# The influence of social networks on welfare and productivity in dairy cattle

Submitted by Natasha Karissa Boyland to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Psychology

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature ………………………………………………

# ABSTRACT

Cattle are gregarious animals that form stable social groups based on affiliative and dominance relationships. However the husbandry practices of the modern dairy industry typically do not take social relationships into consideration, despite a growing body of evidence demonstrating important effects of social relationships on health and fitness in wild animals. Keeping cattle in large, unstable groups can lead to reduced welfare and productivity due to social stress and further research is needed to provide a beneficial social environment that can instead provide stress buffering effects. Social network analysis (SNA) is becoming an increasingly popular method to study animal social groups but until very recently has not been applied in animal welfare studies, where it can offer great advantages. This thesis uses SNA to investigate the social structure of a dynamic group of dairy cattle, and to explore the connection between social network position, and health and productivity. Social data was collected using spatial proximity loggers, allowing remote, continuous recording of associations between cattle. This approach was also used to measure relationships between young calves, investigating the effects of the early social environment.

First, proximity loggers were tested and found to exhibit a significant sampling bias, which had consequences for SNA; a correction method was developed to improve their robustness. The social network structure of 110 lactating dairy cows on a commercial farm was then quantified, over four one-month periods. The network was highly centralised and social stability was low, however there were heterogeneous relationships between cows and we found evidence for assortment by traits. Social network position was linked to the health and productivity of cows; more gregarious individuals had higher milk yields and higher somatic cell counts which may represent a cost-benefit trade-off. Another study assessed the effects of pair-housing calves on weaning stress, health and production during pen rearing. Calves that were paired with a social companion showed a lower stress response to weaning than those housed individually. This effect was further reduced for calves paired earlier, suggesting that social bond strength is important for social support in cattle. The social networks of calves when grouped together showed some stability and relationships were heterogeneous, with social associations being influenced by prior familiarity.

Advancing our understanding of the social requirements of dairy cattle is fundamental for their welfare, and for productivity, and is particularly important in light of recent farming intensification.

## LIST OF CONTENTS

Abstract........................................................................................................... 2

List of figures...................................................................................................... 11

List of tables.......................................................................................................16

Acknowledgements.............................................................................................. 18

Author’s declaration.............................................................................................19

Brief glossary of terms……………………………………………………………21

**Chapter I: General introduction....................................................... 22**

**1.1 Introduction ……………………………………………………………… 23**

**1.2 Group living and social relationships……………………………….………… 23**

**1.2.1 Stress………………………………………………….……………… 25**

**1.2.2 Social support……………………………………...…………… 26**

**1.2.3 Social status……………………………………………...…………29**

**1.3 The social environment on farm…………………..……………………………30**

**1.3.1 Group composition……………………………………...………..…31**

**1.3.2 Group size and density…………………………………………….33**

**1.4 Management procedures inducing social stress…………………………………35**

**1.4.1 Abnormal behaviour…………………………………………………36**

*1.4.1.1 Stereotyped behaviour*……………………………………………………37

*1.4.1.2 Social transmission of abnormal behaviour……………………………….38*

**1.5 Social environment during development……………………………………39**

**1.6 Farm animal welfare……………………………………………..………..42**

**1.7 Social network analysis – an under-utilised tool in welfare science……….……46**

**1.8 The social behaviour of cattle…………………………………………………….52**

**1.9 Conclusions……………………………………………………………..…53**

**Chapter II: Spatial proximity loggers for recording animal social networks: consequences of inter-logger variation in performance…...55**

**2.1 Abstract**……………………………………………………………………56

**2.2 Introduction**………………………………………………………….……57

**2.3 Methods**……………………………………………………………………61

**2.3.1 Proximity devices…………………………..…………………………61**

**2.3.2 Field deployment……………………………..……………………62**

**2.3.3. Standardised test……………………………..……………………63**

**2.3.4 Consequences of inter-logger variability for social network analysis.. 64**

**2.3.5 Analytical model………………………………………….………66**

**2.3.6 Computational model…………………………………...…………67**

**2.3.7 Correction method**…………………………………………..………..68

**2.4 Results**…………………………………………...………………………68

**2.4.1 Field deployment…………………………..………………………68**

**2.4.2 Standardised test……………………..………………………………69**

**2.4.3 Consequences of inter-logger variability for social network analysis...73**

**2.4.4 Modelling……………………………………………………...……75**

**2.4.5 Correction method……………………………………………………75**

**2.5. Discussion……………………………………………………………………77**

**2.5.1 Conclusions…………………………………………………………83**

## Chapter III: Social network structure of dairy cows, *Bos taurus*: from individual to group level patterns...……………………………………….85

**3.1 Abstract……………………………………………………………………86**

**3.2 Introduction……………………………………………………………….87**

**3.3 Methods……………………………………………………………......91**

**3.3.1 Animals and housing…………………………………………………91**

**3.3.2 Spatial proximity loggers……………………………………………….94**

*3.3.2.1 Proximity logger data handling*…………………………………………………94

*3.3.2.2 Logging bias correction*…………………………………………………………95

**3.3.3 Measuring the relationship between proximity data and social relationships…………………………………………...………………96**

**3.3.4 Statistical Analysis……………………………………………………97**

**3.3.5 Generating expected duration matrices……………….………………98**

**3.3.6 Group-level patterns………………………………………………98**

*3.3.6.1 Community structure*………………………………………………98

*3.3.6.2 Centralisation*………………………………………………………99

*3.3.6.3 Network stability*…………………………………………………….99

**3.3.7 Individual-level patterns…………………………………………100**

*3.3.7.1 Social differentiation………………………………………………100*

*3.3.7.2 Assortment…………………………………………………………100*

**3.4 Results…………………………………………………………………….101**

**3.4.1 Measuring the relationship between proximity data and social relationships……………………………………………………………….101**

**3.4.2 Group-level patterns……………………………………………105**

*3.4.2.1 Community structure*……………………………………………105

*3.4.2.2 Centralization*………………………………………………………105

*3.4.2.3 Network stability*…………………………………………….……105

**3.4.3 Individual-level patterns…………………………………………107**

*3.4.3.1 Social differentiation……………………………………………107*

*3.4.3.2 Assortment…………………………………………………………107*

**3.5 Discussion………………………………………………………………110**

**3.5.1 Conclusions……………………………………………………..114**

**Chapter IV: The relationship between social network position and health and productivity in dairy cattle………………………………116**

**4.1 Abstract……………………………………………………………………117**

**4.2 Introduction………………………………………………………………...118**

**4.3 Methods……………………………………………………………………122**

**4.3.1 Animals and housing…………………………………………………..122**

*4.3.1.1 Access to pasture…………………………………………………………….123*

*4.3.1.2 Mobility Scoring…………………………………………………………….123*

**4.3.2 Spatial proximity loggers………..…………………………………124**

*4.3.2.1 Proximity logger data handling……………………………………………124*

*4.3.2.2 Logging bias correction…………….…………………………………………125*

**4.3.3 Statistical Analysis……………………………………………………126**

*4.3.3.1 Is degree centrality associated with individual traits?.........................129*

*4.3.3.2 Is individual somatic cell count related to degree centrality or DIM? 129*

*4.3.3.3 Is individual milk yield related to degree centrality, age or DIM?...... 129*

*4.3.3.4 Are there differences in degree centrality between cows with good or impaired mobility?......................................................................................... 130*

**4.4 Results……………………………………………………………………130**

**4.4.1 Is degree centrality associated with individual traits?.......................130**

**4.4.2 Is the somatic cell count of individuals related to their degree centrality or DIM?..........................................................................................130**

**4.4.3 Is individual milk yield related to degree centrality, DIM or age? 131**

**4.4.4 Are there differences in degree centrality between cows with good or impaired mobility?...........................................................................................131**

**4.5 Discussion..........................................................................................................137**

**4.5.1 Conclusions...................................................................................141**

## Chapter V: Pair housing dairy calves and age at pairing: effects on weaning stress, health, production and social networks…………..……143

**5.1 Abstract...............................................................................................................144**

**5.2 Introduction.........................................................................................................145**

**5.3 Methods...............................................................................................................149**

**5.3.1 Animals, housing and diet.............................................................149**

**5.3.2 Statistical methods………………………………………………150**

**5.3.3 Pen rearing......................................................................................152**

*5.3.3.1 Measures of health, production and weaning stress*……………………153

*5.3.3.2 Between-treatment differences in overall health, growth and intakes* 153

*5.3.3.3 Between-treatment differences in vocalisations, growth and intakes during weaning*…………………………………………………………………………153

***5.3.4* Barn grouping…………………………………………………155**

*5.3.4.1 Spatial proximity loggers*…………………………………………………155

*5.3.4.2 Network stability*…………………………………………………………156

*5.3.4.3 Social differentiation……………………………………………………………*156

*5.3.4.4 Assortment………………………………………………………………………*156

*5.3.4.5 Between-treatment differences in coefficient of variation (CV) in association strength………………………………………………………………………*157

