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Exploring social dynamics in cattle using a social networks approach

Francesca Pells Johansen

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Master by Research in the Faculty of Health Sciences August 2020.

Word count: 25 857

Abstract

Understanding complex social systems requires interactions to be studied as part of a network, not simply at the individual or dyadic scale. Domestic cattle are typically group-housed, thus there exists extensive research on their social patterns. Currently, the farming industry is pursuing information on optimal social conditions for cattle, and to meet that demand, it is necessary to gain a clear understanding of their social dynamics. Few studies have explored the social patterns of domestic cattle as part of a network and/or with a focus on cow-calf dynamics. Here, (i) the effectiveness of a positioning system was tested within a dairy cow barn, and (ii) social network analysis was utilised to quantify social dynamics in a naturally weaning beef herd. The positioning system produced data suitable for social network construction. Related beef cattle had more social connections to other related cattle than unrelated cattle did to other unrelated cattle ($p=0.00002$), and the focal cattle preferred related nearest-neighbours over unrelated nearest-neighbours ($p<0.00$). The social network of a related group of cattle remained stable over time as the weaning period approached ($p=0.007$), and there was no difference between the cow-calf associations before and after weaning ($p=0.49$). The current study shows that a positioning system proved effective in quantifying some aspects of social behaviour in dairy cows, that beef cattle preferentially associate with related animals over unrelated animals when allowed free access to both, that the study animals showed consistent social attachments, and that the calves in the group were important for the social network structure. The necessity of abrupt weaning in calves is challenged due to the strong preference displayed between related animals in the current study. The present study had limitations, most notably technical challenges and limited sample sizes, meaning that the implications of the study must be treated with caution.

COVID-19 statement

The beef cattle trial was interrupted by the COVID-19 outbreak and had to be cut short. The original plan was to continue data collection for another seven weeks, following the cows through the entire weaning period and past the point of the next calf being born, meaning the social dynamics could be further explored with new-born calves in the group. The cows used in the beef cow experiment were also fitted with proximity logger collars which, when the pandemic and subsequent lockdown occurred, I was unable to access as I would have had to 1) travel to the farm and 2) interact with people outside my household (farm staff). This was prohibited by both the government and the university at the time. If I had been able to access the proximity logger data, I would have had better data density as these loggers were running continuously. To date (25.05.2021), they have still not been collected from the farm.

Furthermore, my advisor with social network analysis experience had to refocus her work into primarily COVID-19 disease modelling and as such, had only a very limited availability to advise me on appropriate social network analysis. As a result of this I had to self-teach many of the analyses and concepts used in my thesis.

Acknowledgements

I wish to extend my deepest gratitude to my wonderful supervisors; Dr Suzanne Held, who provided invaluable advice and support, and whose expertise and feedback helped me bring my work to a higher level; and Dr Gina Caplen, who was essential to my positioning system study due to her practical problem-solving skills and advice. Furthermore, I would like to thank Dr Andrew Dowsey and Dr Ellen Brooks-Pollock for their guidance in data analysis, and Dr Joanna Hockenhull and Dr Mike Mendl for their guidance during my Annual Progress Review.

I would like to thank Dorit Albertsen for her extensive help and support, and for being so welcoming towards a house guest, along with Imber Albertsen and Lewis Holcombe for their transportation assistance. Additionally, I would like to thank Linda, Malcolm, Dara, and Mike of Harley Farms South for their help in cattle wrangling and assembling equipment.

I also want to thank Kate Robinson for her kindness in allowing equipment in her office, and I would like to thank the owners and employees of both Wyndhurst Farm and Harley Farms South for allowing me to carry out these studies. I would like to thank Andy Thurman and the rest of the employees of Omnisense Ltd. for their technical support and willingness to work through any arising problems.

I want to thank my friends, Holly Vickery, Jess Henderson and Alfie Joarder-White, for help with proofreading and for always listening when I ramble on about cows. I am also deeply grateful to my parents, Even and Becky Pells Johansen, for their love, support, and sympathetic ears throughout this experience. Finally, I would like to thank the cows themselves, for without them there would be nothing for me to write about.

Author’s declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: Francesca Pells Johansen DATE:05.09.2020.

Table of Contents

Abbreviations

SNA – social network analysis

BVD – bovine viral diarrhea

MYA – million years ago

mtDNA – mitochondrial DNA

DNA – deoxyribonucleic acid

GPS – global positioning system

SSSI – site of special scientific interest

TB – tuberculosis

TMR – total mixed ration

NN – nearest neighbour

FD – fixed device

MD – mobile device

SPA – special protection area

IBR – infectious bovine rhinotracheitis

ID – indentity

PCA – principal component analysis

CINNA – central informative nodes in network analysis

ANOSIM – analysis of similarities

R – related

C – control

IQR – interquartile range

SAC – special area of conservation

ha – hectare

AA – Aberdeen Angus

WP – White Park

Figure list

Table list

1.1 General introduction

One of the remaining challenges in behavioural research is integrating individual and group-level behaviour (Pinter-Wollman et al., 2014). To increase comprehension of complex social systems, social connections must be studied as part of a network, not just at the individual or dyadic scale (Krause et al., 2007). The majority of research within this topic provides evidence for non-random associations in both humans and non-human animals (hereafter animals). Domestic cattle are a social, typically group-housed species, thus there exists considerable research regarding their social patterns (e.g. Val-Laillet et al., 2009; DeVries et al., 2006). Very few studies have, however, documented social patterns as part of a network (e.g. Gygax et al., 2010; Boyland et al., 2016), with specific emphasis on cow-calf dynamics (Swain et al., 2015).

A clearer understanding of the dynamics of interactions between individuals may help interpret processes such as disease transmission (de Freslon et al., 2019), information transfer (Blonder and Dornhaus, 2011), and emotional contagion (Reimert et al., 2013), and has the potential to promote welfare in group-living animals (Krause et al., 2007; Pinter-Wollman et al., 2014). Increasing current understanding of social patterns and preferences of a species allows us to manage them in a way more suited to their optimal social conditions. The purpose of this review is therefore twofold. Initially, it focuses on the current state of knowledge regarding social dynamics in cattle, particularly with reference to highlighting the gaps in our understanding of (i) family dynamics, (ii) social preferences, and (iii) how human management might interfere with (i) and (ii). Secondly, it describes the use of social network theory and analysis in studying social dynamics, focusing on (i) the underlying theory of social network analysis (SNA) and how this may be utilised to track temporal changes, (ii) the advantages of using such an analysis, and (iii) how these techniques may be used within a welfare context.

1.1.1 Definitions

The "social structure" of a group or population is caused by "local interactions between individuals and their environment" (Krause et al., 2007), "social dynamics" are "the emergent effects of interactions within structured groups" (Clark and Fewell, 2014), and "temporal dynamics" are how these interactions change over time. "Natural behaviour" is often held as the gold standard for how animals should be permitted to behave in captive conditions (Spinka, 2006). Natural behaviour in this context is typically defined as how an animal would behave without human involvement. This is often thought to promote positive affective states and good biological functioning (Bracke and Hopster, 2006), although it is worth noting that there exists an ongoing debate regarding which 'natural' behaviours should be promoted within farming systems, e.g. flight behaviours are not thought to promote good welfare (as reviewed by Spinka, 2006). "Natural weaning" in this review is defined as a complete termination of suckling achieved entirely without human intervention in the weaning process (Johansen et al., *in prep*).

1.1.2 Social organisation in cattle

Optimal foraging theory is a model used in behavioural ecology which predicts how animals should prioritise energy acquisition, and states that animals will attempt to obtain a fixed amount of energy in the most time-efficient way, maximise total energy gained, or some combination thereof (Engen and Stenseth, 1984). The former suggests the need to conserve resources for other behaviours such as reproduction. Energy intake is determined by foraging whereas behaviours such as vigilance or reproduction determine energy expenditure (Boggs, 1992). Animals must balance these needs and allocate energy resources accordingly (Kie, 1999). Patterns of social organisation, as with many other behaviours, are typically shaped by such trade-offs and, in turn, can influence energy expenditure. For example, the odds of any one individual in a social group being preyed upon decreases as group size increases (Mooring and Hart, 1992). Jarman (1974) proposed a general framework of social organisation in ungulates based on the ecology of antelope. This framework matched five general sizes of ungulate to five feeding styles and five types of social organisation. Expanding on this, as differences in reproductive state, age and gender also shape biological needs, Rubenstein and Wrangham (1986) suggested that females are primarily selected to solve the ecological problems of resource acquisition and predator avoidance, whereas males are selected to maximise mating opportunities.

Therefore, according to Jarman (1974), female ungulate distribution tends to follow resource distribution, while male ungulate distribution tends to follow female distribution. The Class E detailed in Jarman (1974) includes the largest ungulates such as buffalo (*Syncerus caffer*). These animals tend to graze large amounts of low-quality forage, making resource defence unfeasible. According to this framework, females form stable herds with which males associate. Consequently, in the breeding season, males should be expected to roam amongst females, mating with any receptive females they may come across (male dominance allowing), or to position themselves in areas where female movements converge (leks) (Jarman, 1974). This framework has been confirmed by Lazo (1992, 1994, 1995) in feral cattle (*Bos taurus domesticus)*, where adults were sexually segregated outside of the breeding season, with defence of calves determining the social behaviour of females, and mating success the behaviour of males.

Due to the relative lack of literature detailing free-living, dynamic group behaviour in domestic cattle, to get a comprehensive image of bovine social organisation, information was drawn from research on cattle relatives such as European and American bison, along with literature on extensively managed cattle such as dairy cows, extensively managed animals such as rangeland cattle, and minimally managed animals such as feral cattle.

Most free-living bovids live in fission-fusion groups (Risk et al., 2009; Cross et al., 2005), where larger groups split into subgroups depending on environmental factors (Stephenson and Bailey, 2017).

Both extant species of bison; the European (*Bison bosanus*) and American bison (*Bison bison*), live in groups consisting of females, juvenile animals under three years old, and calves (Green, 1992a; Kemp et al., 2018), although European bison may also have transient males in the group outside the breeding season. These groups vary in size from a few to a few hundred animals (American bison) (Green, 1992b), although the mean size is 13 (Lott and Minta, 1993). European bison tend to live in groups of approximately 20 animals (Kemp et al., 2018). Bison groups are typically organised by dominance relationships. Male bison invest heavily in increasing their dominance during the mating season as the most dominant third of the males mate with two thirds of all receptive females (Lott, 1991). Bison breed seasonally with synchronised calving, which is thought to reduce predation pressure upon the new-born young (Green, 1992b). European bison bulls (4-6 years old) tend to form bachelor herds whereas mature males (7+) are solitary (Kemp et al., 2018).

An important thing to question at this point is the validity of extrapolating information from different species, i.e. comparing bison to cattle when farmed cattle are typically kept under very different conditions to most free-living bovids. The large-sized bovids (bovini tribe) which includes cattle, buffalo and bison, began to diverge approximately four million years ago (MYA), and mtDNA sequencing places the divergence between buffalo and bison/cattle at 1.7 MYA. Both cattle types (taurine (*Bos taurus)* and zebu (*B. indicus))* are descended from the now-extinct aurochs (*B. primigenius)* (Lenstra and Bradley, 1999). Despite cattle, European bison, and American bison, all being distinct species, there is evidence of interbreeding between the two bison species; this is likely due to human attempts to increase genetic diversity since both species have undergone population bottlenecks (Lenstra and Bradley, 1999). Additionally, a fertile American bison-cattle hybrid, the ‘beefalo’, is bred for meat (Porter, 2008). Nonetheless, the literature regarding bison is limited in the extent it can be extrapolated to indicate “normal” behaviour in domesticated cattle. For example, Kohl et al.’s (2013) study found ecological differences between cattle and American bison, with bison grazing and drinking less, and moving faster than cattle.

Interestingly, Hernandez et al. (1999) also found differences between the habitat use and behaviour of domestic and feral beef cattle in the Mapimí Biosphere Reserve, Mexico. In this study, feral cattle represented an ecotype better suited to arid environments than did domestic cattle. For example, feral cattle lived in smaller groups, travelled further and faster, and used more habitats than domestic cattle (Hernandez et al., 1999). As certain behaviours observed in feral cattle (Hernandez et al., 1999) are similar to behaviours observed in bison (Kohl et al., 2013), and the Mapimí Biosphere Reserve had already existed for 22 years (UNESCO, 2020) by the time of the Hernandez et al. (1999) study, one could speculate that the feral cattle had not lost much of the wild-type behavioural repertoire during domestication and were expressing it at the time of the study (such as in Wood-Gush’s seminal study on domestic pigs, see: Stolba and Wood-Gush, 1989). Nonetheless, it is essential to demonstrate caution when extrapolating data regarding cattle behaviour based upon the behaviour of even close relatives such as bison.

In cattle, there is clear evidence of social differentiation, meaning they assort non-randomly (Gygax et al., 2010; Boyland et al., 2016). For example, feral zebu cattle form groups based on kinship, likely due to high levels of philopatry within females (Reinhardt and Reinhardt, 1981a; Lazo, 1992). However, Lazo (1994) found that social affinity in feral cattle is related to age- and sex-class within herds. Resident herd females calved and reared their offspring in their own natal herds, which are maintained by long-term bonds. Male offspring were reared in the herd but tended to associate in clusters with other males upon maturation. Note that group sizes vary between studies, e.g. 19-57 (Lazo, 1995), 1-20 (Hernandez et al., 1999), which may be due to different environmental factors present at the study sites, in-turn influencing resource availability and limiting the number of animals a given area is able to sustain. The social structure seen in feral cattle is analogous to what is known of the social structure of their extinct ancestor, the aurochs (van Vuure, 2002).

Conversely, evidence suggests that in intensively managed dairy cattle, familiarity is the most important factor in establishing and maintaining social bonds. Gutmann et al. (2015) for example, report that recent shared experience has a weaker effect on social relationships than long-term familiarity in dairy cattle and that genetic relatedness had no effect on the observed social relationships. These results could be due to separation from kin at an early age, a common occurrence in many farming systems as a result of management protocols. Within intensively managed dairy systems, cow-calf pairs are generally separated within 24 hours of birth (e.g. DEFRA, 2003; von Keyserlingk and Weary, 2007). Nevertheless, calves remain motivated to form social bonds, as shown in Vitale et al.'s study (1986) on social behaviour in dairy calves. It observed a peak in mean time spent associating with conspecifics at 11-40 days old, and Raussi et al., (2010), concluded that preferential associations between dairy calves are present from 0.5 months of age. Despite the highly unstable social environment which characterises most dairy systems, those dairy cows with longer-term shared histories invest more time in associating with each other (Gygax et al., 2010).

These studies corroborate the older work of Reinhardt and Reinhardt (1981a) who conducted a longitudinal (3-year) study on cohesive associations ("close grazing partner" or "social licking partner") within a zebu (*Bos indicus*) herd. Crucially, as the cattle in their study were kept in a family group (in contrast to dairy cattle) their results showed that the preferential associations formed between the cattle were primarily between family members (Reinhardt and Reinhardt, 1981a). Interestingly, the mother-offspring associations were maintained for at least three years, showing that there is consistent attachment past the point of weaning and subsequent calving - even among the cow and male calves. Veissier et al. (1990) also demonstrated the persistence of mother-offspring attachment past the birth of a subsequent calf in domestic beef cattle (*Bos taurus*) at pasture, when the yearling calves were left in the herd.

As discussed above, most studies focus either on groups where cattle have restricted access to kin at an early age, or on groups where cattle exclusively have access to kin. Even in studies where a mix is present, for example, Veissier et al. (1990), the study focuses only on the cow-calf-yearling relationship and not on relationships the adult cows may have to other cows in the herd. Interestingly, in Lazo's studies (1992, 1994, 1995), the cattle had access to both kin and non-kin, and appeared to associate with kin, and by age- and sex-class within that framework. However, this was not the main focus of the research, and it is important to note that 30-50% of the calves born that year were removed from the herd at around six months of age. As shown above, there is a lack of unified understanding as to which social partners cows would choose if they were unrestricted by management systems.

1.1.2.1 Maternal behavioural influences

This section will focus on the aspects of maternal behaviour which may alter the social structure of a group. For example, how the cow-calf bond might change as the calf approaches weaning, or how the bond between cow and calf may be impacted when a new calf is born. Cattle can alter their social preferences according to maternal state variables, shifting from associating with pregnant cows when in a pregnant state to associating with maternal cows once they give birth (Swain et al., 2015). The initial isolation from the herd which occurs around parturition may not have a large effect on social organisation of the group in itself but one might speculate that this could create the illusion of subgroups or reduced contacts within the herd if the calving cow is particularly sociable or acts as a linking bridge between multiple subgroups within the herd.

Licking the new-born calf begins minutes after birth and is one of the key mechanisms promoting mother-offspring recognition and bonding (von Keyserlingk and Weary, 2007). Indeed, when permitted five minutes of contact, the resulting bond can withstand a separation of up to 12 hours (Hudson and Mullord, 1977). If prevented from licking her own calf, or if allowed to cross-lick other calves, there is a higher risk of calf rejection. Suckling typically occurs within a few hours of birth (von Keyserlingk and Weary, 2007), and is an important aspect of bonding as teat stimulation releases prolactin (Freeman et al., 2000) and oxytocin (Svennersten-Sjaunja and Olsson, 2005) in the cow, and oxytocin in the calf (Lupoli et al., 2001), which play important roles in promoting positive social interactions.

Formation of the mother-offspring bond affects the subsequent social structure of the group. Green (1992b) observed proximity maintenance (within 10m) in mother-offspring dyads of bison (*Bison bison*), concluding that both mother and calf exhibit "following" behaviour of each other. The findings indicate that the calf primarily maintains proximity in larger groups and the mother in smaller groups. Kemp et al. (2018) showed that within a group of 20 bison (*Bison bosanus*), four of the six subgroups were composed of mothers and their offspring. Furthermore, Perez-Barberia and Walker (2018) found that post-lambing, ewes (*Ovis aries)* were less social towards all others in the group in favour of their lamb and became more peripheral, presumably due to a trade-off between maternal care and social interactions.

The subsequent transition from suckling to full independence of the calves, again, may potentially influence the social dynamics in the herd. Weaning is multimodal in the sense that in addition to the removal of the calf's main nutrition source of is the loss of maternal care from the cow (Johnsen et al., 2015). Weaning usually occurs at 8-11 months (Reinhardt and Reinhardt, 1981b) although this can vary depending on the sex of the calf (Green and Rothstein, 1991) and experience of the mother (Green, 1990; Green et al., 1993). Nursing frequency and milk output of the mother gradually decreases, and she rejects increasingly more suckling attempts until weaning is achieved (Trivers, 1974; Johansen et al, *in prep*). Although many aspects of maternal care are terminated at this point, there is evidence of the dyad continuing to associate with each other (Reinhardt and Reinhardt, 1981a; Green, 1992a; Lazo, 1992).

Cow-calf interactions are a well-researched topic, and there is a clear understanding of, for instance, the positive effects of maternal care, or the negative effects of breaking the mother-offspring bond (see section 1.1.3.1). However, the extent to which the relationships within a group are affected by the addition or removal of a calf or calves, or if the patterns of social interactions around natural weaning could be used to identify the weaning window in cattle are not known.

1.1.3 Changes in social structure

Under natural conditions, group sizes self-regulate in the sense that individuals join or leave groups dependent on the net advantages (fission-fusion dynamics: Couzin and Laidre, 2009). Conversely, most farm animals do not have the level of autonomy necessary to self-regulate group size as this is generally organised to benefit production (Estevez et al., 2007). This means that animals have no opportunities to leave "costly" groups which can promote aggressive behaviours (Estevez et al., 2007). The natural mechanisms controlling variations in group size are natality rates, mortality rates, immigration and emigration (Sinclair, 1974; Teas et al., 1981; Bowler and Benton, 2005). Young males are typically the ones who disperse, often into bachelor herds where they develop their social skills (e.g. bison: Kemp et al., 2018). Group fission may also occur when animals differ in physiological capabilities (e.g. locomotion, metabolic). Animals moving at different speeds both incur a cost if they are obliged to synchronise their behaviour/speed (Seebacher and Krause, 2017), which often results in group fission dependent on activity patterns. As discussed in section 1.2, Jarman (1974) and Lazo (1992) found that females are motivated to maximise feeding opportunities, whereas males are concerned with getting females. Another example in cattle is calf creches, where the mothers leave their calves in a group with a “babysitter” while they graze (Wood-Gush et al., 1984).

Intensively farmed cattle are usually kept in artificial groups which are manipulated for husbandry purposes, such as milk production (Grant and Albright, 2001), dietary requirements, or reproductive status (Overton and Waldron, 2004; Roche, 2006). This results in many regroupings where animals are repeatedly added to or removed from groups (Torres-Cardona et al., 2014). Regrouping often produces a short-term increase in agonistic behaviour during re-establishment of the dominance hierarchy which causes distress and can provoke physiological responses such as weight loss (dairy: Torres-Cardona et al., 2014; beef: Leslie et al., 2015). In dairy cattle these adverse effects last between 5-15 days and include reduced feeding and rumination, and increased agonistic behaviours such as threats, butts and fights (Raussi, 2005; Schirmann et al., 2011).

It is likely that health status can also affect the social structure of a group. When confronted with a health challenge, animals show a common suite of behaviours termed “sickness behaviour” regardless of the type of process affecting them (e.g. fungal, bacterial, viral). These behaviours include reduced exploration, reduced feeding; sexual; and social behaviours, poor learning and cognition, and anhedonia (Mazuco et al, 2019; Hart, 1988). These behavioural alterations may be exhibited prior to clinical signs of sickness and as such could have diagnostic value (Szyszka, 2013). For example, Neave (2019) saw behavioural changes in metritic dairy cows three days before they were clinically diagosed. Notably, the affected cows performed worse than previously in competitive social situations (competition at feed bunk).

Fluctuations in group size are one of the key factors regarding alterations in social structure, however, many internal (within-group) influences are present, which also affect social structure. For instance, cows in oestrus typically engage in high levels of urogenital investigation of other cows (de Freslon et al., 2019), thus altering their contact patterns within the group. Moreover, during the breeding season, bulls will keep conspecifics away from cows as they attempt to mate, interrupting spatial relationships with calves (Green, 1992a). Juvenile ungulates are typically more gregarious and less selective in their associations (e.g. giraffes: Carter et al., 2013), causing their sociability to be very high. This can have an indirect effect upon the perceived sociability of their dams. Kemp et al. (2018) found that the within-group influence of lactating bison mothers dropped significantly upon exclusion of their calves from the data analysis, therefore, one would expect to see alterations in the social network structure of cattle during the weaning period. To date, no studies have explored this.

1.1.3.1 Human-induced changes in maternal behaviour

When kept at stocking densities of 0.3-1cow/ha, pregnant cows will increase inter-animal distances, likely attempting to isolate themselves for parturition (Lidfors et al., 1994). This behaviour is less evident in cows group-housed indoors or kept in stocking densities of up to 3 cows/ha (Lidfors et al., 1994). Disrupting pre-birth distancing may interfere with mother-offspring bonding, as other cows may engage in cross-licking the calf, promoting calf rejection by the mother. In fact, some authors believe that isolation is a mechanism evolved to prevent disruption of early cow-calf bonding (e.g von Keyserlingk and Weary, 2007).

