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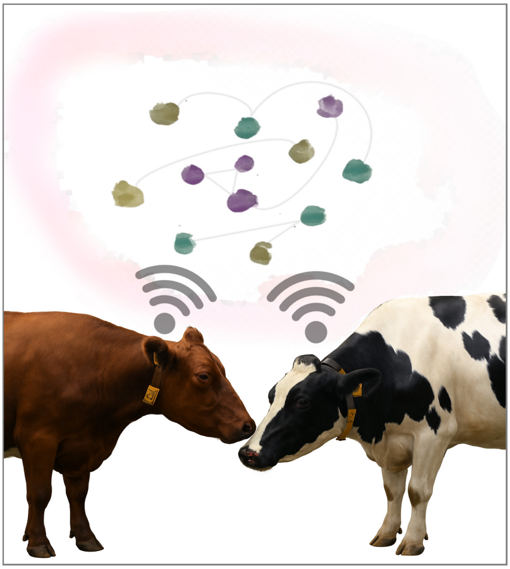
Prospects for including indirect genetic effects in dairy cattle breeding programs

monitoring strategies and methodology

Ida Hansson



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Abstract

Dairy cows are sociable animals and interact with each other daily. These affiliative and agonistic interactions may impact an individual's well-being and production, e.g., milk yield. The environment an individual cow experiences involves the expressed phenotypes of genotypes carried by their social partners. These genotypes can be modelled in terms of indirect genetic effects (IGEs). IGEs have been studied thoroughly in other species, yet information on estimating IGEs for animals moving freely in a large group is still needed. This thesis explored the social behaviour of cows using data from a real-time location system installed in two commercial farms and information from the on-farm milking system from one of the farms. The impact of proximity contacts during milking on a cow's daily milk yield was investigated using milking order information from a milking parlour. Further, the information needed to estimate breeding values for indirect genetic effects was assessed with simulations. The results revealed that the total impact of the neighbours during milking on a cow′s daily milk yield could contribute to or reduce by up to 2 kg of milk. A weak negative correlation existed between the phenotypic direct and indirect effects on milk yield. The variation in indirect effects suggests room for improvement, and future research will assess a possible genetic component. How much contact a cow had with her herd mates in the barn varied between individuals and functional areas and was associated with her parity, lactation stage, reproductive status, udder health, and claw health. The results from the simulation study showed that the magnitude of the IGEs and how accurately we collect the social contacts will influence how well we can estimate IGE in dairy cattle. Collecting the intensities and direction of contacts between individuals was important for achieving better variance component estimates and breeding value accuracies of the IGE. The process of including indirect genetic effects in dairy breeding programs is expected to take time, but this thesis is a first step in approaching this.

Keywords: cow behaviour, social environment, indirect genetic effects, dairy cattle, milk yield, precision livestock farming, real-time location system

Utsikter för att inkludera indirekta genetiska effekter i avelsprogram för mjölkkor

Sammanfattning

Mjölkkor är sociala djur och interagerar dagligen med varandra. Dessa affiliativa och agonistiska interaktioner kan påverka individens välbefinnande och produktion, såsom mjölkavkastning. Den miljö en enskild ko upplever inkluderar de uttryckta fenotyperna av genotyperna hos deras sociala partners. Dessa genotyper kan modelleras i termer av indirekta genetiska effekter (IGE). IGE har studerats ingående hos andra arter, men det behövs fortfarande information om hur man skattar IGE för djur som rör sig fritt i en stor grupp. Denna avhandling utforskade det sociala beteendet hos mjölkkor genom att använda data från ett positioneringssystem installerat på två kommersiella gårdar samt information från mjölkningssystemet på den ena gården. Effekten av närkontakt under mjölkning på en kos dagliga mjölkavkastning undersöktes med hjälp av information om mjölkningsordning från mjölkgropen. Vidare utvärderades med hjälp av simuleringar vilken information som krävs för att skatta avelsvärden för indirekta genetiska effekter. Resultaten visade att den totala inverkan av individer som mjölkade jämsides en ko antingen kunde bidra eller reducera med upp till 2 kg mjölk för en kos dagliga mjölkmängd. En svag negativ korrelation förekom mellan de direkta och indirekta fenotypiska effekterna. Variationen i indirekta effekter antyder att det finns utrymme för förbättring, och framtida forskning kommer att undersöka en möjlig genetisk komponent. Hur mycket kontakt en ko hade med andra individer var associerat med laktationsnummer, laktationsstadium, reproduktionsstatus, juver- och klövhälsa. Resultaten från simuleringsstudien visade att storleken på IGE och hur exakt vi kan registrera de sociala kontakterna kommer att påverka hur väl vi kan skatta IGE hos mjölkkor. Registrering av kontakternas intensitet och riktning visades sig vara betydande för att uppnå bättre skattningar av varianskomponenter och högre säkerhet i avelsvärdena. Processen att integrera IGE i avelsprogram för mjölkkor förväntas ta tid, men denna avhandling utgör ett viktigt första steg i hur vi ska angripa detta.

Keywords: beteende, social miljö, indirekta genetiska effekter, mjölkko, mjölkmängd, precisionsdjurhållning, realtids lokaliseringssystem, sensorteknologi

Preface

This research begins on a blank slate; there are no established rules yet for monitoring social contacts in dairy cows and estimating the underlying genetic structure of these contacts. Social interactions are complex, and incorporating their effects into dairy breeding programs involves many considerations. This thesis represents a first step toward exploring how we should approach this challenge and what methods may be used.

To all the dairy cows around the world
- the unsung heroes of our time.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Hansson, I., Woudstra, S., (2024). Associations of parity and lactation stage with the order cows enter the milking parlor. JDS Communications 5, 416–420. https://doi.org/10.3168/jdsc.2023-04

II. Hansson, I., Marina, H., Fikse, W.F., Nielsen, P.P., Rönnegård, L. (2024). The effect of neighbouring cows within the milking parlour on a cow's daily milk yield. (submitted)

III. Hansson, I., Silvera, A., Ren, K., Woudstra, S., Skarin, A., Fikse, W.F., Nielsen, P.P., Rönnegård, L., (2023). Cow characteristics associated with the variation in number of contacts between dairy cows. Journal of Dairy Science 106, 2685–2699. https://doi.org/10.3168/jds.2022-21915

IV. Hansson, I., Bijma, P., Fikse, W.F., Rönnegård, L. (2024). Towards assessing indirect genetic effects in dairy cattle. (submitted)

The contribution of Ida Hansson to the papers included in this thesis was as follows:

I. Shared co-first authorship with Svenja Woudstra. Contributed equally to the planning of the study, data cleaning, statistical analyses, visualization and writing of manuscript.

II. Planned the study together with the co-authors. Performed all data cleaning, statistical analyses and visualisation. Retrieved R code from Hector Marina for computing the social network within the milking parlour. Drafted the manuscript with inputs from the co-authors.

III. Planned the study together with the co-authors. Retrieved MATLAB scripts from Keni Ren for the data processing of the position data. Performed data cleaning, all the statistical analyses and visualization. Drafted the manuscript with inputs from the co-authors.

IV. Planned the study together with the co-authors. Developed the simulation program together with Freddy Fikse and Piter Bijma. Performed all the data simulations, analyses, and visualization. Drafted the manuscript with inputs from the co-authors.

List of other publications

Other scientific publications by the author that are not included in this thesis:

V. Marina, H., Hansson, I., Ren, K., Fikse, F., Gussmann, M.K., Nielsen, P.P., Skarin, A., Woudstra, S., Rönnegård, L., (2025). How and why to monitor social networks in dairy cows. Frontiers in Animal Science. 6. https://doi.org/10.3389/fanim.2025.1556812

VI. Woudstra, S., Gussmann, M.K., Marina, H., Hansson, I., Kirkeby, C.T., Krömker, V., Nielsen, P.P., Ren, K., Rönnegård, L., (2025). Lessons learnt from strain types, milking order, and mastitis pathogen transmission. Frontiers in Animal Science. 6. https://doi.org/10.3389/fanim.2025.1556831

VII. Marina, H., Ren, K., Hansson, I., Fikse, F., Nielsen, P.P., Rönnegård, L., (2024). New insight into social relationships in dairy cows and how time of birth, parity, and relatedness affect spatial interactions later in life. Journal of Dairy Science 107, 1110–1123. https://doi.org/10.3168/jds.2023-23483

List of tables

List of figures

Abbreviations

AMS	Automatic milking systems
DEE	Direct environmental effect
DGE	Direct genetic effect
DIM	Days in milk
EBV	Estimated breeding value
IEE	Indirect environmental effect
ICC	Intraclass correlation coefficient
IGE	Indirect genetic effect
LRT	Likelihood-ratio test
PLF	Precision livestock farming
RDC	Red dairy cattle
RFID	Radio frequency identification detection
RTLS	Real-time location system
SCC	Somatic cell count
SNA	Social network analyses
UWB	Ultra-wideband

1. Introduction

Dairy production systems must continue to improve and refine to meet future challenges of an increasing human population while ensuring good animal health and welfare and low environmental impact (Brito et al., 2021; Clay et al., 2020). There has been increased awareness of the economic importance of animal health, welfare, and behaviour traits, and there is an increasing concern in society about intensive production systems. More comprehensive breeding goals are expected, involving selection on environmental sustainability (e.g., feed efficiency and methane emission), longevity, animal health and welfare, and overall resilience (Brito et al., 2021; Miglior et al., 2017).

Several factors could influence the environment for cows in dairy farms, such as feed, housing conditions, milking routines, and temperature (e.g., Bargo et al., 2002; Chen et al., 2024; Krohn et al., 1992). One of the essential environmental influences on a dairy cow is also the social environment induced by its herd mates (e.g., Foris et al., 2019; Krahn et al., 2024; Val-Laillet et al., 2008). There is an increasing awareness in the dairy industry of how the social environment can impact both production and welfare. Information on the optimal size and composition of groups is of interest, but a better understanding of cows' social group structure and dynamics is needed to know the optimal social conditions for dairy cows (Boyland et al., 2016).

Social interactions may stress cows, affecting animal welfare and production as stressed cows tend to produce less milk (Hedlund and Løvlie, 2015). Some interactions are, however, positive (Rault, 2012), and our knowledge is still limited in how behavioural traits affect production. To improve both animal welfare and production in dairy farms by considering the effects of social interactions in breeding programs, it is necessary first to quantify and understand the social interactions between cows. The rapid developments and adoption of automated data recording, precision technologies, genomic information, and modern analytical techniques in dairy farms provide opportunities for more objective phenotyping of behavioural traits and new possibilities in dairy cattle breeding (Miglior et al., 2017; Pacheco et al., 2025).

1.1 Social behaviour in dairy cattle

Cattle are sociable animals, living together in dominance-structured groups (Kondo and Hurnik, 1990; Reinhardt and Reinhardt, 1975; Tucker, 2017). Cows separated and isolated from their herd mates will show clear signs of stress (Herskin et al., 2007; Rushen et al., 1999). Cattle, like other ungulates, are a follower species (Bouissou et al., 2001; Lent, 1974; Nogues et al., 2024; Sato, 1982), and feral cattle live in herds of cows and calves, with separate groups of bulls that occasionally interact with the female herd (Tucker, 2017). The specific relationship between the calf and her mother is long-lasting, and the young female remains close to the mother even when the mother has a new calf. The young increase their interactions with the other herd members slowly with age (Bouissou et al., 2001; Lent, 1974; Vitale et al., 1986). In commercial dairy farms, only females are kept, and cows and calves are mostly housed separately after birth. Cows are often grouped within the herds based on their physiological status, whether they are lactating or in the dry period (Bouissou et al., 2001), and by their lactation stage, production, and nutritional requirements to facilitate management.

The dairy industry has several husbandry systems, such as tie-stall barns with pipeline milking systems, loose-housing systems, and free stall barns with either milking parlour or automatic milking systems (AMS), and the barn layout is typically different from herd to herd.

Cows usually spend 4-6 h/day feeding and between 8-12 h/day lying down, where each lying bout is about one hour (Tucker, 2017), and the time budgets differ between individuals (Azizi et al., 2010; Gomez and Cook, 2010; Løvendahl and Munksgaard, 2016).

Cattle communicate with visual and olfactory signals and vocalization to a lesser extent. The visual signals are body language that may involve movements and positioning of the head or the body and are used when displaying, e.g., aggressive or submissive behaviour (Gibbons et al., 2009; Gutmann et al., 2015; Miller and Wood-Gush, 1991). Olfactory signals can help recognize individuals and are important for social relationships (Baldwin, 1977; Bouissou et al., 2001). With olfactory cues and pheromones, cattle can also communicate their psychological state, e.g., when they are stressed or frightened (Boissy et al., 1998; Bouissou et al., 2001; Terlouw et al., 1998). Vocalization is mainly related to situations when animals are frustrated or stressed, such as being isolated from conspecifics or, e.g., in anticipation of food (Bouissou et al., 2001; Hopster et al., 1995).

The social environment is an essential part of the life of dairy cows living together in a group. Cows live in dominance hierarchies and create social relationships based on interactions with their herd mates. These social interactions can be divided into agonistic and affiliative interactions and are necessary for keeping a balanced group and a structured group hierarchy (Tucker, 2017). Agonistic behaviours are either expressed as aggressive acts such as head butts, posturing, chasing, and fighting or responses to aggression which mainly is avoiding behaviour (Bouissou et al., 2001; Gibbons et al., 2009; Gutmann et al., 2015; Miller and Wood-Gush, 1991). Competition for resources is usually a driver for aggressive acts (Foris et al., 2019; Huzzey et al., 2014; Val-Laillet et al., 2008), and these acts can be relatively short in duration and can last less than a minute (Ben Meir et al., 2025; Bouissou et al., 2001). When the social rank is well established in the group, the slightest movement of the dominant cow could lead to a withdrawal or avoidance reaction from the submissive cow, even from far distances (Bouissou et al., 2001; Kondo and Hurnik, 1990).

Affiliative behaviours can be described as positive social interactions, including allogrooming, spatial proximity between particular individuals, and reduced resource competitiveness (Bouissou et al., 2001). Allogrooming is social licking directed mainly toward the head, neck, and front body (Val-Laillet et al., 2009) and has, for example, been shown to lower the heart rate of the receiver (Laister et al., 2011). Affiliative interactions reduce aggression, have a calming effect, and strengthen relationships (Boissy et al., 2007). Animals seek social contact with others as a "social support" when exposed to a stressor and coping with challenges. Stress can be alleviated with familiar and preferential companions, which can also help recover from diseases (Rault, 2012).

Preferential relationships are illustrated by increased spatial proximity between the individuals, affiliative behaviours such as allogrooming, and synchronization of activities (Boyland et al., 2016; Gygax et al., 2010; Val-Laillet et al., 2009). Cows seem to form and maintain preferential relationships with individuals of similar age and relatives (de Freslon et al., 2020; Reinhardt and Reinhardt, 1981; Wood, 1977). Familiarity and growing up together seem to enhance affiliative behaviour (Gutmann et al., 2015; Gygax et al., 2010; Marina et al., 2024b), and these age and familiarity assortments suggest that cows can maintain these preferred relationships even if they are separated from each other during their productive life several times (de Freslon et al., 2020; Marina et al., 2024b). Cows have also been shown to have preferred partners with similar characteristics, such as breed, milk production, and parity (Boyland et al., 2016; Churakov et al., 2021; Marina et al., 2024b). Keeping cows with a long-term familiarity is suggested to contribute to group stability and support animal welfare (Gutmann et al., 2015).

Regrouping cows and introducing new individuals to the group is a standard daily management procedure in dairy herds, which may lead to a disturbance of social relationships and a stressful and unstable social environment for the cows (Chebel et al., 2016; Foris et al., 2021; Raussi et al., 2005). It challenges dominance relationships and can lead to an increase in agonistic interactions. These changes can harm animal welfare and productivity, along with factors such as insufficient space allowance and large group size. It can lead to high competition in feed and resting places, affect feeding and lying behaviour, and reduce milk yield (Hasegawa et al., 1997; Miller and Wood-Gush, 1991; von Keyserlingk et al., 2008). In addition, the social buffering properties of the group can be diminished (Mounier et al., 2006). Cows on pasture, on the other hand, have a greater opportunity to avoid each other and tend to have fewer agonistic interactions on pasture than indoors (Miller and Wood-Gush, 1991). When individuals are sick or injured, they may alter their behaviour and activity level and show more “sickness behaviour” (Fogsgaard et al., 2015; Sepúlveda-Varas et al., 2016; Weigele et al., 2018), which may lower the number of interactions with others in the group (Sepúlveda-Varas et al., 2016; Weigele et al., 2018).

Social interactions between individuals can generate positive or negative effects on animal welfare and production. A dominant cow could, for example, keep other cows away from the milking unit or the feeding station, thus depressing their milk yield directly or also indirectly through reduced feed intake. The social rank of a cow can affect the waiting time in automatic milking systems, where low-ranked cows have longer waiting times (Melin et al., 2006) and consequently get longer milking intervals, which in turn can have a negative effect on milk production (Ayadi et al., 2003; Stelwagen, 2001). A cow's personality may determine the cow's milk yield since nervous cows tend to produce less milk (Hedlund and Løvlie, 2015), and social tension in the herd may lead to stressed cows and a lower milk production (Hasegawa et al., 1997; Hedlund and Løvlie, 2015).

On the other hand, cows receiving allogrooming from their herd mates have been associated with having a higher milk yield (Sato et al., 1991; Wood, 1977), and socio-positive interactions might potentially increase both animal welfare and milk yield (Fadul-Pacheco et al., 2021). To investigate the possibility of genetic selection for increased milk yield, considering the effects of social interaction, knowledge of potential individual differences in the herd mates' influence on a cow's milk yield is needed. The social contacts between individuals need to be quantified, and it is not fully understood what characteristics of a cow determine the number of contacts it has with its herd mates.

1.2 Indirect genetic effects

The phenotype of an individual is influenced by its genotype and the surrounding environment. In the classical quantitative genetic model, the trait value of an individual, P, is the sum of a heritable component, A, referred to as its breeding value, and a residual non-heritable component, E, referred to as environment (P = A + E) (e.g., Bijma et al., 2007a). Individuals living in a group will have social interactions with conspecifics and the environment will then also involve the expressed phenotypes of genes carried by the conspecifics (Bailey and Desjonquères, 2022).

Extensions to the quantitative genetic model have been developed to incorporate the social effects of conspecifics. In these models, the trait value of an individual in a group of n individuals will be the sum of its own direct effect and the sum of the indirect effects of its n-1 social partners (assuming that all individuals in the group interact with each other). Both phenotypic direct and indirect effects can be partitioned into a heritable and a non-heritable component, so the observed phenotype of individual i is given by (Bijma et al., 2007a; Griffing, 1967):

$$P_i = A_{D,i} + \sum_{i \neq j}^{\mathrm{n}-1} A_{I,j} + \sum_{i \neq j}^{\mathrm{n}-1} E_{I,j} + E_{D,i}, \qquad (1)$$

where $A_{D,i}$ is the direct genetic effect (DGE) of the focal individual i, $E_{D,i}$ is the direct environmental effect (DEE) of the focal individual i, $A_{I,j}$ is the indirect genetic effect (IGE) of group mate j, $E_{I,j}$ is the indirect environmental effect (IEE) of group mate j, and $\Sigma_{i\neq j}^{\mathrm{n}-1}$ is the sum over the *n*-1 group mates of focal individual i. In other words, the DGE is an individual's own breeding value for a trait, the effect of the individual's own genotype. IGE, also called competitive-, social-, or associative genetic effects, occurs when an individual´s genotype affects the phenotype of another individual (Griffing, 1967; Moore et al., 1997). However, the social partners are not affected by an individual's genes only, but experience the expressed phenotype of that individual, and the non-heritable components must also be considered (Bijma et al., 2007a; Griffing, 1967). Indoor temperature or a specific feeding regime are examples of non-genetic features in the environment that an individual can experience, which relate to the DEE of the focal individual.

IGEs are heritable effects that are important to consider since they can influence the response to selection (Bijma et al., 2007b; Griffing, 1967). Only DGEs are typically quantified when evaluating the evolutionary potential of traits, and this could lead to less accurate evolutionary predictions since the total genetic variance of traits that originate from other causes, such as IGEs, is neglected (Wolf et al., 1998). The response to selection on heritable traits may differ depending on the correlation between the DGE and IGE. For example, individuals with a genotype for high survival may also show high levels of aggression towards their group mates. Using these individuals as parents in the next generation could reduce the survival of the group mates and possibly for the whole population (Muir and Cheng, 2004). The genetic correlation between the DGE and IGE details competition or cooperation among individuals. A negative correlation indicates a heritable competition, where animals with a high breeding value for the trait have a negative heritable effect on the trait of others (Moore et al., 2002). Oppositely, a positive correlation indicates heritable cooperation, where animals with high breeding value for the trait have a positive effect on the trait of others (Bijma et al., 2007a). The total heritable variation can either increase or decrease due to IGE from social interactions, where a negative correlation between DGE and IGE may decrease the variation.

Two conceptually different theoretical frameworks have been developed for quantitative genetic models of IGE. The first approach is the variance-component model previously described in this chapter (Equation 1). Variance-component models partition the phenotypic variance of a specific trait into a direct genetic variance related to an individual's genotype, an indirect genetic variance related to all of the individual's social partners, and other sources of environmental variance. These models do not specify the specific social interaction trait causing the effect of the social partners. Instead, they evaluate the consequence of the interaction on a response variable (e.g., milk production). The second approach is a trait-based model, specifying the interacting phenotype causing the indirect effect. In these models, the "interaction coefficient," ψ, is used to reveal the relationship between the trait value of the focal individual on the trait value of its social partner. Together with the additive genetic variance, the interaction coefficient defines the size of the IGEs, and the correlation between DGEs and IGEs is determined by ψ (Bijma, 2014; Moore et al., 1997).

In the review of Ellen et al. (2014) and the meta-analysis of Santostefano et al. (2024), IGEs are suggested to increase the genetic variation available for selection and enhance the evolutionary potential. Selecting for IGE in livestock may potentially improve animal welfare and production traits. Research has, for example, shown that selecting on IGE could reduce tail biting and aggressive behaviour in pigs and, hence, increase animal welfare (Camerlink et al., 2015). By targeting both DGE and IGE in genetic selection, mortality in laying hens is expected to be reduced (Alemu et al., 2016; Ellen et al., 2008). Evidence of IGEs on production traits such as growth rate has been reported in e.g., pigs (Ragab et al., 2019) and rabbits (Piles et al., 2017). More and more research within different contexts provides estimates of IGE in livestock and shows genetic variation in IGE for many traits and species (Ellen et al., 2014; Santostefano et al., 2024). Including IGE in breeding programs may improve their efficiency. However, one major challenge is that the IGEs are often small, and more information is needed for accurate predictions than for DGEs (Poulsen et al., 2020).

Indirect genetic effects have been studied primarily on species where the animals are housed in small and homogeneous groups of fixed sizes, e.g., within cages or pens. In these scenarios, the individuals are assumed to have an equal social effect on all their group members. However, methods to estimate IGEs for animals moving freely in a large group with varying levels of interactions, such as cows in a free-stall environment, are currently unavailable. In spatially fixed organisms close to each other, such as trees in a forest, the variance component models have been extended with the intensity of competition (Cappa and Cantet, 2008; Silva et al., 2013). The distance between neighbouring trees is used as a weighting factor in the model to account for the intensity of interaction. There are also examples of studies in pigs that include the variation in interaction level within the model when estimating IGEs (Angarita et al., 2019). A few studies have investigated IGEs of dominance in cattle (Sartori and Mantovani, 2013; Tuliozi et al., 2023). Otherwise, studies on IGEs in cattle are limited. The magnitude and importance of IGEs in dairy cows are unknown, and the number of herds and individuals required to detect these effects will depend on the genetic variance of the studied trait, the population structure, and how much the level of interactions varies within herds (Bijma, 2010a, 2010b). Dairy herds are dynamic due to continuous calving and drying-off events, which constantly change the group compositions of individuals. Therefore, knowing who interacts with whom and how much individuals interact is necessary. The technology to record and quantify social interaction in dairy farms on a large scale was not available until recently.

1.3 Precision livestock farming technologies

The key to estimate IGE in dairy cattle will be to identify which cow is interacting with whom and to quantify these social interactions. Further, a necessity to include IGE in the breeding program is to have automated data collection methods. Traditional visual observations have been the primary method for studying behaviour and social interactions in cattle (Sahu et al., 2020). However, these observations are time-consuming and labour-intensive and are usually limited to presenting representative snapshots of the animal´s behaviour.

In recent years, technical development has provided alternative methods of continuously monitoring animals’ movement and behaviour and systematically collecting behavioural data. Precision livestock farming (PLF) technologies such as electronic feeders, computer vision, proximity loggers, positioning systems, and detailed data collected from milking units have opened up new possibilities to assess social behaviour in cattle. Using data from electronic feeding bins is a promising tool to automatically quantify competitive behaviour between cows, such as displacements at the feed bunk (Huzzey et al., 2014). Computer vision methods have been explored to automatically detect social interactions between cows in the waiting area before milking (Guzhva et al., 2016). However, methods for the identification of the individuals involved in the interactions also need to be addressed (Ren et al., 2021). Spatial proximity loggers can record when two specific individuals are close to each other. In the study of Boyland et al. (2016), proximity loggers were used on 110 dairy cows, and they showed that the proximity contacts between individuals were positively correlated with allogrooming events recorded with visual observations. However, the specific barn area has been suggested to be an important factor when inferring social interactions with proximity measures (Foris et al., 2021; Rocha et al., 2020). The drawback with the proximity loggers is that the information on where these interactions occur in the barn is missing. An ultra-wideband (UWB) indoor positioning system, a real-time location system (RTLS), captures the position of a cow within the barn. With high accuracy, cows can be predicted to be at the feeding trough, alleys, or cubicles (Pastell and Frondelius, 2018; Tullo et al., 2016). Using these positions, detailed information on which area of the barn the time the cows spend in proximity to other cows can be determined (Chopra et al., 2020; Rocha et al., 2020).

On-farm milking systems and associated devices are becoming more complex and can measure increasingly more than just the milk yield produced (Klingström et al., 2024). Information on the milking order of cows can also be used to investigate the behaviour and social interactions. Lame cows and cows with high somatic cell count (SCC) have, for example, shown to come further back in the milking order than non-lame cows and cows with lower SCC (Berry and McCarthy, 2012; Sauter-Louis et al., 2004; Weigele et al., 2018). Social rank has been associated with the order cows enter the milking parlour, yet with contradictory results (Sauter-Louis et al., 2004; Vargas-Bello-Pérez et al., 2020). Detailed information on the identity of each cow, the time of milking, and the position within the parlour can also be used to create social networks during milking. The proximity contacts during milking can be quantified. When the identity of contemporary neighbouring cows in the parlour is known, it is possible to analyse how different cows may affect a cow's milk yield. One of the advantages of this type of data is that it is automatically recorded from systems already installed on the farms.