*5.3.4.6 Between-treatment differences in percentage of time spent with paired calf………………………………………………………………………………………158*

*5.3.4.7 Between-treatment d*ifferences in social network measures…………...158

**5.4 Results.........................................................................................................158**

**5.4.1 Pen rearing..........................................................................................158**

*5.4.1.1 Overall health, growth and intakes……………………….………*158

*5.4.1.2 Vocalisations, growth and intakes during weaning……………………*159

**5.4.2 Barn grouping…………………………………………………...161**

*5.4.2.1 Network stability………………………………….……………………*161

*5.4.2.2 Social differentiation……………………………………………………*161

*5.4.2.3 Assortment………………………………………………………………*162

*5.4.2.4 Between-treatment differences in coefficient of variation (CV) in association strength………………………………………………………………*162

*5.4.2.5 Between-treatment differences in percentage of time spent with paired calf…………………………………………………………………………………*163

*5.4.2.6 Between-treatment differences in social network measures…………*163

**5.5 Discussion……………………………………………………………………..…165**

**5.5.1 Conclusions……………………………………………………………………170**

**Chapter VI: General Discussion………………………………………171**

**6. 1 Main findings…………………………………………………………………172**

**6.1.1 An automated data collection method can measure animal social networks but comes with challenges……………………………...………………………172**

*6.1.1.1 Sampling bias*………………………………………………………………172

*6.1.1.2 Additional challenges with Sirtrack proximity loggers*……….………….…….…174

*6.1.1.3 Spatial proximity data reflects affiliative interactions between cows* …………177

*6.1.1.4 Future directions*…………………………………………………….….………177

**6.1.2 Social structure in dairy cattle……………………………………………..179**

*6.1.2.1 Future directions*……………………………………………….……………….181

**6.1.3 Gregariousness…………………………………………………………………182**

*6.1.3.1 Future directions*………………………………………………………..……….183

**6.1.4 Familiarity, social bond strength and implications for social support…..…184**

*6.1.4.1 Future directions*…………………………………………………………..………185

**6.2 Additional directions for future research………………………………………186**

**6.2.1 Integrating social behaviour and technology on farm……………………186**

*6.2.1.1 Oestrous detection*………………………………………………………………186

*6.2.1.2 Improving voluntary milking systems*……………………………………………………187

**6.3 Conclusions……………………………………………..………………………190**

**References……………………………………..………………………………192**

# LIST OF FIGURES

**Figure 1** Example of a (a) simple social network, where nodes (representing individuals) are shown as green circles and edges (representing associations or interactions) are shown by lines; (b) a weighted network, where thickness of edges represents strength of associations/number of interactions; (c) a directed network, where arrows indicate the direction of the association/interaction

**Figure 2.1** Logging bias (mean percentage difference in contact logging) of each proximity logger, based on total duration of associations over a 3 week period (error bars represent standard deviations)

**Figure 2.2** Mean contact initiation (a) and termination (b) distances of twenty proximity collars and one base station when paired in the standardised test (error bars represent standard errors)

**Figure 2.3** Correlation between the logging bias (as calculated from field deployment) and the mean contact initiation and termination distances of the base station (a & b) and twenty proximity collars (c & d) during the standardised test

**Figure 2.4** Correlation between logging bias (as calculated from field deployment) and in-degree (a) and out-degree (b). The in-degree (total duration of contacts logged by a focal logger) provides a measure of detection sensitivity, while the out degree (total duration of contacts with the focal logger, logged by all other loggers) provides a measure of signal strength

**Figure 2.5** Observed and predicted measures of sociality. a) Inter-logger variation in the observed row sum of the duration matrix generated from field deployment (Table 2.1) and the predicted values calculated from the analytical model (see main text for details).

For both data sets, values are divided by their smallest value. b) Inter-logger variation in observed / predicted sociality

**Figure 3.1** Correlation between the association strength recorded by the proximity loggers and the number of (a) aggressive (r= 0.07, n=63, p=0.51) and (b) affiliative (r=0.51, n=63, p<0.0001) events observed between cows during behavioural observations (p-values are based on permutation tests)

**Figure 3.2** Patterns of community structure during the four logger deployments. There was no significant community structure found at any filter threshold for deployments 1-4 (a-d). Empty circles indicate the observed maximum modularity for each network. Solid circles indicate the maximum modularity generated by the null model, with arrows specifying 95% confidence intervals

**Figure 3.3** Visualisation of cow social networks in deployments 1-4, that have been filtered to only include total associations that were 2 (a), 2.5 (b) or 3 (c) times longer than expected based on networks generated by a null model (controlling for pasture access)

**Figure 3.4** Network betweenness centralisation at increasing filter thresholds for deployments 1-4 (a-d). Empty circles indicate the observed mean betweenness centralisation in each network. Solid circles indicate the mean betweenness centralisation generated by the null model, with arrows specifying 95% confidence intervals. Filtered networks showed significant betweenness centralisation, except for deployment 2 at a threshold of 2.75 (*p*=0.1)

**Figure 4.1** Relationship between DIM (number of days in milk) and weighted degree centrality of cows during deployments 1-4 (a-d respectively)

**Figure 4.2** Coplots show the relationship between somatic cell count (SCC) and predictor variables: weighted degree centrality and DIM (number of days in milk), during

deployments 1, 3 and 4 (a-c respectively). In each graph, each of the six conditioning variable (DIM) bars corresponds to one scatterplot. This correlation begins on the left-hand side for DIM, and this first bar (approx. 0-80 DIM in 2c) corresponds to the scatterplot on the bottom row, left-hand corner. The scatterplots are then read from left to right, and from bottom to top

**Figure 4.3** Coplots show the relationship between total milk yield and predictor variables: weighted degree centrality and DIM (number of days in milk), during deployments 1-4 (a-d respectively). In each graph, each of the six conditioning variable (DIM) bars correspond to one scatterplot. This correlation begins on the left-hand side for DIM, and this first bar (approx. 0-90 DIM for 3a) corresponds to the scatterplot on the bottom row, left-hand corner. The scatterplots are then read from left to right, and from bottom to top

**Figure 5.1** Diagram of arrangement of pens during pen rearing; each of the 8 blocks consisted of one replicate of each treatment (*I*, *P5* and *P28*)

**Figure 5.2** Photograph of study calves in the barn where they were housed from day 60.

**Figure 5.3** University of Wisconsin-Madison Calf Health Scoring Criteria. Reproduced without permission; sourced from: http://www.vetmed.wisc.edu/dms/fapm/fapmtools/8calf/calf_health_scoring_chart.pdf

**Figure 5.4** The total number of vocalisations, during 1 hour observations of calves, over each 3-day period (pre-weaning, weaning and post-weaning)

**Figure 5.5** The coefficient of variation (CV) in association strength for calves in each rearing treatment during week 1 (a) and week 4 (b). Light grey boxes show data when associations between previously reared calves was omitted

**Figure 6** Schematic representation of the VMS waiting area. Cows due to be milked are allowed access to the waiting area via the entrance gate, activated by collar transponders.

Cows are not allowed to exit the milking area and return to the barn until they have been milked by one of two milking units (MU)

# LIST OF TABLES

**Table 1.1** The Five Freedoms, defined by the Farm Animal Welfare Committee in 1992.

**Table 1.2** Examples of studies applying SNA in animal welfare science

**Table 2.1** Association matrix of total duration (seconds) of associations for 20 individuals during the 3 week field deployment

**Table 2.2** Corrected association matrix of total duration (seconds) of associations for 20 individuals during the 3 week field deployment; data for each logger corrected in accordance to its performance with the lowest recorded logger (collar 1)

**Table 3.1** Descriptive statistics of cows included in analyses and others in the milking group during each deployment

**Table 3.2** Spearman's rank correlations between each week-long matrix, measuring network stability for deployments 1-4. Significance was calculated using a null model with edge-level permutations, stratified according to cows' pasture access

**Table 3.3** The social differentiation measured in deployments 1-4, indicates that cows were significantly more heterogeneous than we would expect given a null hypothesis that all cows associate uniformly (while accounting for pasture access)

**Table 3.4** Results of best fitting model (indicated by lowest deviance information criterion) from mixed model regression, measuring assortment of cows by traits in deployments 1-4

**Table 4.1** Correlations between all social network measures in deployments 1-4. Spearman's correlations are used where one of the variables is not normally distributed;

for those where both variables are normally distributed, tests use the Pearson method. All correlations are significant to <0.0001

**Table 4.2** Spearman's correlations were used to test for relationships between variables; significant relationships are highlighted in bold

**Table 4.3** To test for multicollinearity of variables used in our multiple regression models, the variance inflation factor (VIF) from the result of linear models were calculated. If VIF is more than 10, multicollinearity is strongly suggested; the results therefore do not suggest multicollinearity issues.