Most domestic bovids are weaned earlier and more abruptly than would occur naturally (e.g. buffalo: Aref et al., 2016; cattle: Weary and Chua, 2000). Upon cow-calf separation, a strong behavioural (increased activity and vocalisations) and physiological (increased plasma cortisol levels and heart rate) response is triggered (Enriquez et al, 2011; Lefcourt and Elasser, 1995) which increases in intensity if the dyad are permitted prolonged contact prior to separation (von Keyserlingk and Weary, 2007). Abrupt weaning can be extremely challenging for a commercial calf as they often experience multifactorial sources of stress, e.g. the loss of both nutritional and social support from the dam in combination with placement into a novel social group (Enriquez et al., 2011; Taylor et al., 2019). If grouped together at weaning, calves form strong bonds between themselves, which is typically demonstrated by a higher number of social encounters between abruptly weaned calves than among their suckling counterparts (Veissier et al., 1989).

As discussed above, abrupt weaning changes the social network in which calves find themselves. The dominance hierarchy will require re-establishment in an artificially constructed population lacking adults (Taylor et al., 2019). Little is known, however, regarding the potential impact of artificially removing the calves on the social network structure of the adult cows. Associations may shift with changes within the group such as the presence or absence of certain group members (e.g. calves), and are as such, context dependent. As mentioned in section 1.2.1, Swain et al. (2015) found that cows switched from the “pregnant” to the “maternal” group instantaneously upon calving, but also noted this shift was preceded by a general trend towards the “maternal” group over 50 days pre-parturition. Newly born calves have the greatest need for support, and the cows in this study tended to associate most with cows who had calves in the same stage of development, which implies that this switch includes an element of reciprocity. Thus, the ease with which cows integrate into new groups in the absence of maternal reciprocity may be called into question.

1.2 Mapping changes in social dynamics in animals using social network analysis (SNA)

This review turns now to focusing on the ways in which SNA can be utilised within animal behaviour and welfare science research, and how SNA might be used to answer questions highlighted in Section 1, such as how the social network of a group might change over time as a calf approaches weaning.

SNA characterizes the patterns and quality of interactions amongst entities (e.g. groups, individuals, websites etc.) (Makagon et al., 2012). Social networks can be constructed using inferred interactions (e.g. proximity, synchrony) or definite interactions (e.g. allogrooming, bites etc) (Croft et al., 2011). Inferred interactions are easier to track with the currently available technology (GPS, proximity loggers) but also run the risk of "gambit of the group" where individual A and individual B may be in close proximity purely due to the fact that they both associate with individual C (Kemp et al., 2018). Definite interactions are more valuable in the sense that they represent clear ties between individuals, however, there is currently have no way of quantifying them using technology, particularly in free-living animals. Additionally, many species are "undemonstrative", meaning the prevalence of affiliative behaviours are typically low. For example, social licking is a positive social behaviour in bison, but this behaviour is only seen between a bison and her calf (Kemp et al., 2018). Therefore, the purpose of this section is to discuss methods, past and present, of data collection on inferred measures/association data, and how SNA may be used to investigate changes in social interactions in a group.

The basic methodology employed to collect association data has remained fairly constant since SNA was first applied within the context of animal behaviour. For example, primatologists used similar conceptual frameworks as in present-day SNA to construct 'sociograms' (a visualisation of the social interactions within a group) from the early 1960's (Brent et al., 2011). Association data are typically collected using either locations of animals then inferring associations from that data or assessing inter-animal distance. These basic measures are widely used, but the methods used to collect this information have become more sophisticated over time. Despite the availability of recent technological devices such as proximity loggers and GPS trackers, many authors still choose an observational approach (e.g. Kemp et al., 2018).

Proximity studies use a predefined distance between animals to infer a tie. Methods used in the past include "animal-body lengths" as a 'standardised' measure of when an animal is near another (e.g. Green, 1992a). Proximity can also be assessed through video footage. Michelena et al. (2008), for example, investigated cohesion in groups of merino sheep (*Ovis aries)* by video recording groups of varying size and sex composition, and extracting behaviour, orientation and location of each sheep at 1-s intervals. The location data were then used to calculate nearest-neighbour and mean inter-individual proximity. The authors showed that sheep were more aggregated than predicted, and that their social cohesion is influenced by social affinity and activity synchrony. In the last five years, proximity loggers have been increasingly utilised in animal research. Proximity loggers are devices which simultaneously transmit and receive radio signals from other devices within a predefined range (Boyland et al., 2013). Examples include studies such as Swain et al. (2015), who explored the effects of maternal state on association strength between cattle, concluding that cattle with similar maternal states (e.g. calves of the same age) tended to associate more.

Location mapping can be used exclusively on a focal animal; e.g. Hernandez et al. (1999), equipped eight cows from eight different social groups with radio collars in order to map habitat use and behaviour of cattle in the Mapimí Biosphere Reserve, Mexico. The study reports group sizes and that

“The collared animals remained in their respective groups during the study” but does not define the proximity criteria used to classify group membership (Hernandez et al., 1999). Location information may also be collected by observing entire groups. Stephenson et al., (2016), examined associations between rangeland cattle in groups of varying size by collecting association data for every dyad in each group (within 30m) and pasture section by visual observations. They concluded that group size was a key factor in social association patterns, as the cattle in this study only associated non-randomly in groups larger than 40 (Stephenson et al., 2016).

Location can also be derived from physical observations where animals are marked on a map (Stephenson et al., 2016), from video footage (Michelena et al., 2008), or from GPS data. Ganskopp and Bohnert (2009), for example, investigated grazing patterns in cattle, using GPS collars to track cattle movement and activity. Results suggested that forage quantity and quality were important factors regarding the spatial distribution of grazing cattle. An alternative to GPS systems is local positioning systems. For instance, Barker et al. (2018) tested a novel sensor system (Omnisense Ltd., UK) combining local position and activity data to explore the effects of lameness upon feeding behaviour in dairy cows: the sensor system proved effective in detecting differences in feeding behaviour associated with lameness.

Notwithstanding the range of inferred data used, and of the increasingly automated data collection methods available, many social network studies in animals have focused on providing a “snapshot” of the social structure. In other words, they have described an animal group’s network topology at a certain point in time. However, animals often alter their social affiliations in response to internal or external factors. Therefore, a static approach to SNA may be confounded by key individuals being in an abnormal state (e.g. oestrus, migration, sickness) (de Freslon et al., 2019; Farine, 2017). One way to address this potential weakness is to consider both spatial attributions and temporal dynamics of animal social networks. Including temporal dynamics can help to better understand and identify which factors influence sociality (Pinter-Wollman et al., 2014). Temporal dynamics, despite their potential for understanding aspects of social organisation including the prediction of future states (McDonald, 2007), group stability (De Silva et al., 2011; Holekamp et al 2012; Hobson et al., 2013; Boyland et al, 2016; Stanley et al, 2017; Blaszczyk, 2018), and the transmission of information or disease (Blonder and Dornhaus, 2011), have not been widely investigated; the very few empirical studies available have mostly focused on wild animals.

One seminal study demonstrating the predictive power of including changes over time is by McDonald (2007). It showed that early connectivity (i.e. how well-connected one is to the rest of the population) of wild male long-tailed manakins (*Chiroxiphia linearis)* predicts future social success on average 4.8 years later. The interactions between males of this species change between seasons but once an “alpha-beta” pair is established, this affiliation can be long-lasting, likely due to their dualmale song and dance courtship displays (Trainer and McDonald, 1995). Typically, only very few males (alphas) have high copulatory success; the males with the best chance of becoming an alpha are those with the best connectivity in their early (1-6 years old) life, while the odds of rising socially increased five-fold for each unit increase in early connectivity (McDonald, 2007). Temporal dynamics were investigated by constructing a social network for each of five consecutive 2-year blocks and connectivity measures of males in each subsequent network were then compared to their eventual social status and courtship success. This study illustrates the importance of temporal dynamics within this context, as one often cannot fully explain an individual's present success without referencing their social history (McDonald, 2007).

In another study of temporal change in social networks, Stanley et al. (2017) investigated social stability in semi-feral Welsh Ponies (*Equus caballus)* using a 3-year dataset split into seasonal blocks. They concluded that the associations between female ponies were interannually stable but had seasonal fluctuations such as increased gregariousness during the mating season. This line of questioning helps understand how a social group as a unit, and ultimately the individual group members, respond to factors influencing the cost-benefit trade-off of groups such as environmental variability.

Individual consistency in social position can also help comprehension of the evolution and ecology of social behaviour and structure. Blaszczyk (2018), for example, investigated to which degree individuals remain in the same social position in wild vervet monkeys (*Chlorocebus pygerythrus)* across both time and changing environmental conditions. Three grooming networks from different seasons were compared to determine the repeatability of network metrics such as eigenvector centrality, i.e. the influence of an individual within the group (see section 2.2), and clustering coefficient (i.e. how likely conspecifics with which a focal animal is associated with, also sociate with each other, see section 2.2). The effects of dominance and sex upon repeatability (as a measure of consistency) of these metrics were also controlled for. The study found consistency of social position for the majority of direct connectedness measures (e.g. how many animals associate with the focal animal) over time, but indirect connectedness (i.e. the number of animals connected by an individual) was overall less repeatable, and dominance had no effect on direct nor indirect connectedness (Blaszczyk, 2018).

An example from domestic cattle is Boyland et al.'s study (2016) which described the social network topology of a herd of dairy cows. When network stability over time was assessed by comparing four one-week blocks, only 17-57% of the network connections and structure from one week was also present the following week, suggesting a considerable change in social structure between weeks (Boyland et al., 2016).

Utilization of temporal dynamics could allow, for example, tracking of changes in social associations as weaning approaches, prediction of parturition, or perhaps eventually use of social organisation as a predictor for weaning.

1.2.1 Why social network analysis?

The mathematical theorem Network Theory forms the basis of SNA. Within this theorem, a graph is a visualisation of the social relationships present within a group. These are typically displayed as a picture showing distinct shapes (nodes or vertices) linked by lines (edges or ties) (Wey et al., 2008). Nodes are network components representing individuals (sometimes groups). Edges represent relationships between the nodes in social networks, these can be any type of social interaction; definite or inferred, positive or negative (Wey et al., 2008).

SNA offers several advantages in comparison to traditional methods (e.g. measuring group size, mating patterns etc.). Firstly, SNA provides quantitative, standardisable, measures of sociality which have the potential to be used to describe and compare social complexity across taxa (Wey et al., 2008). Using SNA as a tool to describe animal social structures provides a powerful framework with metrics quantifying social structure at different organisational levels (e.g. individual, group, population) (Croft et al., 2011). The relevance of indirect ties (i.e. friends of friends) are an important assumption of SNA (Makagon et al., 2012) as they can, for example, influence rates of information or disease flow through any given node. Comprehension of the factors influencing flow (transfer of disease, information etc. along the edges of a network) is crucial to understanding processes like emotional contagion and disease spread (Croft et al., 2011). SNA can also provide objectivity in determining dominance roles, and centrality measures which are applicable to identification of key individuals in animal social groups (Wey et al., 2008). SNA can also be utilised to calculate the risk of infection based on animal attributes such as body score or gender, and could even be employed to target key animals to treat to prevent the further spread of disease

Secondly, useful variables derived from this approach include “edge density”, which is a gauge of how well-connected a network is; it is expressed as the proportion of possible connections in a network that are actual connections (Darst et al., 2013). For example, if each node was connected to all other nodes, the edge density of the network would be 1. “Clustering coefficient” or “Transitivity” is derived from local connections around each node and is a measure of average local cliquishness in the network (Farine and Whitehead, 2015). It is similar to edge density, but on a local scale; addressing the likelihood of a given node’s neighbours also being neighbours. However, it is important to note that network size limits the detectability of these metrics, meaning that smaller groups are generally less likely to show significant levels of Transitivity (Wey et al., 2019).

“Node Degree” (often simply “Degree”) is a tally of the direct ties leading to an individual (Krause et al., 2015). This has implications for the importance of a given animal as a point of disease transfer or for group stability. For example, Corner et al., (2002) experimentally infected brushtail possums (*Trichosurus vulpecula)* of differing centrality with *mycobacterium bovis* (Bovine TB). Targeted infection of animals with high centrality resulted in 30-63% transmission through their social group, contrasted with only 9% transmission when infections were targeted to random animals. Additionally, secondary infection was more likely between group members with higher centrality scores (Corner et al., 2002).

"Eigenvector centrality" differs from Degree centrality as it takes the centrality of a node's neighbours into account (CentiServer, 2020). A nodes eigenvector centrality is higher if its neighbours also have high eigenvector centrality; an individual with 10 links to well-connected individuals would have higher eigenvector centrality than an individual with 10 links to poorly connected individuals. It can be used as a measure of the influence a node has upon the network during, for example, collective decision-making (Sueur et al., 2018). "Modularity" is a measure of the extent to which clusters or communities are better connected within themselves than to the remainder of the network (Newman, 2006a, b). Kemp et al., (2018), for example, found that bison social network structure shows modularity; specifically, the majority of subgroups were composed of cow-calf pairs or groups of a cow, her calf and her subadult offspring from previous years. "Temporal stability" examines whether the network structure remains consistent over time (e.g. Boyland et al., 2016), and is a measure of social stability within a group.

Social behaviour has been researched across taxa, although the earliest studies typically either produced dominance relationships or examined group composition and did not construct social networks (Wey et al., 2008). A notable exception here includes the work pioneered by Donald Stone Sade, who applied a network-based technique (sociograms) to visualise grooming associations within a group of rhesus macaques (*Macaca mulatta)* (Sade, 1965), which was later applied to several other species of primate (e.g. vervet monkeys: Fairbanks, 1980; patas monkeys: Nakagawa, 1992). Social network theory is flexible and has been utilized to ask questions about species as diverse as bown trout (*Salmo trutta)* (Tentelier et al., 2016), flamingoes (*Phoenicopteridae)* (Rose and Croft, 2017), and primates (Berman et al., 1997; Brent et al., 2017), as well as domestic species such as pigs *(Sus scrofa)* (Buttner et al., 2015) cattle (Boyland et al., 2016), and fish (Kleinhappel et al., 2016).

1.3 The current project and future applications

Understanding social structure and the functions and mechanisms which underpin it is central to understanding of many areas of biology, ecology, and welfare (Croft et al., 2011; Kleinhappel et al., 2016). An individual's behaviour influences and is influenced by the patterns of social interactions exhibited by their conspecifics (Makagon et al., 2012). Social network connections have the capacity to influence fitness, for example through modifications of local social networks to improve mating success (Wey et al., 2008), or access to higher quality feed (Wey et al., 2008). The pattern of an animal's interactions, and by extension the local and global patterns produced by these have implications such as disease spread and population genetic structure on the population level (Croft et al., 2011). Very few studies currently focus on SNA in captive animals towards the end of understanding which social factors and social changes may impact welfare (e.g. hens: (Abeyesinghe et al., 2013); dairy cows (Boyland et al., 2016); dairy calves (Bolt et al., 2017)). Despite their scarcity, they establish the importance of SNA within animal welfare science.

Animal welfare research has conventionally concentrated on minimising the prevalence of negative experiences for animals under human care using frameworks such as the five freedoms (FAWC, 2009). However, FAWC (2009) also argued that aspects of the five freedoms are unobtainable (i.e., an animal might never be free from discomfort but instead experience minimised discomfort as during pregnancy checks), and instead proposes a "good life" framework where animals can have "a life not worth living", "a life worth living" and "a good life". This approach integrates both negative and positive experiences throughout an animal's life. Identifying positive indicators of welfare can be both challenging (e.g. quantifying positive affective state) and time-consuming (e.g. manually logging specific behaviours such as social licking, play) (Vigors and Lawrence, 2019); therefore, when compared to the wealth of empirical studies on negative welfare indicators in cattle, there are relatively few detailing positive welfare (Napolitano et al., 2009). Dawkins (2003) suggests assessing animal welfare in the context of two key questions: "1. Are the animals healthy? 2. Do the animals have what they want?". This approach suggests using the environment as a preference test e.g. determining natural preferences from spontaneous decisions animals make within their environment. This can also be applied to the social environment; if a species maintains a maximally spaced distribution they likely do not 'want' to associate with conspecifics, whereas if the spatial distribution is clumped one could assume they 'want' to be close together. Furthermore, in known social species such as cattle, one can assess the social association patterns present in a population and use this information to make inferences regarding the value placed on specific social partners within a group. However, it is also important to reiterate that when using social associations measured by inter-animal distance, the quality of these associations is not quantified (see section 1.2)

In regard to welfare, most domestic animals face similar types of challenges regardless of species (e.g. disease, injury, social stress). Identifying specific network patterns or roles has the potential to enhance welfare in a suite of ways. For instance, one option might be identifying avenues to improve welfare e.g. through social buffering. Towards this end, Bolt et al. (2017) explored social networks, production, health and stress at weaning in pair-housed dairy calves. The presence of a social companion is thought to help gregarious species cope with challenges, and the social motivation of calves has been well-documented by their willingness to "work" for access to a social companion (Holm et al., 2002). Bolt et al. (2017) report fewer vocalisations from pair-housed calves than from their singly housed counterparts after weaning, indicating that a conspecific acted as a source of social support. Building on this, future studies could measure the modularity of animal groups and move cohesive clusters together, potentially ameliorating the stress of regrouping.

In addition, one could identify aspects of social dynamics underlying positive or negative welfare. Gygax et al., (2010), for instance, quantified the socio-spatial relationships of six herds of dairy cows and found that dairy herds are generally characterised by one connected component which includes the majority of the herd. Within dominance networks, cohesive and well-connected groups tend to be more stable as information travels, or flows, more efficiently through the network (McCowan et al., 2008). This means all the group members are in agreement regarding the hierarchy and as a result, less conflict occurs. The connectivity seen in dairy herds (Gygax et al., 2010; Boyland et al., 2016) may lead one to believe that they might be hierarchically stable, however, this is likely not the case due to the innate instability of group composition caused by management routines within dairy systems. Prospective research might use social network theory to explore these factors in more detail and investigate ways of improving group cohesion.

SNA could prove useful in the identification of individuals who contribute to good or bad welfare since it is uniquely suited to quantifying patterns of associations relating to welfare and identifying individuals in different social roles, particularly in large groups where traditional focuses on direct interactions yields limited information. Flack et al. (2005) explored the indirect role conflict management mechanisms have upon animal societies. They observed heterogeneity in conflict managing behaviours in a group of pigtailed macaques *(Macada nemestrina)*. Individuals responsible for conflict resolution were removed from the social group in a way which emulated natural processes of predation or disease. Knockouts resulted in network destabilisation by increasing mean levels of conflict and aggression. The three knocked-out animals were all adult males who received large amounts of subordination signals (silent bared teeth displays) from group members in peaceful contexts (Flack et al., 2005). Cattle do not have subordination signals *per se* and instead tend to simply avoid dominant individuals or defer to them by turning away. Additionally, studies of agonistic and affiliative behaviours in dairy cows found no correlations between agonistic and affiliative social networks (Foris et al., 2019), meaning it is very unlikely that cattle “reconcile” after conflicts by engaging in affiliative interactions as is seen in other ungulates such as domestic goats (*Capra aegagrus)* (Schino, 1998). Although the identification and targeted management of key conflict managers within a group has the scope to improve welfare within unstable groups, in cattle, it may be more appropriate to instead identify disproportionally aggressive or despotic individuals for targeted management.

Finally, most epidemiological models assume that animals associate randomly, however, in real life animals tend to mix preferentially (Wey et al., 2008). Both the presence of a pathogen within a group (see section 1.1.3, sickness behaviour: Neave et al., 2019) and transmission of a disease through a group can be measured by SNA. Higher centrality values often increase the likelihood of an animal being infected with pathogens (see section 1.2.2, possums: Corner et al., 2002, cattle and badgers: Böhm et al., 2009). Therefore, the collection of SNA-derived information from central individuals could be utilised for the targeted management of susceptible individuals.

The examples outlined above (pathogens, social instability, stress) can all result in decreased productivity in farm animals (Boissy and Le Neindre, 1997; Kossaibati and Esslemont, 1997; Estevez et al., 2007), whereas reduced social stress has been found to improve productivity (dairy cows: von Keyserlingk et al., 2008). Moreover, there is currently a growing demand for information on optimal social conditions, such as stocking density, group size and group composition in commercial cattle strains (Bennett, 1996; Boyland et al., 2016). In order to answer these questions, it is important to first accurately measure and understand their social dynamics (Croft et al., 2016).

The above outlines compelling reasons to study social dynamics in animals, and the current study intends to (i) test a positioning system in a commercial dairy herd for use in social network construction, and (ii) track changing social dynamics in a natural weaning herd of beef cattle. Social networks in cattle has been studied before, but not (to the best of the author’s knowledge) in a natural weaning herd.

1.4 Research aims:

- Determine the effectiveness of a positioning system for use in constructing social networks and quantifying social dynamics in (small) groups of cattle
- Compare and contrast association patterns of a related group of cattle (n=15) managed in a natural weaning system to patterns of unrelated (yet familiar) control individuals (n=15) to assess if unrelated and related cows associate differently
- Investigate whether cattle (sample subset of herd; n=30) within a suckler beef herd (n=268) have preferred social partners
- Determine whether the social network structure of a related group of cattle changes as the calves in the group (n=6) approach weaning

2. Determining the effectiveness of a positioning system for use in constructing social networks in (small) groups of dairy cows

The social environment of dairy cattle is a well-researched topic, likely due to the inherent social instability present within most dairy systems. Regrouping of dairy cows is a common component of husbandry protocols, with cows usually regrouped at least four times per lactation (Schirmann et al., 2011). Dairy units generally calve throughout the year, meaning there is a lack of synchrony regarding the movements of the cows between social groups, and that cows are exposed to a new group of individuals with each regrouping (Schirmann et al., 2011). This regrouping typically results in social instability (Boe and Faerevik, 2003; Estevez et al., 2007) as the cows constantly need to re-establish the dominance hierarchy. The resulting instability can lead to reduced milk production (Hasegawa et al., 1997), increased agonistic interactions (von Keyserlingk et al., 2008), decreased feeding time, rumination and allogrooming (Hasegawa et al., 1997; von Keyserlingk et al., 2008; Schirmann et al., 2011), and increased standing (von Keyserkingk et al., 2008).

Consequently, there have been many attempts to ameliorate these effects. By, for example, introducing cows in pairs which reduced agonistic interactions by 50% (Neisen et al., 2009b). Other strategies include introducing cows at different times of day as in Boyle et al.'s study (2012). It found that dairy cows showed fewer negative effects following regrouping in the evening rather than the morning. Alternative strategies include seeing if cows will eventually habituate to regroupings and reduce their agonistic behaviour accordingly. For example, Raussi et al., (2005) repeatedly regrouped pairs of dairy heifers a total of 16 times over 11 weeks. Agonistic interactions were consistently induced by the regroupings, and interestingly, the heifers showed the lowest amount of agonistic interactions after the seventh regrouping.

Nonetheless, despite the general social instability in the management of dairy cows, there is strong evidence of dairy cows maintaining relationships with preferred social partners. For example, Boyland et al, (2016) found compelling evidence in their study that dairy cows assorted by lactation number, and not as compelling evidence of assortment by breed, gregariousness, and milk production. Furthermore, Gutmann et al., (2015) found four variables predicting a preferred partner; "synchronised group entry", "shared dry period", "shared youth" and "shared adult experience".