2. Aims of the thesis

The overall aim of this thesis was to explore the social behaviour of dairy cows using data from sensors and on-farm milking systems. Furthermore, this thesis aimed to investigate the possibility of including breeding values for indirect genetic effects in dairy breeding programs. To this end, I:

- Studied the entrance order to a milking parlour, with data from the on-farm milking system, to assess whether the milking order is random or has an underlying structure (Paper I).

- Investigated if proximity contacts during milking may impact a cow's daily milk yield using milking order data from the on-farm milking system (Paper II).

- Explored which characteristics of a cow are associated with the number of contacts it has with its herd mates using real-time positioning data (Paper III).

- Studied which data are required to estimate reliable breeding values for indirect genetic effects (Paper IV).

3. Summary of studies

3.1 Farms and data collection

3.1.1 Animals and housing

Data from two commercial farms were used in this thesis (Figure 1, Table 1). Both farms had around 200 lactating cows housed in free-stall barns. Farm A was a Swedish farm with cows housed in two separate milking groups, G1 and G2. The cows were Holstein Friesian, Red Dairy Cattle (RDC), and crossbreds. The cows were milked twice daily in a herringbone parlour from GEA (2×12 GEA Euro class 800 with Dematron 75, GEA Farm Technologies, Bönen, Germany), with two rows of 12 milking units each. Cows in G1 were mainly in early lactation and high-yielding cows, and G2 consisted mostly of pregnant cows and cows decided for slaughter. The cows were routinely regrouped in the herd from G1 to G2 at around 170 days in milk (DIM), when confirmed pregnant, at the decision of slaughter, or depending on the current group sizes. Dry cows were housed in a separate group in another building and were moved to calving boxes before calving. Newly calved cows were introduced to the milking group 24-48 hours after calving. The cows were fed a total mixed ration ad libitum 12 times daily.

Farm B was a farm in the Netherlands, with Holstein Friesian cows housed in one milking group and milked at least twice a day in automatic milking machines (Mlone, 5-box, GEA Farm Technologies, Bönen, Germany). The cows were fed a partial mixed ration ad libitum and additional concentrate in the AMS and the feeding stations according to milk production. The feed was delivered once a day and automatically pushed five times a day. Dry cows were housed in a separate group in another building.

3.1.2 Positioning data

Both farms had the same RTLS (CowView, GEA Farm Technologies), with each lactating cow having a tag on their neck collar connected to the system. Eight anchors located in the ceiling of each barn received ultra-wideband signals from the tags, and the cow's position, in the form of x- and y-coordinates, was collected automatically every second (Figure 1). Positions were estimated through triangulation (Sloth and Frederiksen, 2019), with a reported error distance of approximately 50 cm (Meunier et al., 2018). The position was used to estimate the distance between the lactating cows in the free-stall barn. Positions within two functional areas in the barn, feeding and resting areas, were recorded. Tag IDs were received from the farms to connect each individual to the corresponding positioning tag.

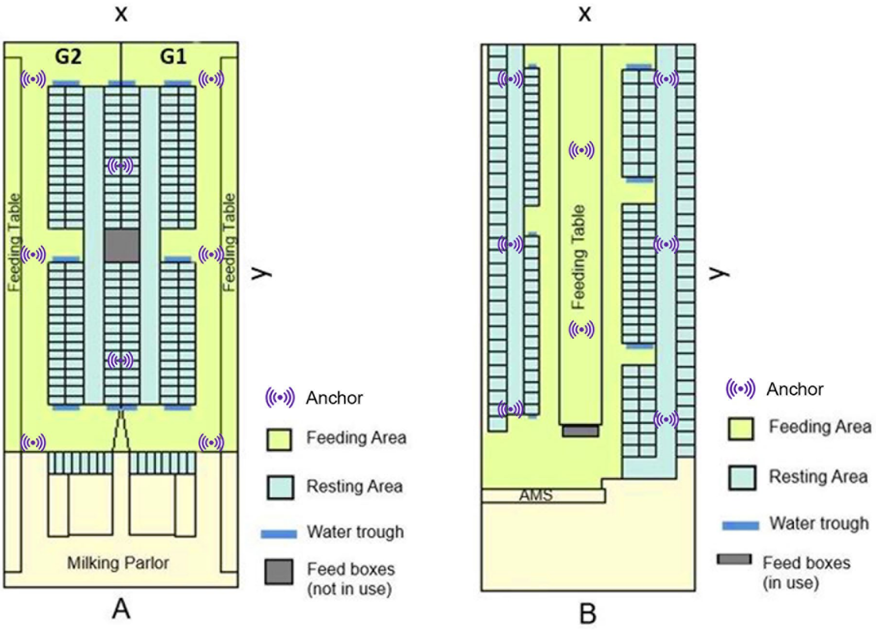


Figure 1. Schematic map of the two free-stall barns, where y and x represent the direction of the y- and x-axes for the positioning system. (A) Farm A holds two milking groups, G1 and G2, each with a 14 m × 56 m pen area. The area shown in beige is out of reach for the cows, except for transport between the pen area and the milking parlour. (B) Farm B contains one big milking group with a pen area of 30 m × 58 m. The area shown in beige is out of reach for the cows except for the automatic milking system (AMS).

3.1.3 Farm data

In farm A, milk records with the position of each cow within the milking parlour during milking and the time-point of the detachment of the milking cluster at the end of the milking were transferred from the milking equipment to the farm computer. The milk records were collected from the farm together with information on individual characteristics such as parity and calving date. Data on insemination records, pregnancy diagnoses, claw trimming records, breed, and pedigree information were extracted from the Swedish official milk recording scheme. In farm B, individual information on parity, calving date, insemination date, and pregnancy diagnoses was received from the farm.

Table 1. Overview of the data used within Papers I-IV

Paper	Farms	Data	Study period	Observations
I	Farm A	Milking data	2020/08/11 - 2020/11/01	33,237
II	Farm A	Milking data	2020/08/31 - 2020/10/06	6,808
III	Farm A & B	Positioning data	2020/10/16 - 2020/10/29	2,282 & 2,814
IV		Simulations		10,000

3.2 Associations of parity and lactation stage with the milking order (Paper I)

3.2.1 Materials and methods

Data from the milking equipment in farm A were collected for this study. The position within the parlour during milking and the timestamp of the milking cluster detachment at the end of each milking for each cow were used to determine the milking order. In front of the parlour, the cows were gathered in a waiting area where they could move freely before entering the parlour (Figure 2). They entered one side of the parlour at a time in a single row and were automatically identified at the entrance with radio frequency identification detection (RFID) technology.

Data from 165 milking sessions and 251 cows were collected. In each milking group, G1 and G2, the milking order was categorized into four groups depending on whether the cows entered the parlour in the First batch of cows milked, the Second, Third, or Last. Each batch included both sides of the parlour. The cows' positions during milking were also categorized into the first six positions (1) or the last six positions (2) (see Figure 2). The cows were categorized into Parity 1, Parity 2, or Parity 3+ and in Early (2–49 DIM), Mid (50–179 DIM), or Late (≥180 DIM) lactation. In one of the milking groups, only cows in mid and late lactation were included.

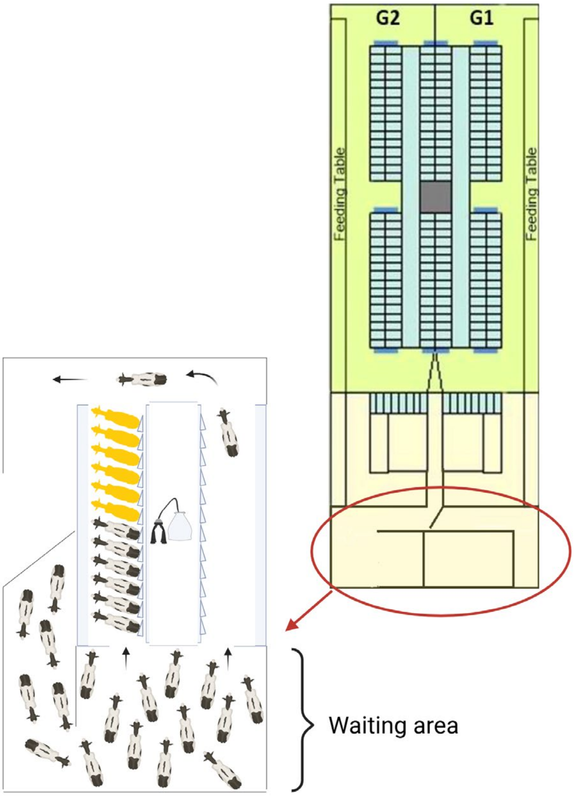


Figure 2. A schematic map of the free-stall barn and the milking parlour. The milking parlour is a 2 × 12-unit herringbone parlour with a waiting area in front of the two entrances. The yellow cows in the milking parlour represent the first six positions on the left side of the parlour.

For the statistical analysis, we fitted two models to assess associations with the entrance order and the preference to enter as one of the first cows within each milking line. First, we fitted an ordinal logistic regression model with the clmm function in the ordinal package in R (Christensen, 2022). The model was fitted with the milking order group (First, Second, Third, Last) as the response variable. Lactation stage and parity were fitted as fixed effects, and the cow ID as a random effect. One model per milking group was analysed. Second, we fitted a logistic regression model with the glmer function in the lme4 package (Bates et al., 2015). The model was fitted with a 0-1 response variable, and the trait was whether or not the cow was milked in the first six positions within each milking line. Parity, lactation stage, group, and milking event were fitted as fixed effects, and cow ID as a random effect. One model, including both milking groups, was fitted. The repeatability was estimated as the intraclass correlation coefficient (ICC) for each model, corresponding to the proportion of the variance of the individual random effects relative to the total variance. The total variance was the sum of the individual random effects and the residual variance, and here, the residual variance was assumed to be equal to $\pi^2/3$ (i.e., the variance of the standard logistic distribution).

3.2.2 Summary of results

We found that the milking order was not random. The repeatability in both milking groups ranged from 0.48 to 0.49 in the first model, indicating that the milking order was relatively consistent. In both milking groups, we found an association of parity with the order the cows entered the milking parlour. Cows in their first parity had higher odds of being in the early milking order groups than cows in higher parities. The entrance order for Parity 2 and Parity 3+ cows did not differ. In the milking group that included cows in all three lactation stages (Early, Mid, and Late), the lactation stage was associated with the entrance order to the milking parlour. Cows in early lactation had higher odds of being in the early milking order groups than cows in mid and late lactation. The entrance order for cows in mid and late lactation did not differ. The probability of being milked in the first or last six positions within one milking line was also associated with parity and lactation stage. Cows in first parity and early lactation were more likely to be milked in the first six positions. However, the repeatability was only 0.09, indicating that the individuals were not consistent in the first or last positions within a milking line.

3.3 Milking neighbours’ effect on milk yield (Paper II)

3.3.1 Materials and methods

Milking order data from farm A was collected from 70 milking sessions, corresponding to 35 days (Figure 3). Daily milk yield records for 219 cows were collected as the sum of the morning and the previous day´s evening yield. A general additive model was used for each milking group to fit a lactation curve and account for the nonlinear relationship with the DIM.

Parity was fitted as a dummy variable in the model to account for the differences in lactation curves between parities. The daily milk yield was used as a response variable, and the resulting residuals from the model, the milk yield residuals, were used in the subsequent model.

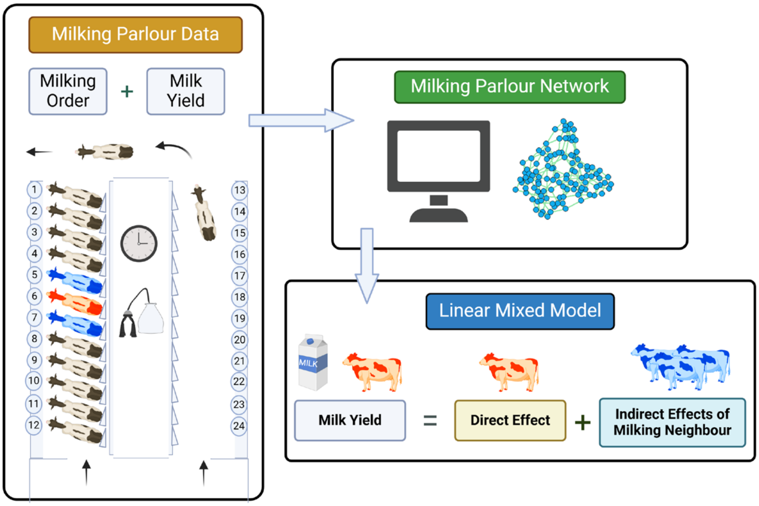


Figure 3. Overview of collected data and methodology for Paper II.

Adjacency matrices of who stood next to whom in each milking session were created. A linear mixed model per milking group (G1 and G2) was fitted with two random effects, the cow ID and the neighbouring cow ID, and the milk yield residuals as the response variable. The random effect of the cow ID was referred to as the direct effect, while the effect of the neighbouring cow IDs was referred to as the indirect effect. The likelihood of the fitted model was compared with a simpler model where the random effect of the neighbour was removed using the lrt function in the hglm package (Rönnegård et al., 2010). The Pearson correlation coefficient was calculated between the estimated direct and indirect effects.

3.3.2 Summary of results

We found a significant effect of the indirect effects of the neighbouring cow during milking in both milking groups (Table 2). The variance of the indirect effects was smaller in G1 than in G2, and the estimates of indirect effects varied from -0.56 to 0.58 kg of milk in G1 and from -1.07 to 0.85 kg of milk in G2. The results indicate that the neighbouring cow during milking affects a cow's daily milk yield, and a cow can impact their group mates' daily milk yield by more than -1 kg milk on average. In this case, the hypothesis is that the neighbouring cow is making the cow feel stressed during milking, and the milk ejection is delayed, leading to increased residual milk and decreased milk yield. However, some individuals had a more positive effect on their neighbours, up to 0.85 kg of milk, indicating that there could be individuals who are more of a social supporter within the group. Neighbours that might, for example, make already nervous cows calmer during milking.

Cows that were regrouped from G1 to G2 during the study period had, in general, a more positive estimated indirect effect in G1 and altered to a more negative effect when moved to G2 (Figure 4). These results could be related to disturbances within the group due to regrouping, indicating that these estimated indirect effects depend on the group's stability and composition. Studies with more extended periods would be necessary to investigate whether these effects belong to the individual or if they rather represent how long the cow has been in the group.

The correlation between the direct and indirect effects in G1 was -0.26 (P = 0.004), and the negative correlation intensified with parity (Figure 5). A negative correlation means that cows with low milk yield, i.e., a low direct effect, have a positive effect on their group mates' milk yield, i.e., a high indirect effect. At the same time, cows with high milk yield have a negative effect on their group mates' milk yield. However, there was no significant correlation between the direct and indirect effects in G2.

Table 2. Variance component estimates of daily milk yield residuals

	G1		G2	
Variance component	Estimate	95% CI[1]	Estimate	95% CI[1]
Direct effects, $\boldsymbol{\sigma_d^2}$	28.8	22.4 – 37.2	27.5	21.3 – 35.5
Indirect effects, $\boldsymbol{\sigma_s^2}$	0.09	0.07 – 0.13	0.19	0.15 – 0.26
Residual, $\boldsymbol{\sigma_e^2}$	6.60		5.04	
LRT[2] statistics	42.1 (P < 0.001)		105.4 (P < 0.001)	

[1] The 95 % confidence interval of the estimated variance components was calculated according to Rönnegård et al. (2010)

[2] LRT = likelihood-ratio test, performed with the lrt function in the hglm package in R (Rönnegård et al., 2010) to test the significance of the indirect effects.

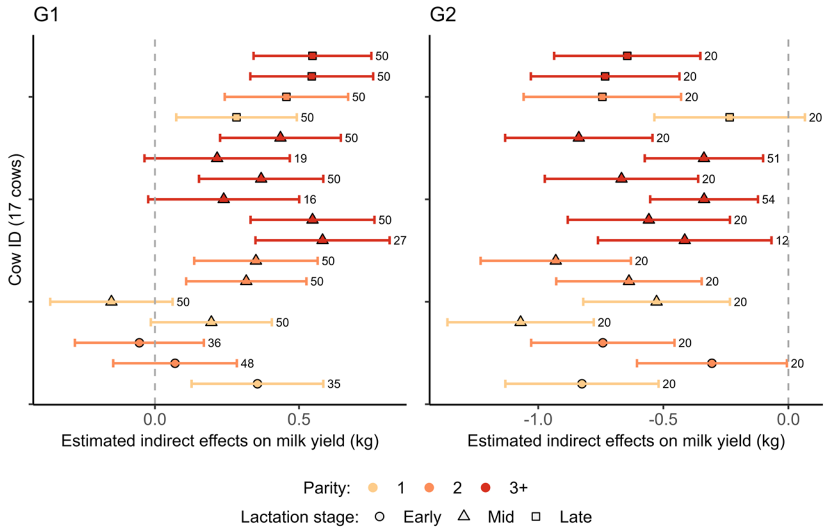


Figure 4. Individual indirect effect estimates on milk yield with standard error bars for cows regrouped from G1 to G2 during the study period. The figure shows the estimates for 17 cows with at least ten records in each group. After the error bars, the numeric value represents the number of records for that cow in the respective group.

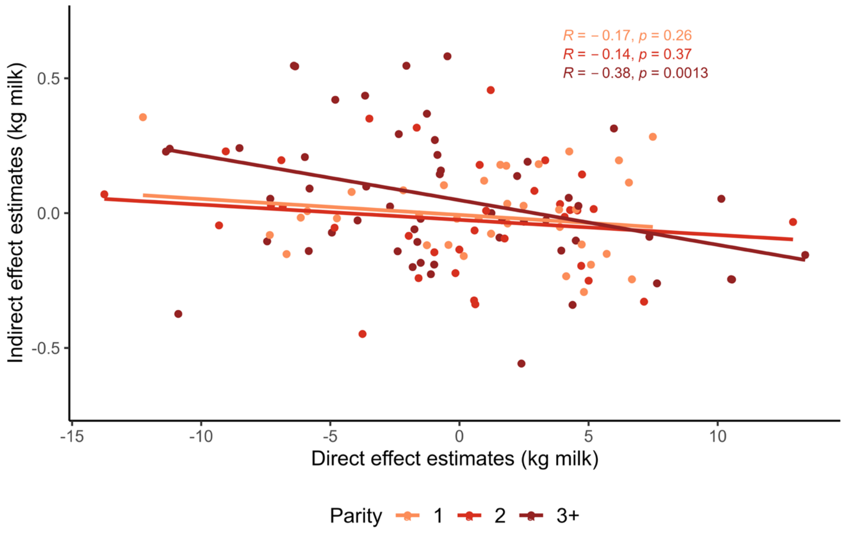


Figure 5. Correlation plot of the estimated direct and indirect effects on milk yield for G1 with a regression line for each parity group. R = Pearson correlation coefficient.

3.4 Characteristics associated with the number of contacts (Paper III)

3.4.1 Materials and methods

The positioning data was used to explore which individuals a cow spent time within proximity. Data was collected from both farm A and farm B. A contact between a dyad was defined with a distance radius of 2.5 m (Figure 6), and the contact duration needed at least 10 min per day between two individuals to reject brief interactions happening by chance. The total duration of contacts, $tcontact_{,i,k}$ for each cow, i, and day, k, was calculated as the sum of durations with all the present group members. The number of contacts a cow had with other individuals was investigated separately in two functional areas: the feeding and the resting area. Since individuals might have different time budgets within these areas, the time spent in these areas, $tarea_{,i,k,}$ were accounted for, and a contact rate was defined as $tcontact_{,i,k}/tarea_{,i,k}$. The contact rate was the instantaneous number of individuals within proximity of a cow at any time during the day and was used as a response variable in our analysis.

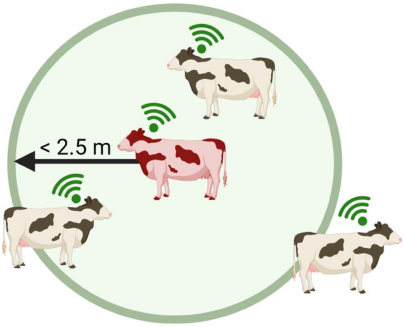


Figure 6. Definition of social contact. A social contact existed between a pair of cows when they were within a distance radius of 2.5 m for at least 10 min in total per day.

A linear mixed model was fitted for each functional area, with contact rate as the response variable, date, parity, lactation stage, breed, oestrus status, pregnancy status, claw health, and udder health as fixed factors, and cow ID as a random effect. Cows were categorized into three parity groups: Parity 1, Parity 2, and Parity 3+, and three lactation stages: Early (7-49 DIM), Mid (50-179 DIM), and Late (≥ 180 DIM) lactation. Oestrus status was estimated based on insemination records. Claw health was based on remarks from claw-trimming records (Remark or No Remark). Udder health was based on SCC analysed from quarter foremilk samples collected at the farm at two different time points and categorized into Low (0 – 130 000 SCC/ml), Mid (130 000 – 300 000 SCC/ml), and High (300 000 > SCC/ml). In farm B, data on claw and udder health was not available.

3.4.2 Summary of results

We found an individual variation of the contact rate in both the feeding and resting areas (Table 3), indicating differences in social behaviour between cows, and the repeatability was relatively consistent between groups and farms. The contact rate was between one and two for most of the cows in the feeding area and between two and three for most cows in the resting area. These results were consistent in all milking groups and farms, which means that at any time during the day, the instantaneous number of individuals within proximity of a cow in the feeding area was between one and two individuals and in the resting area between two and three.

Table 3. Repeatability of contact rate

	Feeding Area			Resting Area		
	Farm A		Farm B	Farm A		Farm B
	G1	G2		G1	G2	
Repeatability[1], %	35	36	30	47	46	47

[1] $\text{Repeatability} = \frac{\text{variance of individual random effects}}{\text{variance of individual random effects} + \text{residual variance}}$

For G1 and farm B, cows in mid and late lactation had a higher contact rate in the feeding area than cows in early lactation (Table 4). The contradictory results for G2 were probably due to different group compositions within this group, since no early lactation cows were included here, and due to cows being newly introduced in G2 from G1 at around 170 DIM. There was no significant association between contact rate and lactation stage in the resting area. Parity was significantly associated with the contact rate in the feeding area in G1 and farm B. The results were contradictory between the two groups. However, the estimated effect size was smaller in farm B. In G1, cows in their first parity had a higher contact rate than cows in higher parities. In the resting area, parity was associated with contact rate in farm B, where cows in higher parities had a higher contact rate than younger cows.

For the additional characteristics included in the model, breed and oestrus were associated with contact rate in the feeding area. In contrast, pregnancy status, oestrus, udder, and claw health were associated with contact rate in the resting area (Table 5). Cows with impaired udder or claw health had a lower contact rate than healthy cows.

Table 4. Summary of the estimated regression coefficients and significance of parity and lactation stage on the contact rate in the feeding and resting area[1]

	Feeding Area			Resting Area		
	Farm A		Farm B	Farm A		Farm B
	G1	G2		G1	G2	
Parity						
1	$\mathbf{0}_a$	0	$\mathbf{0}_a$	0	0	$\mathbf{0}_a$
2	$\mathbf{-0.12}_b$	-0.04	$\mathbf{0.03}_{a,b}$	0.06	-0.00	$\mathbf{0.11}_a$
3+	$\mathbf{-0.20}_b$	-0.03	$\mathbf{0.08}_b$	0.13	-0.00	$\mathbf{0.29}_b$
Lactation stage						
Early (7-49 DIM)	$\mathbf{0}_a$		$\mathbf{0}_a$	0		0
Mid (50-179 DIM)	$\mathbf{0.14}_b$	$\mathbf{0}_a$	$\mathbf{0.15}_b$	0.37	0	0.06
Late (≥180 DIM)	$\mathbf{0.19}_b$	$\mathbf{-0.10}_b$	$\mathbf{0.21}_c$	0.16	0.07	0.09
Residual Std. Dev	0.20	0.19	0.24	0.56	0.48	0.28

[1] Results are shown for G1 and G2 in farm A and B in a Box-Cox transformed scale.

[a–c] Different subscript letters represent significantly different values ($P < 0.05$) between the levels for each factor.

Table 5. Summary of the estimated regression coefficients and significance of the individual characteristics on the contact rate in the feeding and resting area[1, 2]

	Feeding Area			Resting Area		
	Farm A		Farm B	Farm A		Farm B
	G1	G2		G1	G2	
Breed						
Crossbred	0	**0**$_{a}$		0	0	
Holstein	-0.02	**-0.00**$_{a}$		-0.02	-0.08	
Red Dairy Cattle	-0.06	**-0.14**$_{b}$		-0.18	-0.05	
Pregnancy status						
Open	0	0	0	**0**$_{a}$	0	0
Pregnant	0.04	0.05	0.01	**-0.51**$_{b}$	0.08	0.01
Oestrus						
Not in Oestrus	**0**$_{a}$		0	**0**$_{a}$		0
In oestrus	**-0.10**$_{b}$		-0.05	**-0.29**$_{b}$		-0.04
Udder health[3]						
Low	0	0		**0**$_{a}$	0	
Mid	0.01	-0.06		**-0.53**$_{b}$	-0.07	
High	-0.01	-0.07		**-0.19**$_{a,b}$	-0.01	
Claw Health						
No remark	0	0		0	**0**$_{a}$	
Remark	0.01	-0.02		-0.09	**-0.34**$_{b}$	
Residual Std. Dev	0.20	0.19	0.24	0.56	0.48	0.28

[1] Results are shown for G1 and G2 in farm A and B in a Box-Cox transformed scale.

[2] Udder health and claw health data was only available for farm A. Oestrus information was not available in G2. In farm B, all the cows were of the same breed (Holstein).

[3] Udder health levels: Low (0 – 130 000 SCC/ml), Mid (130 000 – 300 000 SCC/ml), High (>300 000 SCC/ml).

[a–c] Different subscript letters represent significantly different values ($P < 0.05$) between the levels for each factor.

3.5 Towards assessing indirect genetic effects (Paper IV)

3.5.1 Materials and methods

Twenty-two different simulation scenarios were performed, and we assessed, amongst others, how the magnitude of IGE and the inclusion of the direction and the intensity of contact could impact the estimation of IGE. The accuracy and precision of the estimated variance components and the accuracy and bias of the estimated breeding values (EBVs) were evaluated. For the basic scenario, we simulated social networks in 100 herds. Each herd contained 100 cows with unrelated dams and sires randomly mated from a parent population of 10,000 cows and 100 sires. Breeding values for the DGE and IGE were sampled from a multivariate normal distribution. The number of contacts for each cow was sampled with a mean of 30 from a Poisson distribution. This number corresponds to an individual's mean number of contacts in a social network of herds with approximately 100 dairy cows, as reported by Chopra et al. (2020) and Marina et al. (2024b). Social networks were constructed within each herd using the sample_degseq function from the igraph package (Csardi et al., 2024). Phenotypes for milk yield were simulated for all 10,000 individuals in the offspring population:

$$y_i = herd_i + a_{D,i} + \sum_{i \neq j}^{n_i} a_{I,j} + \sum_{i \neq j}^{n_i} e_{I,j} + e_{D,i}$$

where y_i is the simulated milk yield for recipient i, $herd_i$ is the fixed herd effect of recipient i, $a_{D,i}$ is the DGE of recipient i, $a_{I,j}$ is the IGE of herd mate j, $e_{I,j}$ is the indirect environmental effect (IEE) of herd mate j, $e_{D,i}$ is the direct environmental effect (DEE) of recipient i, n_i is the number of herd mates recipient i has contact with.