**Table 4.4** Multiple regressions with node-level permutations (30,000 iterations per test) were carried out to test relationships between predictor variables. Nodes were only permuted between individuals that had the same pasture access, in order to control for the effect of management on social associations.

**Table 5.1** Correlations between each week-long matrix, measuring network stability across weeks 1-4. Significance values were generated by comparing the observed values with those from 4999 null networks

**Table 5.2** There was significant social differentiation for each week–long social network; calves spent more or less time associating with other individuals than would be expected by chance

**Table 6.1** Summary of problems encountered when using Sirtrack proximity loggers, and our response to these

**Table 6.2** Five principles underlying a new logger data correction method

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# AUTHOR'S DECLARATION

The work contained in this thesis has involved collaboration with David Mlynski (DM), Sarah Bolt (SB), Joah Madden (JM), Richard James (RJ), and Lauren Brent (LB); their contributions are listed below. As my primary supervisor, Darren Croft (DC) was involved in all chapters and provided comments on the write up. Hence the plural "we" has been used throughout Chapters 2, 3, 4 and 5. All four data chapters were written as free-standing papers, therefore there is some repetition within the thesis as some parts of the methodology were the same.

*Chapter II:* DM wrote the R scripts used to handle the logger data and apply the correction, and helped run tests in the field. JM and RJ were involved in discussion of ideas for the method, and all co-authors provided feedback on the manuscript.

*Chapter III:* LB advised on the use of the Markov Chain Monte Carlo general linear mixed models, DM wrote the R scripts used in the analyses, and all co-authors provided feedback on the manuscript.

*Chapter IV:* DM added null models to the R scripts used in the analyses.

*Chapter V:* R scripts written by DM for Chapter III were used again here. SB designed, collected and analysed data relating to the first part of the study (pen rearing) as part of a MSc research dissertation. SB helped write the manuscript.

In addition, some of the work in this thesis has been published in journals:

*Chapter II*: Boyland, N.K., James, R., Mlynski, D.T., Madden, J.R. & Croft, D.P. (2013) Spatial proximity loggers for recording animal social networks: consequences of inter-logger variation in performance. *Behavioral Ecology and Sociobiology*, 67, 1877–1890.

*Chapter III*: Boyland N.K., Mlynski, D.T., James, R., Brent, L.J.N and Croft, D.P. (2016) The social network structure of a dynamic group of dairy cows: From individual to group level patterns. *Applied Animal Behaviour Science*, 174, 1–10.

# BRIEF GLOSSARY OF TERMS

Definitions of words and terms as used in this thesis:

***Animal welfare*** - ‘the state of the individual as regards its attempts to cope with its environment’ (Radford, 2001).

***Dry cow*** – a cow that is not lactating.

***Drying off*** – a procedure performed by the stockman which stimulates a lactation to end. This can be done by a change in diet (e.g. lowering energy content of diet) and cessation of milking.

***Gregarious*** – a tendency for social attraction; a preference to be in the company of conspecifics. Synonym – *sociable*.

***Stress response*** - an adaptive response allowing for behavioural and physiological adjustments to unpredictable events in the environment (McEwen & Wingfield, 2003).

***Stressor*** – any stimulus (e.g. object, noise, sound, event) that stimulates a stress response.

***Sociality*** - the degree to which individuals of a species tend to associate in social groups and form cooperative societies.

***Year-round calving*** – a farm’s calving pattern, in which cows may give birth at any time of year. This is in contrast to a farm with a *batch-calving* pattern, where pregnancies are synchronised so that all cows on the farm give birth within a short time period.

# Chapter I

## General introduction:

## The importance of social relationships for farm animals and the use of social network analysis to improve welfare

## 1.1 Introduction

In this chapter, I will describe the importance of the social environment for animal fitness and the ways in which social interactions and relationships affect individuals in human-managed populations. As discussed below, social relationships are known to significantly impact animal health and fitness from research into wild populations (Brent, Chang, Gariépy, & Platt, 2014); however these are not generally considered in farm animal management, representing a substantial flaw in our current approach. Innovation in the way we study social behaviour and group living is fundamental for improving farm animal welfare moving forward. I will then introduce social network analysis (SNA) and discuss its potential uses in farm animal welfare.

## 1.2 Group-living and social relationships

Group-living evolved as a strategy to cope with environmental challenges (Wilson, 1975). Simply having more animals in a given space can be advantageous to individuals, by reducing predation (Hamilton, 1971) and heat loss (Krause & Ruxton, 2002), etc. Sociality is a widespread mechanism by which many animals gain further benefits from group-life; for example via sharing information (Reebs, 2000) and cooperation during communal hunting (Creel & Creel, 1995) or predator inspection (Croft et al., 2006). The degree of group-living and sociality varies between and within species, and may also change during the lifetime of an animal. In fact, studies of animal groups have found huge variation in the social organisation of groups, resulting from heterogeneous patterns of social interactions between group members (Croft, James, & Krause, 2008). There are various factors determining how individuals in a group will associate and interact, some of which are outlined below.

In order for animals to function efficiently as a group, the duration and timing of activities such as foraging, travelling and resting should be coordinated (Conradt & Roper, 2000). Depending on classes such as age, sex and size, at times there maybe conflicts of interest between individuals based on different requirements for activities, e.g. larger individuals may require longer foraging bouts. When an individual deviates from its optimal activity budget to match the behaviour of its companions there will be some cost, the magnitude of which will influence whether the individual stays in that group. Group-living animals have been observed to assort by size in both field and laboratory studies, and it is thought that the potentially high cost of activity synchronisation contributes to segregation of smaller groups according to class distinctions (Krause & Ruxton, 2002). This may explain intersexual social segregation in sexually dimorphic species (Conradt, 1998), for example red deer (*Cervus elaphus*) (Clutton-Brock, Guinness, & Albon, 1982).

Associating with familiar conspecifics often makes activities such as foraging and predator inspection more efficient, and allows dominance relationships to develop which lower aggression in groups (Krause & Ruxton, 2002). Choosing to interact with certain conspecifics can increase fitness benefits gained via cooperative acts (e.g. guppies; Croft, Krause, and James (2004)), can increase reproductive success (e.g. house mice: Weidt, Hofmann, and Konig, 2008; horses: Cameron, Setaas, and Linklater (2009); chimpanzees (Schülke, Bhagavatula, Vigilant, & Ostner, 2010)), and alleviate the stress (see section 1.2.1) associated with social instability (e.g. baboons: Wittig et al., 2008). Furthermore, research has revealed that ‘friendship’ is not restricted to humans; animals often choose to associate more with specific familiar conspecifics and maintain relationships by socio-positive behaviours (Sachser, Dürschlag, & Hirzel, 1998). ‘Socio-positive’ or ‘affiliative’ behaviour is frequently characterized by maintaining spatial proximity, food sharing/provision, protection and allogrooming. Interactions of this kind are believed to reduce aggression and strengthen bonds between individuals, which leads to greater group cohesion (Boissy et al., 2007). Social bonds can be found between reproductive pairs (Adkins-Regan, 2002), parent and offspring (Veissier, Boissy, Nowak, Orgeur, & Poindron, 1998) and more distant relatives (Smith, Alberts, & Altmann, 2003). Additionally, bonds can be found between unrelated individuals (Cameron et al., 2009; Langergraber, Mitani, & Vigilant, 2009; Silk, Alberts, & Altmann, 2003).

Individuals differ in their tendency to stay close to others: referred to as their ‘sociability’ (Cote, Fogarty, & Sih, 2012). Group structure is affected by the sociability of individuals in it, as motivation for social proximity partly determines group cohesiveness and relationships (McBride, James, & Shoffner, 1963; Michelena, Gautrais, Gérard, Bon, & Deneubourg, 2008; Cécile Schweitzer, Lévy, & Arnould, 2011). Research into sociability using Japanese quail, *Coturnix japonica*, found that chicks that were selected for low sociability showed preferences for familiar over unfamiliar chicks and formed social bonds with cage-mates, while those that were selected for high sociability showed no preference when given the same choice and were not attracted to their cage-mates any more than non-cage-mates (Schweitzer, Houdelier, Lumineau, Lévy, & Arnould, 2010; Cécile Schweitzer et al., 2011). Unsurprisingly, highly sociable individuals reacted more strongly to stressor of social isolation (Mills, Jones, Faure, & Williams, 1993).