Currently, there exists high levels of farmer interest (Boyland et al., 2016) and public pressure (Weary and von Keyserlingk, 2017) to create optimal welfare environments for farmed cattle. To be able to make decisions about optimal social conditions for cattle, a better understanding of their social patterns is required. Most traditional studies of social behaviour can be time-consuming (e.g. using observational approaches or video cameras) or may not sufficiently capture the dynamism of the social group as members are added and removed. SNA is a good way into this line of questioning.

The use of sensors to track and monitor animal behaviour is increasing, with companies such as Sirtrack Ltd (New Zealand) and Noldus (the Netherlands) developing new products for use in animal behaviour research. Positioning devices have been successfully utilized to construct social networks in the past, most notably by Gygax et al. (2007, 2010), where socio-spatial information was collected in six dairy herds using a radar-based positioning system. Their results showed that groups of dairy cows typically consist of one connected cluster with strong attachment and avoidance relationships. The Omnisense local positioning system (Omnisense Ltd, UK) is a fairly recent addition to the market, having rarely been utilised on farms before. For example, Barker et al.'s study (2018) used the Omnisense positioning system combined with accelerometers to measure feeding behaviour towards the end of identifying lame dairy cows. Position and activity data of 19 cows (ten lame, nine non-lame) were collected over five days on a commercial dairy farm. It found that lame cows had significantly lower mean feeding duration than non-lame cows.

Here, a study was conducted exploring aspects of social behaviour in dairy cattle and testing a positioning system. A positioning system was used to monitor the location of a sample of dairy cows with the aim of (i) testing the system's effectiveness in collecting data appropriate for use in constructing social networks (if successful, the sensors were to be used in the larger beef study (Chapter 3)), and (ii) test if the cows in the study assort by similar traits, specifically age, lactation number or recent shared experience (e.g. Gutmann et al., 2015; Boyland et al., 2016). Given the results of previous work the current study aimed to demonstrate that:

1) the Omnisense positioning system will demonstrate potential for use in social network analysis of intensively housed livestock

2.1. Methods

Ethics

These studies were approved by the University of Bristol's Animal Welfare Ethics Review Board. Handling and collar deployment were coordinated with management practices on farm to reduce stress.

2.1.2 Methods

Animals

This study was undertaken on a subset (n=5) of a dairy herd (n~200) from a commercial dairy farm owned by the University of Bristol, UK. The entire herd was kept in a freestall barn (33.95m x 115.8m). The cows were fed a total mixed ration (TMR) once a day and were milked twice daily (05.00h and 14.00h). The average yearly milk yield for this herd is 11 000L. Cows from the low-yield group (n~80) were used in this study and were kept in a 60m x 14m area within the main barn, with access to 93 lying stalls.

Pilot study

A small pilot study was carried out to inform which cows should be collared in the positioning sensor study (see appendix).

Positioning sensor study

Study cows were selected to ensure they would remain in the low-yield group throughout the 2-week study period (December 2019) and cows of the same age (three years old: n=2, five years old: n=3) were selected based on the results of study 1 (Table 1). These cows were fitted with collars containing the Omnisense positioning devices. These collars were similar to collars worn by the non-pregnant cattle in the group (Dairymaster MooMonitor activity collars, Dairymaster, UK) and as such did not affect the behaviour of the cows. The collars were fitted immediately following milking when the selected cows were diverted into AI stalls at the parlour exit. This area was also used to change collar batteries when necessary.

Position data were collected using a wireless sensor system (Omnisense Ltd, UK). The sensors were defined in two ways by the system based on configuration but were identical in functionality. Fourteen fixed devices (FD) were configured to be fixed and were installed at known locations within the low-yielders pen (Figure 1) to ensure coverage. The sensors affixed to the collars were configured as mobile devices (MD). The local position of each MD was found by measuring the arrival time of messages sent from each MD to all other sensors within range (2m, both FD and MD) in the system.

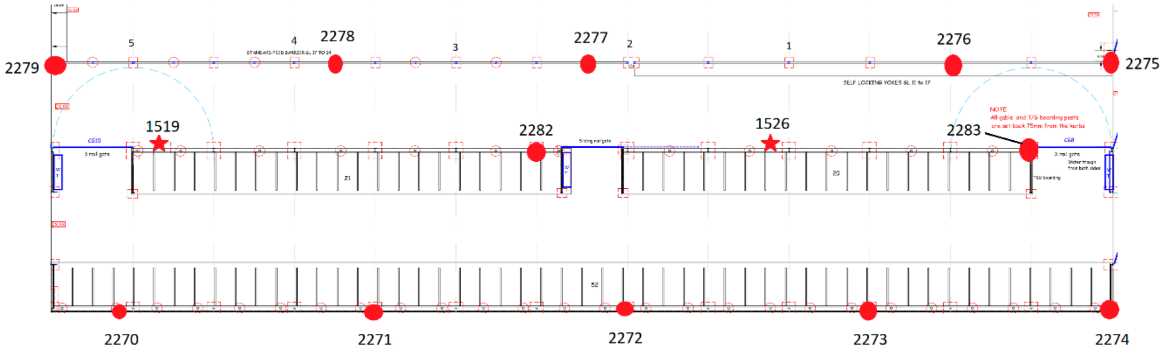

Figure 1: Overview of fixed positioning devices within the low-yielder area. Circles and stars represent different power sources (circles are battery powered whereas stars are mains- powered) and configurations, but no difference in device functionality.

Statistical analysis

Positioning sensor study

Over the study period, (3.12.2019-19.12.2019) there were 116 hours (out of a possible 336) where 4 or more MD and 10 or more FD were fully functioning. These were used for data analysis. This was not optimal (only 34.5% of the possible time) but periods used for further analysis included data where the system was at its most stable and at least 4 (out of a possible 5) of the cow's collar tags were fully functioning. As such, periods used for data analysis are periods where the majority of cows were present.

A frequency distribution of the times of day used for analysis was constructed. The distance between all possible dyads was calculated after synchronising the positioning records in time, and a weighted social network was constructed based on associations between individuals, filtered to include only associations within two metres (as in Boyland et al., 2016).

Social network analysis

To illustrate the kind of social association information which can be extracted from positioning device data, basic network metrics were calculated for each cow in the network (Degree and Strength) along with network-level transitivity (the proportion of network connectivity, e.g., would be 1.0 if every cow associates with every other cow).

The CINNA R package (Ashtiani et al., 2011) was used to conduct a Principal Component Analysis (PCA) on the network to ascertain the best centrality measures for the network according to its structure. The three measures deemed most effective in describing the network by the PCA were extracted and ranked for each cow to examine centrality patterns within the small network.

Quality/pattern of associations

To assess the patterns and quality of the associations of the cows, the social associations were time-ordered for each dyad and plotted to show patterns of social interactions over time.

2.2.2 Results

Positioning sensor study

The positioning system proved effective in producing data suitable for social network construction and for creating time-ordered dyadic social association data. However, there was some challenges with sensor failures leading to variability in the positioning system functionality (Figure 2, 3, 4).

Out of a possible 10 dyads, 7 existed in the social network (Figure 2). The total time the five cows in the network spent within 2m of each other was 17.77 hours. The average contact duration was 2.54 hours.

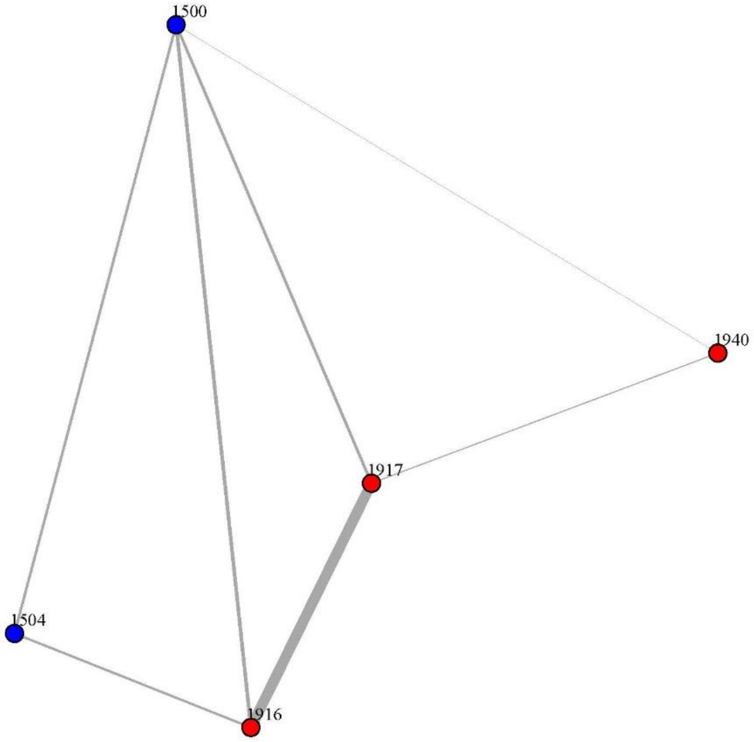

Figure 2: Social network of the five dairy cows in the local positioning study. Node colours indicate age with red = 3 years and blue = 5 years. Edge thickness represents length of time spent within 2 metres, in hours.

Transitivity of the network was 0.64, meaning that 64% of the possible connections in the network existed between the focal cows.

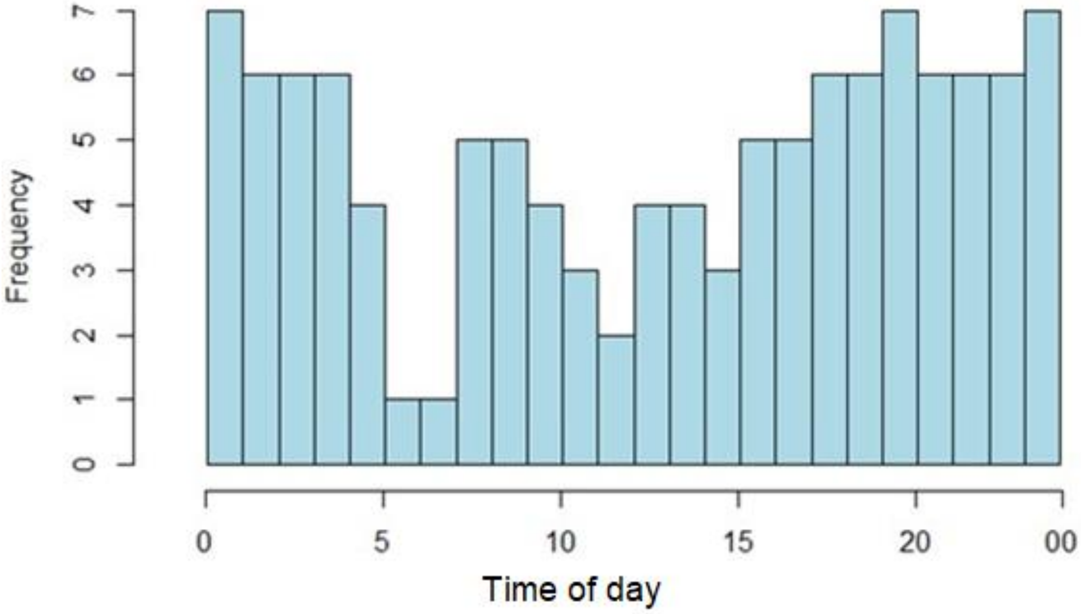

Figure 3: Distribution of the time of day where 10+ FD and 4+ MD were functioning during the study period. Numbers represent the hour starting at that time, e.g., 5=05.00-06.00. Note that the cows were milked each day at 05:00 and 14:00.

Network metrics and centrality ranks (defined in Table 2) are reported in Table 1.

Table 1: Strength and Degree for each cow in the network. Degree is a count (the number of connections each cow had) and Strength is a cumulative value which combines the number and the frequency of interactions (in this case hours spent within 2m of another focal cow). Each cow was ranked in the three centrality measures where 1 is the highest rank (extracted by PCA) (defined in Table 3).

Cow	**Strength**	**Degree**	**Closeness centrality (Freeman) rank**	**Average distance rank**	**Barycenter centrality rank**
1500	6.56	4	1	5	1
1504	3.36	2	4	2	4
1916	13.19	3	5	1	5
1917	11.67	3	3	3	3
1940	0.75	2	2	4	2

Table 2: Definitions of centrality measures used in analysis (in Table 2)

Centrality measure	Definition
Closeness cent. (Freeman)	1 / average distance between node n and all other nodes in the network (CentiServer, 2020)
Average distance	Average distance between node n and all other nodes in the network (CentiServer, 2020)
Barycenter centrality	1 / total distance between node n and all other nodes in the network (CentiServer, 2020)

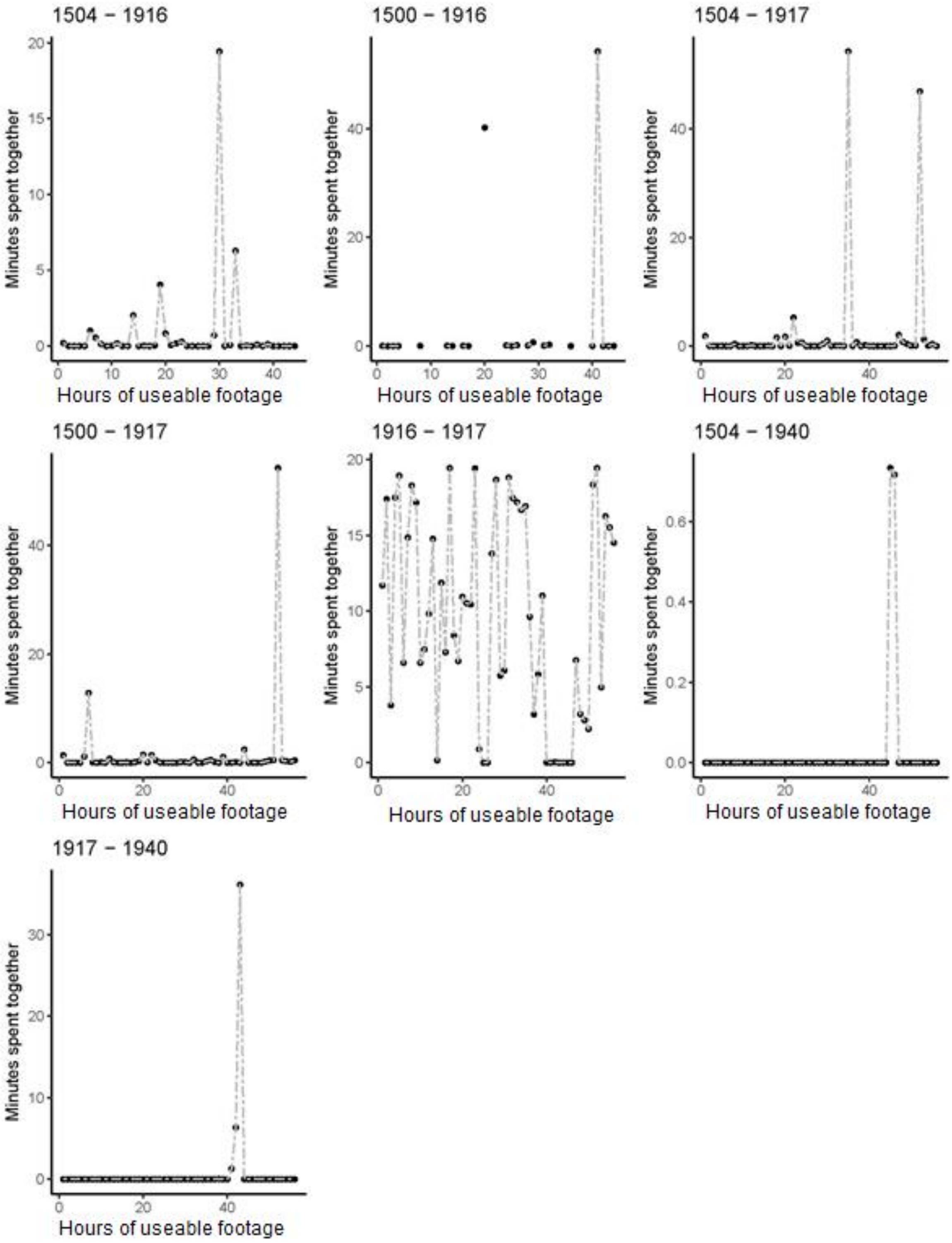

Figure 4: Time-ordered patterns of association for each dyad. X-axis represents each hour where 10+ FD and 4+ MD were functioning. Black points are the number of minutes that dyad spent within two metres of each other in that hour. Dotted lines show if the logger was functioning the subsequent hour. Note that the hours on the x-axis are not necessarily consecutive, just a representation of the hours in which data were collected for that particular dyad. Additionally, there were five collared cows and the threshold for data collection was 4+ MD, meaning that there is likely some overlap in the displayed data.

2.3.2 Discussion

The results from this section are (i) the sensor system proved mostly effective in providing data which could be utilised for SNA during the short pilot deployment; and (ii) the sensor data could also be utilised for other methods of social behaviour quantification such as assessing the nature of social associations or linking social preference to use of different functional areas.

The positioning system utilised in the current study was effective in providing suitable data for social network analysis during the short pilot deployment. The majority of local positioning studies have, to date, focused on validation and potential applications of the technology (e.g. Ipema et al., 2013; Raharijaona et al., 2017; Hasan et al., 2018; Molapo et al., 2018) rather than on answering specific research questions. Once implemented to answer such questions, however, location device studies have provided social association data of high quantity and quality. Barker et al. (2018) conducted a scoping study on the same sensor system as utilised in the present study, with the aim of measuring differences in behaviour between lame and sound dairy cows. The study focused on 20 cows (ten lame, ten sound, matched for days in milk and age) which were fitted with sensor collars. Position within the barn and accelerometer data were continuously collected for five consecutive days. The data were fed into a decision tree algorithm that assessed whether each cow was feeding/not feeding or being milked. The duration and number of feeding sessions were calculated for lame and sound cows, and the study concluded that lame cows fed significantly less than sound cows (Barker et al., 2018).

Gygax et al. (2010) used a radar-based local positioning system to collect location data in six herds of dairy cows. 175 cows from six farms were fitted with collar-fixed transponders and included in the study. The barns were split into functional areas; the feeding area; the lying area, and the activity area. Each farm was continuously observed for six full days (24hrs). Social networks were constructed for (i) synchronicity, or the standardised number of times dyads were in the same functional area, and (ii) median distance, or the median distance between a given dyad when both cows were within the same area. These networks were used to create attachment and avoidance networks for each herd. The network metrics Degree, Edge Density, Diameter and relative size of largest clique were calculated for each attachment and avoidance network. They found that synchronicity and median distance were poorly correlated between the different functional areas, implying that the dairy cows in this study preferred different partners for different activities. The study further concluded that social networks in dairy cows were either tightly connected or almost unstructured, that most of the herd members belonged to the same clustered subgroup, that attachment and avoidance relationships were different, and that there was significant variability in sociality between cows (Gygax et al., 2010).

As shown in Figure 5, the data derived from the pilot deployment of the sensor system was used to plot patterns of dyadic interactions over time. These time-ordered patterns can be useful in determining the nature of a social tie between two animals (Patison et al., 2015). Regular patterns of longer-term close proximity imply affiliative connections such as resting or grazing together or allogrooming (e.g. Reinhardt and Reinhardt, 1981a; Swain et al., 2015). Multiple patterns of shorter encounters may indicate dyads coming together to reinforce relationships or for reassurance, whereas lone short-term encounters may reflect an agonistic encounter which is then followed by avoidance (Foris et al., 2019; Swain et al., 2015). This could be utilised in future studies to identify individuals who engage in disproportionate amounts of lone short-term encounters (potentially agonistic), and as such, may act as an identifier of aggressive individuals who may adversely affect the welfare of the group. For example, Gibbons et al. (2009) found that individual cows showed some consistency in their aggressive-competitive behaviour in different contexts. Therefore, identifying these individuals may be useful for targeted management.

Alternatively, individuals who share many longer-term associations may be identified and regrouped together, potentially ameliorating the stress of regrouping through social buffering. Neisen et al. (2009b) conducted a study examining the effects of regrouping on dairy cows where heifers were regrouped singly or in pairs. The cows within the herd showed lower levels of agonistic behaviour towards heifers introduced into the herd as a pair, and the pair of introduced heifers tended to remain in closer spatial proximity, implying that introduction into a new herd as a pair has a social buffering effect in cattle. However, the paired heifers were simply selected from the same herd and not selected on the basis of any previously known preference between the pair. A future positioning device perspective, therefore, might be to repeat the experiment using pairs of heifers selected based on time-ordered associations (e.g. Figure 5) indicating a social preference. Future studies could further explore the use of functional areas and how preference is reflected in the use of them. As aforementioned, Gygax et al. (2010) found only a weak correlation between synchronicity and median dyad distance in the different functional areas, meaning that cows might select different partners for different activities.

Kilgour et al (2012) found that 51% (±10%) of a beef cow's time budget consisted of grazing and standing/lying resting consisted of 31.8% (±10%) of their daily time budget. Dairy cattle time budgets were found to consist of 59.2% standing/lying and 25.4% feeding (Uzal and Ugurlu, 2010). Considering the fact that these behaviours comprise the majority of a cow's day, they might be selecting tolerant or familiar neighbours for these activities. During feeding, a tolerant neighbour may be preferred as they might not enforce as wide a distance between a high value food resource and themselves, allowing other cows to feed in the same area (Gygax et al., 2010). Whilst resting, a cow might prefer a more vigilant neighbour, thus facilitating a reduction in the cow's own vigilance behaviour (Gygax et al., 2010). The most tolerant cow and the most vigilant cow may not be the same cow, thus causing different preferences in different functional areas. For example, Reinhardt and Reinhardt (1981a) investigated social licking and social grazing in zebu cattle and concluded that the cattle tended to associate with their offspring or siblings. The study did not test for links between the two activities, but grazing associations appeared to be more bidirectional whereas licking associations were more unidirectional. Of course, this may have been caused by the fact that grazing in close proximity is inherently a less directed activity than social licking.

Study limitations

Firstly, when using radio-telemetry there are a number of innate challenges which may cause variations in sensor performance such as the position and orientation of the tag, the size of the tagged animal, and differences in the internal tag components. Furthermore, large or metallic objects within the study area might deflect or absorb signals. The extent to which these factors impacted the present study are unknown.

Secondly, despite near-daily maintenance of the piloted positioning system, out of the 336 possible hours in the study period the sensors were fully functional for only 116 of them (34.5%), which may have biased the data (see e.g. Figure 4). The positioning system had some technical challenges such as sensitivity to the temperature in the barn, sensitive wiring within the devices, and battery capacity which led the pilot study to be carried out in December 2019 rather than as originally planned in August/September 2019. These system issues substantially reduced the available contact data between the cows and may have skewed the results in the sense that many contacts may have occurred between the animals which were not captured by the current system. As such, the present system was not thought to yield an adequate representation of the social relationships between the study cows, and as a result the system was not used in the larger beef cattle study (Chapter 3) as was originally planned.

Conclusions (Chapter 2)

The current pilot study utilised a positioning system to monitor the locations of five dairy cows within a larger herd. Dyadic proximity information was extracted from the positioning data and used to quantify social associations in several different ways. Preliminary results indicated that the cows in the study herd associated by age and lactation number. Local positioning systems may contribute to future studies on animal sociality in a number of ways, some of which have been discussed in the present study. However, it is important to remember that this was only a small pilot study with a limited sample size, and further research is required to explore the suggested options in the future. Although the positioning system currently remains at an early stage, future development of automated systems offer the potential to detect and register social interactions based upon proximity data in real-time, and will undoubtedly facilitate future research on social behaviour in livestock.