A phenotypic standard deviation, σ_P, of 800 kg milk was used to correspond to similar values reported elsewhere (Liedgren et al., 2024; Mohd Nor et al., 2013; Venjakob et al., 2022). A direct heritability, h_D^2, of 0.3 was chosen since it is within the range of the estimated heritability of milk yield in genetic breeding evaluations (NAV, 2024; Oliveira Junior et al., 2021). The simulated variance components are shown in Table 7. The genetic covariance between the direct and indirect genetic effects, $\sigma_{a_{DI}}$, was assumed to be zero. A classical animal model with the added indirect genetic and environmental effects was fitted in DMU (Madsen et al., 2014), where the numerator relationship matrix was calculated from the simulated pedigree.

The importance of the intensity of contacts when estimating IGEs was studied by either including or ignoring them in the analyses or adding noise to the collected intensities (Table 6). The intensity for each contact was sampled from a gamma distribution with shape = 1 and rate = 2. This distribution corresponds with the distribution of the total duration of contacts between dyads of cows in Paper III (unpublished results). The intensities were then standardized to achieve a mean and a variance of 1 to compare the results with the basic scenario, where the intensities are either 1 or 0. The phenotypes for the offspring were generated as in Figure 7, where f_{ij} is the intensity of contact between animal i and j, and the added intensities contributed to a larger phenotypic variance in these scenarios.

We assessed the importance of including the direction of contact, i.e., accounting for which contacts are incoming and outgoing for a cow (Table 6). Within each herd, we simulated directed networks with a mean of 15 incoming contacts and a mean of 15 outgoing contacts. Here, we assumed that half of the social contacts were incoming and half were outgoing for an individual, based on the proportion of mean in and out-degree of displacements and allogrooming events reported by Foris et al. (2019).

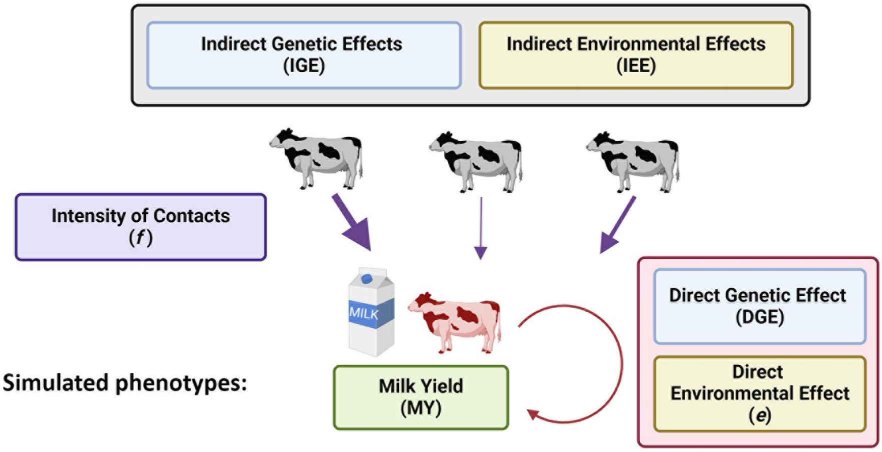
3.5.2 Summary of results

In the basic scenario, the variance component estimates were close to the simulated values with relatively low standard deviations (Table 7), and the accuracy of the EBVs for the DGE and IGE was moderate to high (Table 8). These results show that IGE in dairy cattle could be estimated relatively precisely and accurately from simulated data of dairy herds' dynamic social contact structure.

When the magnitude of the indirect genetic variance was reduced, there were more difficulties with model convergence. The variance component estimates were, on average, close to the simulated values but with larger standard deviations, and the EBV accuracies declined with the size of $\sigma^2_{a_I}$. The size of the IGE will impact the quality of the estimates, where a smaller variance of the IGE will lead to less precise estimates and less accurate EBVs.

Table 6. Description of scenarios for investigating the importance of intensity and direction of contact when estimating indirect genetic effects

Scenario	Description
Intensity of contact	
With intensities	Phenotypes were generated with intensities, and variance components were estimated with these known intensities.
Without intensities	Phenotypes were generated with intensities, and variance components were estimated, assuming there were no intensities but only a contact (1) or no contact (0).
Imprecise intensities	Phenotypes were generated with intensities and random noise (~ N(0,0.16)) was added to the true intensities before the variance components were estimated.
Direction of contact	
With direction	Phenotypes were generated by including only the incoming contacts (a mean of 15 contacts), and the variance components were estimated knowing this direction.
Without direction	Phenotypes were generated by including only the incoming contacts (a mean of 15). However, the variance component was estimated with the undirected network (a mean of 30 contacts), i.e., by including both the incoming and outgoing contacts.



$$MY_i = herd_i + DGE_i + \sum_{i \neq j}^{n_i} f_{ij} IGE_j + \sum_{i \neq j}^{n_i} f_{ij} IEE_j + e_i$$

Figure 7. Simulated phenotypes when including intensity of contacts.

Ignoring the underlying intensities when estimating the variance components led to estimates close to the simulated values with low standard deviations, except for an increased residual variance of 585 % (Table 9). It also resulted in lower breeding value accuracies (Figure 8). Even if the intensity of contacts between individuals was not accounted for in the model, we could still estimate the variance of IGE with accuracy and precision. However, we did not capture the variation of intensities of contacts between individuals, and the individuals' breeding values for IGE were less accurate. Adding random noise to the intensities led to underestimated variance components for the indirect genetic and environmental effects and increased residual variance. The added noise led to imprecise intensities between individuals, changed the scale of the intensities, and led to biased estimates of the variance components. However, the breeding value accuracies were still moderate to high. Ignoring information about intensities in the model appeared to be worse than using imprecise intensities due to lower accuracies of EBVs for both the DGE and IGE (Figure 8).

Table 7. Variance component estimates for simulations of the basic scenario and scenarios with smaller indirect genetic variance

Scenario	$\sigma^2_{a_D}$	$\sigma^2_{a_I}$	$\sigma^2_{e_I}$	σ^2_{e}
Simulated	192,000	6,400	6,400	64,000
Basic Scenario (30% of σ^2_P)	188,572 (28,941)	6,523 (1,123)	6,325 (998)	66,839 (23,006)
Simulated	192,000	640	640	409,600
Smaller $\sigma^2_{a_I}$ (3% of σ^2_P)	191,712 (29,506)	654 (266)	638 (436)	409,569 (24,999)
Simulated	192,000	320	320	428,800
Smaller $\sigma^2_{a_I}$ (1.5% of σ^2_P)	191,904 (35,444)	302 (179)	387 (382)	428,172 (30,065)

The means across the 100 replicates in each scenario with the standard deviation in brackets. $\sigma^2_{a_D}$ = direct genetic variance, $\sigma^2_{a_I}$ = indirect genetic variance, $\sigma^2_{e_I}$ = indirect environmental variance, σ^2_e = residual variance.

When the direction of contact was ignored, the variance components for the indirect genetic and environmental effects were underestimated by roughly a quarter. The EBV accuracies were lower, and for the IGE, the EBVs were biased. Technology that allows monitoring an individual's incoming and outgoing contacts may, therefore, be beneficial.

Table 8. Accuracy of EBVs for simulations of the basic scenario and scenarios with smaller indirect genetic variance

Scenario	Accuracy			
	Sires		Cows[1]	
	DGE	IGE	DGE	IGE
Basic Scenario (30% of σ_P^2)	0.96 (0.01)	0.92 (0.02)	0.74 (0.01)	0.59 (0.02)
Smaller $\sigma_{a_I}^2$ (3% of σ_P^2)	0.93 (0.01)	0.59 (0.06)	0.64 (0.02)	0.33 (0.04)
Smaller $\sigma_{a_I}^2$ (1.5% of σ_P^2)	0.93 (0.01)	0.43 (0.14)	0.64 (0.02)	0.24 (0.08)

The means of accuracies across the 100 replicates with the standard deviation in brackets. DGE = direct genetic effect, IGE = indirect genetic effect

[1] Cows with phenotypes.

Table 9. Variance component estimates for simulations of scenarios with intensity and direction of contact

Scenario	$\sigma_{a_D}^2$	$\sigma_{a_I}^2$	$\sigma_{e_I}^2$	σ_e^2
Intensity of contact				
Simulated	192,000	6,400	6,400	64,000
With intensities	192,202 (30,507)	6,327 (958)	6,460 (773)	63,604 (23,585)
Without intensities	193,502 (32,203)	6,361 (1,266)	6,758 (1,183)	438,631 (29,366)
Imprecise intensities	189,913 (29,893)	5,516 (821)	5,588 (675)	110,420 (24,310)
Direction of contact				
Simulated	192,000	6,400	6,400	64,000
With direction	186,518 (25,060)	6,235 (1,266)	6,567 (1,028)	67,691 (19,634)
Without direction	186,998 (25,950)	1,556 (391)	1,640 (365)	147,755 (20,076)

The means across the 100 replicates in each scenario with the standard deviation in brackets. $\sigma_{a_D}^2$ = direct genetic variance, $\sigma_{a_I}^2$ = indirect genetic variance, $\sigma_{e_I}^2$ = indirect environmental variance, σ_e^2 = residual variance.

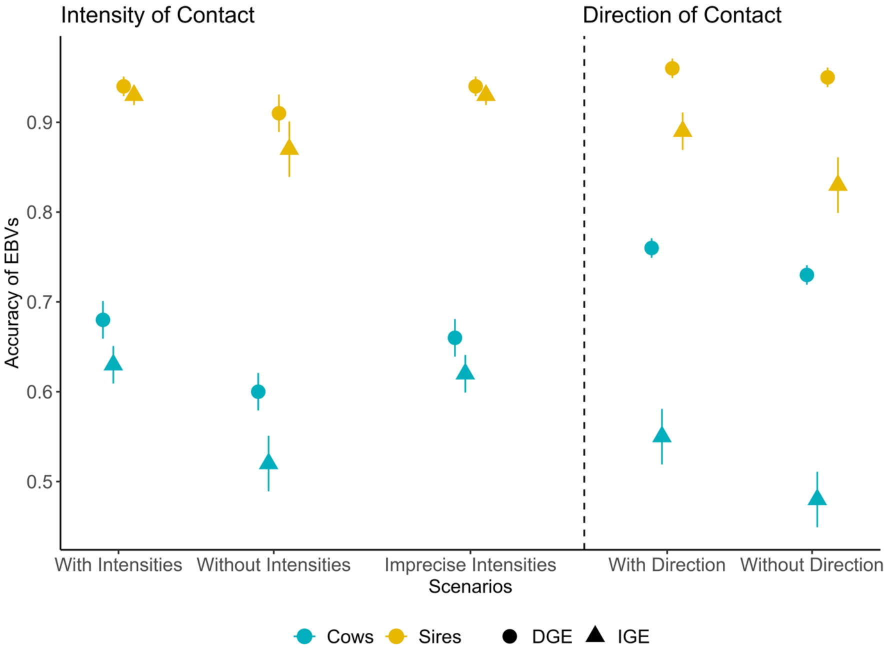


Figure 8. Accuracy of EBVs for scenarios with intensity and direction of contact. DGE = direct genetic effect, IGE = Indirect genetic effect, EBV = Estimated breeding value.

4. General discussion

4.1 Factors associated with behaviour and social contacts

Several factors will influence the social behaviour in dairy herds. In Papers I-III, we found that the behaviour of the cows and their social interplay with their herd mates were associated with different individual attributes. Cows in high parities had fewer contacts in the feeding area, more contacts in the resting area (Paper III), and a higher probability of being last in the milking order than first parity cows (Paper I). Higher parity cows may have a higher social rank than first parity cows and choose their positions in the barn more easily than subordinate cows (Churakov et al., 2021; Wierenga, 1990). A subordinate cow may need to change its position at the feeding table more frequently due to being displaced by other cows and, therefore, getting a higher contact rate in the feeding area. Higher parity cows have been shown to use frequently used cubicles close to the milking area (Churakov et al., 2021). They will, therefore, automatically have a high contact rate in the resting area. First-parity cows, usually more subordinate, tend to use the cubicles in less busy areas of the barn, which are located furthest away from the parlour (Churakov et al., 2021). Cows within the same parity have been seen to spend more time together (Boyland et al., 2016; Churakov et al., 2021; Marina et al., 2024b), and the cows may, therefore, also move together toward the milking parlour. Subordinate cows have also been seen to stay close to the milking unit within an automatic milking system to advance in the milking queue (Melin et al., 2006). A hypothesis is that cows in their first parity are more subordinate than older cows. They try to enter the milking parlour as early as possible to avoid being in the crowded waiting area for too long (Paper I). Nevertheless, Chopra et al. (2020) found no association between parity and proximity interactions. However, they used proximity distance and time thresholds other than those we used in Paper III, which might explain the contradictory results.

Cows in a later lactation stage had more contacts in the feeding area (Paper III), had a higher probability of being last in the milking order (Paper I), and had, in general, a larger and more positive indirect effect on their neighbour's milk yield during milking in comparison to cows in early lactation (Paper II). The difference in behaviour of the early lactation cows, in contrast to the cows in later lactation, might be related to their being less familiar with the other cows in the group and the time they have spent together. Familiarity between individuals living in a group has shown to be important for creating and maintaining social relationships (Foris et al., 2021; Gutmann et al., 2015; Gygax et al., 2010), and cows in later lactation have had the opportunity to create stronger social bonds with more individuals than early lactation cows for example. This could explain why they have more contacts in the feeding area and a generally more positive effect on their herd mates' milk yield. Cows in early lactation might, on the other hand, be less familiar with their herd mates and might therefore be more motivated to leave the crowded waiting area in front of the milking parlour (Paper I).

The reproductive status of the cow was associated with the number of contacts the cow had in the barn. Cows in oestrus had fewer contacts both in the feeding and resting areas (Paper III). Cows in oestrus are usually more active and more engaged in social interactions such as allogrooming and agonistic behaviour (Kerbrat and Disenhaus, 2004), suggesting that they would have had a higher contact rate in the functional areas. However, these cows usually interact with a few individuals within so-called sexually active groups (Sveberg et al., 2013) and will, therefore, only have longer contact with a limited number of herd mates. Oestrus is a brief temporal state and will probably not have any long-term impact on the social relationships within the herd (de Freslon et al., 2020), yet may still be important to account for when analysing social contacts between cows.

Pregnant cows had fewer contacts in the resting area (Paper III). Like other ungulate females, cattle are seeking isolation prepartum. However, this maternal behaviour is usually shown close to calving (Proudfoot et al., 2014; Rørvang et al., 2018a) and would only represent pregnant cows in their late pregnancy state. Nevertheless, behavioural changes due to pregnancy might lead to cows avoiding social confrontations more closely to calving (Rørvang et al., 2018b).

Cows with higher SCC had fewer contacts in the feeding area (Paper III). High SCC indicates udder inflammation, and cows with clinical mastitis have altered their behaviours, so-called sickness behaviour (Dantzer, 2001). Alterations in behaviours such as decreased lying time, feed intake, and feeding rate have been reported (Fogsgaard et al., 2015, 2012; Medrano-Galarza et al., 2012; Siivonen et al., 2011), and also the number of competitive replacements at feeding bins has been shown to decline for cows with clinical mastitis (Sepúlveda-Varas et al., 2016). In contrast to our results, Fielding et al. (2024) found no association between SCC and the mean association strength (the time a cow spent in proximity to other cows divided by all potential contacts). However, their study did not account for the functional area where the contacts occurred due to the use of proximity loggers. Our results might reflect cows with higher SCC showing sickness behaviour and staying away from their herd mates in the feeding area.

Lame cows have been shown to have longer lying time in the cubicles (Walker et al., 2008; Weigele et al., 2018) and visit concentrate feeders (Weigele et al., 2018) and the milking robot (Miguel-Pacheco et al., 2014) less often. Associations have not been proved between lameness and displacements during feeding (Walker et al., 2008) or between lameness and proximity interactions (Chopra et al., 2020). However, cows with claw remarks had fewer contacts in the resting area in Paper III, which could be explained as a social withdrawal response for these cows due to their health status (Dantzer, 2001).

We found differences in contact rate between breeds, where RDC had fewer contacts in the feeding area than Holstein and crossbred cows (Paper III). This could be related to different personalities and temperaments between breeds. For example, Sewalem et al. (2010) found that the Jersey breed had fewer nervous cows than the Holstein and Ayrshire breeds. However, Hedlund and Løvlie (2015) found limited differences in behaviour between Holstein cows and RDC, although the Holstein cows were more consistent in their behaviour than the RDC. More research is needed, and exploring whether social interactions are different within and between breeds would be interesting. Cows have, for example, been shown to have a preferential assortment to individuals of the same breed, which could be related to similar body sizes and energy requirements (Boyland et al., 2016). Many herds in Sweden have a mix of different breeds, and investigating how breeding values for IGE would potentially be different for individuals living in mixed herds or purebred herds would be of interest as to how this should be addressed.

In Paper III, we accounted for the time the individuals spent in the different functional areas when quantifying the social contacts. However, we did not account for the area preference of the individuals. Marina et al. (2024a) showed that the area preference of individuals might shape social contacts between dairy cows, and ignoring area preference in the model could bias the result and yield larger effect estimates. This needs to be considered when we interpret the results from Paper III since the effect sizes might appear larger than the actual ones.

Sociality has been suggested to be a stable trait (Ozella et al., 2023; Rocha et al., 2020). However, the results from Papers I-III suggest that during one lactation, and from one lactation to another, a cow may alter her social behaviour, and that her familiarity with other group mates, her reproductive status, and her health status may influence the behaviour. When we estimated the indirect effects on a cow's daily milk yield during milking (Paper II), we found that the indirect effect changed for regrouped cows. A key question is whether these indirect effects also change within and between a cow's lactation. The length of the study periods in Papers I-III were 82 days (Paper I), 35 days (Paper II), and 14 days (Paper III), and were all within the period between August 2020 and November 2020. Study periods from different years and seasons would be valuable, and longitudinal studies following cows within and between lactations are needed before we can draw any strong conclusions.

4.2 Monitoring strategies and methodology

4.2.1 Positioning data

In accordance with other studies, we found a significant social differentiation between individuals, where some individuals are more social than others (Rocha et al., 2020). Using spatial proximity as a proxy for affiliative interactions between individuals has been widely used (Whitehead, 2008). However, the barn environment, such as the barn layout and the stocking density, will affect a cow’s ability to actively choose whom to be in proximity with or to avoid (Chopra et al., 2020; Sheng et al., 2024). A fundamental challenge with using proximity to determine and quantify social contacts is distinguishing between genuine associations and non-social proximity events (Chopra et al., 2020). Threshold assumptions are required, such as proximity distance and time in proximity. In Paper III, a distance radius threshold of 2.5 m defined a contact between dyads of cows. This threshold aimed to include several proximity interactions, such as two cows standing face to face, a cow standing behind/following another cow, and cows lying next to each other in a cubicle. Table 10 summarises the definitions of contacts from other studies on proximity interactions.

Table 10. A descriptive summary of definitions of social contacts used when analysing proximity interactions

Study	**Distance**	**Time**	**Monitoring system**
Chopra et al. (2020)	< 3m	> 60s	Combined local-position and accelerometer sensor (Oms500, Omnisense Ltd, UK) Mean error distance: 2.66 m
Rocha et al. (2020)	Feeding area: < 1.25m Resting area: < 2.5m	> 600s[1]	Real-time location system (RTLS) (CowView, GEA Farm Technologies) Referred to the mean error distance of 0.5 m guaranteed by the manufacturer (Meunier et al., 2018)
Boyland et al. (2016)	1.5-2m [2]	> 1s[3]	Proximity loggers (Sirtrack Ltd, New Zealand)
Fielding et al. (2024)	1–1.5m [4]	> 20s	Proximity loggers (design by the OpenBeacon project).

[1] The accumulated contacts lasting at least 600s between two cows on a given day.

[2] Logged contacts between individuals when the loggers were within a distance of 1.5–2m. When any two loggers were separated > 120s, the encounter terminated.

[3] Removed all encounters < 1s (considered as noise)

[4] Logged contacts between individuals when the loggers were within a distance of 1–1.5m. When any two loggers were separated > 20s, the encounter terminated.

A short maximum distance would be motivated to distinguish between genuine social interactions and proximity events of non-social character. However, the absence of a few interactions can significantly alter the network's total structure, and reducing false negatives is essential and would, therefore, motivate a large maximum distance as possible (Farine and

Whitehead, 2015). Hence, there is a trade-off between capturing true social interactions and all important connections in the network. In Paper IV, collecting imprecise intensity of contacts led to underestimated variance components of the IGEs, yet the accuracy of the breeding values was not affected to any larger extent compared to ignoring the intensities in the model. These results indicate that capturing all interactions between individuals, even imprecise ones, is better than ignoring the information on intensities. However, the scenarios with the direction of contact in Paper IV showed that including individuals who were false positives led to underestimated variance components of IGEs and biased and less accurate breeding values.

Social interactions of different characters may also differ in duration (Ben Meir et al., 2025; Bouissou et al., 2001; Val-Laillet et al., 2009), and choosing a specific time threshold for defining a social contact may be challenging. Choosing a too high threshold might lead to the exclusion of interactions of social character (Chopra et al., 2020). In Paper III, three different time thresholds were tested for the accumulated duration of contacts between a dyad: 10 min, 20 min, and 30 min. When the time threshold was 30 min, alterations of the results were seen compared to the models with thresholds of 10 and 20 min, with higher p-values for some of the characteristics. A comprehensive sensitivity analysis of these thresholds would be of value, considering the particular system used, its accuracy, stocking density, functional area, and layout.

In the study of Boyland et al. (2016), the association strength (the summed duration of all contacts between dyads), measured by proximity loggers that logged contacts between cows at a distance of 1.5 to 2 m, had a significant positive relationship to social grooming but not to agonistic interactions. However, Foris et al. (2021) showed that after regrouping, the proximity in the walking alley was more associated with agonistic interactions than allogrooming. Rocha et al. (2020) also found that the sociality of cows depends on where in the barn the contacts occur, suggesting that the barn area needs to be considered when evaluating proximity interactions. These findings support the choice of using an RTLS, with information on where in the barn the interactions occur. The quantity and comprehensiveness of the position data can give high certainty when associations between individuals could happen (Farine and Whitehead, 2015).

Agonistic interactions are usually shorter than affiliative interactions (Ben Meir et al., 2025; Val-Laillet et al., 2009) and can be subtle and hard to distinguish (Bouissou et al., 2001). Agonistic behaviours can be observed based on the response to an aggressive act as displacements or replacements at locations containing desirable resources, such as feed bunk or lying areas. Of the total amount of displacements measured by Val-Laillet et al. (2009), 88 % took place by the feed bunk and 12 % in the lying area, and in Foris et al. (2019), the highest displacement frequency was found in the feeding area.

Using the total duration of time in proximity would probably catch more affiliative relationships. However, capturing separate networks for affiliative and agonistic interactions has been stressed (Farine and Whitehead, 2015), and using directed networks. Foris et al. (2019) found that displacements were mostly reciprocal between the individuals, while allogrooming was more asymmetrical. Suggesting that specific cows had different roles in the agonistic and affiliative networks within the herd (Foris et al., 2019). However, in the study of Pinheiro Machado et al. (2020), cows on pasture were engaged more in both allogrooming and agonistic behaviour with their preferential mates than with other herd mates.

One of the original objectives of this project was to investigate whether the RTLS can be used to identify and separate affiliative and agonistic social interactions. With behavioural observations from video recordings, the plan was to connect the observed social interactions with movement patterns from the positioning system. However, the attempt was unsuccessful due to the UWB system's insufficient accuracy. The internal Kalman filter of the CowView system could also distort the actual trajectory of individuals due to a delay in the detected animal movements. Combining computer vision and image analyses with the RTLS could be a promising tool for collecting the direction of contact between individuals (Ren et al., 2021).

4.2.2 On-farm milking systems and the influence of social contacts on milk yield

Our findings that social contacts might influence milk production supports earlier studies. When affinity pairs were separated from each other, their day-to-day variation in milk yield increased, and the overall milk production in the pen was lower (Fadul-Pacheco et al., 2021).

In our analysis in Paper II, we only considered the nearest neighbours standing next to a cow during milking. However, social contact between these individuals is not independent. The behaviour of the nearest neighbour will, in turn, be influenced by their nearest neighbour and so on. Additionally, a cow might be influenced directly by the second neighbour if they can identify each other during milking, since cows can react to subtle interactions even from far distances (Bouissou et al., 2001). Therefore, including the distance between individuals in the milking parlour during milking as intensities of contacts in the model in Paper II might be preferable. Also, in our simulation study (Paper IV), we found that ignoring the intensities of contacts when estimating IGE led to less accurate EBVs. If we would like to extend the model in Paper II to an IGE model, this would motivate us to include intensities.

The advantage of using milking order data when estimating IGE is that information on the specific social interaction trait causing the effect of the social partners is unnecessary. Instead, information on who stands next to whom would be collected and fitted within a variance-component model. Cameras in the milking parlour could, on the other hand, give more information on what type of social interactions occur during milking and also an idea about how much the cows move during milking, which could be related to the potential stress of the cow during that milking event. Information on detached cups and “kick-off” events from the on-farm milking system could also be used as an indirect measure of stress. The effect in the milking parlour is also influenced by what happens in the free-stall barn before the milking event, and investigating if the social networks and the indirect effects in the milking parlour cohere with the social networks in the barn would be of interest.

Another aspect is whether these models could be applied to farms with AMS. In Scandinavia, about one-third of the milk comes from herds with AMS (Olsson, 2022). In the study of Fadul-Pacheco et al. (2021), data on cow movement through a sorting gate in AMS was used to identify affinity pairs, i.e., cows that repetitively move together in close succession. Marumo et al. (2022) and Ozella et al. (2023) used time between milking events in an AMS to assess the consistency of social associations (cows being milked close in time after each other). Both studies revealed the existence of consistent social associations between individuals. Consistent social associations did not influence the average daily milk yield (Marumo et al., 2022; Ozella et al., 2023) but were suggested to influence milk contents of fat and protein (Marumo et al., 2022). The authors stressed that one reason for this could be due to synchronized daily activities between cows that were not associated with the social preferences of specific individuals (Marumo et al., 2022). However, using the milking order from an AMS and implementing our model from Paper II, we could assess if there is an average individual indirect effect of the associated cows on a cow's daily milk yield also in herds with AMS. Ozella et al. (2023) stressed the importance of further research on social interactions in other areas of the barn and at different times. In Paper II, we also investigated the sum of the indirect effects on milk yield during milking for each observation. We assumed that indirect effects were random and additive, and our results show that the indirect effect was negated for some of the observations. Perhaps the hypothesis of a positive effect of milking close in time to social associates (Marumo et al., 2022; Ozella et al., 2023) was cancelled out by other individuals in the herd with a more negative effect on their herd mates.