### 1.2.1 Stress

A stress response is an adaptive response allowing for behavioural and physiological adjustments to unpredictable events in the environment (McEwen & Wingfield, 2003). Yet its direct effects on productivity and welfare make it a key concern for those working with production animals. Short term stress responses can be useful to the animal, allowing adaptation to the environment stimulus, however long term stress responses can be very damaging because when animals experience stress, hormones called glucocorticoids (GC) are released into the blood. GC are principal mediators in allostasis which functions to maintain homeostasis (McEwen, 1998) and can inhibit essential mechanisms such as digestion, growth, reproduction, energy storage, and regulation of the immune system (Goymann & Wingfield, 2004). A “stimulus in an animal’s environment that exceeds the natural regulatory capacity of the animal, and is usually unpredictable and/or uncontrollable” is referred to as a ‘stressor’ (Proudfoot, Weary, and von Keyserlingk (2012), p. 204). The impact of a stressor is thus governed by an animal's behavioural and neuroendocrine response, rather than any physical characteristics it possesses, and this varies for each individual (Koolhaas et al., 1999). An individual's ‘coping style’ in response to stressors (see Wechsler (1995)) is influenced by various factors such as genetics, early development, and the social environment (Koolhaas et al., 1999). A species-specific knowledge of social systems is important for stress management as factors of the social environment can initiate stress responses, these are referred to as ‘social stressors’ (for a comprehensive review see Proudfoot et al. (2012)), or can act as a buffer against stress in the form of social support (described below).

### 1.2.2 Social support

There is increasing evidence from studies of wild animal groups, that individuals who invest in affiliative relationships have increased competitive and reproductive success (Cameron et al., 2009; Joan B. Silk, 2007; J. B. Silk et al., 2009; R. A. Wittig et al., 2008). However, this cannot be explained solely by the adaptive benefits of group-living (as outlined in 1.2). For example, in controlled laboratory experiments the wounds of rats that were given a social companion healed significantly faster than the wounds of rats kept in social isolation. Furthermore, animals in captivity are willing to ‘work’ for social contact with conspecifics (e.g. calves: Holm, Jensen, and Jeppesen (2002), pigs: Matthews and Ladewig (1994), mice: Sherwin (1996)), and it is reasonable to believe the resources that animals are willing to work for are valuable to them and can affect their welfare (Broom, 1988). When farm animals are exposed to a stressor they generally seek social contact with others more so than when they are not stressed (e.g. chickens: Marin et al., 2001, cattle: Ishiwata et al., 2007). Such behaviour can be explained by the phenomenon of ‘social support’: the range of benefits provided by social companions that improve an individual’s ability to cope with challenges (Rault, 2012). In humans, social support can reduce disease-related mortality, morbidity and depression (Biondi & Picardi, 1999; Cohen, 1988; Coyne & Downey, 1991; Miller & Surtees, 1995), and inabilities to maintain social relationships have been linked with psychiatric disorders (House, Landis, & Umberson, 1988; Kiecolt-Glaser & Newton, 2001; Monroe, Bromet, Connell, & Steiner, 1986). Studies of social support in non-human animals also suggest benefits for cardiovascular health (Boissy & Le Neindre, 1997; da Costa, Leigh, Man, & Kendrick, 2004; Ruis et al., 2001; Takeda, Sato, & Sugawara, 2003), immune function (Boccia, Laudenslager, & Reite, 1995; Capitanio, Mendoza, & Baroncelli, 1999; Gust, Gordon, Brodie, & McClure, 1994), and recovery from stressful experiences (Ruis et al., 1999). Studies have also found that when animals were provided with social support they can learn faster; for example heifers that were tested in the presence of conspecifics were able to learn an operant conditioning task more quickly than those tested alone (Boissy & Le Neindre, 1990).

Animals may receive social support from simply being close to conspecifics (even if they are unfamiliar), however the strength of the social relationship between the animals often determines the size of the effect (Rault, 2012). Faervik et al. (2006) demonstrated that dairy calves reacted less negatively when they were provided social support in the form of a companion calf during group separation (rather than separation from the main group alone). When this companion was familiar, calves' response to separation was further reduced, an effect also observed in lambs (Porter, Désiré, Bon, & Orgeur, 2001), and one that should be considered during routine husbandry. Interestingly, individuals may even adjust their behaviour in order to capitalise on this during stressful situations. In fact GC induce behaviours that reduce stress, functioning to lower their own production and hence reduce allostatic load; grooming appears to be one such behaviour (Wingfield et al., 1998). In a study of wild baboons by Wittig et al. (2008), females' GC levels increased substantially when the social group became unstable, however the GC levels of individuals who were only grooming a few preferred partners prior to the group instability did not rise as much as those who were grooming more widely in the group. In subsequent weeks, all females directed their grooming interactions onto fewer individuals, and GC levels decreased the following week. Furthermore, the females that focussed their grooming interactions the most had the greatest decreases in GC. The authors believe that investing more time in social interactions with preferred individuals alleviated stress in this study. Similar behaviour has been observed in humans; women are more likely to use smaller, specific support groups during a stressful period than their wide circle of friends. They are also more motivated for social contact than men in response to stress (Taylor et al., 2000). Taylor et al (2000) propose that sex differences in social tendencies are connected to different levels of oxytocin (and related hormones) which are higher in females and drives maternal and affiliative behaviour. Indeed in herbivores, female-based herds tend to be more stable than male-based herds (Bouissou & Boissy, 2005).

### 1.2.3 Social status

Social hierarchies are commonly observed in animal societies and one important example is a dominance hierarchy (Dawkins, 1976). Dominance is defined as "an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and that of the loser subordinate" by Drews (1993, pg 308). These relationships determine an individual's access to resources and reduce aggression during competition (G. J. Syme, 1974). Dominance rank can also play an important role in an animal's response to stressors (Salak-Johnson & McGlone, 2007) and the way in which positions of social status are obtained and maintained appears to be important for this (Goymann & Wingfield, 2004). In stable social groups, greater stress may be experienced by subordinates who receive agonistic contact from dominants, and additionally have lower access to resources. Yet, in unstable groups, the time that dominant animals spend in agonistic encounters may be much higher than subordinates, making their social position more costly. This is likely to be offset with access to preferred or limited resources and so the overall level of stress experienced will depend on this balance (DeVries, Glasper, & Detillion, 2003). In farm animal management, maintaining group stability and allowing enough space for subordinates to avoid dominants is likely to reduce social stress (Estevez, Andersen, & Nævdal, 2007).

## 1.3 The social environment on farm

Farm animal species are generally gregarious (Estevez et al., 2007) and the social environment is likely to be fundamental to their welfare. In the wild animal groups self-regulate, with individuals joining or leaving in response to costs and benefits of group membership (Krause & Ruxton, 2002). Group housing gives social animals more opportunities to express normal species behaviour, however groups are predetermined with resources limited in space, which can lead to competition and uneven distribution of resources (Estevez et al., 2007). Animals are also frequently regrouped for management convenience (Bøe & Færevik, 2003). Both decisions are currently made with little consideration for group cohesion or individuals' ability to establish social bonds (Færevik, Jensen, & Bøe, 2006). Furthermore, some degree of control over physical and social factors is important to animals (Bassett & Buchanan-Smith, 2007), however farm animals are often unable to control much of their environment, including the freedom to leave a group or avoid certain conspecifics. A consequence of this human-regulated environment is that social behaviour effective in stabilising groups in the wild, e.g. agonistic interactions, can be intensified and create welfare problems on farm.

Different production systems generate different challenges for welfare science, and some management responses only dealing with a problem's effects rather than directly addressing its cause. For instance, in response to feather-pecking in laying hens, beak trimming and light dimming has been widely used. Beak trimming is painful and can have long term problems and cause chronic pain (Gentle, 2011). Lowering light intensity reduces feather-pecking but also reduces hens' ability to recognise conspecifics and navigate the environment (Rodenburg & Koene, 2007). This management approach effectively substitutes one problem for another. Other methods to reduce feather-pecking include provision of nipple drinkers and dark nest boxes (instead of bell drinkers and light nest boxes), litter for foraging during rearing (Asher et al., 2009; Huber-Eicher & Sebö, 2001); and genetic selection (Rodenburg et al., 2003). Providing both a suitable physical and social environment is key in preventing such issues, and identifying the most suitable social environment is therefore critical to the success of any group management system. Group size, density and composition are significant features to consider, and are discussed below.

### 1.3.1 Group composition

The composition of management groups on farm are usually quite dissimilar to that of a free-living groups. It is common practise to group phenotype-matched individuals together for husbandry practicality (e.g. ensuring animals reach slaughter weight at approx. the same time). However as body size often determines individuals' position in the dominance hierarchy, when size-matched individuals are first grouped together, more agonistic encounters may be required to establish dominance between unfamiliar individuals, than in a mixed-size group; this has been shown in pig groups (Moore, Gonyou, Stookey, & McLaren, 1994).

Though farmed poultry are more often kept in same-sex groups, their free-living counterparts are typically found in mixed-sex groups with males guarding females against predators (Keeling & Gonyou, 2001). Group housing with males (at a male: female ratio of 1:100) has been shown to decrease fear in female laying hens (Kristina Odén, Gunnarsson, Berg, & Algers, 2005). Also less female-female aggressive behaviour is observed when laying hens are housed in mixed-sex groups, and this effect is present in large (Odén, Vestergaard, & Algers, 2000) and small flocks (Bshary & Lamprecht, 1994). Reduced aggression may result from the presence of the male as a socially dominant individual (K. Odén et al., 2000). In fact dominant hens can also have this effect on a subordinate dyad, however unlike males, a dominant hen often achieves this through her own aggressive conduct (Ylander & Craig, 1980).