The Omnisense sensors used in study 2 were initially planned to be used for the study in chapter 3, however, due to shortcomings with the sensors (issues with battery connectivity and sensor failures) these plans were altered.

3. Exploring social networks in a group of cows managed in a natural weaning system

As mentioned in Chapter 2, most dairy cows are subject to numerous regroupings throughout their productive lives which may result in adverse effects such as increased agonistic behaviour, reduced milk yield, and prolonged standing bouts (Torres-Cardona et al., 2014). These regroupings are typically carried out to ensure homogeneity within the different groups, meaning that cows with e.g., a high milk yield, a low milk yield, or which are close to parturition, are kept together (Silva et al., 2013). As dairy cows are generally not synchronised in their calving and milk production patterns, this results in frequent regroupings and resultant social instability (von Keyserlingk and Weary, 2008). In contrast to dairy cows, however, the management of extensively grazed beef cattle does not result in the same level of social instability as dairy cows.

Weaning (the transition of young mammals from relying on their dam for social support and nutrition in the form of milk, to social and nutritional independence (Trivers, 1974; Weary et al., 2008) typically occurs earlier in managed systems than under natural conditions. Here, “natural weaning” is defined as a complete termination of suckling achieved entirely without human intervention in the weaning process (Johansen et al., *in prep*).

Extensively grazed cattle typically remain in the same social groups for their entire productive life with herds generally consisting of adult females and their offspring, which are kept with the dams until 3-10 months of age, depending on management system (Smith, 1997; UoA, 2016). Generally speaking, cows are only removed from the established group to be culled (typically due to fertility issues), or for medical interventions (e.g., if they need to be taken to a “sick pen”); and new cows are introduced as replacements when so many cows have been culled that the herd is significantly diminished in size, or when members which were removed for medical reasons are re-introduced to the main herd. In some cases, the female calves may be re-introduced to the herd as replacement stock, but only after they have been weaned by some method of human intervention (e.g., abrupt weaning, fenceline weaning (Weary et al., 2008)). The adult population within a group thus typically remains relatively stable (Sowell et al., 1999). Therefore, one of the key drivers of social instability for extensively managed cattle is not regrouping, but abrupt weaning, where the calf is separated from the dam and put into a new, and non-natural group of peers lacking adult animals (Raussi et al., 2005; von Keyserlingk and Weary, 2007; Taylor et al., 2019).

Abrupt weaning has already been well studied in terms of its behavioural (vocalisations, pacing) and physiological (cortisol, immune response) effects on calves (Weary et al., 2008). Little research, however, has considered how this practice may impact the social dynamics within the group. Indeed, most of the research concerning social behaviour and structure in cattle is undertaken on dairy cows (e.g., Syme et al., 1975; von Keyserlingk et al., 2008; Gygax et al., 2010; Gutmann et al., 2015; Boyland et al., 2016), meaning that much of what is known is based on cattle which are managed quite intensively (typically low/zero grazing, indoor-housed, higher stocking densities), and often in a population with no youngstock (animals less than a year old). As a result, the findings regarding dairy cow social structure may not apply to beef cattle social structure, particularly when youngstock are managed within the herd until weaning. Furthermore, the relatively stable social groups seen in beef cattle management may result in less overt conflict than that which is seen in dairy herds as, once established, the hierarchy persists due to the lack of regrouping within the population (e.g., Lazo, 1994; Sárová et al., 2010; Sárová et al., 2013).

As with dairy cattle, researchers and farmers alike are motivated to optimise social conditions for extensively grazed cattle to promote welfare and productivity (Bennett, 1996; Boyland et al., 2016; von Keyserlingk and Weary, 2017). Therefore, questions relating to social dynamics and resulting preferences in beef cattle are important to answer, such as if social relationships change over time or in relation to life-history events (e.g., weaning), how long the mother-offspring bond persists beyond weaning, or how social associations form within groups, to be able to accurately inform industry regarding optimal social conditions in beef cattle

As discussed in the introductory section, to understand animal preferences, animals must be given the opportunity to make 'spontaneous' choices regarding these preferences (Dawkins, 2003). It is particularly important to give animals these choices within the environment in which they are kept, to ensure on-farm applicability. Therefore, to be able to ask questions relating to the kin/non-kin social preference dichotomy in extensively grazed cattle groups, or regarding social structure around natural weaning, a population where calves are retained in the herd post-weaning, and where the social groups are composed of kin and non-kin alike is required. To date, no studies have investigated social affiliations within this context. A natural weaning system is the ideal model fulfilling these requirements. Use of a natural weaning herd allows creation of a social network which is somewhat analogous to a social network of cattle displaying their "normal" social behaviour – the behaviour they display in a minimally-managed situation. This herd could effectively represent a "baseline" of what social behaviour and dynamics looks like in a group where multiple established family groups interact with each other freely, and the calves are retained within the herd for their entire productive lives. The effects of weaning interventions could then be explored through the lens of how it might differ from this baseline. This is particularly useful as the majority of social network research on cattle has been carried out on dairy cows (e.g., Gygax et al., 2010; Boyland et at, 2016; Bolt et al., 2017), for whom weaning is a completely different process (cow and calf are separated within 48 hours and are not generally permitted to bond (Mikus et al., 2020)).

Social network analysis can, in this case, be used as a tool to help elucidate some of the effects of abrupt weaning. For example, in a natural weaning herd the calves remain in the group past the point of natural weaning. This means that we can quantitatively assess the motivation of cow and calf to maintain their social bond through social network techniques such as measuring any changes in Strength (the frequency of social contacts) between the dyad, or using Modularity (see 1.2.1, page 27) calculations to assess if cow and calf remain in the same subgroup. If the cow-calf bond remains past the point of natural weaning, this means that when given the opportunity to make a 'spontaneous' choice regarding social partner (see Dawkins, 2003 above), the social partner chosen is the cow/calf. Thus, abrupt or early weaning could be disrupting the animal's chosen social ties and causing potential instability within the herd, in addition to the previously established adverse behavioural and physiological effects of abrupt weaning (see Weary et al., 2008).

In the current study, social network analysis is utilised to answer several questions pertaining to social relationships and weaning in extensively grazed beef cattle towards the aim of understanding social preference and alterations in group structure around weaning, specifically:

Do related and unrelated cattle associate differently?

Predictions:

1) Related cattle will associate more than unrelated cattle

Secondly, do the cattle in this herd have preferred social partners, and if so, how are these selected?

Predictions:

1) The cattle will have preferred partners
2) The cattle will assort by age and relatedness

Thirdly, does the social network structure of a related group of cattle change as the calves in the group approach weaning?

Predictions:

1) The social network will be relatively stable throughout the study period
2) Removing the calves from the network will impact the network structure of the group
3) Cows with weaned calves will have lower eigenvector centrality (i.e. fewer social contacts with other animals that themselves have fewer social contact and thus less "importance" within the network) than dams with calves that are still suckling
4) Immediately post-weaning, dams and calves will associate less than previously
5) As they approach weaning, calves will associate with their age-mates more than previously

3.1 Methods

Ethics

Due to routine weekly inspections the study animals were habituated to observers before the study began. The project was approved by the University of Bristol's Animal Welfare Ethics Review Board.

Animals

The cattle used in the study formed part of a commercial organic beef farm (Harley Farms South, Wiltshire, UK). The total number of cattle on the farm varies by season with a larger number during calving (block calving in April-June) and fewer when stock are sold (typically October/November) but averages around 1400-1800 animals split into 12 distinct breeding herds. These herds consist of adult cows (breeding females that currently have a calf or have calved previously), heifers (breeding females before their first calving), steers (castrated males between 12 and 18 months), and calves (<1 year of age). Breeding bulls (intact males) aged 1-10 join the herds between June and August in groups of 1-8. For the remainder of the year the bulls live together.

Location

The farm rents 3300ha of chalk downland on Salisbury Plain, Wiltshire (34.7671° S, 138.6603° E) from the Ministry of Defence. The altitude varies from 120-200 metres over sea level. The annual average temperature is 9.8° C and the annual average rainfall is 743mm.

Management

Calves are ear-tagged, and bull calves castrated by elastration within three days of birth. The cattle on the farm are managed in a natural weaning system where the offspring are not removed from the cow until at least 15 months of age. Heifers stay their entire productive life within these herds (occasionally removed prior to the breeding season for welfare reasons, due to their size). The farm was previously a classic suckler cow operation (cow-calf dyads abruptly separated at approx. 8-10 months) and switched to a natural weaning system (herd by herd) between 2005-2011.

The farm rounds up each herd three times a year to: (1) remove cull animals and small heifers, (2) blood test for Johne's disease, pregnancy check the animals, and remove steers, and (3) health check prior to calving. The cows are also vaccinated for bovine viral diarrhoea (BVD), infectious bovine rhinotracheitis (IBR) and clostridia during these roundups.

Study animals

The focal herd consisted of 269 animals: 106 cows, 49 heifers, 21 steers and 93 calves (45 male and 48 female). The herd was mostly composed of Aberdeen Angus (AA) cattle (n=254), but also included some AA crosses (n=10) and some White Park (WP) cattle crosses (n=5). The herd was kept in electric fenced pens of eight ha or more within their assigned home range of 500ha. These pens were moved on a weekly basis. The cattle had *ad libitum* access to water and mineral licks.

Study cows were selected from the herd on the basis of relatedness. Relatedness was calculated as an absolute value (e.g. cow-calf – 0.5, siblings – 0.25, grandmother-grandchild – 0.25) The ages, breed and kinship information of the animals was taken from the farm's herd database, which was examined to select the largest directly related group within the herd (15 animals) which was then used in the study. The related (R) group (n=15) was matched with a control (C) group (n=15) of unrelated animals of the same age and gender. The sample sizes were selected due to limitations of time during data collection and practicality in selecting completely unrelated animals for the control group. Each group consisted of six adult females (aged 3-13), three heifers (2 years old), two female calves and four male calves. These cows were marked with stock spray using a squeeze crush during a routine husbandry procedure to enable identification from a distance.

Data collection

Behavioural observations were carried out for two days every week during daylight hours for two five-week time blocks (21.11.2019-20.12.2019 and 02.01.2020-31.01.2020), and one 3-week time block (20.02.2020 – 06.03.2020) between November 2019 and March 2020. Observations were carried out by walking around the exterior of the pasture fence until a focal animal was seen whereupon the its contacts (both within the its defined group (R or C) and its nearest-neighbour (NN)) were noted, observations continued until the next focal was seen and so on until all focal animals were observed and a new observation began. The observations began at sunrise on each observation day and concluded at dusk when the cows could no longer be identified. As a result, there were no set data collection times as the timing of sunrise and sunset changed between weeks. Cows were identified by stock spray and the identity (ID) of each cow was confirmed using binoculars (if necessary).

Contacts were defined as an animal being within six metres (lower end of spatial proximity expected in extensively grazed cattle, from Fraser and Broom, 1997) (approx. three cow-lengths or six calf-lengths) of the head of another, and were logged by eye within, not between, the defined groups (Swain et al, 2007; Swain et al., 2015; Kemp et al., 2018). The NN of each study cow within a 30m (as defined in Stephenson et al., 2016) (approx. 15 cow-lengths) radius was also identified and this was not restricted to only study cows but included the entire herd. If the cow had no NN within 30m, the cow was classed as having no NN.

The number of data points collected for each cow varied between weeks due to differences in daylight hours, environmental conditions, and the time taken to locate all study cows which varied between and within weeks. However, despite the number of points varying between weeks (range: 13-21) due to time, terrain and environmental restraints, the same number of data points were collected for all the cows for each week (excluding one cow which was removed from the herd for two weeks due to mastitis). Suckling/nursing events were sampled when observed. The udders of all cows with calves in the Related Group were also scored on a weekly basis using a 7-point scale (Table 3; Fig. 5a-c) novel udder-scoring method (Albertsen, 2016) to determine the point of weaning for each cow-calf pair. Weaning occurred when an udder was scored as “6” or “7” (Table 3) and no subsequent signs of suckling (as defined by scores 1-4, Table 4) or observed suckling occurred for the duration of the study period.

Table 3: Seven-point scoring system used to assess udder status and determine the point of weaning in cow-calf pairs (adapted from Albertsen, 2016)

SCORE	SUCKLING STATUS	UDDER FILLING
1	Used/Suckled	N/A
2	Inconclusive	Inconclusive
3	Inconclusive	Full
4	Inconclusive	Empty
5	Not used	Inconclusive
6	Not used	N/A
7	Not used	Empty

Used: Udder has traces of milk/saliva on teats and underside. Teats are clean and hair on udder is curled.

Inconclusive: Udder has no signs of suckling (see (a)) but are filled with fluid and skin on teats is tightened. Hair is straight and dry.

Not used: Udder has no sign of suckling and is not filled with fluid. Udder may be regressed in size due to lack of milk production at this stage.

Figure 6: Examples of the different types of udder status used to determine the weaning window in cow-calf pairs (see Table 4): (a) used/suckled (score 1), (b) inconclusive (score 2-4), (c) not used (score 5-7).

Statistical analysis

Social network analysis

R (version 3.6.2, R Core team; 2020) was used for data analysis, specifically packages “igraph” (Csardi and Nepusz, 2006), “CINNA” (Ashtiani et al., 2011), “RVAideMemoire” (Hervé, 2018), and “vegan” (Oksanen et al., 2003). The NN data were analysed in IBM SPSS (version 24). During the study period, each cow was seen 132 times; 51 in Time Block one, 46 in Time Block two, and 35 in Time Block three.

Asymmetrical networks (networks where a connection between Cow A and Cow B, and between Cow B and Cow A are represented by a single tie rather than one for each dyad) were constructed for both groups (Related (R) and control (C)) over the entire 13-week block where each node was a cow, edges between nodes represent the data on ‘social contacts’ (e.g. less than six metres between animals) between the dyad (pair of cows), and the width of the edge corresponds to the frequency of social associations between the dyad. These networks were used to examine differences between networks consisting of related animals, and networks consisting of unrelated animals.

In addition, three sequential asymmetrical networks (two over five weeks (Time Blocks 1 and 2) and one over three weeks (Time Block 3) were constructed for Group R to assess changes in social network structure as the calves in the group approach weaning (cf. Boyland et al., 2016). Asymmetrical networks are equipped to deal with the kind of data in the current study, where if Cow A is within six metres of Cow B, Cow B is also within six metres of Cow A. Which means that although ‘Cow A → Cow B’ and ‘Cow B → Cow A’ represents two interactions between a dyad, it is shown as a single bidirectional tie rather than a unidirectional tie per dyad. A symmetrical NN network was constructed for the entire 13-week period to assess if the focal animals had social preferences and how those were selected (Kemp et al., 2018). Symmetrical networks can illustrate the difference in preferences in the sense that if cow A is the NN of cow B, cow B is not necessarily the NN of cow A. The herd records were used to calculate matrilineal relatedness of each dyad within all networks.

Do related and unrelated cattle associate differently?

The 13-week C and R networks were used for this analysis. Two local and four global metrics were calculated for each network; local metrics were Degree and Strength, which were calculated for each individual cow; global metrics were Average Degree, Average Strength, Edge Density and Transitivity. Degree is the number of cattle a given cow is connected to and informs connectivity of a cow to the rest of the network (Wey et al., 2008). Strength is a measure utilised for weighted networks, where both the number of social associations and the frequency of social contacts are considered (Wey et al., 2008). A cow may have high Strength but low Degree if it has numerous contacts with few cows. On a global (entire network) scale, one can also calculate the averages of these measures. Edge Density is a measure of a network's connectedness; it is expressed as the proportion of possible connections in a network that are realised as actual connections (Wey et al., 2008). For example, if every cow was connected to every other cow, the Edge Density of the network would be 1.

In Social Network Analysis, the clustering coefficient is a local measure of cliquishness (Croft et al., 2011). If a cow has x neighbours, that "neighbourhood" has a maximum of 1/2x(x-1) edges, as each edge links two cows. The fraction of possible edges that exist in the real network defines the cliquishness of the node (Croft et al., 2011). This measure can be thought of as the probability of a cow's connections being connected between themselves. Averaging the clustering coefficients across the network gives the average clustering coefficient or Transitivity of the network (Croft et al., 2008). High Transitivity indicates a deviation from a randomly connected network i.e. a network in which the animals associate non-randomly (Croft et al., 2004). To test for non-random associations the observed Transitivity values were compared to Transitivity distributions of 10 000 null models generated for each network. Significance was determined by dividing the number of times the randomly generated values were equal to or higher than the observed value with the total number of generated values (10 000) (Croft et al., 2008).

Unpaired t-tests with permutations (10 000) were carried out to compare the Degree and Strength of cows in Group R to cows in Group C (Boyland et al., 2016; Kemp et al., 2018). To control for effects of calf sociality where the adults may have higher Degree/Strength due to the indiscriminate socialising habits of calves (Kemp et al., 2018), networks for each group were constructed without any calves in them and the tests were run again. Strength is a measure of cumulative frequencies of social interactions, so the calves were also removed from the networks to assess if the R Group had higher Strength as a consequence of suckling interactions between cow-calf dyads (Kemp et al., 2018).

Using the CINNA R package (Ashtiani et al., 2011), centrality measures (the extent of which a given node occupies a position of importance within the structure of the network (Croft et al., 2008)) best suited to each network were extracted. To assess the most important centrality types for each network based on individual network structure, a principal component analysis (PCA) was subsequently carried out (Ashtiani et al., 2011). The resulting centrality measures were used in further analyses. The centrality values were ranked for every cow in each group. Spearman's rank correlation tests were then performed between matched cows from each group to see if centrality positions were consistent across groups (i.e. within age and gender) and within groups (e.g. if certain cows have high centrality scores across the different centrality metrics) to see if relatedness or lack thereof impacts centrality patterns. Average centrality rank was calculated for each cow and within-group Spearman correlations were performed between average centrality rank and age and parity, Degree and age and parity, and Strength and age and parity. Parity was defined as the number of times each cow had given birth.

Analysis of similarity (ANOSIM) is a nonparametric test which "tests the null hypothesis that there are no differences between groups based on a permutation test by assessing if there are more similarities within groups than between groups" (Oksanen et al., 2003). The test uses Monte Carlo permutations where group membership is randomly scrambled, and significance is determined as with the null networks (e.g. the number of permuted values which are equal to or higher than the observed value divided by the total number of permutations) (Oksanen et al., 2003). An ANOSIM was conducted (10 000 permutations) to compare the means of ranked dissimilarities of the C and R networks, essentially testing if there are more similarities within than between groups (Anderson and Walsh, 2013).

Do the cattle in this herd have preferred social partners, and if so, how are these selected?

The 13-week NN network (made up of the NNs within 30m of each focal animal) was used for this analysis. The network includes dyadic contacts which only occurred once, so the network was filtered to include interactions at increasing thresholds; two, three or four times the mean interaction number (edge weight) of the network, meaning that dyadic connections below the selected threshold were removed from the network to reveal more of the underlying network structure (Boyland et al., 2016). To determine if there are tightly knit subgroups within this herd, modularity (Q), or the presence of subgroups that are more strongly connected other members of the subgroup than to the rest of the network, was calculated at each increasing threshold using a clustering algorithm (Newman 2006a, b). The algorithm finds the 'best' way to divide the network into clusters, where the 'best' split maximises Q. The modularity at each filter threshold was compared to a distribution (10 000) of values generated by randomising the node labels of each network (Boyland et al., 2016; Kemp et al., 2018). Significance was determined by dividing the number of times the randomised values were equal to or higher than the observed value with the total number of randomised values (Croft et al., 2008).

As a single association tells us very little about the actual quality of a relationship between individuals (particularly when using proximity as a proxy) (Croft et al., 2008), the NN associations were filtered to only include dyads with three or more social associations, as this was deemed more likely to accurately represent a true preference rather than a random association (Croft et al., 2008; Boyland et al., 2016). The filtered associations were used in further analysis.

To inform the secondary prediction that cows will assort by age and relatedness, Kruskal-Wallis H tests were carried out to examine the patterns of the filtered NN interactions between the focal animals and NNs of different traits (adult NN, juvenile NN, calf NN; female NN, male NN; unrelated to focal animal, MRC (matrilineal relatedness coefficient) between focal animal and NN 0-0.1, MRC between focal animal and NN 0.1-0.45, and MRC between focal animal and NN 0.45-0.75). Post hoc pairwise comparisons of the categories were carried with Bonferroni corrections out on all significant Kruskal-Wallis test outcomes.

Does the social network structure of a related group of cattle change as the calves in the group approach weaning?

The three sequential networks were used for this analysis. Network stability, or the amount of network structure preserved over time, was calculated by calculating Spearman's correlation coefficients between Time Blocks 1 and 2, 2 and 3, and 1 and 3 (Boyland et al., 2016). Significance was determined by comparing the observed coefficient for each Time Block to a suite of values generated by permuting edge weights in null models (10 000) (Croft et al., 2008). The analysis was repeated on binarized (non-weighted) versions of the networks to test if the strength of relationship varied but overarching social connections were consistent over time (Boyland et al., 2016). Finally, to assess the importance of calves in the social network, the calves were removed from the analysis which was then repeated to see if the network was more stable with only adult animals present (Kemp et al., 2018).

In the final Time Block (three weeks), three of the six calves had been weaned. Unpaired t-tests with permutations (10 000) were carried out to test the third prediction that cows without calves will have lower centrality (Einsporn and Habtzghi, 2013). Multiple tests were run to compare the eigenvector centrality of cows with weaned calves and cows with suckling calves, and to compare the eigenvector centrality of non-lactating heifers to both cows with weaned and cows with still suckling calves, to control for any residual effects of recent lactation (Kemp et al., 2018). A paired t-test with permutations was carried out to compare the eigenvector centrality of the cows before and after they weaned their calves (Kemp et al., 2018). Eigenvector centrality was calculated for each cow in each of the three networks.

A paired t-test with permutations (10 000) was conducted to compare the number of associations between cow and calf in the time block before and the time block after weaning to test for any changes which might occur (Kemp et al., 2018).

The proportion of social associations for each calf was calculated for all of their possible social partners within each time block and Spearman's correlations were carried out between time blocks to explore the consistency of their social interactions over time (Boyland et al., 2016). The proportion of time each calf spent with (i) other calves, (ii) juveniles, (iii) adult animals, and (iv) animals of the same gender were also calculated. Friedman tests were carried out to examine changes in social associations by age- and sex- class, and Wilcoxon tests were carried out post hoc to determine the nature of any changes.

3.2 Results

Do related and unrelated cattle associate differently?

The R Group network consisted of 84 dyads (out of a possible 105) with a total of 391 contacts (Figure 6). The mean edge weight or contact frequency per dyad was 4.65 (±4.9SD) and the median edge weight, or contact frequency, was 3 (range 1-33). The C Group network consisted of 43 dyads (again out of a possible 105) with a total of 65 contacts (Figure 6). The mean contact frequency per dyad was 1.50 (±1.0SD) and the median edge weight (contact frequency) was 1 (range 1-5).

Edge density (percentage of potential connections that exist) of the R network was 0.80, whereas edge density in the C network was 0.41, indicating that the R Group was generally more connected than the C Group. Transitivity (the probability of a node's/focal animal's connections being interconnected) of the R network was 0.82, and 0.43 in the C network, suggesting that animals in the R Group were more likely to have social ties with the social connections of their social connections. Transitivity of both networks were significantly higher than random (R network: $p<0.001$ (higher values generated in 0 of 10 000 null values), C network: $p=0.0028$ (higher values generated in 28 of 10 000 null values), indicating non-random associations between the cattle in both groups.