Fielding et al. (2024) used proximity loggers in three different herds. They assessed, amongst others, the relationship between milk yield and SCC with the mean association strength (the time each cow spent in proximity with all other cows in the network divided by the number of potential contacts) and the mean top four contacts. No link between these social contacts was detected to either milk yield or SCC. However, only one week of data was observed, and two herds were housing the cows on pasture, while one herd had indoor housing. All cows were milked in a milking parlour, and in light of our results in Paper II, the social contacts during milking might interfere with the effect of the affiliative interactions the cow has in the barn or on the pasture. Combining the social network within the milking parlour with the different networks in the barn (feeding and resting area) would be interesting. Even if the milking order in the parlour is not random (Paper I), the cows might not be able to choose specific social partners to stand next to during milking. This might, however, look different in herds with AMS. Perhaps avoiding agonistic behaviour from specific individuals in a herd with AMS and free-traffic is easier. The baseline production level of a cow could also probably influence how much the milk yield deviates due to social interactions (Jezierski and Podłużny, 1984). There are fewer opportunities for further improvement in milk yield for cows that already perform close to their physiological potential. In contrast, they are more susceptible to drops in production due to negative social experiences, and detecting negative social interactions might be easier (Fielding et al., 2024).

We might find individual indirect effect estimates on a cow's milk yield by using positioning data with the total duration of time in proximity as intensities in an IGE model, accounting for all interactions a cow has in the feeding area. A high proportion of displacements are reported to occur in the feeding area (Foris et al., 2019; Val-Laillet et al., 2009). These interactions might show a more apparent indirect effect on milk yield than those in the resting area.

4.3 Including indirect genetic effects in dairy cow breeding programs

Including IGEs in breeding programs may contribute to more precise breeding and improve production and animal welfare in dairy farms in the future. This would in turn ensure a more sustainable dairy production and improve the overall image of the dairy industry.

For a potential trait to be considered for selection in a dairy breeding program, the measured trait needs to be clearly defined, economically important, heritable, and have sufficient genetic variation. The trait should also be consistently recorded at a low cost (Miglior et al., 2017; Shook, 1989). The selection of novel traits may be cost-effective when using genomic selection (Strandén et al., 2022). Nevertheless, collecting phenotypes and genotypes from a sufficiently large reference population at selected commercial herds, with well-representative individuals of the breeding population, will be needed to estimate accurate breeding values. Collecting large-scale data is becoming cheaper and more accessible due to rapid advancements in automated data recording technologies and low-cost information and communication technology (Klingström et al., 2024). Developing PLF tools with real-time algorithms also allows for collecting only relevant information and avoids collecting all data (Berckmans, 2017). The interest in behavioural genomics in the livestock sector is growing, and many novel traits are expected to be derived in the near future with the help of sensor data and PLF technologies. However, some key challenges, such as storage, ownership, and data sharing, still need to be overcome (Pacheco et al., 2025). The behaviour of animals will depend on how animals respond to different stimuli in their environment, and it is a complex biological process. When defining novel behaviour traits or indicator traits for genetic selection, factors such as housing and production systems and management practices will probably have an influence. Standardisation of phenotyping protocols and recording guidelines with integrating different data sources may be a solution (Pacheco et al., 2025), yet challenging.

4.3.1 Heritability of sociability and correlation of DGE and IGE

Behavioural traits have usually been estimated to have low-to-moderate heritability. In the study of Agha et al. (2022), heritability for social network traits in pigs ranged from 0.01 to 0.35. Estimates of the heritability of social traits in dairy cattle are, however, scarce. Berry and McCarthy (2012) suggested a partial genetic control of the milking order and estimated a heritability of 0.20. Aggressiveness against herd mates (binomial trait scored by farmers) had a heritability of 0.12 in Brown Swiss cows, and rank order (scored by farmers) had a heritability of 0.16 in the study of Kramer et al. (2013). In Paper III, a repeatability of around 35 % for contact rate in the feeding area was reported and around 45 % in the resting area (i.e., the proportion of variation in contact rate between individuals in relation to the total variance). The repeatability was similar in both farms A and B. How much of this variation was due to genetics was further explored in farm A, where the estimated heritability for contact rate was between 0 and 0.20 and was largest in the resting area (Rönnegård et al., 2022). However, the number of animals was limited, and the estimated heritability was not significant.

In Papers III and IV, we used simple networks with pairwise interaction data; looking into more detailed information about topological network parameters with social network analyses (SNA) will be helpful to increase our understanding of the complex social structure in dairy cattle. Also, investigating if different positions within the social network are heritable will be of value. Wice and Saltz (2023) investigated social networks in Drosophila melanogaster. They found that an individual's position within the network was both affected by their genotype and by the genotypes of their social group member.

In Paper II, we found a weak negative correlation of -0.26 between the direct and indirect effects on milk yield in one of the milking groups. If there is also a negative genetic correlation between the DGE and IGE of milk yield, there would be a risk of breeding for animals with a high genetic potential of producing milk but simultaneously having a negative effect on their herd mates. The variation seen between individuals in Figure 5 suggests that some cows could be high-producing cows that also positively affect the milk yield of their herd mates. This variation shows that there might be room for improvement, and the next step would be if there is a genetic component to these effects.

In the meta-analysis of Santostefano et al. (2024), which included 47 studies across 21 species, they estimated a correlation between DGE and IGE to be positive (0.26), although statistically no significant. Nonetheless, the direct and indirect genetic correlation appears not to follow any general systematic pattern. In laying hens, a strong negative correlation was found for survival time, suggesting that individuals that live longer are more likely to perform cannibalistic behaviour (Peeters et al., 2012). In contrast, the correlation for bite score in mink was strongly positive, indicating that individuals who bite more also receive more bites (Alemu et al., 2014). A strong negative correlation was found for growth in quail, meaning that birds that grew fast also reduced the growth of other individuals due to negative interactions (Muir, 2005).

4.3.2 Magnitude of IGE

Information on the magnitude of IGE in dairy cattle is still unknown. Studies on maternal indirect genetic effects have reported a mean magnitude of 10.8 % of the phenotypic variance (across 116 studies and 64 species) (Moore et al., 2019). Maternal indirect genetic effects are the effects the mother has on her offspring´s traits beyond the genetically inherited part of the trait. Maternal indirect genetic effects on milk yield traits were reported in the study of Schutz et al. (1992a) to account for between 4.1 and 10.5 % of the phenotypic variance. In the meta-analysis of Santostefano et al. (2024), the contribution of IGE variance of social partners to the phenotypic variance in a variety of traits and species was expected to be between 0-12 %, with a mean of 3 %. IGE in less harmful situations, such as interactions through the scent of individuals, has been found to explain 1-2 % of the phenotypic variance (Dewan et al., 2019).

In Paper II, we found that the indirect effect of the neighbour during milking on a cow's daily milk yield had a mean variance of 0.09 and 0.19 in the two milking groups (Table 2). We could speculate by calculating the proportion of these indirect effects in relation to the total variance of a cow’s milk yield. The mean number of milking neighbours, *n*, a cow, had per day was 3.6 in both groups. The mean total variance of a cow's daily milk yield could be calculated with the following equation (corresponding to Equation

6 for the simulated phenotypic variance in Paper IV): $\sigma_{Tot}^2 = \sigma_d^2 + n\sigma_s^2 + \sigma_e^2$, where σ_d^2 = variance of direct effects, σ_s^2 = variance of indirect effects, σ_e^2 = residual variance. We insert the values from Table 2 for G1: σ_{Tot} = 28.8 + (3.6*0.09) + 6.6 = 35.72 and G2: σ_{Tot} = 27.5 + (3.6*0.19) + 5.04 = 33.22. We can then calculate the proportion of indirect effect variance to the total variance for G1: $\frac{n\sigma_s^2}{\sigma_{Tot}} = \frac{(3.6*0.09)}{35.72}$ = 0.009, and G2: $\frac{n\sigma_s^2}{\sigma_{Tot}} = \frac{(3.6*0.19)}{33.22}$ = 0.02. These calculations would then suggest that 0.9 % of the variation in a cow's daily milk yield is explained by the social phenotype of the neighbours in G1 and 2 % in G2, which would be consistent with the results from the meta-analysis by Santostefano et al. (2024).

However, we did not estimate any genetic parameters in Paper II. Further, we only studied one farm for a short period, with differences in results between the groups. We also found that for regrouped cows, the indirect effect estimates changed, which could indicate that this effect does not belong to the specific individual but depends on the dynamics of the group. Therefore, no conclusion about the magnitude of potential IGE could be drawn at this point. Nonetheless, if we hypothesize that the variance explained by the social phenotype of the neighbours is 2 % of the total variance of a cow's daily milk yield, and compare this value with our calculated values for S_P^2 (the total social indirect variance, genetic + environmental, relative to the phenotypic variance) in Paper IV (Paper IV; Table 1). The 2% is smaller than the smallest size of S_P^2 (S_P^2 =0.03) we tried to simulate when the IGE explained 1.5 % of the phenotypic variance. Model convergence was more of a problem in our simulations when we simulated with an IGE of this size. Additionally, the standard errors of the variance component estimates were larger (Table 7), and the accuracy of the estimated breeding values for IGE was, in the basic scenario, low to moderate: 0.24 (0.08) for cows and 0.43 (0.14) for sires (Table 8).

A major challenge for accurate predictions is that the IGEs are often small, and more information is needed than for DGEs. Using genomic information instead of only pedigree might improve the predictions (Poulsen et al., 2020). In our simulations, we had 10000 cows with phenotypes distributed in 100 herds in the basic scenario, and we could estimate the variance components quite well, even for the small magnitude of IGE. However, since the S_P^2 = 2 % was smaller than the smallest size of S_P^2 we simulated, it is unclear if using genomic information may allow us to reduce the number of individuals and herds required. The number of herds and individuals required to detect IGE in dairy cows still needs to be investigated and will depend on the size of IGE and the genetic variance of the studied trait. We used a simple population structure in our simulation. In real life, familial relationships are more complex, and to separate preferential bonding between related animals and inheritance patterns, the modelled population structure might need more attention in the future. The variation in number of interactions between herds also needs to be explored.

4.3.3 Modelling

The variance-component model allows for estimating IGEs without information on the specific social interaction between the animals, but it requires knowledge of who is interacting with whom. The mechanisms and underlying biology of the IGE are mainly left unclear, and the total magnitude is instead quantified as a variance component (Bijma, 2014). In contrast, the trait-based models need information on all traits that functionally underlie the IGE on the trait of interest. A challenge with this model is that some of these underlying traits might be difficult to define or record. However, when these causative traits are known, using a trait-based model should be able to estimate the strength of the interaction more precisely, and the required sample size could be smaller than what is needed for estimating genetic parameters (Bijma, 2014).

In our simulation study in Paper IV, we stress the importance of including the direction of contact to achieve more accurate estimates of variance components and breeding values. In many social interaction events, individuals can play two roles, either as performers or receivers; the interactions are directional. Wang et al. (2023) presented a generalised linear mixed model (GLMM) with a binomial probability distribution for large-scale longitudinal data on social interactions between animals in large groups. They defined two latent traits: the tendency to engage as a performer or recipient in a social interaction. The probability that individual *i* performed an interaction towards individual *j* was fitted as a response variable, and BV for the performer effect of individual *i* and BV for the recipient effect of individual *j* were fitted as random effects. They suggested that if we can clearly distinguish the performer and the recipient, two distinct quantitative genetic traits should be defined.

More information is needed on the genetic basis of directional social interactions, and one of the key questions to answer before including IGE in breeding programs is how these correlate with other traits. One aspect of this is how IGE for milk yield is correlated with IGE for other traits, e.g., udder health and feed efficiency.

The accuracy of the estimated IGE from field data will depend on the accuracy of the social networks we collect. In terms of how we model and include IGE in breeding programs, the definition of a social contact between individuals will depend on which social network we collect data from (e.g., milking parlour or network in the barn). In the milking parlour network, social contact would be defined as standing next to each other during milking (yet with a possibility to include intensities of contact depending on the distance between individuals during milking). If we use social networks in the feeding area, we might need to evaluate separate breeding values for affiliative and agonistic interactions. Instead of using the total duration in proximity, we might need to quantify the number of specific interactions as intensities, for example. Furthermore, depending on how the networks (e.g., feeding area, resting area, pasture, milking parlour) correlate, we might need different breeding values for different networks and feasibly different breeding values depending on the milking system (milking parlour, AMS). More information is needed on which network would be the most representative for the specific studied trait, e.g., milk yield. Suppose the social contacts in the milking parlour interfere with the effect of interactions the cow has in the barn or on the pasture. In that case, the genetic evaluation must account for this correlation between networks. There is a long way to go until we can include breeding values for indirect genetic effects in the breeding evaluation for dairy cattle, but this thesis is a first step on how we could address this.

5. Final conclusions

- Cows are not interacting randomly, and there is variation in how much contact individuals have with their herd mates. Some cows had a higher contact rate, while others were more solitary.
- Characteristics such as parity and lactation stage seem to be associated with a cow's behaviour and number of contacts, as well as impairment of udder and claw health.
- Validation of different thresholds for social contacts is needed.
- There exists individual variation in the average indirect effect on the milk yield of the neighbour. An individual's neighbours' total effect during milking could contribute to or reduce by up to 2 kg of milk.
- A weak negative correlation was found between the direct and indirect effects on milk yield. The variation in indirect effects suggests there is room for improvement, and the next step would be to investigate if there is a genetic component to these effects.
- Regrouping of cows seems to disrupt the individual indirect effect, and longitudinal studies are needed to see how these effects evolve during a lactation period and over several lactations.
- Collecting the intensities of contacts is necessary to yield breeding values of IGE of good accuracy, even if there is some noise in the collected intensities.
- Ignoring the direction of contact when collecting data on social contacts could lead to an underestimation of the variance components of IGE and lower breeding value accuracies.
- Combining RTLS and camera vision might open up the possibility to include breeding values for indirect genetic effects in dairy breeding programs.

6. Future research

More scenarios are of interest as a follow-up to Paper IV. These include a more complex and realistic pedigree and population structure for dairy cattle breeding programs. The relationships between interacting animals could be included in the model, and their effects on the estimates could be assessed. In addition, the non-random social structure in dairy herds has yet to be studied. Some individuals interact more with some cows than others (Boyland et al., 2016; Marina et al., 2024b), and different individual attributes could influence the number of contacts (Paper III). Together with the included genotypic information, the sufficient number of herds and animals that would be needed to estimate IGE in dairy cattle for different magnitudes of IGE could be explored.

The Swedish University of Agricultural Sciences (SLU) infrastructure for dairy data collection, Gigacow (Klingström et al., 2022), offers the possibility to test the models and methods used in this thesis in other herds and on a larger scale. SLU Gigacow collects data from over 5,000 dairy cows in 17 Swedish commercial farms (Klingström, 2024). The data is gathered from the farm management system, with daily data updates, from farms with either a robot milking system or a milking parlour. For some animals, genotypes are also linked to the individual data and data extracted from the Swedish official milk recording scheme, such as pedigree and health events. All calves born on the farms are genotyped, increasing the number of genotyped animals even further (Klingström et al., 2022). Connected sensor technology and cameras will also be available in the future (Klingström, 2024). Replicating the model used in Paper II for the farms with a milking parlour would be possible, as well as extending the model to an IGE model by including the genotypes of the individuals. Longitudinal studies over several lactations are also possible. More information is also needed on how these milking parlour networks relate to the social environment and networks in the barn. This can be achieved by combining the milking parlour network analyses with social network analyses in different functional areas in the barn to compare the coherence of the networks.

Using information on milking events and cow traffic through sorting gates from the farms with an AMS, we could replicate the studies in Fadul-Pacheco et al. (2021), Marumo et al. (2022), and Ozella et al. (2023) with more farms and animals. In addition, using the milking order information from the AMS, one could also assess if the individuals milked before or after a cow could affect the cow's milk yield by using an IGE model. Some AMS herds also have an enclosed waiting area with sorting gates in front of the milking robot. In these waiting areas, there is a risk for agonistic interactions (Guzhva et al., 2016), and low-ranked cows have been shown to queue longer in front of the milking robot compared to higher-ranked cows (Lauwere et al., 1996). One could hypothesize that the individuals standing in the waiting area at the same time could have an impact on each other's milk yield. Cameras in the waiting area will give more detailed information on possible social interactions between the individuals (Guzhva et al., 2016).

There are 3D camera systems, such as the Cattle Feed Intake (CFIT) (Lassen et al., 2018), that identify the individual cow and measure both feed intake and body weight (Lassen et al., 2023). The system is installed in both commercial and research farms (Lassen et al., 2023; Stephansen et al., 2021), and it would be interesting to investigate if these cameras could also be used to record e.g. displacements at the feeding table or assess if cows stand at the feeding table in a random order or not.

Using camera vision and the RTLS for social networks in the barn could also be a way to collect the direction of social contact between individuals (Ren et al., 2021). Many cows spend a significant part of their life on pasture, and having sensors indoors and on pasture would be valuable and allow monitoring of all individuals continuously throughout the year.

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Popular science summary

At the moment, we know relatively little about the social lives of cows in loose housing systems. Yet, it is an important area from several perspectives. Cows are sociable animals that live together in large groups, and they interact with each other on a daily basis. These interactions help to maintain balance and form the social ranks within the herd. Still, they will also influence a cow's welfare, health, and production. Some interactions are positive, such as when cows perform social grooming on each other or spend their time close to specific chosen individuals. Such behaviours make the cows calmer and strengthen the social relationship between animals. Other interactions can be more negative and more stressful for a cow. Such as a cow being pushed away from the feeding table by a cow with a higher rank or blocked from entering the milking robot.

Dairy production systems must keep improving to ensure sustainable dairy production with good animal welfare, improved productivity, and low environmental impact to meet the future challenges of an increasing human population. Breeding programs are constantly evolving, and even more widespread breeding goals are expected to tackle these challenges in the future. The social interplay between individual cows also influences breeding opportunities. A cow's behaviour towards other individuals will partly depend on the genes it carries, and when a cow's behaviour impacts another individual's productivity, it is called "indirect genetic effect" (IGE). These effects could be built into the breeding model to breed for cows with high milk production while at the same time accounting for the effects of social interactions. This would improve both production and animal welfare. Studies on IGE in other animals living in small groups have been done, but we still need to know how to study these social effects in dairy cows that live in large groups. We need to understand how the cows interact, especially who is interacting with whom and be able to measure these interactions.

New advanced technology at the farms has made it possible to automatically follow the cows' movement around the barn and collect data on their behaviour on a large scale. With information from different sensors and the farm's milking system, we can learn more about the social interplay between cows and how it will influence the production.

This thesis aimed to study the behaviour and social interplay between dairy cows by using data from a positioning system installed at two commercial farms and data from the milking system at one of the farms. Furthermore, the thesis focused on what information we would need to collect in the future to include social effects in the breeding program.

The first study only used information from the milking system. It inspected the order cows entered the milking parlour when it was time for milking. The results showed that how the cows entered the milking parlour was not just a random order. Cows in their first lactation and cows in an early lactation stage entered the milking parlour early and were milked first. Older cows and cows in a later lactation stage entered the parlour later and were milked last.

The second study also collected data from the milking system. It used the information on milking order to see which cow was standing next to whom during milking and if the neighbouring cow during milking could affect a cow's daily milk yield. Cows seem to influence each other's milk yield during milking. Some cows had a more negative impact on their milking neighbour's milk yield, while others seemed to be more socially supportive. In one of the groups, cows with a high milk yield tended to impact their neighbour's milk yield negatively. Cows that were moved from one milking group to another went from having a positive effect on their neighbour's milk yield in the original group to a more negative impact on their neighbours in the new group.

The third study collected each cow's position within the barn every second with the help of the installed positioning system. With these positions, we could see how much time a cow spent close to other cows in the barn and which individuals the cow spent time with. If two cows were within 2.5 m of each other for more than a total of 10 min per day, they were said to have social contact. Where in the barn the interactions occur, whether during feeding or when they lay down to rest, was important for how many contacts the individuals had. Some cows spent much of their time close to other individuals in the herd, while others kept more to themselves. Individual features of a cow, such as her lactation number, lactation stage, reproductive status, udder health, and claw health, were linked with the number of contacts a cow had with the other herd mates.

In the last study, simulations were used to explore what kind of information that is important to collect if we want to include breeding values for social effects in the future. How large these social effects are and how well we collect information on social contacts will decide how accurate and reliable the breeding values will be. Information on how much and intense each pair of cows interacts with each other will be necessary for achieving accurate breeding values. Also, information on who is performing the behaviour between an interacting pair will be important.

In future research, it may be beneficial to use cameras to record specific social interactions between cows and integrate this information with data from the positioning system. This approach could provide more insight into whether the interactions are positive or negative and identify which cow is the performer and which is the receiver of the behaviour. Applying the method from study two across more farms and incorporating genetic information about the individuals will be essential. Additionally, exploring how social contacts in the barn influence milk production will enhance our understanding of the social dynamics between individuals and inform what data we need to gather moving forward.

Populärvetenskaplig sammanfattning

För närvarande vet vi relativt lite om kornas sociala liv i lösdriftssystem. Ändå är det ett viktigt område ur flera perspektiv. Kor är sociala djur som lever tillsammans i stora grupper och interagerar dagligen med varandra. Dessa interaktioner hjälper till att upprätthålla balansen och forma den sociala rangordningen inom flocken. Samtidigt påverkar de även kons välfärd, hälsa och produktion. Vissa interaktioner är positiva, till exempel när kor utför social putsning på varandra eller väljer att vistas nära specifika individer. Sådana beteenden har en lugnande effekt och stärker de sociala banden mellan djuren. Andra interaktioner kan vara mer negativa och stressande för kon, till exempel när en ko blir bortknuffad från foderbordet av en ko med högre rang eller hindras från att gå in i mjölkningsroboten.

Mjölkproduktionssystemen måste ständigt förbättras för att säkerställa en hållbar mjölkproduktion med god djurvälfärd, förbättrad produktivitet och låg miljöpåverkan för att möta framtidens utmaningar med en växande befolkning. Avelsprogram utvecklas kontinuerligt, och ännu bredare avelsmål förväntas i framtiden för att hantera dessa utmaningar. Den sociala interaktionen mellan individuella kor påverkar också avelsmöjligheterna. En kos beteende gentemot andra individer beror delvis på de gener den bär på, och när en kos beteende påverkar en annan individs produktivitet kallas det för en ”indirekt genetisk effekt” (IGE). Dessa effekter skulle kunna integreras i avelsmodeller, för att avla på kor med hög mjölkproduktion samtidigt som man tar hänsyn till effekterna av sociala interaktioner. Detta skulle kunna förbättra både produktionen och djurvälfärden. Studier av IGE har genomförts på andra djur som lever i små grupper, men vi behöver fortfarande lära oss hur man studerar dessa sociala effekter hos mjölkkor som lever i stora grupper. Vi behöver förstå hur korna interagerar, särskilt vilka individer som interagerar med varandra, och kunna mäta dessa interaktioner.

Ny avancerad teknik på gårdarna har gjort det möjligt att automatiskt följa kornas rörelser i ladugården och samla in beteendedata i stor skala. Med information från olika sensorer och gårdens mjölkningssystem kan vi lära oss mer om det sociala samspelet mellan kor och hur den påverkar produktionen.

Denna doktorsavhandling har studerat kornas beteende och sociala samspel med hjälp av data från ett positioneringssystem installerat på två kommersiella gårdar samt data från själva mjölkningssystemet på en av gårdarna. Vidare har avhandlingen fokuserat på att undersöka vilken typ av information vi behöver samla in för att kunna inkludera avelsvärden för sociala effekter i avelsprogrammen.

Den första studien använde data från mjölkningssystemet på gården och inspekterade i vilken ordning korna gick in till mjölkgropen när det var dags för mjölkning. Resultaten visade att hur korna gick in till mjölkning var inte någon slumpmässig ordning. Förstakalvare och kor i ett tidigt laktationsstadium gick in till mjölkgropen tidigt och blev mjölkade först. Äldre kor och kor i ett senare laktationsstadium gick in till mjölkgropen senare och var mjölkade sist av alla kor.

Den andra studien använde också data från mjölkningssystemet. Informationen om mjölkningsordningen användes för att se vem som stod bredvid vem under mjölkningen och om de individer som stod bredvid en ko under mjölkning kunde påverka hennes dagliga mjölkmängd. Kor verkade kunna påverka varandras mjölkmängd under mjölkningen. Vissa kor hade en mer negativ påverkan på deras mjölkningsgrannes mjölkmängd medan andra kor verkade agera mer som ett socialt stöd. I en av grupperna, hade högmjölkande kor en tendens att påverka andra kors mjölkmängd mer negativt. Kor som flyttades från den ena mjölkningsgruppen till den andra gick från att ha ett positivt inflytande på de andras mjölkmängd till att gå till att ha en mer negativ effekt på kornas mjölkmängd i den nya gruppen.

I den tredje studien registrerades varje kos position i ladugården varje sekund med hjälp av det installerade positioneringssystemet. Med dessa positioner kunde vi se hur mycket tid en ko tillbringade nära andra kor i ladugården och vilka individer hon vistades tillsammans med. Om två kor befann sig inom 2,5 meters avstånd från varandra under mer än totalt 10 minuter per dag ansågs de ha social kontakt. Var i ladugården interaktionerna ägde rum, till exempel vid foderbordet eller när de låg och vilade, påverkade hur många kontakter individerna hade. Vissa kor tillbringade mycket tid nära andra individer i flocken, medan andra höll sig mer för sig själva. Individuella egenskaper hos kon, såsom hennes laktationsnummer, laktationsstadium, reproduktionsstatus, juverhälsa och klövhälsa, var kopplat till hur många kontakter hon hade med de andra korna.

I den sista studien, användes simuleringar för att ta reda på vilken typ av information som är viktig att samla in ifall vi vill inkludera avelsvärden för sociala effekter i framtiden. Hur stora dessa effekter är och hur bra vi kan samla in information om sociala kontakter kommer avgöra hur pålitliga avelsvärdena kommer att vara. Hur mycket kontakt individer har, hur intensivt de interagerar och umgås, var nödvändig information att ha för att få mer exakta avelsvärden. Det visade sig också vara viktigt att ha information om vilken ko som utför beteendet i en interaktion.

