairy cows.

Our study includes extensive data but only from one farm and some data were missing. How to deal with missing data in SNA is indeed challenging and therefore only individuals with complete data were included in the current study. Future studies should compare the result from different herds and combine different sensor technologies, such as accelerometers, camera vision, proximity loggers for recording outdoor social contacts, and milk sensors with the UWB system. The integration of these technologies would allow the thorough study of indoor and outdoor social networks combined with milk production data over long periods of time.

CONCLUSIONS

The present study applied RTLS technology to describe the effect of different cow characteristics on the likelihood of formation and persistence of social contacts in dairy cattle. The findings of our study support the theory that dairy cows do not interact uniformly but spend different times with particular individuals than would be expected by chance. Our results reveal that cows of the same parity interact more consistently, as well as those born within 7 d of each other or closely related by pedigree. The repeatability of the topological parameters indicates a stable short-term consistency in the individual animal roles within the social network structure. The use of this knowledge could improve the stability of the social structure and promote dairy cow welfare and hence production. Further studies focusing on social network information, constructed from automated position data and disease transmission information, could enhance the design of prevention and intervention protocols for transmissible diseases in dairy cattle.

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