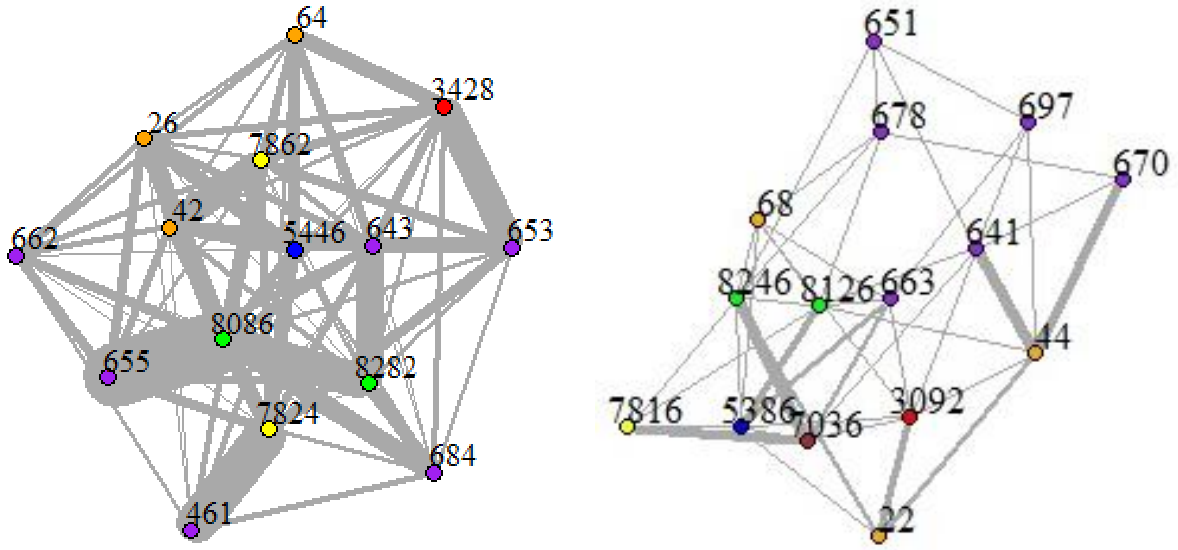

Figure 6: Social networks of the Related group (left) and the control group (right) using data from the entire 13-week period. Node colours represent cow age. Red=13 years, blue=9 years, maroon=5 years, yellow=4 years, green=3 years, orange=2 years, purple=10-12 months. Edge width (width of the connections) represents total frequency of contacts between the dyad.

Average Degree, or "connectedness", was 11.20 in the R network and 5.73 in the C network, showing that related focal animals have a higher number of connections with other related focal animals than control animals have with other control focal animals. Average Strength (connectedness that accounts for edge weights) of the R network was 52.13, and 8.67 in the C network, implying that animals in the R Group associate at a higher frequency than the C Group. Average Degree was significantly higher for cows in the R Group compared to the C Group (unpaired t-test: t(14)=(8.477, p(perm)=0.00002, Figure 7), as was Average Strength (unpaired t-test: t(14)=8.458, p(perm)=0.00002, Figure 8), meaning that animals in the R group not only had more social connections within the group, but also associated more with their connections.

Degree and Strength were also significantly higher for the R group compared to the C group when calves were removed from the networks (Degree: unpaired t-test: t(8)=-6.5, p(perm)=0.00004, Strength: unpaired t-test: t(8)=-8.044, p(perm)=0.00004), implying that the R group maintains a higher level of social association which is not caused by gregariousness of calves (Kemp et al., 2018) or the strength of the mother-offspring bond to an unweaned calf (Reinhardt and Reinhardt, 1981b).

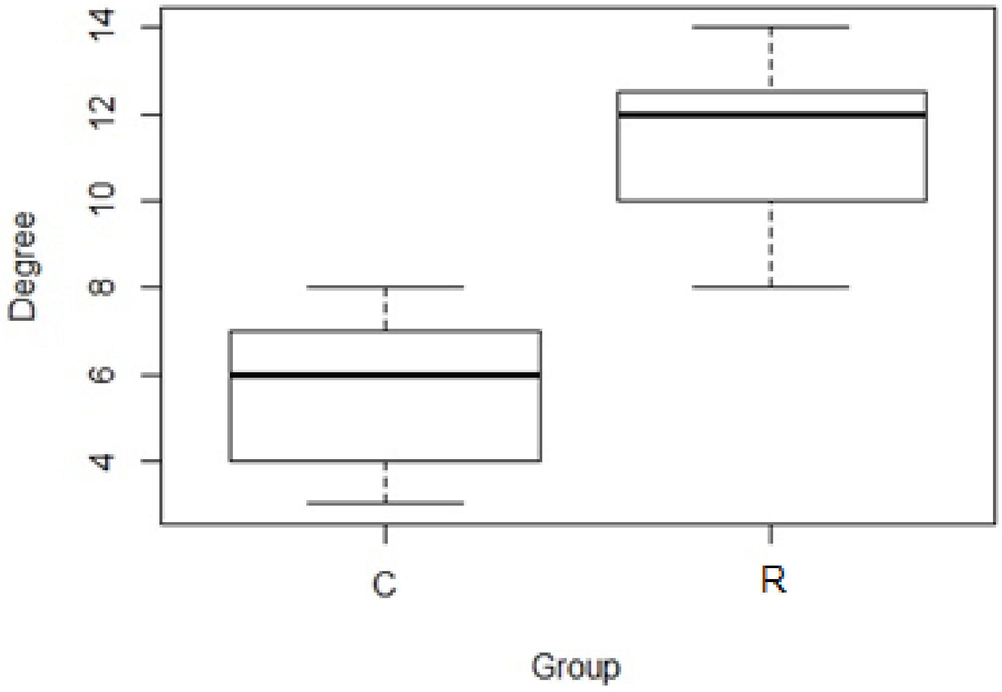

*Figure 7: Boxplot showing the Degree (number of social connections) of the cattle in the Control Group and the Related Group. Thick black lines are the group median, boxes are the interquartile range (IQR), and whiskers are 1.5*IQR.*

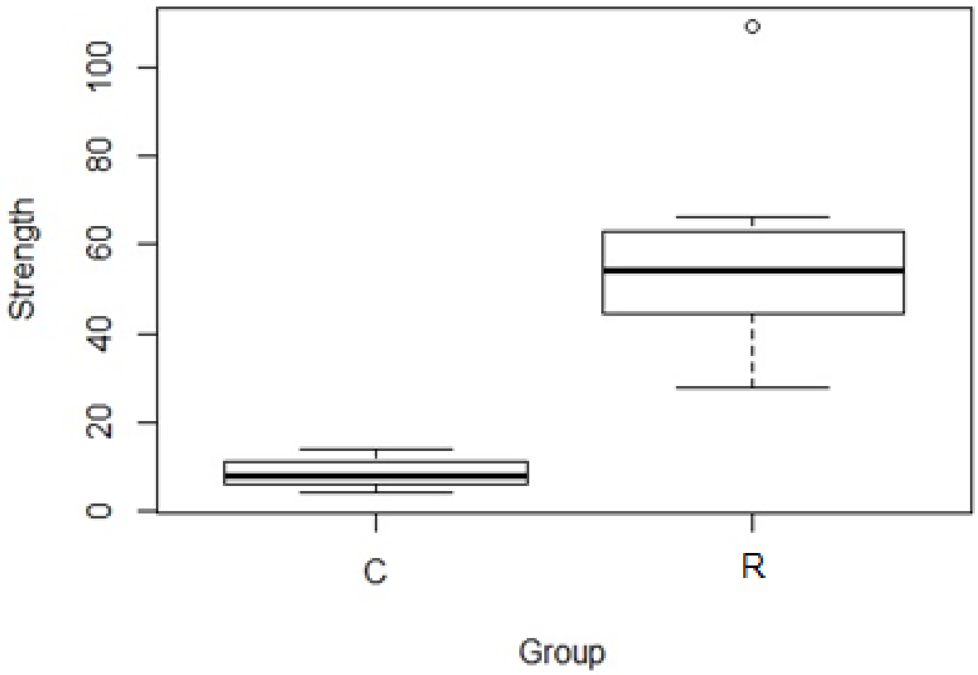

Figure 8: Boxplot showing the Strength (number ***and*** *frequency of social connections) of the cattle in the Control Group and the Related Group. Thick black lines are the group median, boxes are the interquartile range (IQR), and whiskers are 1.5*IQR. Hollow circles represent outliers.*

Local network measures (Degree and Strength) along with the ranked centrality measures (defined in Table 4) derived from the PCA are reported in Table 5 and 6.

Table 4: Definitions of centrality measures used in analysis (Table 4 and 5)

Centrality type	***Definition***	***Example***
Stress centrality	Number of shortest paths between nodes that pass through node n (Brandes and Erlebach, 2005; CentiServer, 2020)	A measure of how important a node is in terms of information flow e.g. how quickly and how many other nodes will be reached during a collective movement
Flow betweenness centrality	Stress centrality divided by the total number of shortest paths in the network (Brandes and Fleishcer, 2005; CentiServer, 2020)	A measure of how important a node is in terms of information flow but standardised to account for network size

Table 5: Network metrics for the cattle in group R. The centrality measures are ranked, the cow with the highest centrality (definitions in Table 5) of each type is given a "1" and the lowest a "15". Degree and Strength are absolute values.

Cow ID	*Degree*	*Strength*	*Flow betweenness centrality*	*Stress centrality*
3428	10	48	1	2
5446	12	46	15	15
7824	13	66	3	1
7862	13	54	8	9
8086	13	109	11	11
8282	12	55	6	3
26	12	47	10	4
42	12	55	14	14
64	11	64	12	13
662	11	28	5	7
684	10	32	9	10
655	8	62	7	8
461	9	36	13	12
643	14	65	2	6
653	8	43	4	5

Table 6: Network metrics for the cattle in group C. The centrality measures are ranked, the cow with the highest centrality of each type is given a "1" and the lowest a "15". Degree and Strength are absolute values.

Cow ID	*Degree*	*Strength*	*Flow betweenness centrality*	*Stress centrality*
3092	7	9	6	5
5386	8	11	15	15
7036	6	14	1	1
7816	4	7	12	12
8126	8	10	11	6
8246	8	13	14	14
22	4	8	13	13
44	6	14	10	11
68	6	6	4	4
670	3	6	7	9
678	5	5	8	10
697	4	4	9	8
663	6	8	5	7
641	7	11	3	3
651	4	4	2	2

Results of Spearman correlations indicated a significant positive association between flow betweenness centrality (Table 4) and stress centrality (Table 4) ($r_s(13)=0.864$, $p<0.001$), within the R group (Table 5). Furthermore, results of the Spearman correlation indicated a significant positive association between flow betweenness centrality and stress centrality ($r_s(13)=0.93$, $p<0.001$) within the C group (Table 6). This suggests that within both groups, the same cows are ranked in the same place for each of the two centrality metrics.

Spearman correlations of centrality measures between groups indicated no significant associations between flow betweenness centrality rank in groups R and C ($r_s(13)=0.507$, $p=0.056$) and stress centrality rank in groups R and C ($r_s(13)=0.318$, $p=0.248$), meaning there is no evidence of cows of a particular age or gender being the most central individuals in each group.

Within-group (R) Spearman correlations indicated no significant association between average centrality rank and age ($r_s(13)=-0.16$, $p=0.57$), average centrality rank and parity ($r_s(13)=-0.23$, $p=0.4$), Degree and age ($r_s(13)=0.44$, $p=0.098$), Degree and parity ($r_s(13)=0.36$, $p=0.19$), Strength and age ($r_s(13)=0.32$, $p=0.24$), or Strength and parity ($r_s(13)=0.2$, $p=0.47$), suggesting that age and parity have no impact on centrality rank, Degree or Strength within in the R group. However, within-group (C) Spearman correlations indicated significant associations between Degree and age ($r_s(13)=0.52$, $p=0.045$), Degree and parity ($r_s(13)=0.571$, $p=0.026$), and Strength and age ($r_s(13)=0.57$, $p=0.026$), implying that within the C group, as the cows age, they increase their Degree and Strength, and as they have more calves, they increase their Degree. There was a trend between Strength and parity ($r_s(13)=0.502$, $p=0.056$), indicating that as the cows have more calves, they might increase the number and frequencies of their social connections. The correlations found no significant associations between average centrality rank and age ($r_s(13)=0.19$, $p=0.5$) or average centrality rank and parity ($r_s(13)=0.095$, $p=0.74$), indicating that the social importance of a focal animal is not associated with age or parity.

The results of the ANOSIM indicated a significant difference in the patterns of social associations between the two groups ($R(13)=0.97$, $p=0.00009$) as the mean of the ranked dissimilarities were high within groups and low between groups, meaning that the groups were more similar to themselves than to each other.

Do the cattle in this herd have preferred social partners, and if so, how are these selected?

There were 8040 possible dyads between the focal animals and all other animals in the herd, 1240 (15.4%) of which were observed as actual NN contacts (nearest neighbour within 30m) during the study period, meaning that every focal animal was not observed associating with every other possible animal in the herd. Within the observed NN contacts, 78.5% of dyads were only observed as each other’s NN once, 16.2% were observed as NNs twice, 3% were observed three times, and 2.3% four times or more (range 4-13).

The unfiltered network had eight subgroups with membership ranging from 9-60 (mean=28) (Fig. 10; Table 7). Modularity of the unfiltered network (Fig. 9a) was 0.185, and significant after node permutation ($p=0.0085$), meaning that there were social clusters within the networks which had more connections to other members of the cluster than to the rest of the network and indicating a social preference between cattle within that cluster. Modularity of the two times (9b), three times (9c), and four times (9d) mean filtered networks was 0.547, 0.881, and 0.901, and had a significance of $p<0.001$, $p<0.001$, and $p<0.001$ when compared to randomly permuted values (higher values generated in 0 of 10 000 null networks), suggesting that there are subgroups within the networks which are interconnected more closely to members of the subgroup than to the rest of the network (these subgroups become more apparent in Figure 9c-d and Figure 10) and suggesting that the cattle in the herd have preferred social partners.

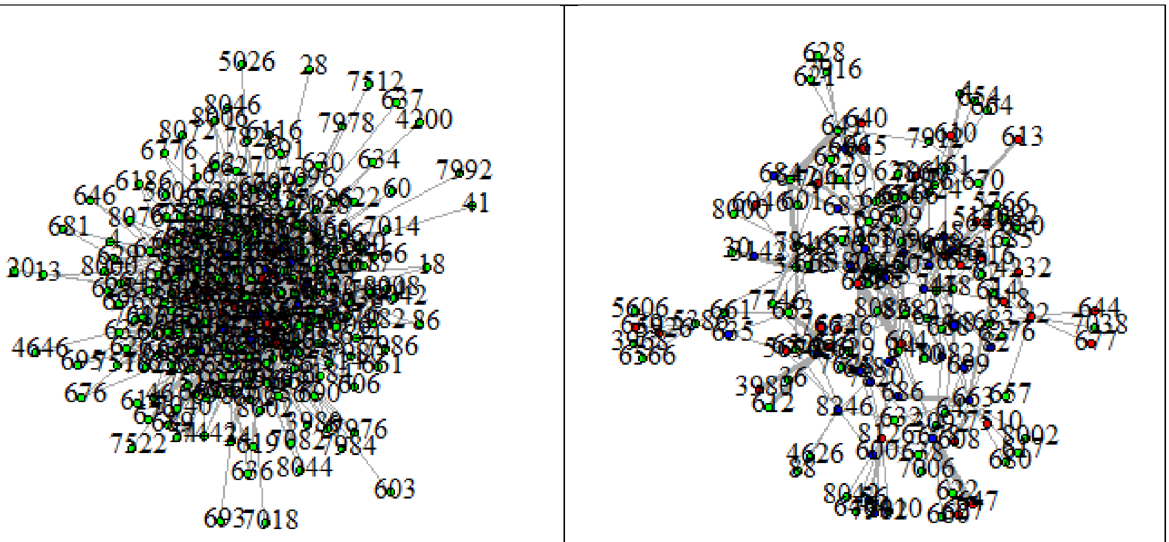

Figure 9a: Unfiltered

Figure 9b: Filtered at 2 times mean interactions

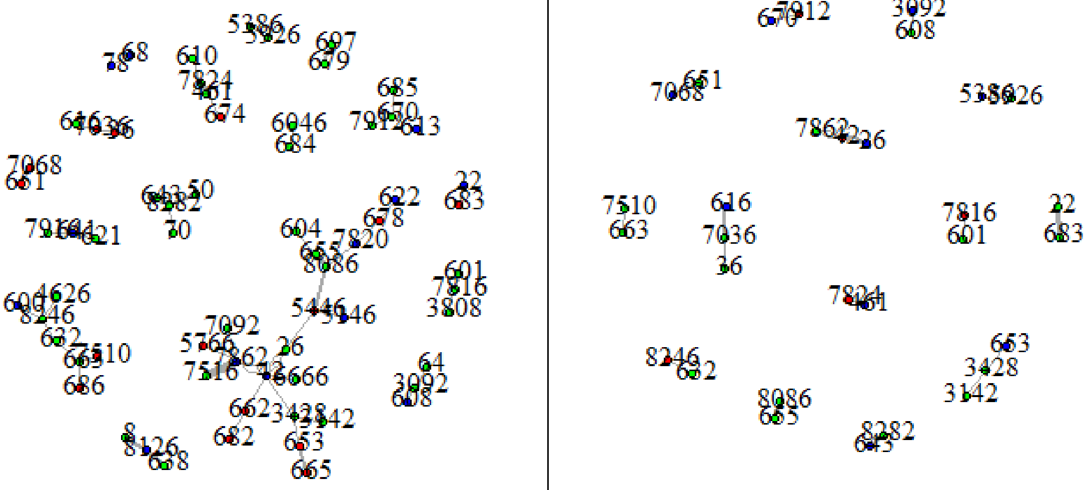

Figure 9c: Filtered at 3 times mean interactions

Figure 9d: Filtered at 4 times mean interactions

Figure 9: NN networks filtered at increasing interaction thresholds. Node colours represent group membership: red nodes are in group R, blue nodes are in group C, and green nodes are "all others" in the herd.

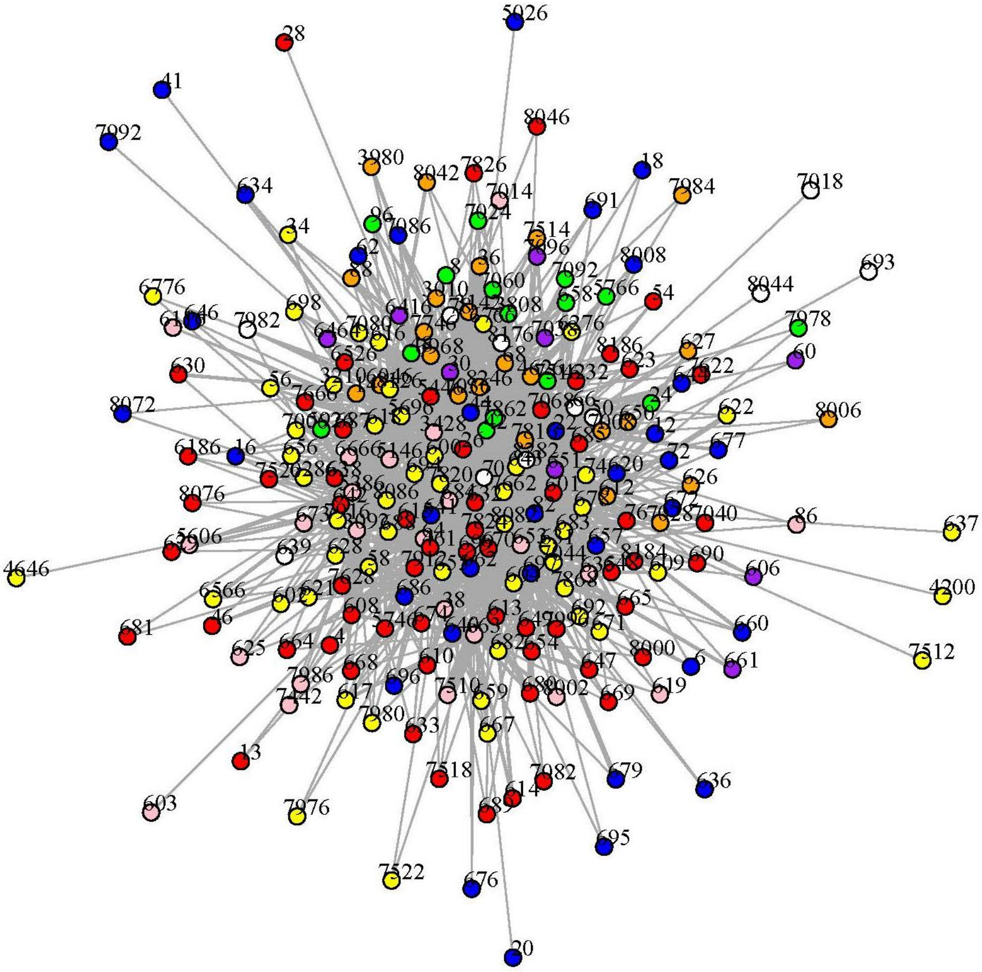

Figure 10: Unfiltered NN network showing subgroups (as measured by modularity) by colour. Each colour represents a subgroup of cattle more strongly connected to each other than to the rest of the network.

Table 8: Frequency table of herd subgroups (shown in Figure 11)

GROUP	***MEMBERS***
1	60
2	35
3	52
4	15
5	9
6	23
7	24
8	11

A Kruskal-Wallis H test revealed a statistically significant difference in NN frequency between dyads of different degrees of relatedness ($x^2(3)=24.87$, $p<0.000$; Figure 11), with a mean rank of 24.45 for unrelated dyads, 50.50 for dyads with MRC 0-0.1, 30.25 for dyads with MRC 0.1-0.45, and 45.85 for dyads with MRC 0.45-75, where a higher mean rank indicates a higher frequency of NN associations between the focal animals and NNs of that category. These results indicate that the cows in the current study showed a social preference towards related NNs rather than unrelated NNs, meaning that relatedness could be the factor for which social connections are selected.

Further Kruskal-Wallis H tests revealed no statistically significant differences between NNs of different age classes ($x^2(2)=0.033$, $p=0.98$; mean rank calf 33.27, juvenile 32.18, adult 33.06; Figure 12) or sex classes ($x^2(1)=0.608$, $p=0.44$; mean rank female 32.22, male 36.46; Figure 13)), meaning the cows in the current study showed no social preference towards a NN of a particular age or sex, thus implying that age and sex do not play a major role in determining social connection in the current study.