I framtida studier, kan användning av kameror vara möjlig för att registrera specifika interaktioner mellan kor och på så sätt kombinera denna data med information från positioneringssystemet. Då kommer vi kunna få mer uppgifter om interaktionerna är positiva eller negativa och vilken ko som utför beteendet och vem som är mottagaren. Att upprepa försöket som utfördes i den andra studien med fler gårdar samt att inkludera individernas genetiska information kommer vara nödvändigt. Att studera hur de sociala kontakterna i ladugården påverkar mjölkproduktionen generellt kommer ge oss mer kunskap om det sociala samspelet mellan individer och vilken data vi behöver samla in i framtiden.

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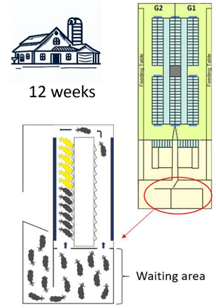
Short Communication
Health, Welfare, and Behavior

Associations of parity and lactation stage with the order cows enter the milking parlor

Ida Hansson[1]*† and Svenja Woudstra[2]*

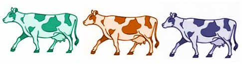
Graphical Abstract

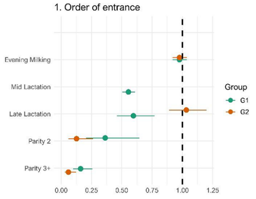
251 cows



12 weeks

Milking Order





Estimated odds ratios and 95% confidence intervals

Conclusions:
Cows do not mix homogeneously.
First-parity and early-lactation cows tend to enter the milking parlor earlier compared with the rest of the herd.

Importance for:
- ☐ the understanding of mastitis infection dynamics and the design of bio-economic disease transmission models
- ☐ future studies on how social contacts affect cows during milking

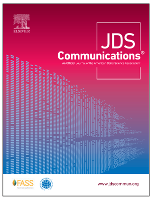
FORMAS

Summary

This study investigated the milking order to a milking parlor in 1 commercial farm with 251 cows over 12 weeks. Two analyses were conducted to determine whether parity and lactation stage were associated with the entrance order and a preference to enter as one of the first cows within one milking line. The milking order turned out to be fairly consistent, and cows in their first parity, as well as cows in early lactation, tended to enter the parlor early. The preference of entering a new milking line first gave similar results, but there were no large individual differences.

Highlights

- Cows do not mix homogeneously during milking.
- Parity 1 and early-lactation cows enter the milking parlor earlier than other cows.
- Cows tend to keep their rank within the milking order constant.
- The results should be considered when planning grouping strategies.



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The list of standard abbreviations for JDSC is available at adsa.org/jdsc-abbreviations-24. Nonstandard abbreviations are available in the Notes.

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Short Communication
Health, Welfare, and Behavior

Associations of parity and lactation stage with the order cows enter the milking parlor

Ida Hansson[1]*† and Svenja Woudstra[2]*

Abstract: To explore the effect of lactation stage and parity on the milking order of cows, we collected milking order data of all lactating cows (n = 251) over a period of 12 wk in one commercial Swedish dairy cow herd using a herringbone milking parlor. Cows were kept in 2 housing groups (G1 and G2) and moved from G1 to G2 at approximately mid lactation. Two analyses were conducted to investigate if lactation stage (early: 2–49 d in milk, mid: 50–179 d in milk, and late ≥180 d in milk) and parity are associated with the entrance order to the parlor or a preference of entering a new milking line first. In G1 and G2, cows in first parity entered the milking parlor earlier than cows in higher parities. In addition, in G1 cows in early lactation entered the milking parlor earlier than cows in later lactation. Similar effects were observed for the preference of entering a new milking line first. No effect of mid versus late lactation could be observed in either G1 or G2. The study also found that cows tend to keep their rank within the milking order constant. The results of the study indicate that cows of presumably lower hierarchy (first parity and early lactation) leave the waiting area earlier compared with other cows. This should be considered when planning grouping strategies and preventive measures against mastitis pathogen transmission.

The entrance order of individual cows into a milking parlor, the milking order, is not random, and some cows constantly tend to enter the milking parlor earlier than other cows (Grasso et al., 2007; Vargas-Bello-Pérez et al., 2020). In the study of Sauter-Louis et al. (2004), high-dominance cows tended to be milked first and low-dominance cows last. In other studies, cows with higher milk yield and lower SCC showed a tendency to enter the milking parlor early (Rathore, 1982; Berry and McCarthy, 2012). However, only weak correlations have been reported, and other studies did not find the same correlations for milk yield and social rank (Vargas-Bello-Pérez et al., 2020) as well as SCC (Dias et al., 2019).

Milking management is one important factor that can influence the udder health situation in dairy cow herds, and mastitis caused by IMI is one of the costliest health disorders in dairy farms (Ruegg, 2017). Pathogens causing mastitis can have either a host-related, contagious transmission pathway, where the udder tissue of infected cows forms the major reservoir, or be mainly transmitted from extra-mammary sites (e.g., feces of cows). Pathogens that show a contagious transmission pathway often cause strong inflammatory reactions measured as SCC, long-lasting infections, and milk yield losses (Heikkilä et al., 2018; Woudstra et al., 2023). Until now, however, it remains unclear if cow characteristics that are associated with the probability of being infected with mastitis pathogens (i.e., parity and lactation stage; Mekonnen et al., 2017; Taponen et al., 2017) also influence the position in the milking order.

Beyond pathogen transmission, understanding cow characteristics that influence the milking order is also essential from an animal behavior and welfare perspective. Sufficient lying time has been considered important for cow welfare (Tucker et al., 2021). Short lying time has, for example, been associated with lameness (Galindo and Broom, 2000), and cows entering the milking parlor late have also been seen to have an increased risk of lameness (Sauter-Louis et al., 2004). Cows with a long waiting time in the waiting area will also be away from feed for longer, affecting milk production (Dias et al., 2019). In addition, long intervals between milkings also harm milk yield (Stelwagen, 2001), with even only occasionally prolonged intervals influencing the yield (Ayadi et al., 2003). Parity and lactation stage have shown to affect the number of social contacts between dairy cows (Hansson et al., 2023). To be able to further study how social contacts could potentially affect the cows during milking in a parlor, the milking order needs to be investigated more closely.

Previous research has shown that the entrance of cows to the milking parlor does not happen randomly. However, it has not been extensively studied if a cow's parity or lactation stage influences her rank in the milking order. Therefore, the present study aimed to investigate if the order in which cows enter the milking parlor is associated with their lactation stage or parity. In addition, we wanted to explore over a period of 12 wk the cow level variability of positions within the milking order.

Data were collected from one commercial dairy farm in Sweden that housed around 210 lactating dairy cows in a noninsulated freestall barn. The cows were divided into 2 housing groups, G1 and G2, where cows in G1 were primarily in early to mid lactation and cows in G2 were in mid to late lactation. Cows were routinely regrouped from G1 to G2 at approximately 170 DIM when confirmed pregnant or designated for slaughter. The lactating cows were milked in a 2 × 12 unit herringbone milking parlor (2 × 12 GEA Euro class 800 with Dematron 75, GEA Farm Technologies, Bönen, Germany) twice daily (start of milking around 0430 and 1630 h). The milking sessions lasted around 1.5 h for each group and G1 was always milked first. Before milking, the cows were

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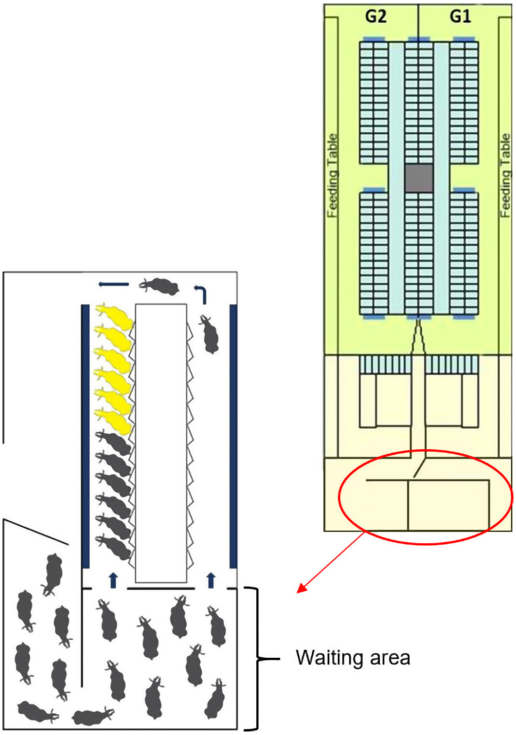

Figure 1. A schematic map of the freestall barn and the milking parlor used within the study. The barn holds 2 milking groups, G1 and G2, where the green area in the barn map represents the feeding tables and allocated alleys, and the blue area represents the cubicles and the alleys between the cubicles. The area shown in beige is a separate area with calving boxes, drying off area, and the milking parlor in the bottom of the map. The milking parlor is a 2 × 12 unit herringbone parlor and has a waiting area in front of the 2 entrances of the parlor. The yellow cows in the milking parlor represent the first 6 positions within the left side of the parlor. The figure was partly adapted from Hansson et al. (2023).

gathered in the waiting area in front of the parlor, where they could move freely and alter their position to the entrance of the milking parlor (Figure 1). The cows enter the parlor in a single row to one side of the parlor at a time and are automatically identified at the entrance to the milking parlor. After milking, the cows exit in a single row. Each cow's position within the parlor and the timestamp when the milking cluster detached were transferred from the milking equipment to the farm computer.

Data from 165 milking sessions were collected between August 11, 2020, and November 01, 2020. Records from 251 cows (148 cows in G1 and 154 cows in G2, with 52 of these cows present in both groups during the study period) were collected. Data from one complete milking session was missing due to late data transfer (from the farmer to the researchers). For the 165 milking events we collected, the proportion of missing records was 1%, and the mean proportion of missing records per cow was also 1%. The total number of observations used in the analyses was 33,237. One reason for missing records was that the milking records of cows that had entered the gradual drying-off process were not included in the files from the farm for some of the weeks. In Sweden, such a gradual drying-off process is common. In the study herd, the gradual drying-off process started on Tuesdays; the cows were moved to a separate area within the barn, and milked subsequently only Wednesday morning, Friday morning, and Monday morning. Then the dried-off cows were moved to another building. They were moved to the calving boxes before calving and then introduced to the milking groups 24 to 48 h after calving. The milking order was determined based on when a cow finished milking and its position within the parlor. All cows at each milking session and within each group were numbered from first to nth order depending on the number of lactating cows daily and the milking spot number in the parlor.

The milking order was divided into 4 groups for each housing group: first, second, third, and last. The first group represents the first batch of cows milked, including both sides of the parlor (positions 1–12 on the right-hand side and 13–24 on the left-hand side), the second group was the second batch of cows (positions renamed as position 25–48 including both sides), the third as the third batch of cows (positions 49–72), and the last group representing positions >72. Thus, there were milking groups 1 to 4 for G1 and again 1 to 4 for G2, reflecting that cows could choose their milking order freely within each housing group, but could not switch freely between housing groups. The milking event was classified as either morning milking (1) or evening milking (2). The cows' positions within the parlor during milking were also categorized into the first 6 positions (1) or the last 6 positions (2) within each side and each milking batch (see Figure 1). In the analysis, records for cows during the drying-off process and less than 2 d after calving were then removed because the cows stayed in a separate area during this time.

The number of records per cow ranged between 14 and 165, with a mean of 148 and a median of 164 records. Parity ranged between 1 to 6 and 1 to 7 in G1 and G2, respectively, where cows were classified as parity 1 (41 cows in G1 and 44 in G2), parity 2 (42 in G1 and 51 in G2), or parity 3+ (65 in G1 and 60 in G2). Each cow was categorized into one of 3 lactation stages depending on the current DIM: early (2–49 DIM), mid (50–179 DIM), or late (≥180 DIM) lactation. During the study period, 83, 112, and 29 cows in early, mid, or late lactation, respectively, were for a minimum of 10 milkings in G1. Accordingly, 7, 49, and 130 cows in early, mid, or late lactation, respectively, were in G2 for at least 10 milkings. Since the 7 cows in early lactation in G2 were exceptional cases and most of them in higher parities (e.g., cows with specific problems designated for slaughter from start of lactation on), they were removed from the first analysis when the model was fitted group-wise.

The statistical analyses were performed with the statistical software R version 4.0.3 (R Core Team, 2020). Two different analyses were conducted to investigate if lactation stage and parity are associated with the entrance order to the parlor and the variability of position within the milking order:

First, an ordinal logistic regression model with milking order group (first, second, third, or last) as response variable and parity, lactation stage, and milking event as fixed effects and cow ID as random effect was used to investigate associations of cow characteristics with the overall entrance order. One model per milking group (G1 and G2) was fitted using the clmm function in the ordinal package (Christensen, 2022). The proportional odds assumption was graphically assessed according to the recommendations from Harrell (2001) and concluded to hold. Second, a logistic regression model with the first 6 positions as the response variable and parity, lactation stage, group, and milking event as fixed effects, and cow ID as a random effect was used to investigate if specific cow characteristics are associated with a preference to enter as one of the first cows within each milking line. One model, including records from both milking groups, was fitted. The logistic regression model was analyzed with the glmer function in the lme4 package (Bates et al., 2015). The intraclass correlation (**ICC**) was estimated for each model as the proportion of the variance of the individual random effects in relation to the total variance (i.e., the sum of the residual variance and the variance of individual random effects). The residual variance is assumed to be $\pi 2/3$ for all 3 models (Nakagawa and Schielzeth, 2010).

In the first model, we found an effect of parity on the order of entrance to the milking parlor in G1 and G2, and an effect of lactation stage in G1 (Figure 2), where it seems that first-parity cows and cows in early lactation tend to be first in the milking order. In G1, cows in parity 2 had 64% lower odds of being in higher rather than lower categories of the outcome compared with cows in parity 1 (odds ratio [**OR**]: 0.36, 95% CI: 0.20–0.65), and cows in parity 3+ had 84% lower odds of being in higher rather than lower categories of the outcome compared with cows in parity 1 (OR [CI]: 0.16 [0.10–0.26]). In G2, cows in parity 2 had 87% lower odds of being in higher rather than lower categories of the outcome compared with cows in parity 1 (OR [CI]: 0.13 [0.06–0.26]), and cows in parity 3+ had 94% lower odds of being in higher rather than lower categories of the outcome compared with cows in parity 1 (OR [CI]: 0.06 [0.03–0.12]). These results show that cows in parity 1 have higher odds of entering the milking parlor early than cows in higher parities. However, there was no difference in entrance order between cows in parity 2 and parity 3+, indicating that the behavior of cows in these categories is more similar.

Berry and McCarthy (2012) found a nonlinear relationship between milking order and parity, where the youngest and oldest parity cows entered the parlor last. They argued that the younger cows might be more hesitant to the milking system and probably have a lower social rank, which has also been seen as correlated with milking order (Sauter-Louis et al., 2004). However, Melin et al. (2006) concluded that cows most likely find it rewarding to be milked and that cows of low social rank within an automatic milking system monitored every chance to advance in the milking queue by staying close to the milking unit. In the study herd, we also observed that cows of higher parity used different cubicle areas than first parity cows, which preferred areas with less cow traffic (Churakov et al., 2021). The waiting area in front of milking parlors is usually full at the beginning of milking. First-parity cows, with often lower rank in the hierarchy, might therefore prefer to enter the milking parlor early and leave the crowded waiting area. Furthermore, it has been observed that cows with similar attributes tend to stay together and create preferential bonds (Boyland et al., 2016; Marina et al., 2023), which might also explain the cows' division by parity within the milking order.

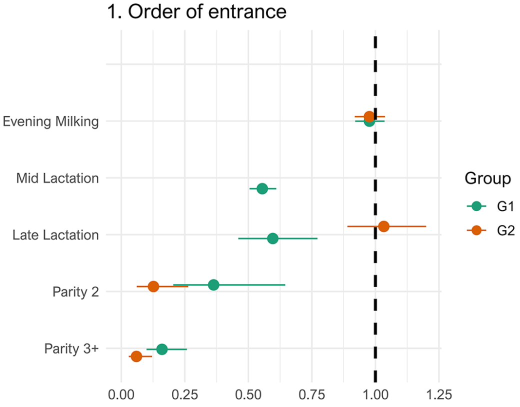

Figure 2. Estimated odds ratios and 95% CI of the entrance order model estimated with an ordinal logistic regression model (large dots = estimated odds ratios; error bars = range of 95% CI; G1 = group 1, G2 = group 2).

In G1, cows in mid lactation had 45% lower odds of being in higher rather than lower categories of the outcome compared with cows in early lactation (OR [CI]: 0.55 [0.50–0.61]), and cows in late lactation had 40% lower odds of being in higher rather than lower categories of the outcome compared with cows in early lactation (OR [CI]: 0.60 [0.46–0.77]). These results show that cows in early lactation have higher odds of entering the milking parlor early than in mid and late lactation. There were no differences between the entrance order of mid- and late-lactation cows in G1. This matches the results of G2, where we did not include any early-lactation cows in the analysis and did not see any effect of the lactation stage when comparing mid- and late-lactation cows. In G1, 61 cows went from early to mid lactation during the study period. To capture the behavior of cows concerning the entrance order when they transitioned from one lactation stage to another, we ran an additional model for G1, where we treated the lactation stage as a continuous trait. The model showed same results and similar effect sizes for all the coefficients as the previous model, and the estimated odds ratio for DIM was OR [CI]: 0.992 [0.990–0.993], which means that with a 1 unit increase in DIM, the odds of being in higher rather than lower categories of the outcome decreases by 0.8%.

That early-lactation cows show a different behavior than cows in later lactation could perhaps be related to the time the cows have spent in the group and their familiarity with the other cows, which seem to affect the number of contacts the cows have with each other (Gygax et al., 2010; Hansson et al., 2023). This might explain why early-lactation cows seem to have similar behavior as subordinate first-parity cows. The ICC was 0.48 in G1 and 0.49 in G2, which shows that there is variation between cows regarding the order in which the cows enter the milking parlor and indicates that the milking order is somewhat consistent.

In the second model, we saw a parity and lactation stage effect on the probability of being milked in the first 6 positions or the last 6 positions within one milking batch (Figure 3). Cows in parity 2

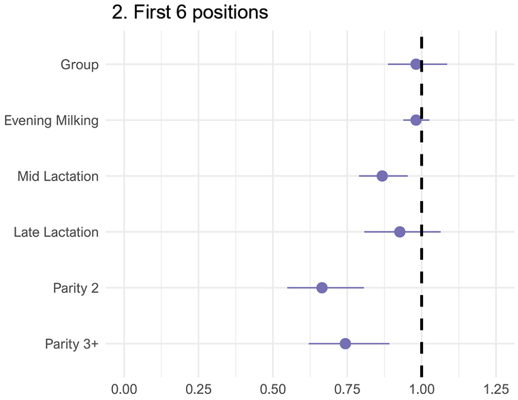

Figure 3. Estimated odds ratios and 95% CI of the first 6 positions model estimated with logistic regression (large dots = estimated odds ratios; error bars = range of 95% CI).

had 34% lower odds of being in the first 6 positions than those in parity 1 (OR [CI]: 0.66 [0.55–0.81]). Cows in parity 3+ had 26% lower odds of being in the first 6 positions than cows in parity 1 (OR [CI]: 0.74 [0.62–0.90]). There was no difference between the cows in parity 2 and parity 3+. Cows in mid lactation had 13% lower odds of being in the first 6 positions than early-lactation cows (OR [CI]: 0.87 [0.79–0.95]). There was, however, no difference between cows in early and late lactation or between cows in mid and late lactation. These results align with the results from our first model. However, the effects are of lower magnitude, and the ICC was only 0.09, indicating no consistency for individual cows to be in the first or last 6 positions. In both models we considered the milking event time (morning vs. evening) to control for an effect of the time of milking. We did not expect any effect, and this was confirmed for models 1 and 2. The data from the present study show that in the study herd, cow characteristics were associated with their order in the milking parlor. Cows in later lactation and higher parities tended to be later in the milking order and it is known that these animals are also those more likely to be infected with mastitis pathogens (Mekonnen et al., 2017; Taponen et al., 2017). That older cows and those later in lactation seem to be later in the milking order might contribute to their higher probability of having IMI. However, several mastitis-causing pathogens cause long-lasting infections and the higher probability of being infected at later stages of lactation might also simply be the result of low spontaneous cure rates, at least for some pathogens (Woudstra et al., 2023).

One of the measures regularly named in the literature for the prevention of the transmission of mastitis pathogens is the implementation of a milking order based on the cow's infection status (sometimes deducted from SCC measurements; Nielsen and Emanuelson, 2013). However, for this the milking herd needs to be split into separate housing groups, which is often difficult to implement, especially in smaller herds. Additionally, a study by Hansson et al. (2011) has shown only a limited economic effect of this measure. If cows in their first lactation and those that are still early in lactation anyhow show a tendency of coming first into the milking parlor, this might contribute to the limited effect of implementing a milking order. Another important reason, however, is probably that it is not possible to correctly identify all infected animals and that spread of contagious pathogens can still occur in a group of presumably uninfected cows. Knowing that cows do not mix homogeneously during milking with regard to parity and lactation stage contributes to a further understanding of mastitis infection dynamics and needs to be taken into account when designing bio-economic disease transmission models like those of Gussmann et al. (2018). Such bio-economic models could also be used in the future to quantify the impact of the here observed effects of parity and lactation stage compared with assuming a random milking order. However, the present study was conducted in one herd only, and similar studies need to be repeated in a larger number of herds to confirm our findings and investigate further the management factors influencing the order in which cows with certain characteristics enter the milking parlor.

In conclusion, the present study indicates that cows do not enter the milking parlor in a random order and that first-parity cows and those earlier in lactation tend to enter the milking parlor earlier compared with the rest of the herd. These results indicate that early-lactation and first-parity cows have a higher motivation to leave the waiting area early. In addition, the results of the present study should be considered when simulating the effect of preventive measures against the transmission of contagious mastitis pathogens or planning these for dairy farms.

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Notes

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The authors declare that according to the Swedish Animal Welfare Act, no ethical approval is needed for this type of study.

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Nonstandard abbreviations used: G1 = housing group 1; G2 = housing group 2; ICC = intraclass correlation; OR = odds ratio.

III

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Cow characteristics associated with the variation in number of contacts between dairy cows

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ABSTRACT

In modern freestall barns where large groups of cows are housed together, the behavior displayed by herd mates can influence the welfare and production of other individuals. Therefore, understanding social interactions in groups of dairy cows is important to enhance herd management and optimize the outcomes of both animal health and welfare in the future. Many factors can affect the number of social contacts in a group. This study aimed to identify which characteristics of a cow are associated with the number of contacts it has with other group members in 2 different functional areas (feeding and resting area) to increase our understanding of the social behavior of dairy cows. Inside 2 herds housed in freestall barns with around 200 lactating cows each, cow positions were recorded with an ultra-wideband real-time location system collecting all cows' positions every second over 2 wk. Using the positioning data of the cows, we quantified the number of contacts between them, assuming that cows spending time in proximity to one another (within a distance of 2.5 m for at least 10 min per day) were interacting socially. We documented in which barn areas these interactions occurred and used linear mixed models to investigate if lactation stage, parity, breed, pregnancy status, estrus, udder health, and claw health affect the number of contacts. We found variation in the number of contacts a cow had between individuals in both functional areas. Cows in later lactation had more contacts in the feeding area than cows in early lactation. Furthermore, in one herd, higher parity cows had fewer contacts in the feeding area than first parity cows, and in the other herd, cows in third parity or higher had more contacts in the resting area. This study indicates that cow characteristics such as parity and days in milk are associated with the number of contacts a cow has daily to its herd mates and provides useful information for further research on social interactions of dairy cows.

Key words: dairy cow, real-time location system, social interactions

INTRODUCTION

Social interactions in dairy cattle play an important role in their everyday activities and could be crucial to the understanding of optimal management, welfare, and disease transmission. Domesticated cattle are gregarious and live in herds, based on dominance hierarchies, where they form relationships based on social interactions between individuals (Bouissou et al., 2001). These interactions can be categorized into agonistic or affiliative interactions having either negative or positive effects on individuals. Management procedures such as mixing of groups, introducing new individuals, large group sizes, and insufficient space allowance can cause social tension in the herd and increase the agonistic behaviors (Talebi et al., 2014; Foris et al., 2021; Scheurwater et al., 2021). Social tension can cause stress, which may not only affect animal welfare but also production, as stressed cows tend to produce less milk (Hedlund and Løvlie, 2015). Furthermore, the contact intensity between individuals is also a major factor for the transmission of diseases (Chen and Lanzas, 2016). Positive social behavior, in contrast, defined as either spatial proximity between certain individuals or allogrooming, is believed to reduce aggression, have a calming effect, and strengthen relationships between

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individuals (Boissy et al., 2007), hence potentially increasing both animal welfare and milk production.

Cows differ in their tendency to stay close to other individuals (Boyland et al., 2016; Rocha et al., 2020) and they may form strong bonds with other cows, especially when sharing long-term experiences (Gutmann et al., 2015; de Freslon et al., 2020). Cows also seem to have preferential assortment to individuals with similar attributes, such as parity, breed, milk production, or gregariousness (Boyland et al., 2016; Churakov et al., 2021). Other studies have shown that cows can have preferred feeding partners, which has mostly been seen in pairs of primiparous cows (Val-Laillet et al., 2009).

There are many factors that can affect the number of social interactions in a group. Different functional areas of the housing system are, for example, important to consider because the social network patterns can alter between the walking alley, feeding, and lying areas (Gygax et al., 2010; Foris et al., 2021). Cows more familiar with each other have spent longer time together and formed stronger social bonds compared with cows less familiar with each other (Gutmann et al., 2015). In addition, more active cows may have more opportunities to interact with other individuals in the group than less active cows. For example, the activity increases significantly on the day of estrus for a cow (Schofield et al., 1991). Veissier et al. (2017) also found that cows in early or late lactation and younger cows tend to be more active. However, Chopra et al. (2020) did not find any correlation between parity and spatial proximity to specific individuals. Sickness and injuries may cause alterations in a cow's behavior and activity levels, and the individual may potentially decrease interactions with other group members (Fogsgaard et al., 2015; Sepúlveda-Varas et al., 2016; Weigele et al., 2018).

Automated bio-logging technology has opened up a myriad of possibilities to study social interaction between animals in both wild environments (Smith and Pinter-Wollman, 2021), and conventional production systems (Foris et al., 2019; Rocha et al., 2020). This includes a systematic sampling or collecting of individual animals' behavior without affecting the observed animals as much as traditional behavioral studies can (Altmann, 1974). Using a real-time locating system (**RTLS**) we can get detailed information about spatiotemporal co-occurrences and investigate which cows tend to spend more time close to other cows. A major benefit of studying a production animal is the fine-scale individual information retrieved on for example age, pregnancy status, or time at the feeding table. Combining individual information with positioning data, we can try to explain the differences in proximity using individual characteristics. Investigating social interactions of cows opens up the possibility to improve animal welfare and production by improving the social environment of individual cows.