The success of modifying housing design to allow more normal behaviour can been demonstrated with 'get-away' housing systems for sows nursing piglets which enable sows to regulate the amount of time spent socialising with other sows versus time nursing piglets (Van Nieuwamerongen, Bolhuis, Van Der Peet-Schwering, & Soede, 2014). This reduces demand on sows for nursing and allows socialisation. These systems are also beneficial to piglets, which have contact with piglets from other litters (Weary, Pajor, Bonenfant, Fraser, & Kramer, 2002).

When deciding on group composition it may also be important to consider how different personality types interact and integrate within a group. In a study by (Hessing, Hagelsø, Schouten, Wiepkema, & Van Beek, 1994), certain group composition based on coping strategies were better for pig production. Using a 'backtest' (piglets are restrained in supine position for 1 minute (Bolhuis, Schouten, Schrama, & Wiegant, 2005)) pigs were determined to have either a 'low-resisting' or 'high-resisting' coping strategy, a trait that has shown to have consistency in pigs (Kooij et al., 2002). Groups comprising pigs of both strategy types were more productive than groups made exclusively of one type, having significantly less disease and greater, and more uniform, weight gain. This suggests there are advantages to diversity in coping strategy; it may be that individuals with different strategies assume different social roles that are important for the group. 'Bold' and 'shy' personalities (behavioural traits that vary between individuals but are consistent within individuals (Gosling, 2001) have been identified in a number of species (e.g. fish: Huntingford (1976); birds: Verbeek, Boon, and Drent (1996); rodents: Koolhaas et al. (2001)). Both personality types are useful in a group, as bold individuals are more likely to explore new resources and thus contribute to the spread of the group, while shy individuals may have a greater role in group cohesion (Michelena, Sibbald, Erhard, & McLeod, 2009).

### 1.3.2 Group size and density

In natural populations, group size and density are determined by environmental conditions and availability of resources (e.g. food and water availability or mating opportunities), with individuals joining or leaving a group based on a trade-off between costs and benefits at a particular time (Estevez et al., 2007). However, modern farming often involves large group sizes and high stocking densities, and this can have negative effects on health and productivity (Estevez et al., 2007). The size of an animal group is a central feature defining the complexity and structure of its social system (Pollard & Blumstein, 2008), and is one factor that determining whether the benefits of membership outweigh the costs (Conradt & Roper, 2000). Group size affects social relationships by altering the frequency and context of social interactions. As groups become larger, social encounters between each pair may effectively be diluted (Gygax, Neisen, & Wechsler, 2010) and the number of conspecifics for each individual to recognise and remember increases. This can mean that social bonds do not become as strong as those in small groups which may be reduce group cohesion and effectiveness of social support. In a study of young Japanese quail, *Coturnix japonica*, by Schweitzer et al. (2011) there was a reduction in affiliative behaviour and calming effect conferred by a conspecific, with increasing group size. In primates, grooming behaviour is an important bonding mechanism and as groups increase in size, the amount of time spent grooming increases in accordance (Dunbar, 1991). When groups reach a certain size, the time required for grooming becomes too costly and group cohesion will decrease, eventually leading to group fission (Dunbar, 1991; Lehmann, Korstjens, & Dunbar, 2007).

An interesting trend has emerged when investigating the effects of increasing group size on aggression. At large group sizes less aggression has been observed in some species, such as pigs (Turner & Edwards, 2004), laying hens (Estevez, Keeling, & Newberry, 2003; Estevez, Newberry, & Keeling, 2002; Lindberg & Nicol, 1996), and fish (Syarifuddin & Kramer, 1996). For example in a study by Andersen, Nævdal, Bakken, and Bøe (2004), after mixing pigs into different sized groups, a greater number of fights (per individual) occurred in groups of six and 12 pigs than in groups of 24 pigs; larger groups also had the greatest proportion of pigs not involved in fights. This trend may occur because as group size increases, the probability of re-encountering an individual declines sharply and the cost of engaging in agonistic interactions increases as there are more individuals with whom to compete. In this case, it may be more beneficial to use alternative social strategies that do not rely on individual recognition or extensive memory of conspecifics, such as those that employ status signals and direct assessment (Preuschoft & van Schaik, 2000).

Increased stocking density is inevitable in intensive farming systems (Estevez et al., 2007). However, space allowance is a key determinant of welfare for farm animals (Fregonesi & Leaver, 2002). High stocking density can lead to higher competition for resources, and uneven distribution of food, water and resting spaces etc. Animals also experience social stress due to aggression during competition and crowding (Craig, 1981). This can lead to reduced performance (Fregonesi & Leaver, 2002; Turner, Ewen, Rooke, & Edwards, 2000) and despotic behaviour (Mendl & Newberry, 1997). Providing enough space is important for the formation of social relationships and overall group structure. However, allocating animals to housing systems is not as simple as maintaining a set density per animal, as space requirement does not necessarily increase uniformly. This is partly due to the variable social patterns we observe in groups of different sizes (mentioned above) but we should also consider the required ‘interaction space’ that allows for fighting, fleeing, play etc., and space for self-isolation during sickness (Spoolder, Geudeke, Van der Peet-Schwering, & Soede, 2009).

As groups in the farm environment are controlled externally, social behaviour is forced to adapt to group composition, density and size (Estevez et al., 2007). In response, farm animals may use dynamic social systems to adapt to their environments. Though some systems may involve less aggressive behaviour they may also involve less affiliative behaviour and individuals may not gain the benefits of social support associated with social relationships. There is also evidence that damaging behaviours and fear increase with group size (Rodenburg & Koene, 2007). The larger effects of these social systems remain unclear.

## 1.4 Management procedures inducing social stress

Farm management practises that cause social disruption, social instability, crowding and short-term isolation represent significant social stressors (Proudfoot et al., 2012). Social instability hinders the development of social relationships and is associated with various adverse effects, (Sachser et al., 1998). When individuals are added into a group of unfamiliar conspecifics they experience more social stress and have less access to resources than the resident animals (Mench, Swanson, & Stricklin, 1990). ‘Regrouping’ is a common practice on dairy farms despite the negative effects that result, e.g. increased frequency of agonistic encounters (Raussi et al., 2005) and short-term milk decline (von Keyserlingk, Olenick, & Weary, 2008); (Hasegawa, Nishiwaki, Sugawara, & Ito, 1997). There also appears to be long-term consequences of this social stressor; Hultgren and

Svensson (2009) demonstrate a negative correlation between the number of times a cow was regrouped and her productive lifetime. Alternative ways to regroup or introduce new individuals have been suggested with the aim to alleviate social stress, including introducing new animals during the night/during low activity (Lamb, 1976; Nakanishi, Kawamura, Goto, & Umetsu, 1993). The introduction of small sub-groups into a larger group has shown some benefits (heifers: O'Connell, Wicks, Carson, and McCoy (2008) and pigs: O'Connell, Beattie, and Moss (2004).

### 1.4.1 Abnormal behaviour

Although it is expected that  animal behaviour will differ in captivity to that expressed in the wild, it is generally unusual for well-adapted animals to invest much energy or time in activities that do not promote their fitness on some level (Rushen & Passillé, 1992). Yet 'abnormal behaviours' are found in many captive groups; these behaviours are largely absent in wild, healthy individuals (i.e. are not a result of selection) and cannot be accounted for by captive breeding (Mason, 1991b). Abnormal behaviours are often linked to mental and/or physical suffering and include food refusal, self-injurious behaviour (e.g. feather plucking), and stereotyped motor reactions (Hosey et al., 2009). Some abnormal behaviour can only occur in group housing and are significant problems in animal agriculture. Examples include: tail-biting in pigs (Schrøder-Petersen & Simonsen, 2001); vulva-biting in pigs (Van Putten & Van De Burgwal, 1990); cross-sucking in calves (de Passillé, 2001); feather-pecking in poultry (Blokhuis & Wiepkema, 1998);  and increased aggression towards conspecifics (Rodenburg & Koene, 2007).

#### *1.4.1.1 Stereotyped behaviour*

Patterns of behaviour that are "repetitive, unvarying and apparently functionless...typical of animals in some conditions of captivity and are generally associated with poor welfare" are referred to as stereotypes (Mason, 1991a, p. 103). Stereotypical behaviour has been linked to altered responses of the brain; for example Garner and Mason (2002) found associations between bar-mouthing stereotypies of bank voles, *Clethrionomys glareolus*, and altered responses by their basal ganglia. These findings are analogous to studies documenting the disruption to basal ganglia functioning and occurrence of stereotypies in humans, and are associated with cognitive deficits (Garner, Mason and Smith 2003). Stimulus-poor environments, situations of physical restraint, and experience of unavoidable fear or frustration will most often elicit stereotypies initially (Mason, 1991a). However, once established, stereotypies can be stimulated by neutral factors with little discernible welfare significance (e.g. Kennes, Ödberg, Bouquet, and De Rycke (1988)). Hence, expression of these behaviours has been used as an indicator of inadequate conditions in captivity (Fraser & Broom, 1990; Wiepkema, 1993); and they may direct us toward issues causing reduced welfare, however the amount/frequency of stereotyped behaviour is not necessary a good measure of how poor welfare may be (Rushen & Passillé, 1992). Further, the presence or frequency of a stereotypy does not necessarily reflect the animal's state in relation to its *current* environment. It appears that subsequent to development, behaviours become part of an individual's repertoire and frequently persist regardless of altered and/or improved conditions (Mason, 1991b). Thus our best chance at eradicating these behaviours from captive populations, lies in understanding the conditions that cause their development, and consequently those required to prevent them.