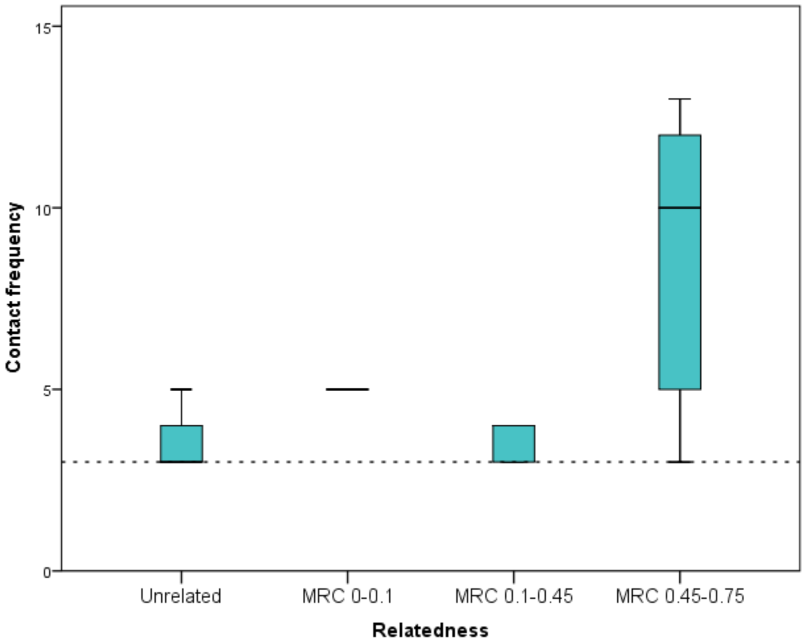

Figure 11: Bar chart showing contact frequency of all focal animals with NNs of different relatedness. The dotted line represents the filter threshold of 3+. Whiskers represent error bars and the thick black line is the category median.

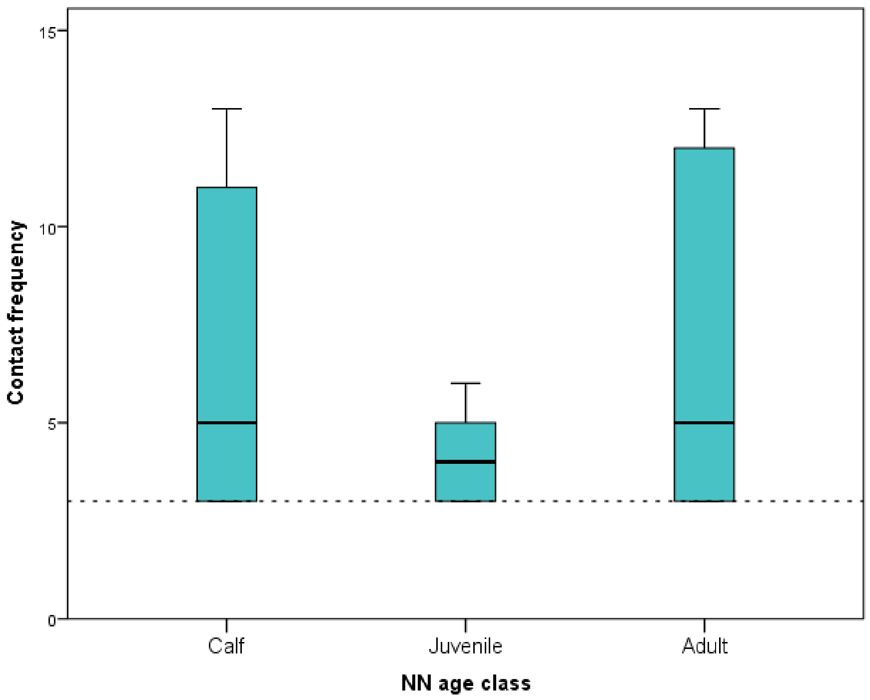

Figure 12: Bar chart showing total contact frequency of all focal animals with NNs of different age groups. The dotted line represents the filter threshold of 3+. Whiskers represent error bars and the thick black line is the category median.

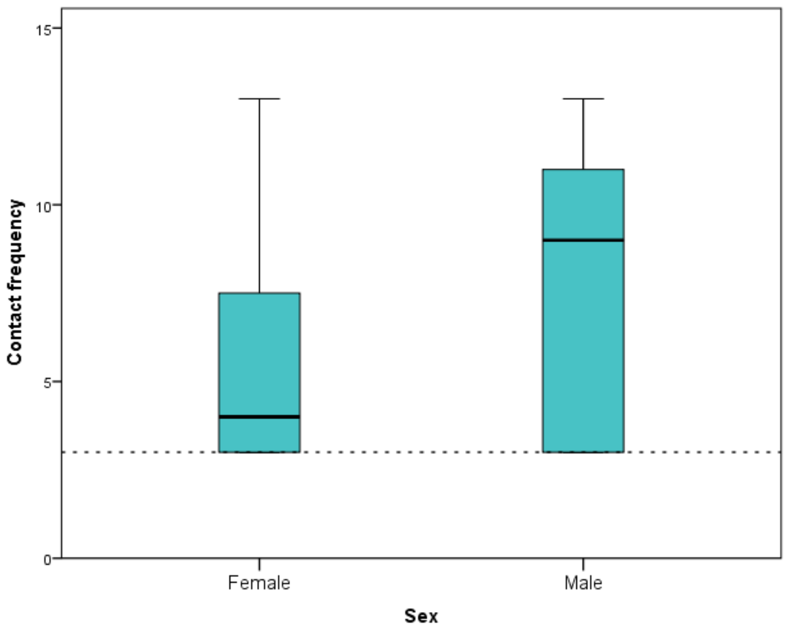

Figure 13: Bar chart showing total contact frequency of all focal animals with NNs of each sex. The dotted line represents the filter threshold of 3+. Whiskers represent error bars and the thick black line is the category median.

Does the social network structure of a group of related cattle change as the calves in the group approach weaning?

The social network for Time Block 1 consisted of 64 dyads with a total of 223 contacts (Fig. 14a). The mean edge weight, or contact frequency, was 3.54 (±3.03SD) and the median edge weight was 2 (range 1-15). Time Block 2's network consisted of 43 dyads with a total of 120 contacts (Fig. 14b). The mean edge weight was 3.3 (±2.8SD) and the median edge weight was 2 (range 1-22). The social network for Time Block 3 consisted of 69 dyads with a total of 173 contacts (Fig. 14c). The mean edge weight was 2.5 (±2.3SD) and the median edge weight was 2 (range 1-13).

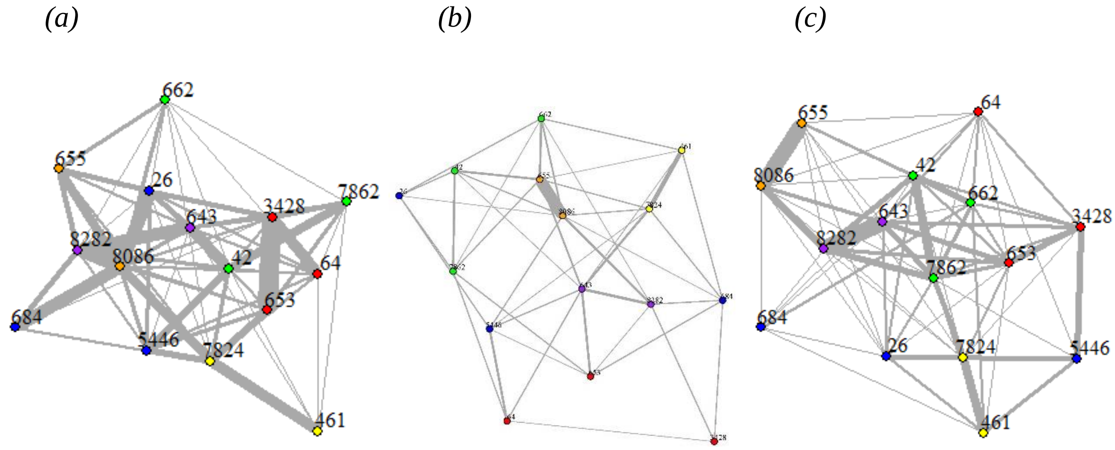

Figure 14: Social networks of Group R for each 5-week block (a, b) and one 3-week block (c). Colours represent different cow-calf pairs or cow-calf-yearling groups if the cow had a yearling as well as a calf. Yearlings have two-digit tag numbers, calves have three-digit numbers, and cows have four-digit numbers such that the three red nodes in (a) represent a cow-calf-yearling group. Edge width represents frequency of contacts between dyads.

Edge density (the fraction of potential ties that are present in the observed network) of weeks 1-5, 6-10, and 10-13 were 0.6, 0.409, and 0.66, respectively, meaning that there were fewer total connections within the network during Time Block 2. Transitivity (the likelihood of there being connections between a node's connections) was 0.64 in weeks 1-5, 0.375 in weeks 6-10 and 0.67 in weeks 10-13, meaning that during Time Block 2 the network was less connected overall.

Network stability (consistency of social connections) and their frequency over time, as measured by Spearman's correlation coefficient is reported in Table 8.

*Table 8: Spearman's rho and p-values for the different network types between time blocks. Full networks are networks which include frequency of interactions. Binarized networks have the same edges as the full networks but ignore the frequency of interactions. Adult-only networks are binarized networks with the calves removed. Significant results are marked with "***"*

Full networks	*df*	*S*	r_s	*p*
Time Block 1-2	104	142436	0.26	0.007 ***
Time Block 2-3	104	170152	0.12	0.23
Time Block 1-3	104	131672	0.32	0.00097 ***
Binarized networks				
Time Block 1-2	104	144319	0.25	0.009 ***
Time Block 2-3	104	192166	0.0039	0.96
Time Block 1-3	104	161994	0.16	0.10
Adult-only networks				
Time Block 1-2	35	6153.7	0.167	0.33
Time Block 2-3	35	6153.7	0.21	0.22
Time Block 1-3	35	7213.6	0.072	0.68

Eigenvector centrality, or influence, was not significantly higher for cows who had not weaned their calves compared to cows who had weaned calves (unpaired t-test: t(2)=-0.79, p(perm)=0.49), for heifers when compared to cows with weaned calves (unpaired t-test: t(2)=-0.312, p(perm)=0.71), for heifers compared to cows without weaned calves (unpaired t-test: t(2)=-1.22, p(perm)=0.29), nor when comparing the eigenvector centrality of the same cows pre- and post-weaning (paired t-test: (2)t=-0.327, p(perm)=0.993), suggesting no link between social influence and presence of a calf.

Cow-calf association frequency, was not significantly lower for cows post-weaning when compared to pre-weaning values (paired t-test: t(2)=1.12, p(perm)=0.49, Figure 15), nor for cows with weaned calves when compared to cows without weaned calves, e.g. still suckling (unpaired t-test: t(2)= -3.39, p(perm)=0.092, Figure 16), implying that there might be a trend towards fewer associations between weaned cow-calf dyads compared to cow-calf dyads where the calf is still suckling.

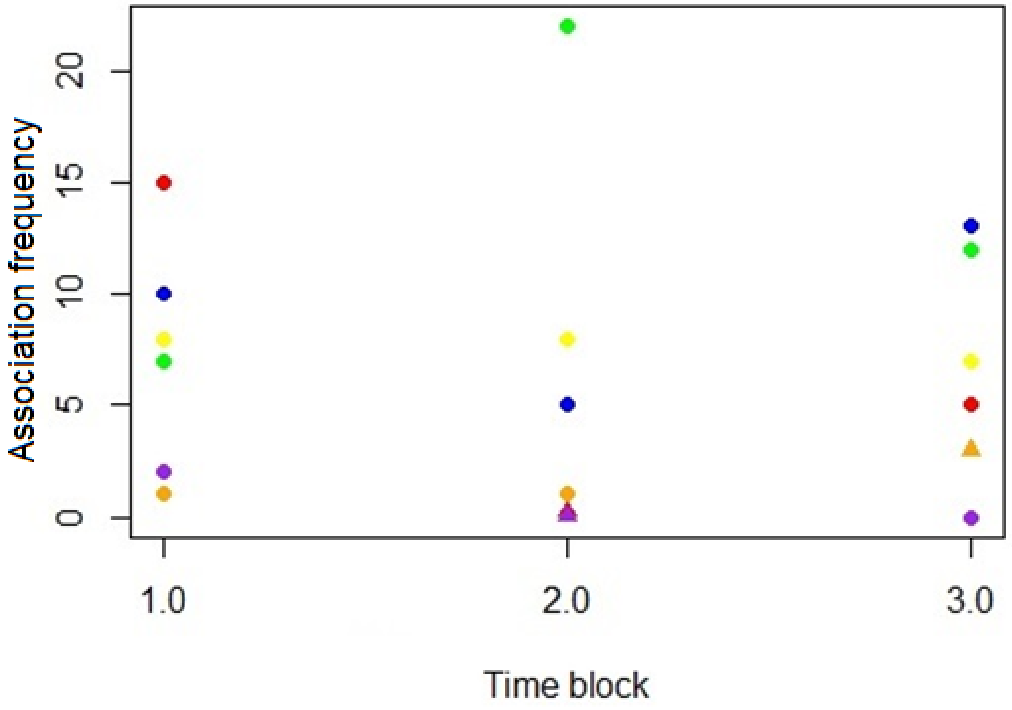

Figure 15: Association frequency (measured as number of times a cow-calf dyad were within 6m of each other) of each cow-calf dyad in each time block. Colours represent cow-calf dyads. Triangles represent the time block in which that calf was weaned.

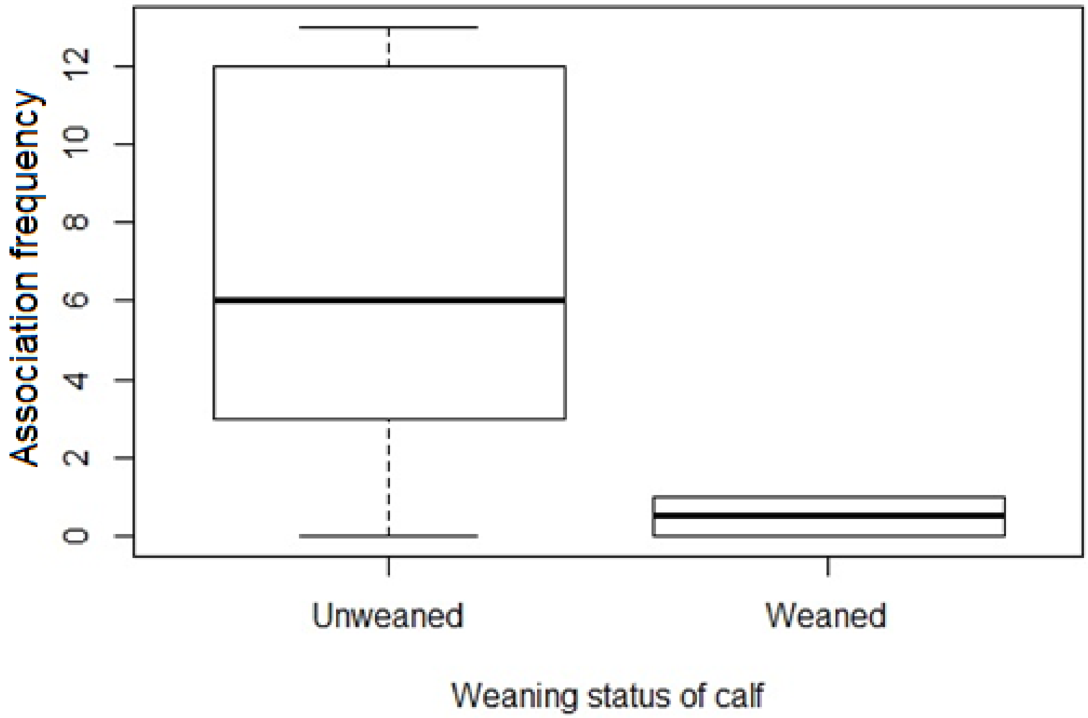

*Figure 16: Boxplot showing the association frequency (number of times each cow-calf dyad were within 6m of one another) of weaned and unweaned cow-calf dyads. Thick black lines are the group median, boxes are the interquartile range (IQR), and whiskers are 1.5*IQR.*

Only two calves showed consistency in their social partners over time (full results reported in Table 9).

*Table 9: Consistency of social partners for each calf in each Time Block. Significant results are marked with a *.*

Calf	*Time Block 1-2*	*Time Block 2-3*	*Time Block 1-3*
461	(r_s(9)=0.84, p=0.81)	(r_s(9)=0.19, p=0.57)	(r_s(9)=-0.053, p=0.88)
643	(r_s(12)=-0.002, p=0.994)	(r_s(12)=-0.04, p=0.896)	(r_s(12)=0.67, p=0.009)*
653	(r_s(11)=0.21, p=0.498)	(r_s(11)=0.157, p=0.61)	(r_s(11)=0.42, p=0.15)
655	(r_s(7)=0.029, p=0.94)	(r_s(7)=0.38, p=0.29)	(r_s(7)=0.517, p=0.126)
662	(r_s(11)=0.59, p=0.033)*	(r_s(11)=-0.254, p=0.4)	(r_s(11)=-0.217, p=0.48)
684	(r_s(7)=0.175, p=0.61)	(r_s(7)=-0.46, p=0.16)	(r_s(7)=-0.142, p=0.678)

A Friedman test of differences among repeated measures revealed no significant differences in calf-adult associations between the three time blocks (x^2(2)=2.33, p=0.331; Figure 17). Additional Friedman tests of differences among repeated measures of differences in calf-juvenile associations (Figure 18), calf-calf associations (Figure 19), and same-gender associations (Figure 20) also found no significant difference between time blocks but suggests a trend towards significance (x^2(2)=5.33, p =0.0695; x^2(2)=5.33, p=0.0695; x^2(2)=5.33, p=0.0695). This means that calves in this study might associate more with other calves or juveniles of the same age as they mature.

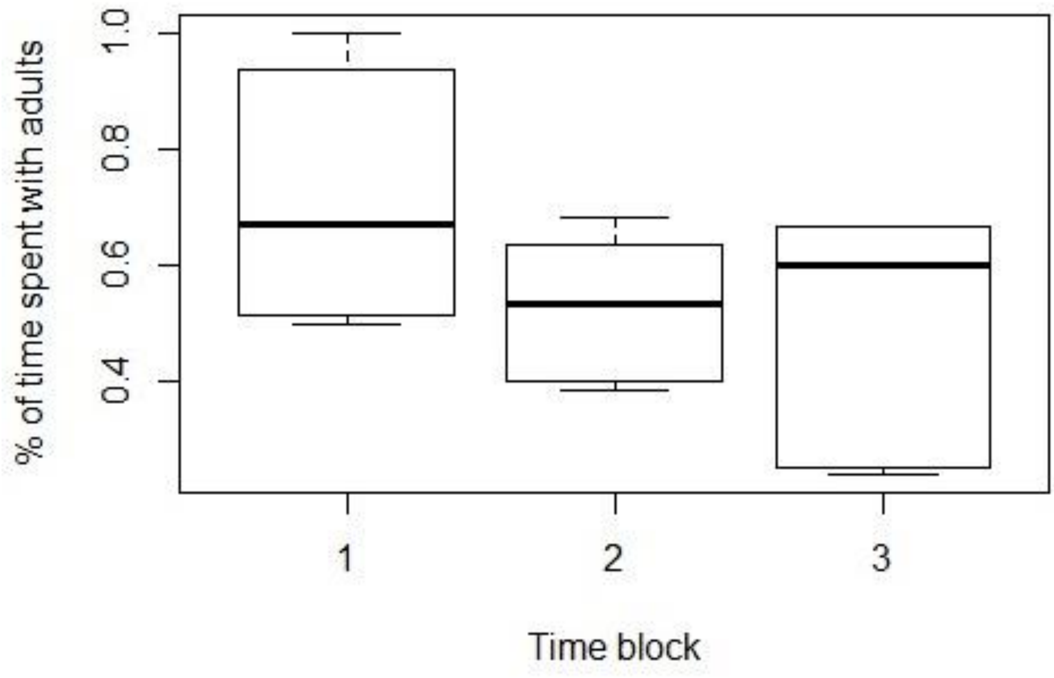

*Figure 17: Changes in calf-adult associations over time. Thick black lines are the group median, boxes are the interquartile range (IQR), and whiskers are 1.5*IQR.*

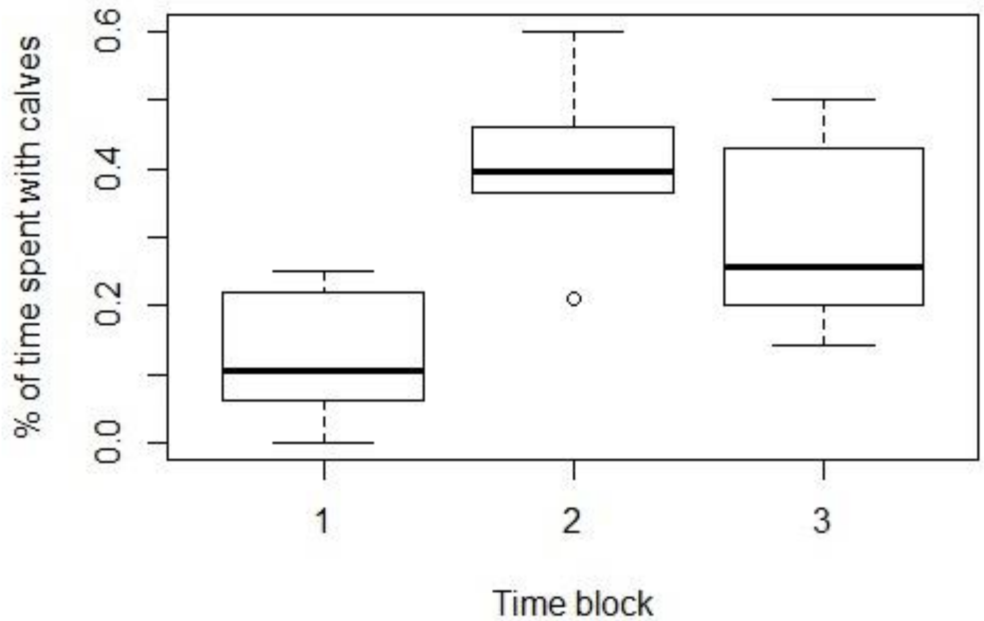

*Figure 18: Changes in calf-calf associations over time. Thick black lines are the group median, boxes are the interquartile range (IQR), and whiskers are 1.5*IQR. Hollow circles represent outliers*

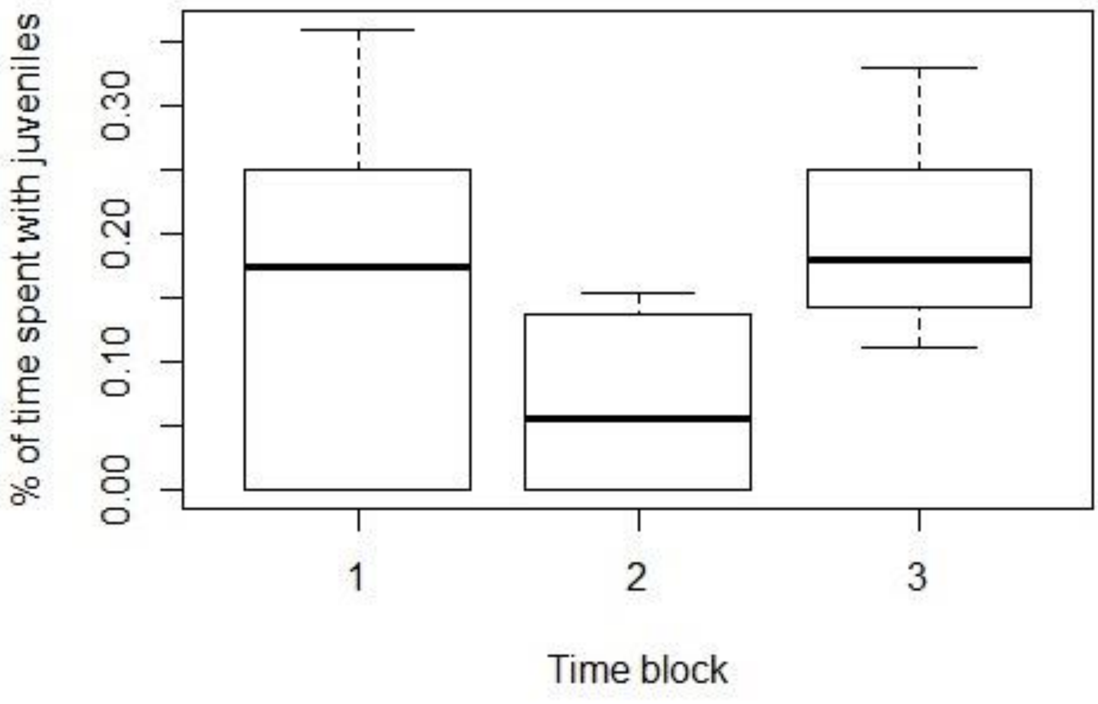

*Figure 19: Changes in calf-juvenile associations over time. Thick black lines are the group median, boxes are the interquartile range (IQR), and whiskers are 1.5*IQR.*