Increased understanding of factors driving social interaction can help disentangle the most effective social conditions for dairy cattle and optimize the size and composition of dairy cow groups. The aim of this study was, therefore, to identify which characteristics of a cow were associated with the number of contacts it has with other group members in 2 different functional areas (feeding and resting area) to increase our understanding of the social behavior of dairy cows. Using positioning data of cows from 2 indoor dairy farms, we (1) quantified and explored the variation of the number of contacts between cows in 2 separate areas in the barn (feeding and resting) and (2) investigated if lactation stage, parity, breed, pregnancy status, estrus, udder health, and claw health affected the number of contacts.

MATERIALS AND METHODS

All data were collected in accordance with the Swedish Animal Welfare Act. No ethical approval was needed for this type of study; thus the research was not submitted to an Animal Ethics Committee.

Animals and Housing

Data were collected from 2 commercial dairy farms, one in Sweden (farm A) and one in Netherlands (farm B). Farm A housed around 210 lactating dairy cows (Holstein Friesian, Swedish Red, and crossbreds) in a noninsulated freestall barn. The barn was divided into 2 milking groups, G1 and G2, each with a pen area of 14 m × 56 m and 102 and 103 cubicles, respectively, with rubber mattresses and sawdust as bedding material (Figure 1). Approximately 2 wk before the start of the study period a sample of 22 cubicles all over the barn was measured in farm A. These 22 cubicles were chosen as a representative sample of all cubicles because all cubicles in the farm could not be measured due to time limitations. The width was on median 120.5 cm (range: 108–126).

Group 1 consisted predominantly of newly calved cows and cows with high milk yield, and G2 contained mainly pregnant cows or cows decided for slaughter. Cows were routinely moved, usually at approximately 170 DIM, from G1 to G2 when confirmed pregnant, or at the decision of slaughter. However, the group compositions were also dependent on the current sizes of the 2 groups. The dry cows were housed in a separate group in another building.

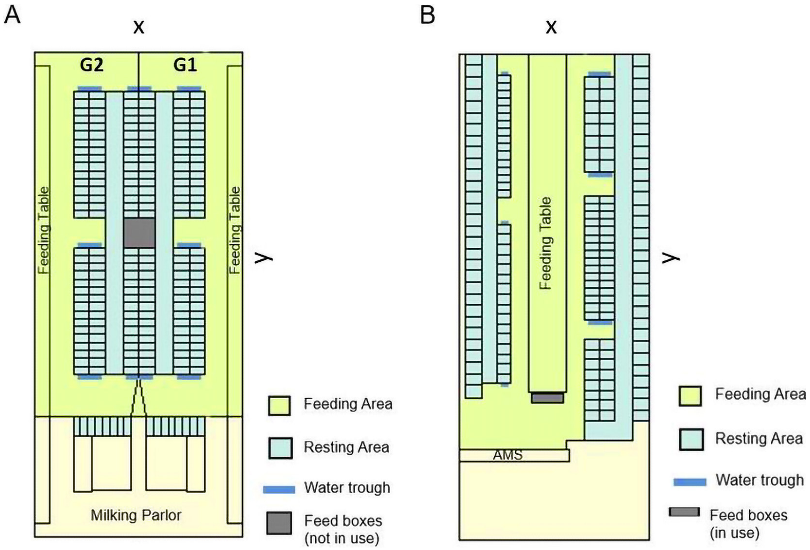

Figure 1. Schematic map of the 2 freestall barns used in the study, where y and x represent the direction of the y- and x-axes. (A) Farm A holds 2 milking groups, G1 and G2, where the cubicles are located in the middle of the barn and the feeding tables along the sides. The area shown in beige is out of reach for the cows in the milking group, except for transport between the pen area and the milking parlor. (B) Farm B contains one big milking group, where the feeding table is located in the middle of the barn and the cubicles along the sides. The area shown in beige is out of reach for the cows in the milking group except for the automatic milking system (AMS).

The cows were fed a TMR 12 times a day, and had approximately 0.57 m of feed space per cow in G1 and 0.62 m in G2. The cows were milked twice a day (around 0430 h and 1630 h) in a milking parlor from GEA (2 × 12 GEA Euro class 800 with Dematron 75, GEA Farm Technologies), and each group spent around 1.5 h in the milking parlor during each milking event.

Farm B housed around 210 lactating Holstein Friesian cows in a noninsulated freestall barn, consisting of one milking group with the feeding table in the middle of the barn (Figure 1). The pen area was 30 m × 58 m. The cows in the milking group had access to 228 deep-litter cubicles (median width 112 cm, range 110–125 cm) with compost made of the cow's manure as bedding material. The dry cows were housed in a separated group in another building. The cows were milked at least twice a day in 2 double-automatic milking machines (Mlone, 5-box, GEA Farm Technologies) and were fed a partial mixed ration ad libitum, delivered once a day, with additional concentrate in the milking robots and feeding stations according to milk production. The cows had approximately 0.51 m of feed space per cow at the feeding table. Both farms had water troughs evenly distributed in the whole barn, placed at the end of the cubicle rows.

Positioning Data

Data Collection. In both farms, each lactating cow was equipped with a tag mounted on the top of the collar connected to an RTLS (CowView, GEA Farm Technologies) automatically collecting individual positioning data of the cows with a 1-s fix rate. The tags sent ultra-wideband signals, which were received by anchors located throughout the barns' ceiling. Cow positions were estimated through triangulation and preprocessed through a chain of built-in data-processing modules in the CowView system (Sloth and Frederiksen, 2019), with a reported accuracy of 50 cm (Meunier et al., 2018). Positioning data files were downloaded directly from GEA's server on each farm from October 16 to 29, 2020. The files (referred to as FA data files in the CowView system) contained a tag-ID, timestamp, and the (x, y) coordinates. We validated the accuracy in the 2 farms by computing the mean error distance for the fixed performance tags (13 tags in farm A, 21 tags in farm B), with a mean error distance of 78 and 54 cm in farms A and B, respectively. The variation between days for the same tag was negligible, whereas the standard deviation (SD) between tags was 88 cm in farm A and 35 cm in farm B. Following the recommendation by

Melzer et al. (2021), we also inspected heatmaps of the cows' positions during entire days and did not observe any apparent shifts in the data given the blueprints of the farms (Supplemental Material S1; https://pub.epsilon.slu.se/29185/; Hansson et al., 2022).

Data Processing. After downloading the position data from the GEA system, we used MATLAB (MATLAB, 2020) to interpolate missing positions and calculate the total duration of proximity interactions. Farm A had on average 33.8% missing positions over the 14 d with a SD of 9.3% between individuals and days. The average for farm B was 27.1% (SD 9.3%). Only tags mounted on cows were considered, whereby tags on cows with more than 70% of missing data during a 24 h period were also excluded [9 tags in farm A (6 in G1 and 2 in G2) and 1 tag in farm B] following Ren et al. (2021). Interpolation was performed using the Modified Akima Interpolation (Akima, 1970; Fried and Zietz, 1973) following the recommendation by Ren et al. (2022). Missing data at the beginning and the end of a day were treated separately. If a tag was missing data at the beginning of a day, the first nonmissing position was filled in for that period. Similarly, if a tag was missing data at the end of the day, the previous nonmissing position was filled in. Furthermore, if an interpolated position was out of range (i.e., outside the barn given the coordinates of the barn; Figure 1), it was positioned at the border of the barn. Farm A did not have enough tag collars for both the lactating and dry cows and therefore moved the tag collar from a dried-off cow to a newly calved cow. The tag-ID was linked to the correct cow using start and end date for a tag to the cow's calving and dry-off date, respectively.

Definition of the Response Variable: Contact Rate

This study focuses on the number of contacts a cow had with other group members in 2 different functional areas, the feeding area and resting area, in both farms (Figure 1), where the feeding area also includes space where the cows can walk and drink. The time spent in the 2 areas needs to be accounted for, as there might be an individual variation of time budgets. Therefore, a contact rate was defined, which represents the instantaneous number of individuals within proximity of a cow at any time during the day. Positioning data were used to find individuals within proximity of a cow, as detailed below.

A distance-radius threshold of 2.5 m defined a contact between dyads of cows (Rocha et al., 2020). The total duration of contacts $t_{contact,i,k}$ for each cow i and day k was calculated separately for the 2 functional areas, feeding and resting. The duration of contacts for each cow and day was obtained by summing contact durations with all other cows present in each group. The time spent in each area $t_{area,i,k}$ was also calculated. The fitted response variable in our analyses was the contact rate defined as $t_{contact,i,k}/t_{area,i,k}$. A cow that, for example, spends half of the time in the resting area with one conspecific and the other half of the time with another will have a contact rate of 1. Another cow that spends half of the time in the resting area with 2 conspecifics and the rest of the time alone will also have a contact rate of 1, reflecting the expected number of conspecifics within proximity at any point in time she is in the resting area.

The total duration of contacts between 2 individuals was required to be at least 10 min per day to be included in the analysis (Rocha et al., 2020). This threshold was applied to eliminate brief interactions due to cows just passing by each other.

Cow Characteristics

Data Collection. For farm A, individual attribute data such as parity, calving date, and tag-ID were provided by the farm and information about breed, insemination records, pregnancy diagnoses, and claw-trimming records was extracted from the Swedish official milk recording scheme. Quarter foremilk samples for analysis of SCC were collected on October 8 and October 22 from all lactating cows during afternoon milking. After disinfection of the teat ends with ethanol (70%), the first 3 milk streams were discarded. Then samples were collected in sterile 13-mL tubes. The SCC was measured by flow cytometry (SomaScope Smart, Delta Instruments B.V.). For farm B, lists with individual attribute data on parity, calving date, insemination date, pregnancy diagnoses, and tag-ID were provided from the farm. Summary of data collected of cows included in the analysis at each farm and group for each characteristic is presented in Table 1.

Data Processing. The parity of the cows in farm A varied between 1 to 6 and 1 to 7 in G1 and G2, respectively, and between 1 to 8 in farm B. The cows were categorized into 3 groups (parity 1, parity 2, and parity 3+). The average DIM during the study period was calculated and each cow was assigned to 1 of 3 lactation stages; early (7–49 DIM), mid (50–179 DIM), or late (≥180 DIM) lactation. Cows with breed proportion of the dominant breed >75% were defined as purebred, otherwise they were defined as crossbreds.

The pregnancy status of a cow was defined with the last insemination date and a later confirmed pregnancy found in the pregnancy status records. Cows confirmed pregnant were assumed to be pregnant one day after the successful insemination and then categorized as pregnant; otherwise, they were categorized as open.

Table 1. Summary of data collected for cows included in the analysis at each farm and group (farm A divided into milking groups G1 and G2) for each characteristic

Characteristic	Farm A G1 (n = 83)	Farm A G2 (n = 80)	Farm B (n = 201)
Parity			
1	23	21	70
2	22	28	36
3+	38	31	95
Lactation stage			
Early (7–49 DIM)	17	0	29
Mid (50–179 DIM)	60	16	77
Late (≥180 DIM)	6	64	95
Breed			
Holstein	27	21	201
Red Dairy Cattle	19	22	—
Crossbred	37	37	—
Estrus			
In estrus	28	2	51
Insemination date[1]	14	1	18
Insemination date −21 d[2]	8	0	23
Insemination date +21days[3]	3	0	2
Insemination date −42 d[4]	2	0	6
Insemination date +42 d[5]	1	1	2
Not in estrus	54	65	150
No information	1	13	0
Pregnancy status			
Pregnant	39	62	106
Open	47	18	95
Udder health			
Low (0–130,000 SCC/mL)	58	50	—
Mid (130,000–300,000 SCC/mL)	11	8	—
High (>300,000 SCC/mL)	14	22	—
Claw health			
Remark	24	24	—
Digital dermatitis[6]	1	1	—
Digital dermatitis[7]	8	11	—
Heel horn erosion[6]	2	4	—
Heel horn erosion[7]	1	1	—
Sole hemorrhage[6]	2	0	—
Sole hemorrhage[7]	8	3	—
Other diseases			—
White line abscess	0	4	—
Double sole	0	1	—
White line separation	6	1	—
Interdigital hyperplasia	0	2	—
Verrucose dermatitis	1	1	—
No remark	58	54	—
No information	1	2	—

[1] Cows were inseminated during the study period. Estrus is estimated as equal to the insemination date.

[2] Cows were inseminated after the study period. Estrus is estimated to 21 d before the insemination date.

[3] Cows were inseminated before the study period. Estrus is estimated to 21 d after the insemination date.

[4] Cows were inseminated after the study period. Estrus is estimated to 42 d before the insemination date.

[5] Cows were inseminated before the study period. Estrus is estimated to 42 d after the insemination date.

[6] Remark for minor lesions.

[7] Remark for major lesions.

Insemination records were used to estimate when cows were in estrus during the study period. The optimal time to inseminate a cow is 12 h postestrus (Dransfield et al., 1998), and estrus behavior may be expressed for 2 to 24 h (Forde et al., 2011). A cow was therefore defined to be in estrus on the insemination day and the day before. The estrus cycle in dairy cows is between 18 to 24 d (Forde et al., 2011). For cows inseminated before or after the study period, the estrus was estimated from the average length of a cow's estrus cycle (21 d). For cows inseminated after the study period, the estrus was estimated to be 21 and 22 d before insemination or 42 and 43 d before insemination (2 estrus cycles). For cows inseminated before the study period, the estrus was estimated to be 21 and 22 d after insemination or 42 and 43 d after insemination. A cow was recorded to be in estrus if the estimated date was within the study period and after the calving date. Most dairy cows resume normal ovarian activity within 15 to 45 d postpartum (Forde et al., 2011). Therefore, we assumed that a cow started to ovulate at the earliest 32 d after calving (Opsomer et al., 1998). If a cow was pregnant, it was categorized as not in estrus. The cows were categorized into 3 groups with respect to estrus (estrus, not in estrus, and no information). One cow in G1 and 13 cows in G2 did not have any insemination records and categorized as no information.

The current health status of cows influences their behavior and 2 of the most important health problems in adult dairy cattle are mastitis and claw disorders. Therefore, we decided to include the available data on these 2 conditions in our analyses. Claw and udder health records were only recorded at farm A.

Lameness due to claw lesions is often a long-lasting condition and regular claw trimmings were only conducted every 6 to 8 wk on a subset of cows. Therefore, we decided to use the latest 2 claw-trimming records before and after the study period to get claw-trimming records for all cows under study [August 12, 2020 (1 cow in G1, 12 cows in G2), September 28, 2020 (27 cows in G1, 22 cows in G2), November 24, 2020 (26 cows in G1, 30 cows in G2), and January 5, 2021 (28 cows in G1, 14 cows in G2)]. Remarks were based on either minor or major lesions of claw disorders: digital dermatitis, heel horn erosion, sole hemorrhage, white line abscess, double sole, white line separation, interdigital hyperplasia, verrucose dermatitis. For the analysis, all animals with at least one record of a claw disorder (minor or major) were considered to be “with claw health remark.” One cow in G1 and 2 cows in G2 did not have any claw-trimming records and these were categorized as no information.

The quarter sample with the highest SCC for each cow was selected from each sampling event. The geometric mean of the 2 consecutive samples were calculated and a Box-Cox transformation of the SCC was performed. The transformed SCC was adjusted to parity and breed in accordance with Nyman et al. (2014, 2016) and back transformed to adjusted SCC. All cows were classified into 3 risk categories: low (≤130,000 SCC/mL), mid (130,000–300,000 SCC/mL), and high (>300,000 SCC/mL) according to udder health classes used in the Swedish official milk recording scheme (Funke, 1989; Brolund, 1990). Four cows were only sampled in the second sampling (October 22, 2020), and this value was used instead of the geometric mean. Somatic cell count is usually elevated in the colostrum period in newly calved cows. Two cows were newly calved and in their colostrum period at the first sampling date, and their SCC records for this date were removed.

One cow in farm B did not have any individual attribute information and was therefore removed from the analysis. In farm A, G1 contained between 96 and 100 lactating cows during the study period, G2 between 87 and 94, and farm B had between 206 and 211 lactating cows. All groups were dynamic, with cows leaving and entering the groups depending on dry-off dates and calving dates, in addition to culling. Seven cows spent the first 7 d of the study in G1, and on October 23, they were moved to G2. During the study period, the number of unique cows in G1, G2, and farm B was 108, 98, and 216, respectively. Only cows present during the entire study period in one of the groups (G1, G2, or farm B) were included in the analysis. In total, 163 cows were present during the whole study period in farm A (83 in G1 and 80 in G2) and 201 cows in farm B.

Statistical Analysis

R statistical software version 4.0.3 (R Core Team, 2020) was used for the statistical analyses. For each of the 2 areas, feeding and resting, a linear mixed model was fitted using the lmer function in the lme4 package (Bates et al., 2015). The response variable was contact rate, and date, parity, lactation stage, breed, estrus, pregnancy status, claw health, and udder health were included as explanatory variables, and cow ID as random effect to account for repeated measurements (days within study period). In G2, there were only 2 cases of estrus, and the variable was removed from the model in this group. In farm B, the variables claw health and udder health were not available and therefore not included in the model. For models producing skewed distributions of residuals, Box-Cox transformation was applied on the response variable using the boxcox function in the MASS package (Venables and Ripley 2002). The Box-Cox transformation parameter lambda used for the feeding area was 0.6, 0.4, and 0.6 for G1, G2, and farm B, respectively. The lambda was equal to 1.4, 1.3, and 0.2 for G1, G2, and farm B, respectively, for the resting area. The repeatability was calculated as the proportion of variation between individuals (i.e., the variance of individual random effects) with respect to the total variance (i.e., the sum of the variance of individual random effects and the residual variance). The skewness of the distributions of the response variable was calculated with the skewness function in the moments package (Komsta and Novomestky, 2015) in R. The Anova function in the car package (Fox and Weisberg, 2019) was used to compute P-values.

Model Validation and Sensitivity Analysis

Contact rate is dependent between individuals as it is a measure that involves pairs of cows in contact with each other. Consequently, the assumption of independence between individuals in the fitted linear mixed model is violated and significance levels in hypothesis testing may be affected. This was examined with a permutation test. The permutations were made between cows and between dates within cows. Hence, the explanatory variables for a record were coupled with a randomly sampled response variable from another record while retaining the structure of observations within cows. The original F-test statistic was compared against the F-test statistics obtained after fitting the linear mixed model to 10,000 permuted data sets. This permutation test is referred to as node-level permutation in Farine (2017). These node-level permutations produce random associations between the response variable and the explanatory variables, but at the same time keeps the dependency structure between observations. The ANOVA P-values from the 10,000 linear mixed models, fitted to the permuted data sets, should be uniformly distributed if deviations from the assumption of independence can be ignored. Consequently, the proportion of fitted models producing P-values below 5% should be around 0.05. This was the case and there was no need to adjust the significance level for deviations from the assumption of independence.

To further understand the 2 variables underlying the calculations of contact rates, $t_{contact,i,k}$ (total duration of contacts) and $t_{area,i,k}$ (time spent in each area), they were analyzed separately and the results are displayed in Supplemental Material S2 (https://pub.epsilon.slu.se/29185/; Hansson et al., 2022).

The residual variance was checked for consistency using the hglm package (Rönnegård et al., 2010) in R. The variance of the residuals was found to decrease with the time spent in an area, indicating that the number of contacts a cow had when only spending a shorter time in an area was more stochastic. However, the P-values of the estimates in the hglm output were similar to those from the linear mixed model fitted using the lmer function. Consequently, it was concluded that there was no need to adjust the P-values from lmer for variance heterogeneity.

Variance inflation factors were computed to test for multicollinearity between explanatory variables, using the vif function in the car package (Fox and Weisberg, 2019) in R. The variance inflation factors were close to 1 for all explanatory variables, indicating no multicollinearity problems between the models' variables and that the fixed factors essentially represented different effects.

An exhaustive sensitivity analysis for the distance and time thresholds used to define a social contact was out of the scope of this study; however, for farm A both distance thresholds of 1.5 m and 3.0 m were tested, and a time threshold of 20 and 30 min was also tested (Supplemental Material S3; https://pub.epsilon.slu.se/29185/; Hansson et al., 2022).

RESULTS

Feeding Area

The contact rate in the feeding area ranged between 1 and 2 for most cows in all groups and farms (Figure 2). Hence, the instantaneous number of individuals within proximity of a cow at any time during the day ranged between 1 and 2 individuals. The distribution of contact rates in the feeding area had a positive skewness in all 3 groups (G1: skewness = 0.22, G2: skewness = 0.51, farm B: skewness = 0.29). The estimated repeatability was 35, 36, and 30% in G1, G2, and farm B, respectively. The contact rates differed between days in both farms and groups ($P < 0.001$, Table 2).

Lactation stage had an effect on all groups and farms in the feeding area (G1 $P = 0.013$, G2 $P = 0.029$, farm B $P < 0.001$). Estimated effect sizes are given in Table 3. In G1 and farm B, cows in mid and late lactation had more contacts in the feeding area than the cows in early lactation. In G2, late lactation cows had fewer contacts than the cows in mid-lactation.

There was an effect of parity in G1 ($P < 0.001$) and farm B ($P = 0.009$) in the feeding area, but not in G2. Older cows in G1 had fewer contacts than younger cows. In farm B, on the contrary, Cows in parity 3+ had more contacts than cows in parity 1, although the estimated difference was not as large as in G1.

Breed had an effect in the feeding area in G2 ($P = 0.008$) but not in G1 ($P > 0.05$). Red Dairy Cattle had a lower contact rate than crossbreds and Holstein cows in G2. Pregnancy status did not have an effect in any of the groups, and udder health and claw health did not have an effect in either G1 or G2. Estrus, however, did have an effect in G1 ($P = 0.002$) but not in farm B ($P = 0.069$). Cows in estrus in G1 had contact with fewer individuals in the feeding area and the results in farm B pointed in the same direction.

Resting Area

The contact rates in the resting area ranged between 1 and 3 for most cows in all groups and farms (Figure 3). The distribution of the contact rates in the resting area had a negative skewness in farm A (G1: skewness = −0.32, G2: skewness = −0.25) and a positive skew-

Table 2. *P*-values from the ANOVA test for the relation between the contact rate (Box-Cox transformed) and the individual characteristics in the feeding and resting areas for the studied farms (farm A divided into milking groups G1 and G2)

	Feeding area			Resting area		
	Farm A		Farm B	Farm A		Farm B
Characteristic	G1 (n = 83)	G2 (n = 80)	(n = 201)	G1 (n = 83)	G2 (n = 80)	(n = 201)
Date	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Parity	<0.001	0.685	0.009	0.773	0.999	<0.001
Lactation stage	0.013	0.029	<0.001	0.089	0.646	0.366
Breed	0.468	0.008		0.513	0.815	
Pregnancy status	0.319	0.266	0.688	<0.001	0.583	0.725
Estrus	0.002		0.069	0.002		0.240
Udder health	0.967	0.264		0.017	0.936	
Claw health	0.109	0.327		0.454	0.008	

ness in farm B (skewness = 0.55). The repeatability was 47, 46, and 47% in G1, G2, and farm B, respectively. The contact rates were also different between days in both farms and groups ($P < 0.001$, Table 2).

There was no effect of lactation stage on the response variable in any groups or farms in the resting area ($P > 0.05$). Parity had an effect on the contact rates in farm B ($P < 0.001$) but not in farm A ($P > 0.05$). Estimated effect sizes are given in Table 4. Cows in parity 3+ had a higher contact rate than younger cows in farm B. Breed had no effect in any group in the resting area ($P > 0.05$). Pregnancy status had an effect in G1 ($P < 0.001$) but not in G2 or farm B. Pregnant cows had a lower contact rate than open cows in G1. There was an effect of estrus in G1 ($P = 0.002$) as well, but not in farm B ($P > 0.05$). Similar to the results in the feeding area, cows in estrus had a lower contact rate than cows not in estrus.

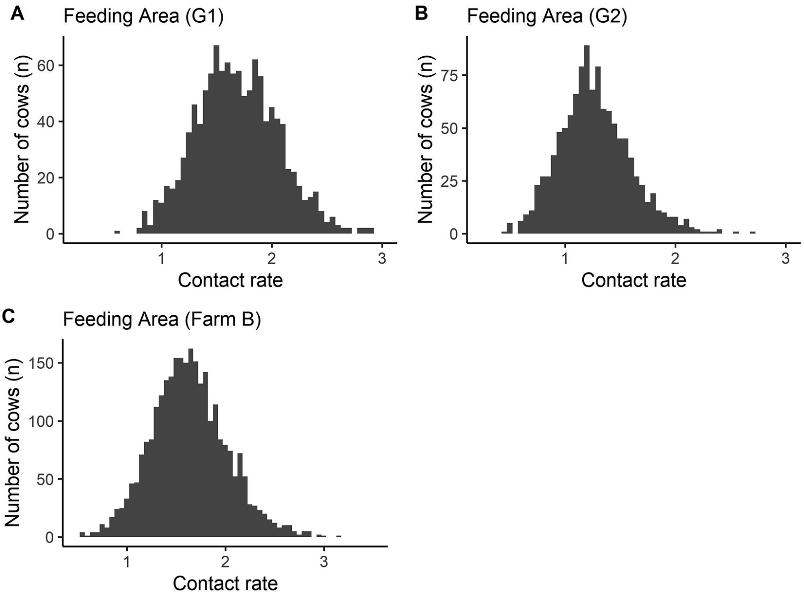

Figure 2. Distribution of the contact rates in the feeding area for all 3 groups: (A) for farm A milking group 1 (G1), (B) for farm A milking group 2 (G2), and (C) for farm B.

Table 3. Summary of the estimated regression coefficients and significance of the individual characteristics on the contact rate in the feeding area for each farm (farm A divided into milking groups G1 and G2)[1]

	Farm A		Farm B
Fixed effect	G1 (n = 83)	G2 (n = 80)	(n = 201)
Parity			
1	0^{a}	0	0^{a}
2	-0.12^{b}	−0.04	$0.03^{a,b}$
3+	-0.20^{b}	−0.03	0.08^{b}
Lactation stage			
Early (7–49 DIM)	0^{a}		0^{a}
Mid (50–179 DIM)	0.14^{b}	0^{a}	0.15^{b}
Late (≥180 DIM)	0.19^{b}	-0.10^{b}	0.21^{c}
Breed			
Crossbred	0	0^{a}	
Holstein	−0.02	-0.00^{a}	
Red Dairy Cattle	−0.06	-0.14^{b}	
Pregnancy status			
Open	0	0	0
Pregnant	0.04	0.05	0.01
Estrus			
Not in estrus	0^{a}		0
In estrus	-0.10^{b}		−0.05
Udder health			
Low (0–130,000 SCC/mL)	0	0	
Mid (130,000–300,000 SCC/mL)	0.01	−0.06	
High (>300,000 SCC/mL)	−0.01	−0.07	
Claw health			
No remark	0	0	
Remark	0.01	−0.02	

[a–c]Different superscript letters represent significantly different values ($P < 0.05$) between the levels for each factor.