#### *1.4.1.2 Social transmission of abnormal behaviour*

The mere presence of a conspecific can affect an individual's behaviour, and the behaviour of one animal can induce the same behaviour in another; imitation may play a role in the transmission of abnormal behaviour (Nicol, 1995). Feather pecking is a serious problem in flocks of laying hens, and one that is very rarely limited to a few birds (Wechsler, Huber-Eicher, & Nash, 1998), appearing to 'spread' between conspecifics (Appleby, Hughes, & Elson, 1992). Zeltner, Klein, and Huber-Eicher (2000) tested for social transmission of feather-pecking experimentally, by introducing feather pecking chick 'tutors' into groups where feather-pecking had been absent. At the end of the experiment, groups given tutors showed significantly higher frequencies of feather-pecking than control groups. Aside from feather-pecking, control tutors did not differ from feather-pecking tutors in their behaviour, and feather-pecking tutors were not pecked more often than other birds. The authors conclude that development of feather-pecking in the study can be explained by social transmission. Wechsler et al. (1998) similarly found feather pecking to spread throughout a group so that it was expressed by the majority of hens, however higher rates and more severe forms were observed in certain individuals, making them more likely to cause feather damage and decrease overall group welfare. Behavioural and physiological responses to environmental challenges vary between individuals, including the expression of stereotyped behaviour. For example in a study by Geverink, Schouten, Gort, and Wiegant (2003), the duration of stereotyped chain-biting by stall-housed gilts was significantly higher in 'high resisting' than those with a 'low resisting' coping style (see section 1.3.1). Quantifying individual variation in the propensity to develop or imitate abnormal behaviour may also help us understand the spread of abnormal behaviour through a group.

## 1.5 Social environment during development

The effects of group composition and management practices have been considered broadly above, however, the social requirements of animals are dependent partly on age; animals are motivated to seek different social relationships throughout their lives. For instance in group living mammals, very young animals generally centre their attention on their mother. As juveniles develop, their awareness of conspecifics increases and they begin to socialise with a broader selection of individuals, forming social relationships that define their position in the group (Veissier et al., 1998).

Early rearing conditions are very important to an animal's development and can affect their personality (Bergmüller & Taborsky, 2010), stress response (Meaney (Meaney et al., 1996), susceptibility to disease (Kanitz, Tuchscherer, Puppe, Tuchscherer, & Stabenow, 2004), adult social behaviour (Sachser & Renninger, 1993) and their potential to develop abnormal behaviours (Mason & Rushen, 2006). Environmental stressors can even influence the development of an animal in gestation, with the maternal stress response altering neuroendocrine, reproduction, immune system and behaviour of offspring (Weinstock et al., 1992; Herrenkohl, 1979; Kay et al., 1998; Ward et al., 1972) Disrupting or withholding interactions between a mother and infant induces a range of biological effects in mammals (Coe et al., 1985) and these separations are widespread in farming practise today. Passive behaviour and lethargy is observed in non-farm animals following maternal separation, and researchers suggest this represents stress-induced sickness behaviour due to mental "despair" (Michael B. Hennessy, Deak, & Schiml-Webb, 2001). Maternal separation can be connected to development of abnormal behaviours in some cases, however multiple factors are likely to play a role, as abnormal behaviour is not present in all farm animals subjected to the same weaning processes

(Latham & Mason, 2008). A critical stage for stereotypy prevention could mean the quality of early social life is even more important for welfare. Hadley, Hadley, Ephraim, Yang, and Lewis (2006) demonstrated that enriched housing for deer mice (*Peromyscus maniculatus*) grouped during 24–84 and 84-124 days of age, was associated with substantially lower levels of stereotypy when focal animals were then transferred to standard housing. This effect was not seen in older deer mice (11-14 months of age). The authors put forward their findings as support for a sensitive period for prevention of stereotypy development, and suggest that early experience provides a neuroprotective effect.

Certain sensitive periods during an animal's early life may also be crucial for their ability to integrate into a group as an adult. The guinea pig, *Cavia porcellus*, has been well studied in this respect (Sachser, 1994). Sachser (1993) demonstrated that when juvenile male guinea pigs are reared in a colony, male-male dominance in adulthood is established with less aggression than if males were reared with a single female companion. The relatively passive way in which two former colony males may form a stable dominance relationship was attributed to their opportunities for agonistic interactions with dominant adult males at puberty, giving them experience in a subordinate role and practise of appropriate signals and behavioural responses (Sachser, 1993). When two males that were deprived of these social encounters at puberty were introduced, aggression and severe injury to one or both was observed. The different response of these two categories of males (and their behavioural strategy) was reflected in their cortisol levels; clear and consistent increases were observed in (usually) subordinate males (Sachser, 1994; Sachser & Lick, 1991). When colony-reared male guinea pigs were introduced into a new colony, they gradually integrated into the group (Sachser & Renninger, 1993) with few agonistic encounters and no change in weight or plasma-cortisol levels. This contrasted significantly with guinea pigs that were reared individually: these individuals were repeatedly involved in fights and threat displays, and suffered considerable weight loss and increase in plama-cortisol in response to the change in social environment.

In cattle, behavioural differences associated with opportunities for social interactions at a young age have been found. Studies demonstrate that calves from group rearing conditions are more confident (Bøe & Færevik, 2003), show less fear (Jensen, Vestergaard, Krohn, & Munksgaard, 1997), play more (Jensen, Munksgaard, Mogensen, & Krohn, 1999), are involved in less agonistic encounters and achieve higher social rank (at 8 months) (Broom & Leaver, 1978) than individually reared calves. Different responses to regrouping can also be seen with age. For example, studies have found that cattle aged ~4.5 months old habituated to repeated regrouping (Veissier et al., 2001) however by the age of 18 months old they do not (Raussi et al., 2005) and regrouping is a known stressor for adult dairy cattle (Proudfoot et al., 2012).

The social environment also affects how animals respond to humans. Veissier et al. (1998) found that veal calves that were housed individually were less stressed by handling than those housed in groups. Price and Wallach (1990) tested individually housed and group housed Hereford bulls at 19 months old, for aggressiveness towards humans. Both groups were hand-reared, yet the individually housed bulls showed more threatening and aggressive behaviour towards handlers, while group housed bulls were more cooperative. Again this may be due to the group environment providing opportunity for agonistic contexts between bulls, where appropriate contest manners (e.g. when aggression should be limited) can be learnt. When a relevant social environment is provided and motivation for social interactions is satisfied, the practise of social skills may allow animals to be more receptive to the signals of others; both conspecifics and humans. In a study by Søndergaard and Ladewig (2004), group-rearing of horses reduced aggression during training and improved training progression compared with those kept individually (Rivera, Benjamin, Nielsen, Shelle, & Zanella, 2002). Lensink, Fernandez, Cozzi, Florand, and Veissier (2001), assessed the reaction of calves to being loaded individually onto a truck. Group housed calves were less compliant, however they may have been distracted and/or more stressed than individually housed calves due to the added stress of peer separation (though no evidence in the study could demonstrate this). Grignard, Boissy, Boivin, Garel, and Le Neindre (2000) showed that calves housed in groups were easier to handle when completely separated from the group than when they had visual contact with peers.

## 1.6 Farm animal welfare

With a human population expected to reach 9 billion by 2050, the demand for animal and other food products is increasing and the pressure to improve productivity is felt in all farm industries (Godfray et al., 2010). Agriculture has intensified since the Second World War; farms have become fewer but larger and much has changed in the way we manage farm animals (Fraser, 2008; MacDonald & McBride, 2009; Vanhonacker, Verbeke, Van Poucke, Buijs, & Tuyttens, 2009). However there is also growing public and political interest in the treatment of captive animals (Appleby, Hughes, & Mench, 2011) and animal welfare is currently a major topic, alongside sustainability and environmental damage, in the ethical debate surrounding food production (Woods, 2012).