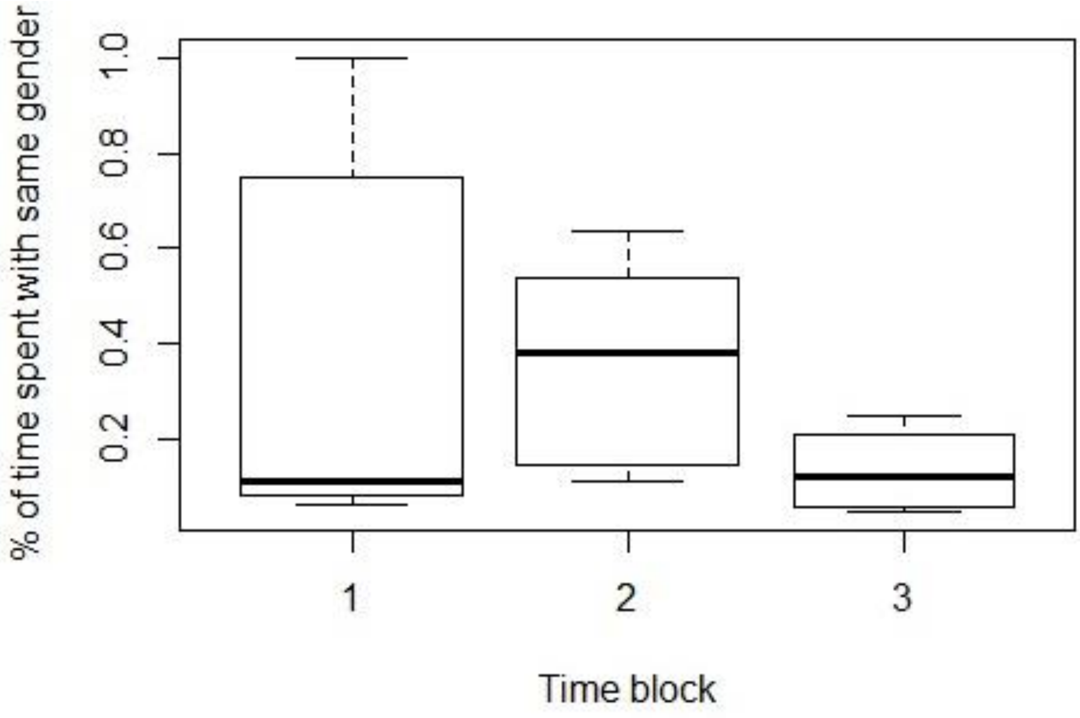

*Figure 20: Changes in associations with animals of the same gender over time. Thick black lines are the group median, boxes are the interquartile range (IQR), and whiskers are 1.5*IQR.*

3.3 Discussion

Do related and unrelated cattle associate differently?

The study results show cattle within both the C and R groups associate non-randomly, meaning that there are individuals in the herd that they associate with more than others (cf. Boyland et al., 2016). The current study demonstrates the two networks were significantly different, since the network metrics Strength and Degree were significantly higher within the R Group compared to the C Group. Strength and Degree were also significantly higher in the R Group when the calves are removed from the analysis, meaning the differences between the groups was independent of cow-calf interactions e.g. suckling.

There is considerable evidence of non-random associations in species from a range of taxa such as sharks (Schilds et al., 2019), bats (Kerth and König, 1999; Zeus et al., 2018), flamingos (Rose and Croft, 2017), and bovids (European bison: Kemp et al., 2018; dairy cows: Gygax et al., 2010; Boyland et al., 2016; dairy calves: Bolt et al., 2017; rangeland cattle: Stephenson et al., 2016; zebu cattle: Reinhardt and Reinhardt, 1981) which are further supported by the results of this study.

Notwithstanding the range of evolutionary costs (e.g. parasite spread: Patterson and Ruckstuhl., 2013, competition: Fortin and Fortin, 2009) and benefits (e.g. reduced predator pressure: Fortin and Fortin, 2009, protection of young: Brunetti and Scornavacca, 2010) associated with group living in animals, there is a question as to whether group living is driven by “passive” or “active” mechanisms. As discussed in chapter 1.2, the data collection approach cannot explicitly determine which mechanisms are at play within a group of animals. Passive mechanisms include shared interest in a finite resource such as a food or water source (Schilds et al., 2019), whereas active mechanisms include social preference (Couzin et al., 2005). For example, Best et al., (2013) found that Eastern grey kangaroos (*Macropus giganteus*) are philopatric and associate by matriline, but generally speaking, the strongest associations were between females whom had overlapping territories. This indicates that space use is a key driver of social relationships in this species. However, it is important to note that the underlying mechanisms of this behaviour remains unknown, and the authors note that it remains unclear whether the overlapping home ranges are the reason behind the high levels of social association, or if the high level of social association is the reason behind the overlapping home ranges (Best et al., 2013).

Passive associations are largely driven by spatio-temporal resource availability and would likely result in a high level of social interactions between dominant individuals (as discussed in section 1.2) as they would have primary access to the best resources (Neisen et al., 2007, in Gygax et al., 2010). Lott and Minta (1983) did not test for dominance but concluded that American bison associate randomly, and associations are primarily driven by common space-use. This hypothesis was tested on dairy cows by Neisen et al (2007) (in Gygax et al., 2010), who found no causal link between dominance and lying areas, meaning that active preference appears to be present in dairy cows. The herd in this study had access to a large pasture (8 ha or more) at a low stocking density (298.5m^2 per cow). Therefore, it was predicted that competition would not be an active driver of passive associations within the study herd. Additionally, reciprocity is not a characteristic of passive associations, and the evidence of maternal reciprocity (e.g. Swain et al., 2015) in cattle further supports the claim that the non-random associations displayed by the cattle in this study are a result of active associations driven by social preference, and not by passive associations such as competition.

As discussed in section 1.2, there exists a level of uncertainty as to the type of individuals cattle prefer to associate with, specifically whether familiarity or relatedness is the most important factor underlying group formation. Considering the case of social dynamics of American bison groups. Green (1992a,b) concluded that American bison preferentially associate with kin, particularly along matrilines, as in European bison (Kemp et al., 2018), whereas Lott and Minta (1983) determined that American bison associate randomly, despite calves associating with their mothers “well past weaning age”. These contrasting results may be due to the temporal differences between the studies. Green (1992a,b) tracked 13 bison calves and their mothers for approximately one year (Green, 1992a) or 5 months (Green, 1992b), whereas Lott and Minta (1983) utilised a longitudinal approach, following 16 bison cows and 8 calves for 44 months. Green (1992a) states that female calves remain within 10m of their mothers at least until sexual maturity (approx. 3 years) and this cow-calf spatial proximity is primarily maintained by the calf. Therefore, the results seen in Lott and Minta (1983) may be due to the longer-term nature of their study, where calves passed the age of sexual maturity and were therefore no longer as motivated to maintain contact with their dam.

In cattle, the majority of studies are conducted on dairy cows which typically have little or no access to related conspecifics from a young age. The preferential bonds formed between familiar dairy cows (see section 1.2) is most likely explained by Kilgour (1972)’s suggestion that a key factor influencing cohesive bonds in groups of cattle is the human management practices which allow these bonds to develop. Lazo (1992; 1994)’s studies found that the feral Doñana cattle formed stable herds with fixed home ranges, herd formation was driven by high levels of philopatry within females, and social associations were formed based on familial ties (Lazo 1994). The overarching group structure remained the same whereas at the lower level of social organisation herds split into smaller, unstable groups termed “parties” which vary in size and composition depending on resource availability and distribution (Lazo, 1992;1994). Furthermore, Reinhardt and Reinhardt (1981) found that cattle showed a preference for their offspring of both sex over all other non-related animals for as long as five years post-partum. These preferential associations were also seen between siblings and the authors concluded that “the ensuing family units were strikingly stable and cohesive”. The higher Transitivity value seen in the R Group in the current study indicates a high level of cohesion within the group (Kemp et al., 2018), which further validates the claims put forward in Reinhardt and Reinhardt (1981).

Philopatry is a fundamental aspect of minimally-managed bovine groups (Lazo, 1992; 1994; 1995), but beyond that, animals tend to associate with animals with whom they share similar traits (bison: Kemp et al 2018, dairy cows: Boyland et al 2016; rangeland cattle: Stephenson et al., 2016). Relatedness, therefore, has been identified as the most likely basis for cattle grouping under minimally managed conditions (Stephenson et al 2016; Reinhardt & Reinhardt 1981; Lazo 1994; 1992). This observation is supported by the current study, as the R Group had a significantly higher prevalence of within-Group contacts, significantly higher Degree, and significantly higher Strength than the C Group.

Social relationships between an animal and the members of its herd develop with age and rely on learning the characteristics of future social partners (Veissier et al., 1998). In cattle, the cow-calf bond develops soon after birth (von Keyserlingk and Weary, 2007), and soon thereafter to other individuals in the herd (Phillips, 2008; Raussi et al., 2010). In minimally-managed conditions, associations between siblings are likely to develop within the “sensitive period” (11-40 days old) as in Vitale et al. (1968), who conducted a study on feral Maremma cattle and found that the calves in the study spent over half of their day separate from their dams, socialising with other calves, even before 10 days of age. It is important to note here that their conclusion, that Maremma cattle preferentially associate with age-mates rather than related animals is contrary to many other authors results (e.g. Reinhardt and Reinhardt, 1981; Lazo, 1994) and may be caused by the limited mobility of calves during early life. Reinhardt and Reinhardt (1981) posit that the dam acts as a linking agent between siblings which often leads to the establishment of family units.

Interestingly, there is also evidence of kin discrimination in cattle reared separately. Coulon et al., (2010) published a paper on social preference and kin discrimination in a group of heifers. Seven of the 24 individuals in the study were clones from the same somatic line. Calves were singly-housed until six months of age when they were grouped together in a barn. Preferential associations between cloned heifers within the mixed herd were observed, in addition to cloned individuals differentiating between pictures of heifers from the same social group and a different social group, as well as between pictures of cloned heifers from the same donor and heifers from a different donor, all from the same social group (Coulon et al., 2010). These results indicate that cattle can use visual cues to discriminate between kin and non-kin, however, it remains unclear if phenotype matching is the only mechanism used to identify kin/members of the social group. For example, twin lamb associations in sheep are not only due to genetic relatedness but also experience (Ewbank, 1967a; Shilito-Walser et al., 1986). Twin lambs born as a result of embryo transfer associate as much as twin lambs conceived naturally (Shilito-Walser et al., 1981), and there is no difference between social associations of heterozygous and monozygous twin calves (Ewbank, 1967b; Veissier et al., 1998). Wiley (2012) suggested that all sensory modalities are used for discrimination of members of an animal’s social group but specified that animals may simply be categorising conspecifics based on “kin” and “non-kin” groupings rather than individual recognition.

As a result of the mother-offspring bond, and the associated close spatial proximity due to suckling interactions and lack of independence in the calf, associations between mother and offspring should be expected to be higher than between the mother and any other cow. Therefore, the presence of the calves in the related network might be the reason the Related Group has higher Degree and Strength than the Control Group. Without the presence of calves in the network for analysis, the adult cows in the Related Group maintained a significantly higher Degree and Strength than in the Control Group. One explanation for this may be in line with the results from Swain et al., (2015) where cows with calves spend more time associating with other cows who also have calves. However, if the cow-cow associations were purely based on “maternal class” one would expect to see the same level of associations in the C Group within the current study, as all cows had calves, meaning that the higher network metrics seen in the R Group did not occur purely as a result of maternal reciprocity. The evidence for continued mother-offspring associations over at least 5 years in zebu cattle shows that adult offspring continue to interact with their parents over a long period of time (Reinhardt and Reinhardt, 1981). Additionally, Veissier et al. (1990) observed that cows still favour their yearling calf over all other yearling calves past the point of a new calf being born, and spend more time in closer proximity to their new calf on day one postpartum only (Veissier et al., 1998). Therefore, it may be possible that the strong associations seen in the R Group within the current study are a consequence of older mother-offspring bonds that cause the cows to maintain closer contact, and as a result, the calves are exposed to other family members at an earlier age, further reinforcing the associations within the group. More generally speaking, high relatedness between individuals who have a high level of association may increase their fitness by improving offspring survival through, for example, calf creches (Vitale et al., 1986) which can improve calf safety (Hamilton 1964; Swain et al., 2015), while allowing the mother more time to graze.

Interestingly, when comparing the centralities, or social importance, of the matched cows within and between groups the results indicate that these measures are characteristic of individual cows rather than linked to age or gender. Finally, within the C Group, there were significant positive correlations between network metrics (Strength, Degree) and traits of the cows (age, parity), such that older cows with higher parity are more likely to have a higher number and frequency of social contacts. Such correlations were not evident in the R Group.

The lack of consistency in the centralities between the defined groups indicates that individual centrality is not tied to age, gender, or parity but is instead a characteristic of an individual cow. This is consistent with previous results on individuality in livestock (sheep: Marino et al., 2019). For example, Gibbons et al., (2010) used a runway test to determine sociability in dairy cows measured by latency to reach 5m from the rest of the herd. The latency was then compared to spontaneous behaviours such as synchrony with the herd observed within the home pen and was highly repeatable within cows. The utilisation of a PCA approach led Kemp et al. (2018) to combine the variables "age" and "dominance" into "experience", and the variables "Strength" and "eigenvector centrality" into "sociability"; interestingly, these two new variables were not correlated, further supporting the weak effect of age on centrality. Additionally, the selected control cows may have been a mix of cows with very high and very low dominance within the larger herd. Some studies have shown that animals with low dominance do not tend to select dominant individuals as their preferred social partners, perhaps as a mechanism to reduce aggression. For example, Briard et al. (2015) found that domestic horses distributed their social preferences among other horses of similar rank and personality. This study did not examine the role of dominance on social connections, which could be an interesting avenue for further study. The absence of any correlation between traits (age, parity) and network metrics (Degree, Strength) in the R Group compared to the C Group, within the current study, may be attributed to the importance of the matrilineal group within the social structure of cattle (e.g. Kemp et al., 2018), meaning that related animals preferentially associate with other relatives regardless of their traits. For example, Godde et al. (2015) used a social network approach to quantify associations between female mountain goats (*Oreamnos americanus*) and found that while the goats in the study assorted by reproductive status, they also associated with related animals at the expense of associations on the basis of similar traits

This section had the aim to compare and contrast association patterns of related and unrelated cattle from a single herd. The results were consistent with the prediction that related animals would associate more than unrelated animals. A key point here is the fact that all the study animals were reared in the same herd, under identical conditions yet associations were maintained at a higher rate and with a higher number of group members within the Related Group compared to the Control Group. This indicates that the cows are willing to invest more into relationships with related conspecifics than unrelated conspecifics and calls into question common management routines on farms today such as early cow-calf separation in both beef and dairy systems.

It is worth noting that the study cows represent a limited sample size so any results should be generalised with caution.

Do the cattle in this herd have preferred social partners, and if so, how are these selected?

In this section, the key results were (i) that cows showed a preference towards certain NNs over others, as shown by the significant modularity of the network; and (ii) overall, the cows showed no preference for NNs of a certain age- or sex-class, but did show a preference towards related NNs.

Modularity measures community structure within a network, and as such, the significant modularity measures within all NN networks (Fig. 9) in the current study indicates that there exist subgroups within the study herd which are more closely connected to other subgroup members than to the rest of the network/population, and during a fission event, the herd would likely split along the subgroups indicated by the modularity results (Fig. 10). It has been theorised that modularity acts as a survival strategy to increase benefits in large groups by reducing competition (Grilli et al., 2016; Lorenz et al., 2011) or disease spread (Sah et al., 2017). However, it may also be caused by factors such as cognitive limitations (Lehmann et al., 2007; Kerth et al., 2011) or time restraints (Lehmann et al., 2007). Bovids are fission-fusion species, and the presence of subgroupings within a herd, as seen in the current study, has been well-established in the literature (Lazo, 1992; 1994; 1995; Stephenson et al., 2016). For example, Lazo (1994) observed fission-fusion grouping in feral cattle at two levels of organisation; an unstable lower level where subgroups merged and split according to environmental conditions, and a stable higher level of organisation within the subgroups themselves. Interestingly, Stephenson et al (2016) conducted a five-year study on extensively grazed beef cattle and established subgroup size as ranging from 3-39, which is slightly less than the observed range in the current study, but generally consistent with the overall results.

Once the presence of subgroups has been established, the logical next step is to examine their composition to ascertain which factors play a role in forming these groups. The observed subgroups in Lazo (1994) were composed of related mother-young pairs, along with cattle of the same sex and similar age, although it is worth noting that male participation in the observed herds was low as mating occurred seasonally and during the study there were a low proportion of adult males (9%) within the study area (Lazo, 1994). Furthermore, maternal bonds are the key condition informing social preference in European bison (Kemp et al., 2018) and zebu cattle (Reinhardt and Reinhardt, 1981a) and also appear to be the general driver of NN associations in the current study as the only significant NN preference shown by the focal animals was towards related animals. The results of the current study may thus be in line with the results of Reinhardt and Reinhardt (1981a) where the dam acts as a connection between multiple generations of her offspring.

The lack of assortment by age- and sex-class is inconsistent with previous results on the topic (e.g. Lazo, 1994; Boyland et al., 2016). Boyland et al (2016) found significant assortment by milk production, breed, lactation number, and pasture access in dairy cows, but noted that the assortment patterns did not account for a large part of the variation in association patterns.

Milk production may have impacted the observed NN associations in the current study and could be measured as “stage of weaning”. This would further support the results of Swain et al. (2015) by showing a switch in associates linked to the end of a lactation as well as the start of one (measured as “maternal” cows). However, only the focal animals were assessed for signs of weaning during the study and as a result the relevant analyses could not be run. Furthermore, this would only be applicable to NN associations between adult cows with calves.

Assortment by breed has been documented in cattle (e.g. Huber et al., 2008; Braghieri et al., 2011; Boyland et al., 2016), and has even been substantiated by testing cows on 2D-images of familiar and unfamiliar cows from the same or different breeds, where the tested cows consistently showed recognition of images of cows of the same breed (Coulon et al., 2009). Braghieri et al. (2011) examined time budgets, ingestive behaviour and social behaviour in three native Italian cattle breeds (Podolian, Chianina, and Romagnola) managed as a single herd, and found that the cattle showed a preferential spatial relationship with other animals from the same breed (Braghieri et al., 2011). In the current study, the herd was mostly composed of AA cattle, and as a result only one of the study cows (7036) was of a different breed. Therefore, breed preferences were not assessed and as a result further research on this topic is required.

Lactation number reflects age (Boyland et al., 2016) and as such, contrast the results of the present study. However, the management differences between extensively grazed beef cattle and intensively managed dairy cows must be considered; dairy calves are typically removed from their dam soon after birth (Veissier et al., 2013; Bolt et al., 2017) and mixed with other calves of the same age (or even housed individually) (Bolt et al., 2017), thereby reducing the pool of potential associates to bond with during the “sensitive period” in calves (Vitale et al., 1986; Raussi et al., 2005) to only animals of similar age. Conversely, Lazo (1994)’s study was conducted on a feral cattle population where management was restricted to culling of 30-50% of the calves on an annual basis. Why, then, do the results of the current study contradict those of Lazo (1994)? A key difference between the current study and that of Lazo (1994) is data collection methodology. The current study noted only a single NN per focal animal per scan whereas Lazo (1994) derived preferences from group membership where all animals showing “cohesive behaviour and spatial distribution and were more than 150m from other individuals or groups” were classed as a social unit and all animals within the same social unit were used to assess preference. Therefore, since the study also found that these social units were often made up of cow-calf pairs (Lazo, 1994), it follows that these groups of maternal cows and their offspring (as in Swain et al., 2015) would often be associating with animals of the same age (cows with cows and calves with calves).

An alternative explanation might be the duration of each study. Lazo’s (1994) took place on 309 days over two years, and as mentioned, a large proportion of the calves born each year were culled as part of management routines. Since the data were pooled across the entire study period, a considerable proportion of the data may have been collected on cows whose calves were culled and might have subsequently associated with other cows of the same age (Lazo, 1994). In contrast, the current study took place over five months during one production season where no new animals were introduced, and no animals were removed from the herd. Perhaps if the study animals had been observed throughout weaning and until the birth of the subsequent calf, the results of the current study may have been more similar to those of Lazo (1994). Unfortunately, the COVID-19 disease outbreak prevented further data collection.

The aim of this section was to investigate if the focal animals had preferred social partners, and if so, to examine how these were selected. The first prediction, that the cows had preferred partners, was consistent with the results of the current study, whereas the second prediction was only partially accurate; the cows showed a preference towards related animals, but not towards animals of the same age. This section did not restrict which conspecifics each animal could associate with and as such, functioned as a free-choice test. The fact that the study cows could choose any animal from the entire herd as their NNs and preferentially selected related animals further underlines the perceived importance of related animals to cattle, and the potential welfare deficit caused by restricting that access.

The data may also have been skewed by the data collection technique, that is, by only noting a single NN per cow per scan preferred social partners may have been overlooked due to them not being the nearest to the focal animal, despite the fact that they may have been in close proximity. Additionally, it is worth mentioning that the focal animals consisted of adults, juveniles and calves whose social association data were combined for the analyses. This might explain the lack of preference for any one age group as the different ages may have had preferences for different age-classes. However, when split into age categories, the sample sizes in the current study were too small to be successfully analysed.

Does the social network structure of a related group of cattle change as the calves in the group approach weaning?

The key findings were (i) that network structure was significantly stable in the binarized networks (networks with simple yes/no ties without multiplicity of contacts) between the first and second time blocks, but not between the second and third nor between the first and third, meaning that not only the frequency of interactions changed between Time Blocks 2 and 3, but also the pattern i.e. connections between cows in the Related group either ceased to exist or were established between previously non-connected dyads; (ii) that network stability was significantly consistent in the full networks (networks showing both the number and frequency of ties) between the first and second, and first and third time blocks but not between second and third, meaning that the pattern and frequency of associations between cows in the R group changed in Time Block 2; (iii) that eigenvector centralities did not differ between cows with and without calves, suggesting that the calves in the current study did not boost the importance (see 3.0 Predictions) of their dams within the network; and (iv) cow-calf pairs continued to associate past the point of weaning, with no significant difference in the association strength of the cow-calf pairs before and after weaning. Furthermore, (v) only two calves (643, 662) showed consistency in the ranking of their social partners (dams included); 643 between Time Blocks 2 and 3, and 662 between Time Blocks 1 and 2.