[1]Results are shown for G1 and G2 in farm A and farm B in a Box-Cox transformed scale. The residual SD of the estimates were 0.20, 0.19, and 0.24 in G1, G2, and farm B, respectively.

Udder health had an effect on the contact rates in G1 ($P = 0.017$) but not in G2 ($P > 0.05$) and claw health had an effect in G2 ($P = 0.008$) but not in G1 in the resting area ($P > 0.05$). Cows with udder health categorized into the mid-risk group had lower contact rates than cows in the low-risk group in G1, and cows with remarks on claw health had a lower contact rate than cows with no remarks in G2.

DISCUSSION

We used an RTLS at 2 commercial dairy farms to identify which individual characteristics of a dairy cow were associated with the contact rate it had with other cows in the feeding and resting area. We found that lactation stage, parity, breed, and estrus with some variation affected the contact rates in the feeding area, whereas pregnancy status and udder and claw health did not seem to have any affect. In the resting area we found that the number of contacts were affected by parity, pregnancy status, estrus, as well as udder and claw health although it varied between groups, whereas lactation stage and breed did not.

There was an individual variation in contact rate among cows and a variation in contact rates between days, both around the feeding table and the resting areas in both farms. This was expected as the groups were dynamic with cows continuously entering and leaving the groups. Unstable and dynamic groups can result in more dynamic and temporal social bonds (Boyland et al., 2016). The health status and the circadian rhythm of the individual cows can also alter between days (Veissier et al., 2017) and may affect the number of contacts between individuals. Additionally, the daily management routines on the farms and the interference of the farm staff can differ from day to day and affect the possibilities to maintain social networks.

Association of Cow Characteristics with Contact Rate

Lactation Stage. Our results showed that cows in later lactation in G1 and farm B had a higher contact rate in the feeding area than cows in early lactation. Cows in later lactation on farm A (i.e., G1) also spent less time in the feeding area than early lactation cows

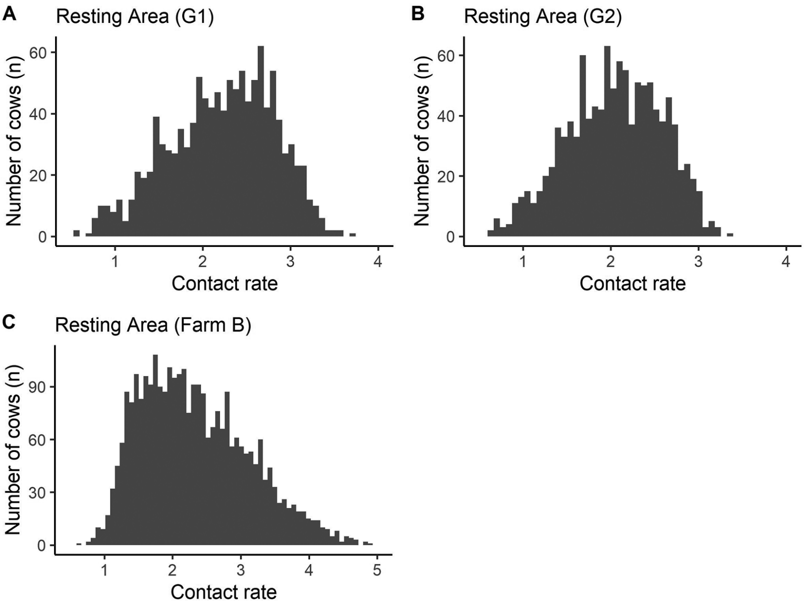

Figure 3. Distribution of the contact rates in the resting area for all 3 groups: (A) for farm A milking group 1 (G1), (B) for farm A milking group 2 (G2), and (C) for farm B.

(Supplemental Material S2, Supplemental Table S5; https://pub.epsilon.slu.se/29185/; Hansson et al., 2022), similar to the findings by Løvendahl and Munksgaard (2016), which may be related to the energy requirements in the different stages of the lactation. The lactation stage was related to time within the lactating group and cows in late lactation could thus have had the opportunity to create stronger social bonds with more individuals compared with early lactation cows. On the contrary, late lactation cows in G2 had a lower contact rate than cows in mid-lactation. However, we remind the readers that G2 consisted predominantly of cows in late lactation, and G1 contained mainly cows in early and mid-lactation. There were no early lactation cows present in G2, which could explain the contradictory results. Additionally, because cows were usually moved from G1 to G2 at approximately 170 DIM, many cows in G2 were relatively new to the group and might not have had as much time to create social bonds. The previous experience of conspecifics and familiarity between individuals has been identified as essential for social relationships (Gygax et al., 2010; Foris et al., 2021), and our findings suggest that the lactation stage and the time spent in the group seem to be important factors for the number of contacts cows have.

Parity. In G1 and farm B, parity significantly affected the contact rate in the feeding area. Older cows had fewer contacts than younger cows in G1, whereas in farm B, older cows had more contacts than younger cows. However, the estimated effect for parity in farm B was smaller in comparison to the effect in G1. High parity cows have been shown to spend less time feeding (Azizi et al., 2010), and our results also showed that older cows spend a shorter time in the feeding area than younger cows (Supplemental Material S2, Supplemental Table S5; https://pub.epsilon.slu.se/29185/; Hansson et al., 2022). Higher parity cows are older and more experienced and can have a high dominance position in the herd (Wierenga, 1990). A cow with a higher social rank can most likely choose positions in the barn more freely than subordinates (Wierenga, 1990; Churakov et al., 2021). Therefore, if a dominant cow goes to the feeding area to eat, it will probably keep the same position at the feeding table, eat what it needs and then leave. A subordinate cow may be pushed away from its spot at the feeding table and may need to change position several times, getting a high number of contacts. Hence, our results suggest that parity has an effect on the number of contacts a cow has, which might be related to dominance and social rank. At the

Table 4. Summary of the estimated regression coefficients and significance of the individual characteristics on the contact rate in the resting area on each farm (farm A divided into milking groups G1 and G2)[1]

Fixed effect	Farm A		Farm B (n = 201)
	G1 (n = 83)	G2 (n = 80)	
Parity			
1	0	0	0^{a}
2	0.06	−0.00	0.11^{a}
3+	0.13	−0.00	0.29^{b}
Lactation stage			
Early (7–49 DIM)	0^{a}		0
Mid (50–179 DIM)	0.37^{b}	0	0.06
Late (≥180 DIM)	$0.16^{a,b}$	0.07	0.09
Breed			
Crossbred	0	0	
Holstein	−0.02	−0.08	
Red Dairy Cattle	−0.18	−0.05	
Pregnancy status			
Open	0^{a}	0	0
Pregnant	-0.51^{b}	0.08	0.01
Estrus			
Not in estrus	0^{a}		0
In estrus	-0.29^{b}		−0.04
Udder health			
Low (0–130,000 SCC/mL)	0^{a}	0	
Mid (130,000–300,000 SCC/mL)	-0.53^{b}	−0.07	
High (>300,000 SCC/mL)	$-0.19^{a,b}$	−0.01	
Claw health			
No remark	0	0^{a}	
Remark	−0.09	-0.34^{b}	

[a,b]Different superscript letters represent significantly different values ($P < 0.05$) between the levels for each factor.

[1]Results are shown for G1 and G2 in farm A and farm B in a Box-Cox transformed scale. The residual SD of the estimates were 0.56, 0.48, and 0.28 in G1, G2, and farm B, respectively.

same time, Chopra et al. (2020) did not find any connections between parity and proximity interactions.

Parity was only significant in the resting area in farm B, where the older cows had more contacts than younger cows. These results could be related to where the cows chose to lie down in the barn. In the study of Churakov et al. (2021), conducted in the same 2 herds as the present study, older cows preferred to lie down in cubicles close to the milking area, and cows in the first lactation occupied cubicles in a less busy area of the barn. Older cows use the more frequently used cubicles (Churakov et al., 2021) and will automatically have more contact with other individuals in the resting area, similar to the study by Boyland et al. (2016), where cows in similar parity formed preferential bonds.

Breed. For breed, we found that Red Dairy Cattle had fewer contacts than crossbreds and Holstein cows in the feeding area in G2. Boyland et al. (2016) found that cows have a preferential assortment to individuals with similar breeds, which might be related to body size and energy requirements. The explanation for our results is unclear but indicates that there could be some difference in the social behavior between breeds and might also, for example, be related to temperament or personality (Sewalem et al., 2010; Hedlund and Løvlie, 2015), which would be interesting to investigate further.

Estrus. Cows in estrus are more restless and show sexual behaviors such as mounting or standing to be mounted and chin-resting on the rump of another cow. They are also more engaged in other social interactions, such as allogrooming and agonistic behavior (Kerbrat and Disenhaus, 2004). Estrus had a significant effect on the contact rate in G1, in both the feeding and resting area, where cows in estrus had fewer contacts than cows not in estrus. We might have expected that cows in estrus would have contact with more individuals because they usually are more active and solicit other cows to mount (Kerbrat and Disenhaus, 2004). However, this contact would probably be short when a cow in estrus was trying to mount a cow that was not in estrus and does not want to be mounted. Because we used a threshold of 10 min for the accumulated duration of contacts between 2 individuals during a day, many of these brief contacts would have been eliminated. Cows in estrus also usually stay close to one or more other individuals within so-called sexually active groups (Sveberg et al., 2013) and would, therefore, only have longer contact with a limited number of individuals. We did not observe significant results for estrus in farm B; one reason for this could be that we used indirect measures such as insemination dates and did not know if the cows actually were in estrus or which stage of the estrus they were in.

Udder Health. Udder health showed significant effects in the resting area in G1. Cows within the mid-risk group had fewer contacts than the low-risk group. These results could be related to sickness behavior and a tendency for the cows to stay away from other individuals. High SCC is a sign of inflammation in the udder. It is documented that cows with clinical mastitis show signs of sickness behavior, such as changes in feeding behavior, activity, and lying time (Siivonen et al., 2011; Medrano-Galarza et al., 2012; Fogsgaard et al., 2015). Decreased feed intake, feeding rate, and lying time were even seen in cows with rather mild naturally occurring clinical mastitis (Medrano-Galarza et al., 2012; Fogsgaard et al., 2015). Sepúlveda-Varas et al. (2016) saw a decline in competitive replacements at the electronic feeding bins for cows diagnosed with clinical mastitis. In this study, we investigated the association of behavior and SCC, as an indicator of subclinical mastitis. Our study did not reveal any differences in the time spent in the resting and feeding area between cows of the 3 udder health classes (Supplemental Material S2, Supplemental Tables S5 and S6; https://pub.epsilon.slu.se/29185/; Hansson et al., 2022), and we did not find significant results for udder health in G2.

Claw Health. Claw health showed significant effects in the resting area in G2. Cows with claw remarks had contact with fewer individuals than cows with no remarks. Lameness can cause alterations in cow behavior and influence lying time, general activity, feeding behavior, and milking order (Weigele et al., 2018). Weigele et al. (2018) recorded fewer visits to the concentrate feeders by lame cows than nonlame cows, which could be interpreted as a strategy to avoid aggressive encounters or to avoid moving at all due to pain. Other studies found no correlation between agonistic behaviors and lameness (Walker et al., 2008; Chopra et al., 2020). Our study did not reveal any differences in the time spent in the resting and feeding area between cows with and without claw health remarks (Supplemental Material S2, Supplemental Tables S5 and S6; https://pub.epsilon.slu.se/29185/; Hansson et al., 2022), and we did not find significant results for claw health in G1. For claw health, we used indirect measures such as claw-trimming records from several dates and did not know if the cows were lame at the time of the study, which could explain the contradictory results.

Study Design and Limitations

Social Interactions. In our study, we cannot know for sure if proximity was connected to true social interaction or simply to an individual being more wide-ranging and therefore encountering more other individuals (Albery et al., 2021). Therefore, conclusions on social interactions should be drawn with caution. Proximity could also be due to nonsocial events such as the positioning of the other group members at the feeding table or in cubicles. This is one of the major challenges with using automated positioning data to identify proximity interactions (Chopra et al., 2020).

Defining Contacts. An appropriate distance threshold for a proximity interaction in cubicles would be 2.5 m to account for the maximum distance between the tags when 2 cows are lying in adjacent cubicles (Rocha et al., 2020). Choosing a distance threshold for proximity interactions in the feeding area and walking alley is slightly more complicated because an individual cow's ability to actively choose whom to be close with or to avoid will be affected by the stocking density in the herd and the layout of the barn (Chopra et al., 2020). The study of Chopra et al. (2020) defined proximity interactions between cows when the individuals were 3 m apart, and social interaction between 2 cows standing nose to nose would represent a distance-radius threshold of 1.25 m, according to Rocha et al. (2020). However, a social interaction between 2 cows where one cow is standing behind another cow or closely following another cow would approximately represent a cow's distance. Positioning data collected from collar-based tracking devices do not describe the entire space occupied by individuals' bodies. Therefore, conclusions drawn regarding the social network or potential disease transmission may be incorrect when body parts not wearing tags are excluded from the network or misidentified as noise (Farthing et al., 2020). A short maximum distance would be motivated to distinguish between genuine social associations and nonsocial proximity events. However, reducing false negatives is essential as the absence of a few associations can significantly alter the network's global structure (Farine and Whitehead, 2015), which would motivate as large maximum distance as possible. Hence, there is a trade-off between capturing genuine associations and capturing all important edges in the network structure. Our investigations in Supplemental Material S3 (https://pub.epsilon.slu.se/29185/; Hansson et al., 2022) showed no qualitative change when altering the distance threshold to 1.5 or 3.0 m. Gibbons et al. (2010) showed that a cow observed less than 1 m to 2 neighbors could be a suitable indicator of sociability but that it was in a context where the cows had little possibility to keep larger distances, which was not the case in our current study.

We also tested different thresholds for the accumulated duration of contacts between 2 individuals. We found that a 30 min threshold in the feeding area resulted in higher *P*-values for lactation stage and estrus in G1, which suggests further investigation into the most suitable threshold. Different social interactions may also differ in duration. Grooming bouts can vary a lot in duration, from 2 to 814 s (Val-Laillet et al., 2009) and in stable groups of cattle, agonistic behaviors are few and subtle and can be hard to distinguish (Bouissou et al., 2001). Choosing a threshold that is too high might lead to the exclusion of interactions of social character.

Housing Conditions. The layout of the building and the stocking density are factors that must be considered when studying the social structure among dairy cows in freestall systems (Collings et al., 2011; Lobeck-Luchterhand et al., 2015). These factors may affect the individual's ability to choose whom to be in proximity with or avoid actively (Chopra et al., 2020). There were more cubicles available in relation to the number of cows in G2 and farm B than G1. Having fewer cubicles to choose from probably limits the voluntary proximity interactions in the resting area. The barn layout of the 2 farms within this study was also quite different. The feeding tables were located along the sides of the barn in farm A and in the middle of the barn in farm B. The feed space per cow was a little bit less in farm B than in farm A, which may have limited the potential for individuals to actively avoid other cows. In farm A, the cows were divided into 2 groups, whereas in farm B, all cows were housed in one big group. These differences between farms may affect how the cows move around the barn and might explain why the results sometimes differed. Other aspects that might also have an affect are the differences in milking system, management practices of the farm, bedding material, feeding regimen, and geographical location.

Housing conditions also affect the accuracy of RTLS data. Ren et al. (2021) showed that the accuracy of the RTLS varied between the 2 areas on farm A, where group G1 and G2 are kept, with more missing data along one of the feeding tables. However, these are rather short events of missing data and we expect that our applied data interpolation should be sufficient to capture all contacts of substantial importance between pairs of cows.

CONCLUSIONS

This study aimed to associate characteristics of a cow to the number of contacts it has with other group members by the feeding table and in the resting area in the barn, to increase our understanding of the social behavior of dairy cows. Our findings suggest that cows in late lactation have more contacts in the feeding area than cows in early lactation and higher parity cows have fewer contacts in the feeding area than cows in the first lactation, which might be related to familiarity and social rank. Our results also revealed that higher parity cows seem to have more interactions in the resting area. Furthermore, cows with impaired claw health or udder health had fewer contacts with other cows in the resting area, compared with healthy cows. Further analyses and additional data collection to distinguish between positive and negative interactions are needed to increase our understanding of different management scenarios and effects on animal welfare.

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Supplementary Material 1

We inspected heatmaps of the FA data for one day (2020-10-18) and for both farms to investigate any apparent shifts in the data. Additionally, we also tracked a subset of individuals and inspected heatmaps of their positions to be able to exclude any apparent shifts in the data.

1. We examined the individual heatmap for randomly selected 20 cows from Farm A (10 from G1 and 10 cows from G2) and 20 from Farm B.
2. We examined the heatmaps for these individuals as groups.
3. We examined the heatmap for all the cows included in our study.

Figure S1 (below) shows the heatmaps of two individuals from Farm A and two from Farm B as examples. The black dots plot the trajectory of the individuals, and the heatmap overlays the trajectory. In total, the positions of 20 cows in each farm were inspected individually. Figure S2 shows the heatmap of these selected individuals as a group. Figure S3 shows the heatmap of all the individuals (163 cows from Farm A, 201 cows from Farm B, at 2020-10-18).

We used Figure S1 to observe potential data shifts in the cubicle areas. When individuals spend a long time in the resting area, we can see the position data spread around the single cubicle. However, the spread is still inside the resting area and show similar mean error distance as the performance tags. Thus, we could not find any apparent data shift in the resting area that will affect our social network analysis. Figure S3 gives more general information on data quality. The feeding area showed narrow and high-density areas over the metal bars of the feeding bank. The resting area showed a clear boundary of the beds' layout. Therefore, we could not find apparent shifts in the data given the blueprints of the farms.

Supplementary Material 1 to: Cow characteristics associated with the variation in number of contacts between dairy cows. *Journal of Dairy Science*

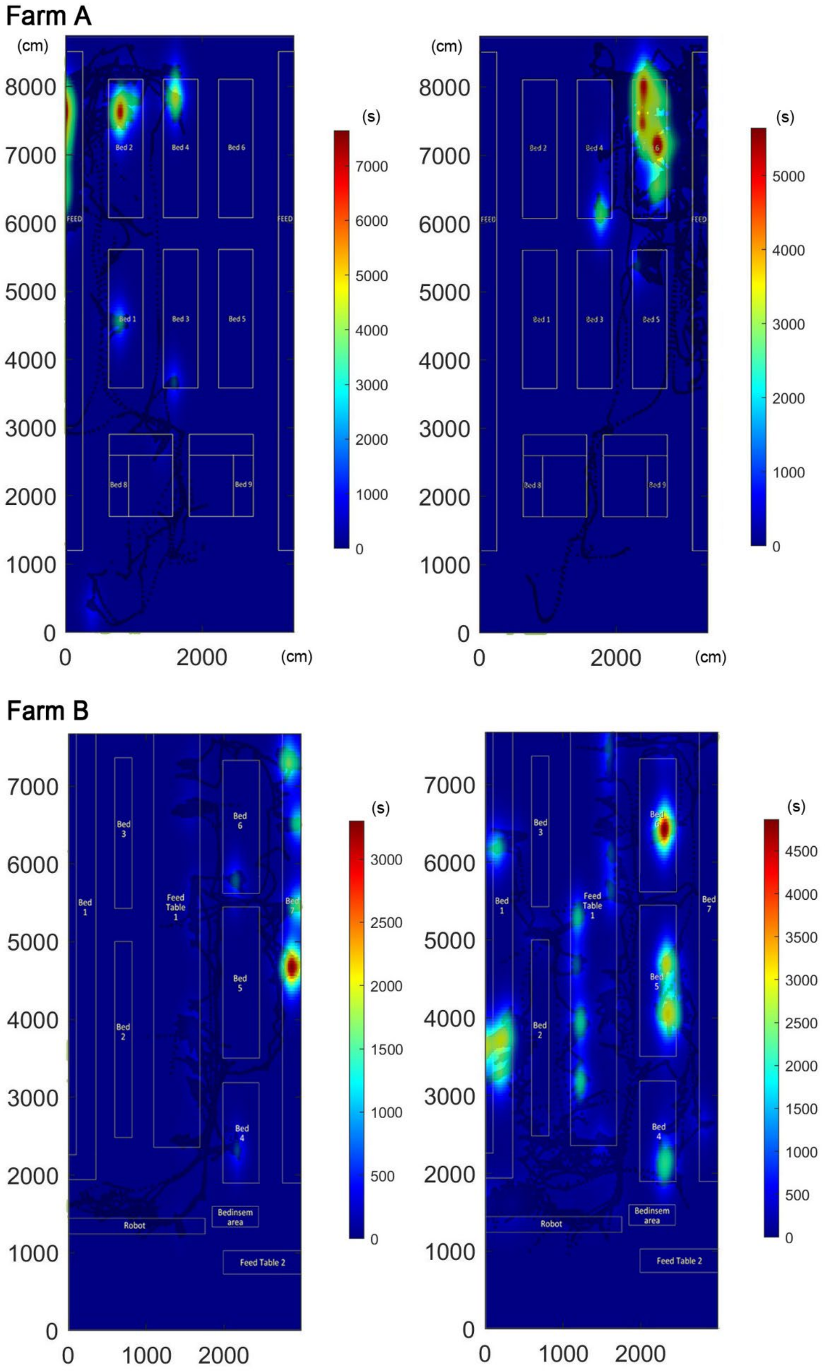

Figure S1. The heatmaps of two example individuals from Farm A and two from Farm B. The black dots plot the trajectory of the individuals, and the heatmap overlays the trajectory. The layouts of the barns are shown in the figure using white outlines.

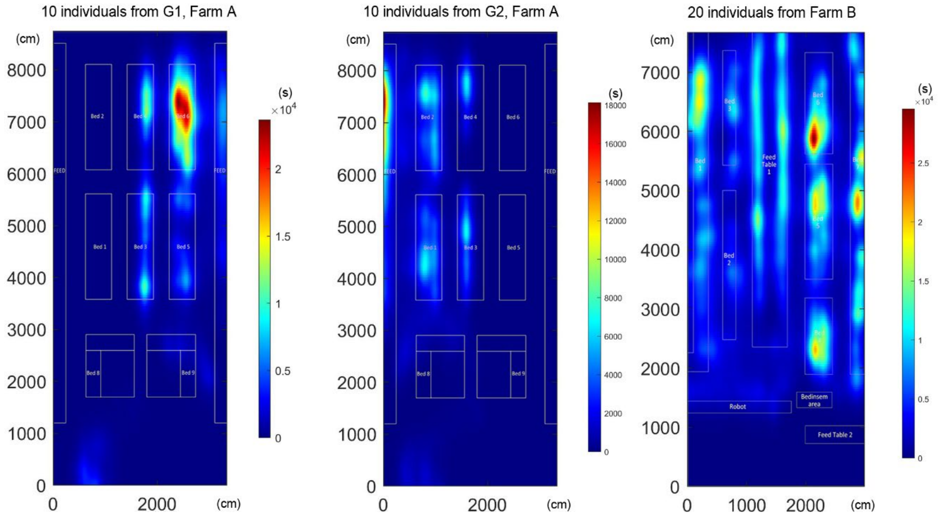

Figure S2. The heatmap of the three groups of cows where the positions of every individual were first inspected individually.

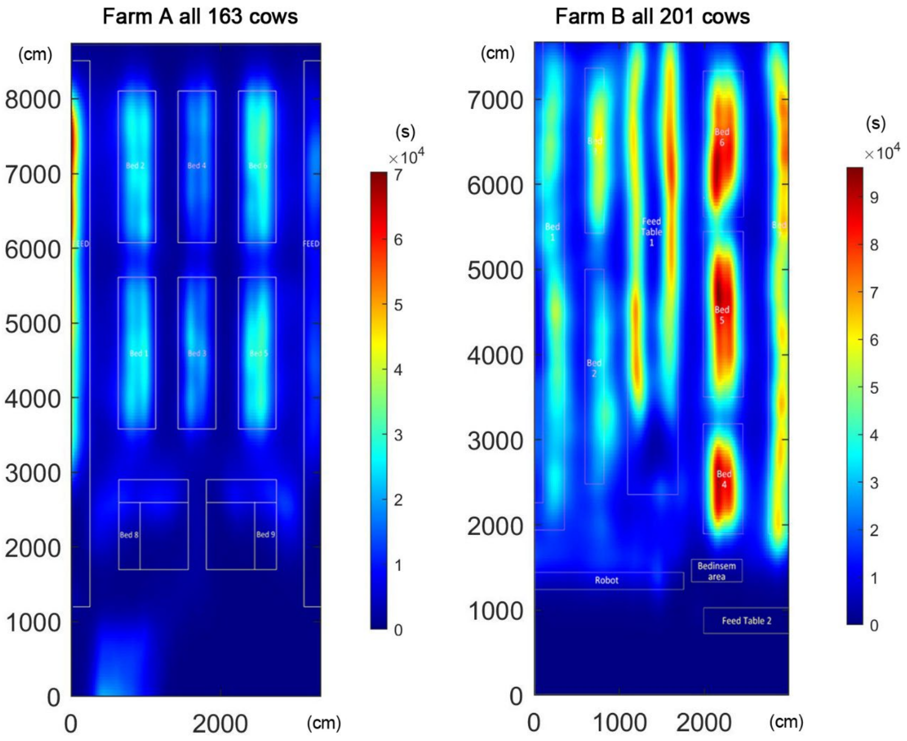

Figure S3. The heatmap using all 163 cows from Farm A and 201 cows from Farm B, on 2020-10-18.

Supplementary Material 2

Description and analysis of the response variables *total duration of contacts*, and *time spent in area*. The same explanatory variables as for the response variable *contact rate* in the main text were used.

Total duration of contacts is defined as the sum of all durations of contacts during 24 h. Note that these values can be greater than 24 h since there can be multiple simultaneous contacts. Time spent in area is defined as the total time an individual spends during 24 h within the predefined area, either feeding area or resting area as described in the main text

Total duration of contacts

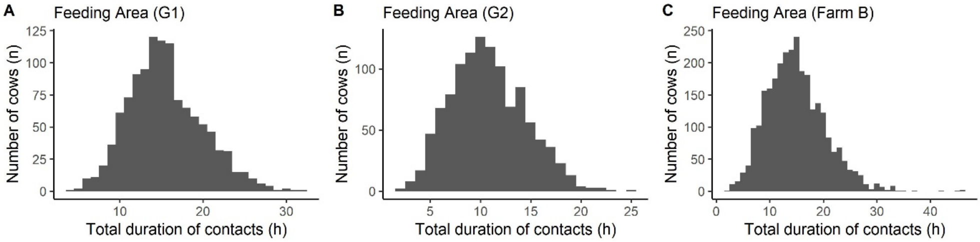

Figure S1. Distribution of the total duration of contacts in the feeding area for all three groups: A) for G1, B) for G2 and C) for Farm B.