Farm animal welfare legislation in the EU is underpinned by the Five Freedoms (Table 1.1), as defined by the Farm Animal Welfare Committee in 1992. However complete freedom from these factors simultaneously may be impossible, and not ideal for welfare (Korte, Olivier, & Koolhaas, 2007). Though numerous definitions exist, animal welfare is commonly considered 'the state of the individual as regards its attempts to cope with its environment' (Radford, 2001); therefore instead of focusing on freedom from these factors, a more effective approach may be to assess the capacity of animals to adapt to environmental demands. For example rather than aiming for a situation where an animal never feels hunger, it may be more appropriate to aim for a situation where it can respond to hunger with a normal behaviour, i.e. foraging, and finding suitable food. The term 'normal behaviour' should be used with caution as this technically includes responses such as fear and escape behaviour thus conflicting with fifth freedom. Though these responses are adaptive and serve vital purposes for wild animals, they are rarely required for survival in captivity and are generally considered indicative of poor welfare. In this context 'normal behaviour' has been redefined as "behaviour that animals tend to perform under natural conditions, because it is pleasurable and promotes biological functioning'' (Bracke & Hopster, 2006, p. 80). This definition includes behaviours such as play, foraging, grooming and exploration. In order to offer such behavioural opportunities, the environment provided should be suitable for the species and meet the needs of the animals, both physically and socially.

Table 1.1 The Five Freedoms, defined by the Farm Animal Welfare Committee in 1992.

| | |
|---|---|
| **1.** | Freedom from thirst, hunger and malnutrition |
| **2.** | Freedom from discomfort |
| **3.** | Freedom from pain, injury and disease |
| **4.** | Freedom to express normal behaviour |
| **5.** | Freedom from fear and distress |

Within the existing farm animal welfare literature most attention has been given to the effect of the physical environment, yet the social environment is central to the expression of normal behaviour. The living conditions of many animals in captivity are vastly different to those experienced by their wild counterparts, however this disparity is arguably most pronounced for farm animals. Other captive populations, such as those in EU accredited zoos, are usually provided with more complex environments, and close attention is paid to the physical and psychological health of individual animals. Zoos encourage animals, where possible, to perform behaviour that is observed in the wild which can involve mental stimulation in the form of training or enrichment etc., along with provision of enclosures, forage and social groups that are (or are at least believed to be) relevant to the species (Hosey, Melfi, & Pankhurst, 2009). The barren conditions of many farming systems are alien by comparison. For example, domestic poultry breeds are believed to descend from the red jungle fowl (*Gallus gallus*) (West & Zhou, 1989; Yamashita, Okamoto, Maeda, & Hashiguchi, 1994), a bird native to forests of southeast Asia (Zuk, Thornhill, Ligon, & Johnson, 1990) with an average breeding density of approximately 2.5 acres per adult bird (Collias & Collias, 1967). In stark contrast, laying hens in the EU can be cage housed with a living space of 750cm² per bird (CEC, 1999). Council Directive 1999/74/EC (implemented on 1st January 2012) banned the use of conventional 'battery' cages, and revised the minimum living standards for laying hens (*Gallus gallus domesticus*). The current 'enriched' cages have only an additional 50cm² of useable space per bird (compared with battery cages) and contain items that should allow hens to perform normal behaviours: a perch, nest box and litter. However these are misleading in description; for example a 'nest box' can consist of a section of the cage partitioned by a plastic curtain with a small matt of AstroTurf. The welfare improvements actually made for hens since the battery cage ban is under scrutiny, as 'enriched' cages are still considered insufficient for full expression of the behavioural repertoire, and thus do not meet the basic needs of the laying hen (FAWC, 2007). ‘Enrichment’ items can even be detrimental in the cage environment; one study found that perches (placed 6cm from the cage floor) exposed hens to cloacal cannibalism and resulted in increased mortality (Moinard, Morisse, & Faure, 1998). Incidentally, the ban of the battery cage is still referred to as one of the most significant welfare advances across the European Union (FAWC, 2007) which may serve to highlight how much work is left to be done in this field.

When making such comparisons we must also acknowledge that hens and other farm animals are domesticated, and have thus undergone physiological and morphological changes. According to Price (1997) these changes are the result of: the relaxation of natural selection, selection for desirable traits by humans, and ‘natural selection’ under captivity leading to adaptation. Unintentional selection of traits also occurs as some attributes are correlated, and these are referred to as ‘side-effects’ of selection (Rauw, Kanis, Noordhuizen-Stassen, & Grommers, 1998). Genetic selection has increased production considerably but in some cases is linked with a decrease in fitness traits (Goddard, 2009) such as poor fertility in high-producing dairy cows (Pryce, Royal, Garnsworthy, & Mao, 2004). Behavioural changes have also occurred during farm animal domestication, including a reduced anti-predator response (Johnsson, Petersson, Jonsson, Bjornsson, and Jarvi (1996) and increased sociability (Price, 1997). Providing domestication is taken into account, knowledge of wild animal behaviour, and the complex mechanisms that determine how animals interact, is extremely useful for understanding the requirements of captive animals.

## 1.7 Social network analysis – an under-utilised tool in welfare science

The use of social network analysis (SNA) is a relatively recent approach in animal behaviour science (Krause, Croft, & James, 2007) and is based on graph, statistical and probability concepts (Asher et al., 2009). It is set apart from more traditional methods in that it is centred on the assumption that actors are interdependent rather than independent: it takes into account that individual behaviour affects and is affected by the presence and behaviour of others (Wasserman & Faust, 1994). In fact dyadic interactions seldom take place in isolation (Croft et al., 2005) and can have short and long–term effects on group structure and flow (of resources, disease, etc.). SNA allows for the quantification of relational ties between actors that often consist of complex interaction patterns varying in type, function, frequency, intensity and duration, with multiple participants and observers (Croft et al., 2008).

In a social network, individuals are represented by 'nodes', and a measure of the interactions or associations between them are represented by 'edges' (Croft et al., 2008). We may simply record whether there are edges between each node (Figure 1a), or we may add more detail to the network by measuring how strong these edges are. For example if edges in a network represent grooming interactions, rather than just recording that two individuals were involved in grooming, we could record the duration of time they were observed to do so – this would result in a 'weighted network' (Figure 1b). Additionally, we could record whether grooming events were mutual (individuals groomed each other) or one-way (one individual was always groomed and the other always did the grooming), which can add important detail to the network; this is referred to as a 'directed network' (Figure 1c) (Croft et al., 2008). We can also add detail to the nodes of the network by assigning these with attribute data. The effects of individual attributes on relationships or social structure can then be measured, for example we could test whether the age, body size or sex of individuals affects their position in a network; it might be that larger individuals occupy central positions, and we might find that individuals are assorted in the network by size (e.g. Croft et al. (2005). This type of analysis can provide useful information on the biological relevance of social structures that are observed.

Intricate patterns of sociality have been revealed using a network approach, in an increasing number of wild animal populations (Croft et al., 2008). Differences in association are firstly restricted by the social organisation of the species (Faust, 2011), then are likely due to the function of the association, and the benefits that certain individuals can provide for that function. Structured networks are described in a continually increasing collective of studies with extensive fitness implications including:: infant survival (e.g. baboons; Silk et al. (2009); shaping of vocal behaviour (e.g. cowbirds; Miller et al. 2008); and, cooperation (guppies; Croft et al. (2006); plains zebra: Fischhoff, Dushoff, Sundaresan, Cordingley, and Rubenstein (2009)). The social fine structure of animal groups is shown to be significantly influenced by personality, of individuals, e.g. aggression influences associations with females for male sleepy lizards, *Tiliqua rugosa*, (Godfrey, Bradley, Sih, & Bull, 2012). Also, in a study by Croft et al (2009) the shy/bold personality of guppies influenced network connections, with shy fish generally having more (and stronger) connections than bold fish. These associations are complex, and guppy social networks are influenced by additional factors such as predation risk (Edenbrow et al., 2011). The application of a network methodology has also been used to study transmission of disease (e.g. in brushtail possum: Corner, Pfeiffer, and Morris (2003), between badgers and cattle: Böhm, Hutchings, and White (2009), bats: Fortuna, Popa-Lisseanu, Ibáñez, and Bascompte (2009), meerkats: Drewe, Eames, Madden, and Pearce (2011)) and can provide valuable insight for conservation biology and disease control.

The strong prevalence of important social relationships among wild animals has clear implications for the management of animals in captivity, yet our understanding of the networks in production animals groups is largely unknown. Though becoming more popular for the study of animal systems (Croft et al., 2008; Sih, Hanser, & McHugh, 2009), SNA is currently underutilised in the field of animal welfare science (Asher et al 2009). To analyse animal social structure, we require detail of interactions between known individuals over a considerable time period (Hinde, 1976). This is sometimes impossible for wild populations due to the nature of their environment or behaviour, however this is attainable for farmed populations, which are contained, observable, and often routinely marked for identification. Two key areas in welfare that would benefit from the methods of SNA are: (1) determining the dynamics of disease and social transmission, (2) quantifying the direct impact of social factors on animal welfare (Asher et al., 2009). We can use these methods to compare snapshots of social structure in space/time, enabling investigation of social requirements through ontogeny and how relationships develop through time. SNA can be used to investigate group cohesion and formation of subgroups. It could also be used to identify which animals are most socially central and well connected; these individuals may be important for group stability or disease spread, or it may be advantageous to train these influential individuals with novel equipment to allow more rapid social facilitation. Additionally, changes in behaviour are commonly observed due to illness (Dantzer & Kelley, 2007) and changes in network metrics over time could be used to predict health problems.