Binarized network connections are simple yes/no ties that simply inform the presence of a connection rather than explaining the intensity of said connection, meaning alterations in binary networks over time reveals absolute changes in network topology where existing connections are broken or non-existent connections are established (Croft et al., 2008). Therefore, the fact that network structure of the binarized networks in the current study was only significantly stable between Time Blocks 1 and 2 means that between Time Block 2 and 3 the study cows participated in some combination of breaking and establishing social ties. Considering the biological factors at play at this time, a plausible reason for this social upheaval is weaning of calves, which was substantiated by the current study as two of the six calves were weaned during Time Block 2 (Fig. 11) (one calf was weaned during Time Block 3 and the remaining three were not weaned during the study period). Furthermore, this is consistent with the current literature on natural weaning age in calves, which has been recorded as occurring at around 10 months of age (Reinhardt and Reinhardt, 1981b).

Alternatively, the change from Time Block 2 to 3 occurred in early February which is the middle of the dormant season in the UK (Statista, 2020). Therefore, observed changes may be due to a restructuring of the cost-benefit balance where maintaining closer social ties with conspecifics is less beneficial and energy is better invested in foraging (Engen and Stenseth, 1984), especially as the study cows were not provided with supplemental feed during winter months. Interestingly, Hall (1989), in a study of Chillingham Cattle, found a seasonal cycle of social behaviour which peaked in the summer. This study included sexual behaviours as part of “social behaviour”, making generalisation more challenging as sexual behaviour was not examined in the current study. However, the results from Hall (1989) concluded that there was no evidence of seasonal breeding in this population. In line with those results, the changes in network structure in the current study may be indicative of a seasonal cycle of social behaviour related to forage availability.

The most likely solution is some combination of the two previous suggestions. The current understanding of weaning behaviour is based largely on parent-offspring conflict theory (Trivers, 1974; Godfray, 1995) where, as lactation progresses, the dyad reach a point where the costs of lactation and maternal care incurred by the mother are greater than the benefits of continued suckling are to the offspring and weaning is likely to be initiated (Trivers, 1974; Martin, 1984). As such, the lack of consistency between the binary networks in Time Blocks 2 and 3 might be indicative of weaning, which although likely already in progress at this time, was accelerated by the lower levels of food resources available to the cows.

Of course, as mentioned previously, an increase in previously un-established connections may also have caused the lack of consistency between networks in time periods 2 and 3 and could be a result of the study calves establishing new social connections within the herd either following or approaching weaning (Daleszczyk, 2005). Prior to, but particularly during weaning, youngstock tend to form stronger bonds with their age-mates (Veissier et al., 1989), which may have also occurred in the current study.

The full networks (which include frequency of social connections) also showed significant consistency over time, indicating that consistencies in social interactions are not only characterised by the binary measures of who associates with whom, but also the magnitude to which that occurs e.g. the number of associations. Time Block 2 was the Time Block with the most weaning activity (two out of six calves were weaned during this time block). The results further support the theory that changes in the social network occurring around weaning are substantial enough to cause the lack of correlation seen between Time Block 2 and Time Block 3. Additionally, as shown in Swain et al. (2015), adult cows switch group membership between (in this study) maternal and pregnant cows. Therefore, one might speculate that despite still being a "maternal" cow past the point of weaning, the adult cows might be reaffirming bonds within the rest of the herd after weaning.

Perez-Barberia and Walker (2018) examined the social dynamics of sheep around parturition and found that parturition leads to a greater interindividual distance between maternal sheep, as well as between maternal and non-maternal sheep. Furthermore, maternal sheep were more likely to occupy peripheral positions in the flock. Interestingly, the authors posit that pre-parturient isolation in sheep may be an adaptive strategy to reduce agonistic interactions by familiarising herd-mates to the new spacing between animals. There is currently no research regarding how peripheral positions are maintained in sheep, particularly in populations which are continually in movement (e.g. grazing) or how reintegration and subsequent reduction of interindividual distances occurs (Perez-Barberia and Walker, 2018). Sheep are herd animals, and as such one might expect a reaffirmation of bonds once the lamb ceases to be the primary focus of the mother, and this may be echoed in the results of the current study, which found no correlation between networks within different time blocks.

In contrast to results from Kemp et al. (2018), the current study found no significant differences between the eigenvector centrality of heifers and cows with calves (weaned or unweaned). There was also no significant difference between the eigenvector centrality of the same cows before and after their calves were weaned. "Sociability" in European bison is significantly higher for females with calves than for females without calves, but upon removal of the calves from the social network, the opposite was revealed: lactating bison had the lowest centralities and Strength (Kemp et al., 2018), that is, the lowest "influence" within the group and the lowest total frequency of social interactions.

The lack of significant differences in eigenvector centrality between cows with and without calves seen in the current study may be explained by the fact that most of the adult cows in the herd were lactating during the study period. Comparing cows to non-lactating heifers is challenging since there may be age-related effects of sociality present in the herd (Carter et al., 2013). Perhaps in a natural population with a higher proportion of non-lactating females as in Kemp et al. (2018) the result of the current study may have shown significant differences in eigenvector centrality.

Additionally, the high Edge Density (0.80) of the R Group's network indicates that 80% of the possible connections are realised in the network, meaning that each cow in the network is connected to most other cows in the network (Table 4, Degree; Figure 7). This implies that affinity to other related members of the group is high regardless of the associations of calves meaning that most family members associate with other family members either directly through associations or indirectly through the association of other family members, and the presence of the calf is not changing the overall social structure. Eigenvector centrality is a measure of "influence", where a nodes eigenvector centrality is higher if its neighbours also have high eigenvector centrality; an individual with 10 links to well-connected individuals would have higher eigenvector centrality than an individual with 10 links to poorly connected individuals. As such, the high Edge Density in the current network means that since most of the cows in the network are connected, no one cow is likely to have high influence as they are all interconnected to the same individuals.

Furthermore, the premise of calves increasing the eigenvector centrality of their dams has the prerequisite of the calves having the highest Strength and Degree, meaning calves are the most sociable age group. This was not the case in the current study (Table 4). Instead, in the R Group only one calf was in the top five highest for Degree and only two were in the top five for Strength, whereas for both Strength and Degree four of the lowest five were calves (Table 4). This means that most of the calves would have a minimal effect upon the eigenvector centrality of their dams, as was seen in the current study.

In line with results from Reinhardt and Reinhardt (1981), the cattle in the current study continued to associate with their calves past the point of weaning although there was a slight trend towards fewer associations between weaned cow-calf pairs. The analysis was underpowered (three weaned pairs and three pairs still suckling) and as such may have resulted in a false negative, meaning that the suggested trend could be more indicative of the behaviour of these cows if the current study had a larger sample size. Veissier et al. (1990) conducted a study on social behaviour of 11 Salers cows at pasture where the yearling calves were also left in the herd past the birth of the subsequent calf. In this study 64% of the yearlings suckled their dams prior to calving, and there were clear indicators of preferential attachment even for those who were weaned; expressed by the higher levels of proximity and synchronisation between the dyad relative to other animals, along with the higher levels of licking and non-agonistic behaviours between the dyad compared to other group members. The cow remained in closer spatial proximity to her new calf than to her yearling on the first day post-partum only ($p<0.05$). The cow licked and engaged in non-agonistic behaviours at a higher rate with the calf than the yearling. During the post-calving observations 36% of yearlings were observed suckling. The cows engaged in licking and non-agonistic behaviours significantly more often with their calves than with their yearling ($p<0.01$) yet were more often in closer proximity to and synchronised with their yearling rather than their calf ($p<0.01$), perhaps due to the similarities in grazing behaviour between the cow-yearling dyads. The cows consistently preferentially engaged in licking and non-agonistic behaviour with their own yearlings over other yearlings throughout the study period. The yearlings were not observed to strengthen bonds between themselves as had been observed in abruptly weaned yearlings in Veissier et al. (1989). In fact, non-agonistic associations were significantly lower ($p<0.01$) between yearlings after the calving period (Veissier et al., 1989). These results show that the attachment between the cow and yearling persist past the point of weaning and the birth of the subsequent calf. However, this study focused exclusively on the triad of cow, calf and yearling within an artificially constructed herd where no other relatives were present, and only lasted until two weeks after the calving period, so draws no conclusions regarding the duration of mother-offspring attachment past the point of weaning.

The lack of consistency in social partners seen in the current study may be caused by not sampling the preferred individuals as these may have been part of the rest of the herd rather than within the Related Group; several of the calves (653, 684, 662) were weaned during the study period and subsequently altered their association patterns with their dams. Previous work on the subject suggest that calves associated with their age-mates after weaning (abrupt weaning), and the calves may be altering their associations from within the family group to include the rest of the herd. Carter et al., (2013) found that young female giraffes had the most social partners upon reaching maturity before settling into a "regular pattern" of associations, and this may reflect that same behaviour in cattle where the young animals are establishing new ties following weaning.

Integration into the herd is a process many young animals go through. Moose (*Alces alces*), for example, show sequential periods of social development (Altmann, 1958); first the moose calf imprints on its mother and begins "following" where it remains in close proximity to its mother at all times. From approximately 20 days of age, the calf begins to explore the area more independently, but the mother restricts social interactions by defending the calf from any other animal within a certain distance. At 90 days old, the mother breeds, and the calf socialises with the adult males, in fact, adult males who show aggression towards the calf during the rut are rejected by the moose cow (Altmann, 1958). Daleszczyk (2005) investigated the integration of European bison calves into the herd. Eleven calves were observed during the first 14 weeks of their lives. Three main phases were identified in a calf's social integration: first the formation of the mother-offspring bond, second the integration of the calf into a group of conspecifics, and finally the calf is incorporated into the larger herd. This integration is informed by activity patterns of the calf, where the early stage is represented by large amounts of time resting, e.g. in calf creche with other young calves (Vitale et al., 1986). As calves transition from an entirely milk-based diet to a diet where most of their sustenance come from grazing, they associate more with all members of the herd as they will typically be performing more of the same behaviours (Daleszczyk, 2005).

American bison show two processes as they reach maturity; first, the behaviour of the young calf develops to become more analogous to the behaviour of the adults in the social group, then the mother-offspring bond gradually loosens until the calf becomes independent from the cow (Egerton 1962, in Shult, 1972). The lack of consistency of social associations seen in the current study may be due to the calves in the study being near/at weaning age and subsequently transitioning into integration within the larger herd. This is substantiated in several studies on cows (Walker, 1962; Reinhardt and Reinhardt, 1981b; Das et al., 2000; Paranhos da Costa et al., 2006), which saw that once the cow produces less milk, the suckling events between cow and calf also decrease, and the calf spends more of its time with other cattle in the herd.

This section aimed to assess if and how the social dynamics of a related group of cattle changes as the calves in the group approach weaning. The first prediction, that the social network would remain relatively stable, was generally consistent with the results of the current study. The second, third, fourth and fifth predictions were not reflected in the results as calves proved important to the overall network structure, did not reduce the centralities of their dams, did not show a drop in cow-calf associations after weaning, and did not appear to associate more with their age-mates as weaning approached. In short, the social network of related cattle does undergo changes as the calves approach weaning and/or are weaned, but the calves still represent an important part of the social network and maintain social contact with their dam without impacting the effectiveness of their weaning or the apparent ability of their dams to maintain production (all adult cows calved again in 2020). This questions the necessity of abrupt weaning and the related welfare challenges. Further study is required into the production aspects of natural weaning before it can be recommended as a commercial weaning system. However, there are weaning methods (two-step weaning, noseflap weaning) that allow the calf to remain part of the social group whilst restricting udder access. In the context of the results from the current study, these methods might be preferable to current practice.

It is worth emphasising again that data collection towards this section was curtailed by the COVID-19 disease outbreak. Sample sizes used in the analyses are thus limited (e.g. there are only three juvenile cows and only two female calves) and as such some analyses are underpowered which makes it challenging to generalise the results of this section to the cattle industry as a whole.

4.1 Conclusions and Final remarks

The results of the present study indicate that the cattle in this herd invest more into social relationships with related animals than unrelated animals when allowed free-choice access to both. Moreover, the established social relationships within a related group of cattle remained generally consistent throughout the start of the weaning period (when the current study ended), the calves in the group proved important for the overall network structure. Furthermore, the use of positioning devices appear to be effective in quantifying aspects of social associations in dairy cattle.

There is extensive evidence of early cow-calf separation causing stress and impaired welfare (e.g. strong behavioural and physiological responses (Lefcourt and Elasser, 1995; Newberry and Swanson, 2007; Enriquez et al., 2011) in both cow (Ungerfeld et al., 2011) and calf (Hickey et al., 2003; Enriquez et al., 2009). The results of the current study further underline the issues with cow-calf separation by emphasising the strong preference cattle have toward related conspecifics and illustrating the importance of both weaned and unweaned calves within a social network.

However, the implications of the present study must be treated with some caution due to study limitations. Firstly, the sample sizes in (i) the Omnisense pilot trial and (ii) the beef cattle study were limited ((i) n=5), (ii) n=30), meaning that many of the statistical tests were underpowered and thus may have been false negatives (e.g. Figure 17 and the associated statistical test are conflicting), there was also only one treatment and one control group in the beef trial due to time limitations and practicality in selecting control group members. Secondly, both studies had time constraints which resulted in lower data density. The beef cattle trial was interrupted by the COVID-19 outbreak, and as such, had to be cut short by seven weeks. Furthermore, the data collection technique used for the NN networks may have contributed to a lower data density (see discussion). Finally, the Omnisense system had technical issues which caused challenges during the pilot trial, leading to the devices only functioning 34.5% of the time.

Building on the results from the current project, however, there are a number of future research avenues, such as using positioning devices to quantify social association through e.g. identification of individuals in particular social roles for future targeted management. Potential studies on beef cattle could, for example, extend the current study past the weaning period and the birth of the subsequent calf (as was planned and subsequently interrupted by COVID-19 in the current study) to investigate if changes in social dynamics occur during the calving period and if so, what those changes might mean in terms of welfare and productivity; alternatively, studies could investigate if there are social preference patterns between focal animals and multiple NNs; or even if social preferences are based on traits not covered in the current study such as body condition, weaning date, or body size.

On a more general scale, future studies could continue exploring alternative strategies to abrupt weaning. At present, several strategies have been explored, such as fenceline weaning (separating cow and calf by a fence thus allowing continued partial contact (Enriquez et al., 2009)), noseflap weaning (placing a noseflap on the calf which prohibits suckling but allows social contact (Enriquez et al., 2009)) or natural weaning in beef systems, and cow-calf systems (management systems which allow prolonged cow-calf contact (Johnsen et al., 2015)) on dairy farms.

In conclusion, the current study demonstrates the effectiveness of automated tools in understanding aspects of social behaviour in dairy cattle, and represents an initial exploration of social dynamics during a period of biological change (weaning) in extensively grazed beef cattle managed in a natural weaning system. It has yielded a number of novel findings that open up a range of future research avenues relevant to cattle management and welfare.

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Appendix 1

Methods pilot study: selection of cows for positioning system trial

Animals

This study was undertaken on a subset (n=12) of a dairy herd (n~200) from a commercial dairy farm owned by the University of Bristol, UK. The entire herd was kept in a freestall barn (33.95m x 115.8m). The cows were fed a total mixed ration (TMR) once a day and were milked twice daily (05.00h and 14.00h). The average yearly milk yield for this herd is 11 000L. Cows from the low-yield group (n~80) were used in this study and were kept in a 60m x 14m area within the main barn, with access to 93 lying stalls.

Selection of cows

Due to the limited number of sensors (n=5) available for use in study 2, a small, pilot study was carried out on cows from the herd to test for general trends in social preference before deployment of the Omnisense system. This was done to enable targeted collaring of cows deemed likely to associate. Cows were selected upon inspection and observed for 90 minutes. Behavioural data were collected using a combination of continuous observation where behaviours from Table 1 were recorded *ad lib* along with the identity of the cow with which the focal cow was interacting. Scan samples were completed every five minutes, as well as recording nearest neighbour (NN) identity, NN activity and focal cow activity. This was carried out for 12 (limited number due to time constraints) cows from August to September 2019, prior to study 2. All observations took place between 9.00 and 14.00h, before the afternoon milking. Due to the dynamic nature of dairy systems, and challenges regarding sensor functionality, none of these 12 cows were eventually collared but the results from these cows guided selection of focal cows for the sensor study (by similar traits).

Table A1: Ethogram of behaviours recorded during behavioural observations of dairy cows.

Agonistic/negative	
Butt	Physical contact where one cow uses its forehead, horns or horn base to strike or push another cow
Displacement	Physical contact where one cow forces another to give up its position within the barn
Affiliative/positive	
Groom	Oral contact (licking) by one cow (actor) to another (receiver). Excludes anal region, udder, teats and hooves. If there is a switch between actor and receiver, a change of receiver, or a pause lasting 10 seconds or longer, a new event is recorded.
All behaviours were coded with (A/R) to indicate actor/receiver as the focal cow could act as either.	

Statistical analysis

Selection of cows for use in position device trial

The following analyses were carried out on the behavioural data (Table 1) collected on the 12 cows which were not later used in the Omnisense trial. To inform which cows were collared and subsequently used in the Omnisense trial, Chi-square statistics were calculated to examine if cows were likely to have positive or negative interactions with other cows of the same age, lactation number, and same date of entry into group (Lavrakas, 2008). Each data point represented a cow-cow dyad. Binary variables were created for each of the trait-specific variables, where dyads were awarded a ‘1’ if they were, and a ‘0’ if they were not the same age, had the same lactation number, or were moved into a new group within 2 weeks of each other, respectively. Positive and negative interactions were scored as ‘1’ and ‘0’. If a dyad had multiple different types of interactions, the interaction which occurred most frequently was awarded to that dyad.

The positioning system (Chapter 2) was scheduled to be installed in September 2019, and as such, data collection for study 1 was terminated at this stage, resulting in a limited sample size.

Results

Focal cow selection

Eleven of the twelve observed cows performed at least one of the behaviours from Table A1. A total of 89 interactions were observed overall: 73 negative and 16 positive. In total, the 11 cows interacted with 56 other cows. Cows where the traits in question (age, lactation number, date moved to group) were unknown were removed from the analysis. Out of all of the interactions, nine were between cows moved to the group within two weeks of each other and 25 between cows moved to the group at different times. 20 were between cows with the same lactation number and 22 between cows of different lactation numbers. 21 were between cows of the same age and 23 between cows of different ages.

The Chi-square tests showed that cows moved into the low-yield group within two weeks of each other exchanged a similar amount of positive and negative interactions with one another whereas cows moved to the group at different times exchanged more negative than positive behaviour ($x^2(1)$ = 0.022, p=0.882) (Fig. A1a).

Cows with the same lactation number were significantly more likely to have positive interactions with each other ($x^2(1)$ = 17.432, $p \leq 0.001$) (Fig. A1b), as were cows of the same age ($x^2(1)$ = 22.837, $p \leq 0.001$) (Fig. A1c), meaning that cows of the same age and lactation had a tendency to engage in positive rather than negative interactions than those of differing age and lactation.

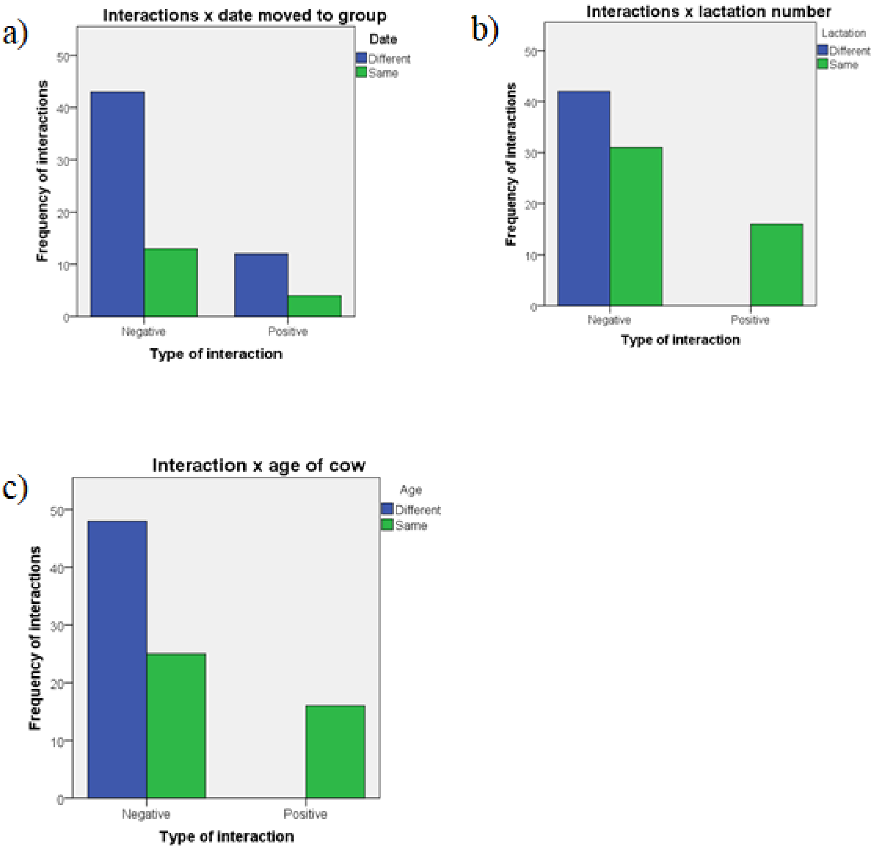

Figure A1: Bar charts showing the total frequency of positive and negative behaviours between the 12 cows observed to inform focal cow selection for the Omnisense study, and the cows they associated with (behaviours from Table 1). Frequency of positive and negative interactions performed by cows moved to the group within 2 weeks of each other (a), with the same lactation number (b), and of the *same age (c). Multiple interactions of different types were assigned to the most frequent type, e.g. if Cow A and Cow B had 5 positive interactions and 2 negative interactions, the dyad was assigned to "positive interactions".*

Discussion

The results from this section are (i) that cows of similar age and lactation number were more likely to have positive interactions with each other than cows moved into the low-yield group within two weeks of one another.

Cows assorting by similar traits has been previously established in the literature (Lazo and Soriguer, 1993; Lazo, 1994; Gutmann et al., 2015; Boyland et al., 2016). The majority of studies on dairy cows conclude that cows of similar age, similar lactation and with a shared history tend to assort together (Gygax et al., 2010; Boyland et al., 2016). Boyland et al (2016), in a study on dairy cows, found that cows assorted by breed, lactation number, milk production, and pasture access. Comparably, Gutmann et al. (2015) concluded that synchronised group entry, shared dry period, shared youth and shared adult experience predicted a preferred partner in dairy cattle (Gutmann et al., 2015). In cattle, age and lactation number are often correlated as most farmers aim to get dairy cows into calf annually from the age of two onwards (Mourits et al., 1999; Le Cozler et al., 2008). Therefore, it is unsurprising that both age and lactation number were significantly associated with positive interactions in the current study. It is surprising, however, that there was no link between positive interactions and synchronised group entry (±2 weeks) in the present study. This discrepancy between the results of the current study and the results from Gutmann et al. (2015) may be explained by the low sample size of cows in the present study that were moved to the social group within two weeks of one another (nine cows) compared to cows moved to the social group at different times (25 cows).