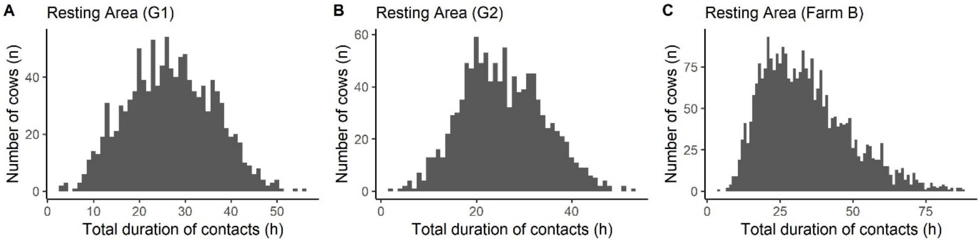

Figure S2. Distribution of the total duration of contacts in the resting area for all three groups: A) for G1, B) for G2 and C) for Farm B.

Supplementary Material 2 to: Cow characteristics associated with the variation in number of contacts between dairy cows. *Journal of Dairy Science*

Table S1. P-values from the ANOVA test for the relation between the total duration of contacts and the individual traits in the feeding and resting area for all groups and farms

	Feeding Area			Resting Area		
	Farm A		Farm B	Farm A		Farm B
Trait	G1 (n = 83)	G2 (n = 80)	(n = 201)	G1 (n = 83)	G2 (n = 80)	(n = 201)
Date	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Parity	< 0.001	0.011	0.052	0.190	0.597	< 0.001
Lactation stage	0.927	0.021	0.013	0.009	0.531	0.639
Breed	0.338	0.015		0.762	0.974	
Pregnancy status	0.550	0.408	0.075	0.002	0.693	0.158
Estrus	0.371		0.493	< 0.001		0.139
Udder Health	0.736	0.080		0.016	0.669	
Claw Health	0.609	0.463		0.724	0.132	

Supplementary Material 2 to: Cow characteristics associated with the variation in number of contacts between dairy cows. *Journal of Dairy Science*

Table S2. Summary of the estimated regression coefficients and significance of the individual traits on the total duration of contacts in the feeding area. Results are shown for G1 and G2 in Farm A and Farm B in a Box-Cox transformed scale. Different characters in subscript represents significantly different values ($p < 0.05$) between the levels for each factor

Feeding Area	Farm A		
Fixed Effects	G1 (n = 83)	G2 (n = 80)	Farm B (n = 201)
	Estimate	Estimate	Estimate
Parity			
1	0_a	0_a	0_a
2	-0.41_b	-0.68_b	$-0.25_{a,b}$
3+	-0.97_c	-0.84_b	-0.37_b
Lactation stage			
Early (7-49 DIM)	0		0_a
Mid (50-179 DIM)	-0.02	0_a	0.46_b
Late (≥180 DIM)	-0.10	-0.65_b	0.66_b
Breed			
Crossbred	0	0_a	
Holstein	-0.13	-0.27_a	
Red Dairy Cattle	-0.22	-0.78_b	
Pregnancy status			
Open	0	0	0
Pregnant	-0.07	0.23	-0.23
Estrus			
Not in estrus	0		0
In estrus	-0.11		-0.08
Udder health			
Low (0 – 130 000 SCC/ml)	0	0	
Mid (130 000 – 300 000 SCC/ml)	0.13	-0.67	
High (>300 000 SCC/ml)	0.05	-0.48	
Claw Health			
No remark	0	0	
Remark	-0.03	0.12	
Residual Std. Dev	0.53	0.80	0.99

Table S3. Summary of the estimated regression coefficients and significance of the individual traits on the total duration of contacts in the resting area. Results are shown for G1 and G2 in Farm A and Farm B in a Box-Cox transformed scale. Different characters in subscript represents significantly different values ($p < 0.05$) between the levels for each factor

Resting Area	Farm A		
Fixed Effects	G1 (n = 83)	G2 (n = 80)	Farm B (n = 201)
	Estimate	Estimate	Estimate
Parity			
1	0	0	0_a
2	-0.27	0.48	0.32_b
3+	1.48	0.75	0.71_c
Lactation stage			
Early (7-49 DIM)	0_a		0
Mid (50-179 DIM)	3.36_b	0	0.11
Late (≥180 DIM)	$2.71_{a,b}$	0.45	0.13
Breed			
Crossbred	0	0	
Holstein	0.27	0.09	
Red Dairy Cattle	-0.55	-0.09	
Pregnancy status			
Open	0_a	0	0
Pregnant	-2.28_b	0.28	0.11
Estrus			
Not in estrus	0_a		0
In estrus	-1.92_b		-0.10
Udder health			
Low (0 – 130 000 SCC/ml)	0_a	0	
Mid (130 000 – 300 000 SCC/ml)	-3.42_b	0.73	
High (>300 000 SCC/ml)	$-0.92_{a,b}$	0.45	
Claw Health			
No remark	0	0	
Remark	-0.31	-1.15	
Residual Std. Dev	3.11	2.34	0.60

Time spent in area

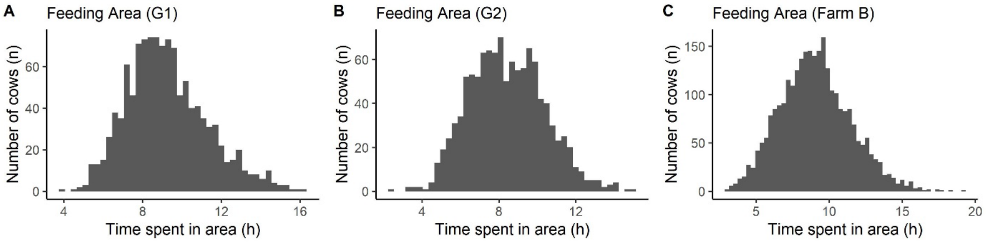

Figure S3. Distribution of the time spent in the feeding area for all three groups: A) for G1, B) for G2 and C) for Farm B.

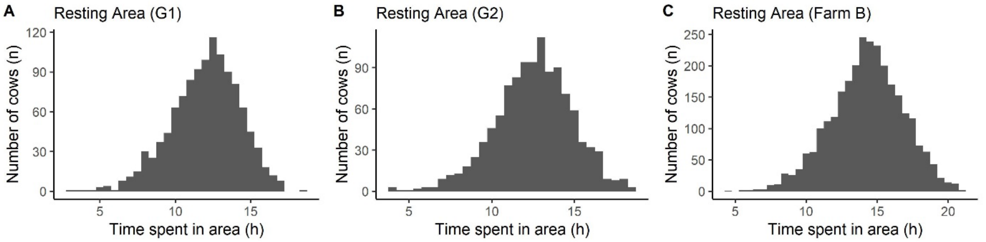

Figure S4. Distribution of the time spent in the resting area for all three groups: A) for G1, B) for G2 and C) for Farm B.

Table S4. P-values from the ANOVA test for the relation between the time spent in area and the individual traits in the feeding and resting area for all groups and farms

	Feeding Area			Resting Area		
	Farm A		Farm B	Farm A		Farm B
Trait	G1 (n = 83)	G2 (n = 80)	(n = 201)	G1 (n = 83)	G2 (n = 80)	(n = 201)
Date	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Parity	0.001	0.006	< 0.001	0.013	0.196	< 0.001
Lactation stage	0.025	0.303	0.934	0.011	0.512	0.801
Breed	0.769	0.215		0.757	0.569	
Pregnancy status	0.139	0.835	0.017	0.490	0.672	0.011
Estrus	0.138		0.382	0.088		0.234
Udder Health	0.775	0.204		0.515	0.177	
Claw Health	0.770	0.558		0.929	0.849	

Table S5. Summary of the estimated regression coefficients and significance of the individual traits on time spent in the feeding area. Results are shown for G1 and G2 in Farm A and Farm B in a Box-Cox transformed scale. Different characters in subscript represents significantly different values ($p < 0.05$) between the levels for each factor

Feeding Area	Farm A		
Fixed Effects	G1 (n = 83)	G2 (n = 80)	Farm B (n=201)
	Estimate	Estimate	Estimate
Parity			
1	0_a	0_a	0_a
2	-0.06_a	-0.46_b	-0.31_b
3+	-0.22_b	-0.63_b	-0.58_b
Lactation stage			
Early (7-49 DIM)	0_a		0
Mid (50-179 DIM)	-0.15_b	0	0.01
Late (≥180 DIM)	-0.23_b	-0.20	0.05
Breed			
Crossbred	0	0	
Holstein	-0.03	-0.25	
Red Dairy Cattle	-0.04	-0.27	
Pregnancy status			
Open	0	0	0_a
Pregnant	-0.06	0.04	-0.23_b
Estrus			
Not in estrus	0		0
In estrus	0.05		0.07
Udder health			
Low (0 – 130 000 SCC/ml)	0	0	
Mid (130 000 – 300 000 SCC/ml)	0.04	-0.40	
High (>300 000 SCC/ml)	0.03	-0.22	
Claw Health			
No remark	0	0	
Remark	-0.02	0.17	
Residual Std. Dev	0.17	0.50	0.66

Table S6. Summary of the estimated regression coefficients and significance of the individual traits on time spent in the resting area. Results are shown for G1 and G2 in Farm A and Farm B in a Box-Cox transformed scale. Different characters in subscript represents significantly different values ($p < 0.05$) between the levels for each factor

Resting Area	Farm A		
Fixed Effects	G1 (n = 83)	G2 (n = 80)	Farm B (n = 201)
	Estimate	Estimate	Estimate
Parity			
1	0_a	0	0_a
2	$-3.46_{a,b}$	2.31	2.83_b
3+	$4.09_{a,c}$	3.63	4.32_b
Lactation stage			
Early (7-49 DIM)	0_a		0
Mid (50-179 DIM)	7.88_b	0	0.33
Late (≥180 DIM)	10.21_b	1.29	-0.22
Breed			
Crossbred	0	0	
Holstein	1.64	1.91	
Red Dairy Cattle	1.69	0.58	
Pregnancy status			
Open	0	0	0_a
Pregnant	1.33	-0.82	1.73_b
Estrus			
Not in estrus	0_a		0
In estrus	-2.68_b		-0.67
Udder health			
Low (0 – 130 000 SCC/ml)	0	0	
Mid (130 000 – 300 000 SCC/ml)	-3.41	4.35	
High (>300 000 SCC/ml)	-0.04	2.34	
Claw Health			
No remark	0	0	
Remark	0.76	0.59	
Residual Std. Dev	8.18	5.14	5.01

Supplementary Material 3

Distributions and correlations for the response variable *contact rate* when the distance threshold is changed from 2.5 m to either 1.5 m or 3.0 m, and the threshold for accumulated duration of contacts is changed from 10 minutes to 20 or 30 minutes are presented here.

The primary distance threshold of 2.5 m was chosen as it is approximately one body length and captures pairs of cows when one cow is standing in front of the other. The lower threshold of 1.5 m was chosen as it captures cows very close to each other. The longer threshold distance of 3 m was chosen because it encompasses the outer boundaries of two neighbouring cubicles and therefore captures all possible interactions between neighbouring cows in the cubicle area.

When the time threshold was changed from 10 minutes to 30 minutes for group G1 (Farm A) in the feeding area the correlation was 0.77 (Figure S15 panel A), and among the lowest correlations investigated. (Feeding area group G2 had a slightly lower correlation but several values equal to 0 for the 30-minute threshold caused difficulties in comparing model results since the Box-Cox transformation is not uniquely defined for outcome values equal to 0, see Figure S15 panel B.) In Table S1, the changes in p-values are compared for the two time thresholds. The results show that the same explanatory variables (date and parity) are significant at the 5% significance level, except for lactation stage and estrus where the p-value changed from 0.013 to 0.189 for lactation stage and from 0.002 to 0.069 for estrus.

When the distance threshold was changed from 2.5 m to 1.5 m for group G2 (Farm A) in the resting area the correlation was 0.83 (Figure S4) and among the lowest correlations investigated. In Table S2, the changes in p-values are compared for the two distance thresholds. The results show that the same explanatory variables (date and claw health) are significant at the 5% significance level.

Table S1. P-values from the ANOVA test for the relation between the contact rate and the individual traits in the feeding area for G1 in Farm A, using a 30 min threshold for the accumulated duration of contacts, compared to the results in the main text for a 10 min threshold.

	G1 (n=83) Farm A	
	Feeding Area	
Trait	30 min [a]	10 min
Date	< 0.001	< 0.001
Parity	< 0.001	< 0.001
Lactation stage	0.189	0.013
Breed	0.182	0.468
Pregnancy status	0.951	0.319
Estrus	0.069	0.002
Udder Health	0.847	0.967
Claw Health	0.229	0.109

[a] Two records where the contact rate was equal to zero were removed to enable a Box-Cox transformation.

Table S2. P-values from the ANOVA test for the relation between the contact rate and the individual traits in the resting area for group G2 (Farm A) using a 1.5 m distance threshold, compared to the results in the main text for a 2.5 m distance threshold.

	G2 (n=80) Farm A	
	Resting Area	
Trait	1.5 m [a]	2.5 m
Date	< 0.001	< 0.001
Parity	0.946	0.999
Lactation stage	0.825	0.646
Breed	0.791	0.815
Pregnancy status	0.382	0.583
Estrus		
Udder Health	0.748	0.936
Claw Health	0.034	0.008

[a] One record where the contact rate was equal to zero was removed to enable a Box-Cox transformation.

Distance threshold: 1.5 m

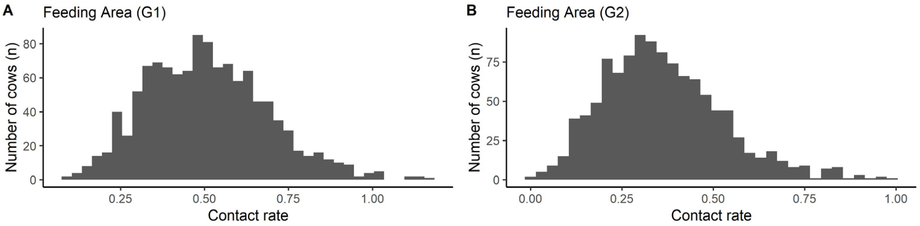

Figure S1. Distribution of the contact rate in the feeding area for the two groups in Farm A, with a distance threshold of 1.5 m: A) for G1, B) for G2.

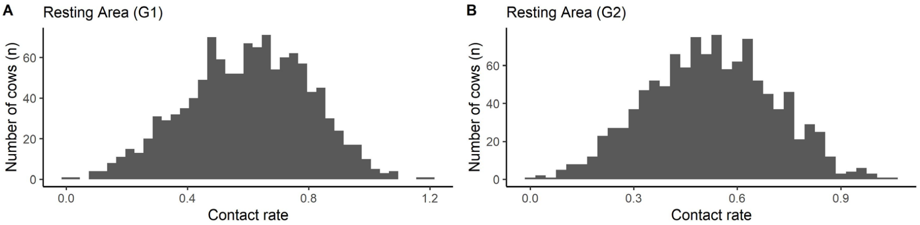

Figure S2. Distribution of the contact rate in the resting area for the two groups in Farm A, with a distance threshold of 1.5 m: A) for G1, B) for G2.

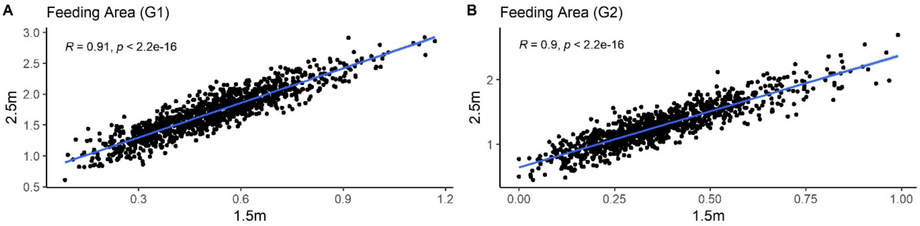

Figure S3. Correlation plot of the contact rate using either a distance threshold of 1.5 m or 2.5 m, in the feeding area: A) for G1, B) for G2.

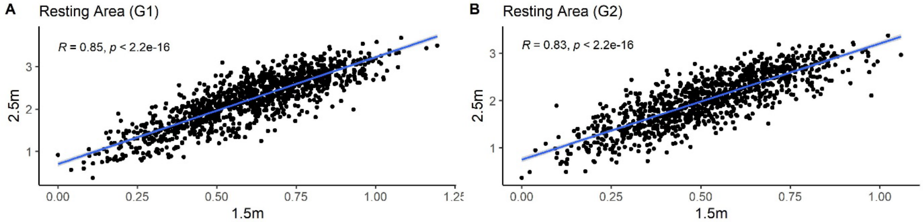

Figure S4. Correlation plot of the contact rate using either a distance threshold of 1.5 m or 2.5 m, in the resting area: A) for G1, B) for G2.

Distance threshold: 3.0 m

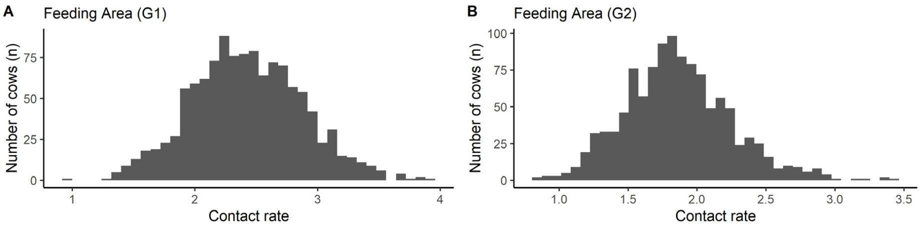

Figure S5. Distribution of the contact rate in the feeding area for the two groups in Farm A, with a distance threshold of 3.0 m: A) for G1, B) for G2.

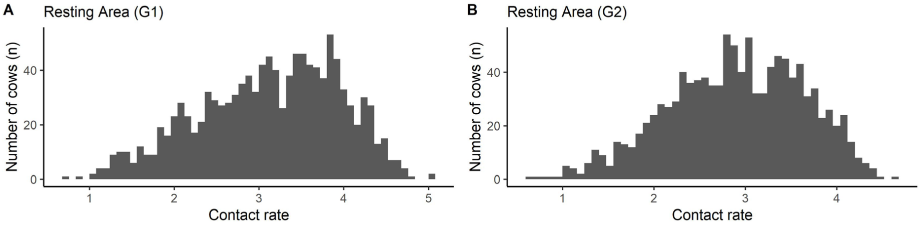

Figure S6. Distribution of the contact rate in the resting area for the two groups in Farm A, with a distance threshold of 3.0 m: A) for G1, B) for G2.

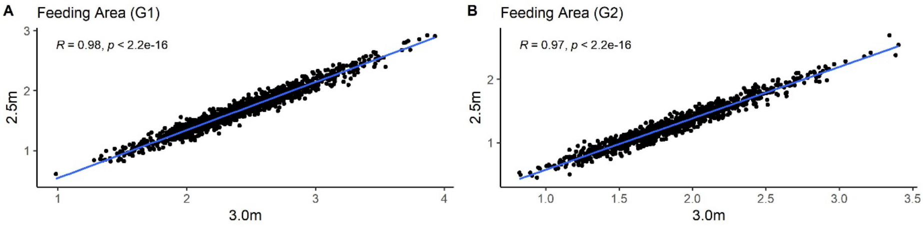

Figure S7. Correlation plot of the contact rate using either a distance threshold of 2.5 m or 3.0 m, in the feeding area: A) for G1, B) for G2.

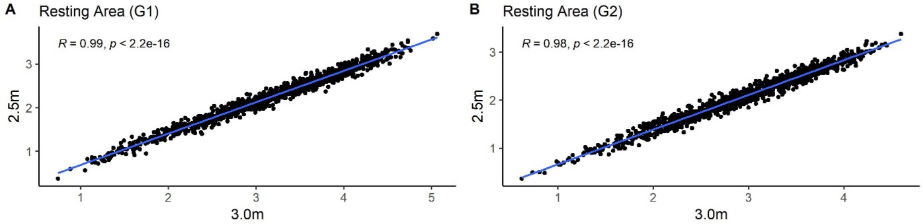

Figure S8. Correlation plot of the contact rate using either a distance threshold of 2.5 m or 3.0 m, in the resting area: A) for G1, B) for G2.

The accumulated duration of contacts: 20 Min

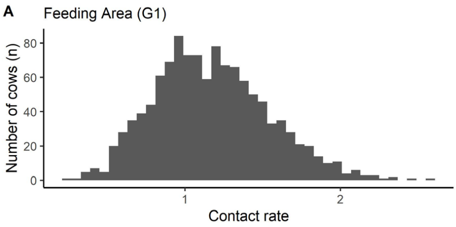

Figure S9. Distribution of the contact rate in the feeding area for the two groups in Farm A, with the accumulated duration of contacts set to 20 Min: A) for G1, B) for G2.

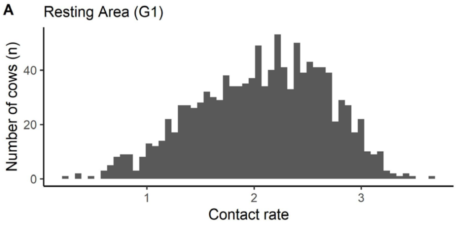

Figure S10. Distribution of the contact rate in the resting area for the two groups in Farm A, with the accumulated duration of contacts set to 20 Min: A) for G1, B) for G2.

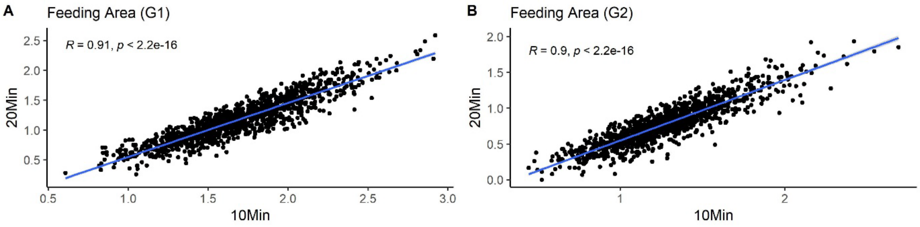

Figure S11. Correlation plot of the contact rate using either an accumulated duration of contacts threshold of 10 Min or 20 Min, in the feeding area: A) for G1, B) for G2.

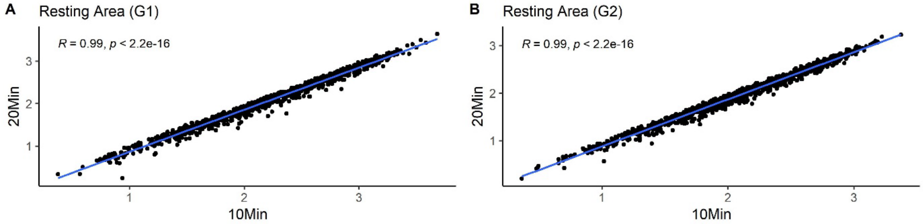

Figure S12. Correlation plot of the contact rate using either an accumulated duration of contacts threshold of 10 Min or 20 Min, in the resting area: A) for G1, B) for G2.

The accumulated duration of contacts: 30 Min

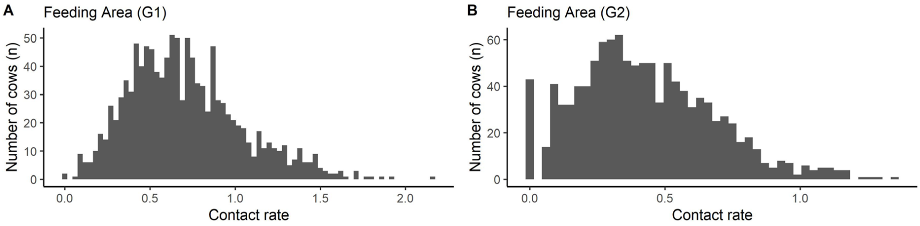

Figure S13. Distribution of the contact rate in the feeding area for the two groups in Farm A, with the accumulated duration of contacts set to 30 Min: A) for G1, B) for G2.

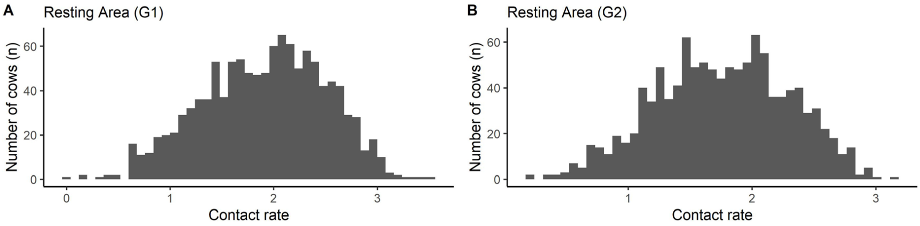

Figure S14. Distribution of the contact rate in the resting area for the two groups in Farm A, with the accumulated duration of contacts set to 30 Min: A) for G1, B) for G2.

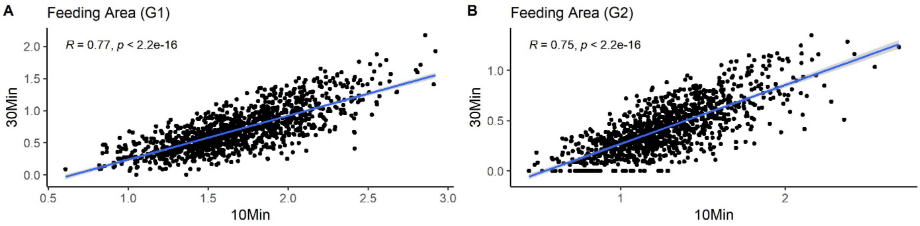

Figure S15. Correlation plot of the contact rate using either an accumulated duration of contacts threshold of 10 Min or 30 Min, in the feeding area: A) for G1, B) for G2.

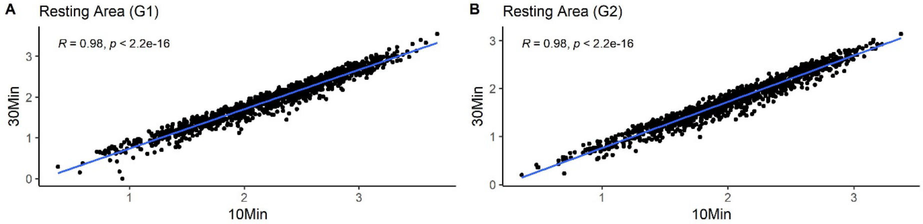

Figure S16. Correlation plot of the contact rate using either an accumulated duration of contacts threshold of 10 Min or 30 Min, in the resting area: A) for G1, B) for G2.

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Social interactions may impact an individual's productivity and can have a genetic component, so-called indirect genetic effects (IGE). This thesis explored the social interplay of cows using sensors and milking data and assessed the necessary information to include IGEs in breeding programs. Individual attributes were associated with social behaviour, and proximity contacts during milking influenced milk yield. Collecting intensities and contact direction was important for accurate IGE estimates. This thesis is a first step in approaching IGEs in dairy cattle.

Ida Hansson received her doctoral education at the Department of Animal Biosciences, Swedish University of Agricultural Sciences (SLU). She received her undergraduate degree from SLU and her MSc from the University of Edinburgh.

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