SNA methods are now being promoted by researchers in this field (e.g. Asher et al. (2009), Beisner and McCowan (2014), Koene and Ipema (2014) Rose and Croft (2015)) and studies employing these methods to improve welfare are emerging (see Table

1.2 for a summary of findings). Additionally, SNA has been used to investigate farm-farm disease transmission, analysing information on the movement of animals as a mechanism for disease spread in cattle (Dubé, Ribble, Kelton, & McNab, 2008), and sheep (Kiss, Green, & Kao, 2006). Providing a deeper understanding of social complexity, these methods could have strong welfare application for all captive animals by informing management practises and optimising the social environment in captivity.

SNA may be useful for studying numerous farm animal species that are kept in groups, and in this thesis the method is used to investigate the social networks of cattle. Information on cattle behaviour and social grouping is given in subsequent chapters, however in the next section I provide a short summary of our current understanding of cattle social behaviour.

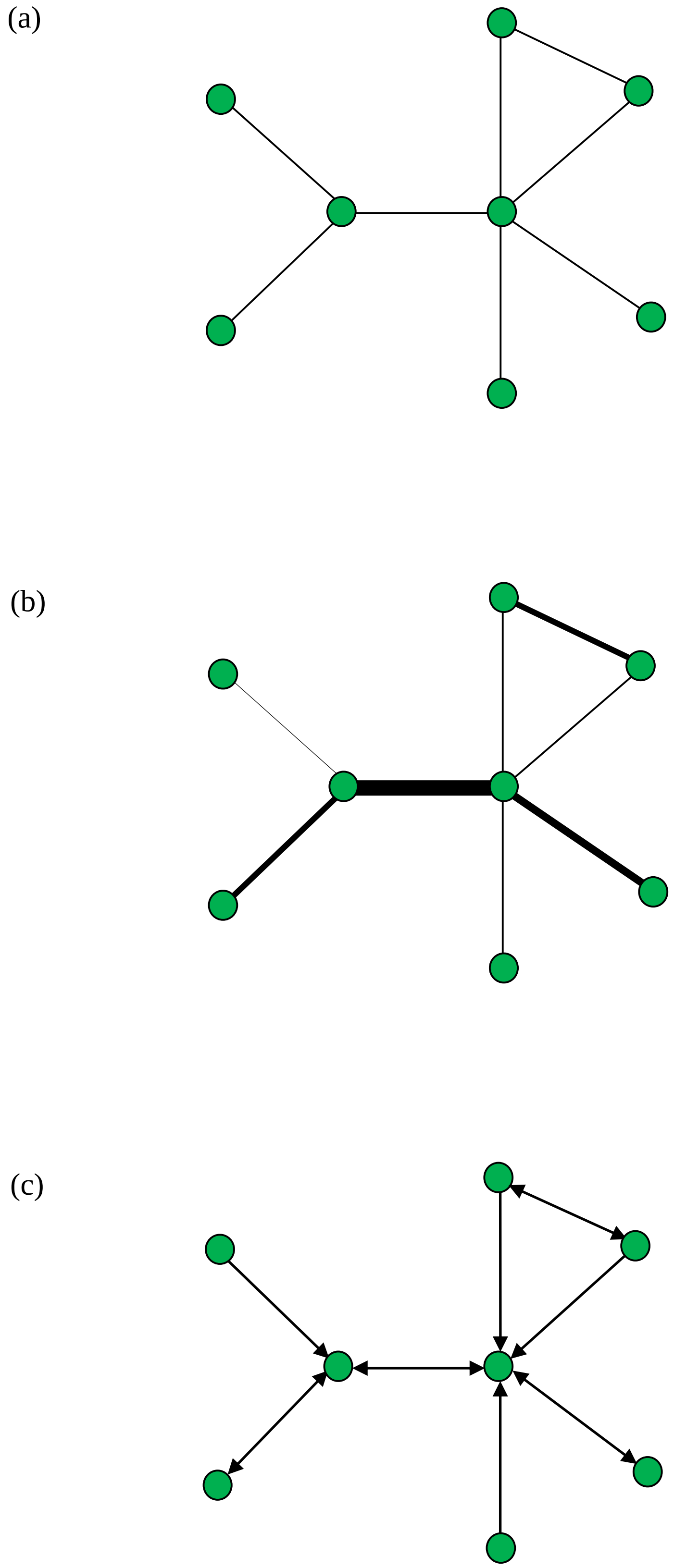


Figure 1 Example of a (a) simple social network, where nodes (representing individuals) are shown as green circles and edges (representing associations or interactions) are shown by lines; (b) a weighted network, where thickness of edges represents strength of associations/number of interactions; (c) a directed network, where arrows indicate the direction of the association/interaction

Table 1.2 Examples of studies applying SNA in animal welfare science

| Citation | Species | Study information | Measures used to construct networks | Main findings and implications for welfare |
|---|---|---|---|---|
| **McCowan, Anderson, Heagarty, and Cameron (2008)** | Rhesus macaques; *Macacca mulatta* | 3 year study of ~1300 individuals housed at the California National Primate Research Center. | Social interactions - direct observation | Demonstrated that SN measures can be used to predict aggression (allowing preventative measures to be taken by managers to minimise this) and to aid in group modifications that promote group stability and social cohesion. |
| **Koene and Ipema (2014)** | Horses; *Equus caballus* | Measured networks of a 9 Dartmoor ponies in an all mare semi-feral herd, including mares with foals. | Nearest neighbour distance, allogrooming and agonistic behaviour – direct observation | Foals are often removed from the group to be sold. SNA was used to identify which foal could be removed from the herd with lowest risk to social structure and welfare of the group. |
| | Brown bears; *Ursus arctos* | Investigated the social structure of 15 brown bears housed in a large forest enclosure. | Activity, location and nearest neighbour distance – direct observation | Showed that there were some strong positive associations between individuals, despite wild brown bears being mostly solitary. Management should consider these associations when removing bears and during feeding/cleaning the enclosure. |
| | Laying hens; *Gallus gallus domesticus* | Investigated the social structure and feather-pecking behaviour of 8 pen-housed hens. | Location and nearest neighbour distance – video recorded | Identified the most central hen in both socio-positive and socio-negative networks suggesting that this individual may play a key role in the group. They found that the nearest neighbour network was significantly correlated with the feather-pecking network. They suggest that information on laying hen social structure may be relevant for understanding and reducing problem behaviour in (large) flocks of laying hens. |
| | Veal calves; *Bos taurus* | Measured social networks of 10 calves aged 3-4 months in a pen. | Nearest neighbour distance – automated recording of location | Network structure differed daily and showed no social preferences. When associations were summed over 12 days, preferences could be found. |
| **Cañon Jones et al. (2010)** | Atlantic Salmon; *Salmo salar* | The development of fin damage and behavioural interactions during feed-restriction was examined. | Spatial position, aggressive interactions - Video recorded | Fin damage was due to social aggression between fish. Groups under feed-restriction had higher fin damage, and had denser and more centralised networks than control groups. Fish that were more central in the network were the initiators of aggressive interactions, gained more weight, and had less fin damage. |

## 1.8 The social behaviour of cattle

Cattle are a gregarious species, living in herds, with individuals having high social attraction. Given the opportunity, cattle form long-term stable social relationships and live in groups that are based on matriarchal family units, interconnected by non-kin social bonds (Lazo, 1994; Reinhardt & Reinhardt, 1981). Allogrooming and spatial proximity between cattle, reflect the social relationships between individuals (Bouissou, Boissy, Le Neindre, & Veissier, 2001). Cattle form dominance hierarchies, and dominance between individuals is determined by various agonistic interactions such as chasing, heat butting and fighting. In a natural environment (e.g. extensive free-range herds) calves are often left to rest in small groups away from their dams (Sato, Wood-Gush, & Wetherill, 1987; Vitale, Tenucci, Papini, & Lovari, 1986), and social bonds and familiarity may begin to form from a few weeks old. There is a strong bond between a cow and her calf, but as the calf gets older it will spend more time with others in the herd and the cow will start the weaning process (starts refusing to feed the calf) when the calf is around 10 months old (Reinhardt & Reinhardt, 1981).

In the UK dairy industry there is considerable diversity in the way animals are grouped and managed, however there are a number of common practices that disrupt social relationships between cattle, which are likely to impact welfare. Firstly, group composition (including group size) and stocking density is controlled by the farmer, rather than being self-regulated based on costs/benefits of group membership. This means there can be high competition for resources such as food and space, which often leads to aggression, and individuals may experience stress. Secondly, regrouping is often part of farm management, in which social groups are split or individuals are moved from one group to another during lactation, e.g. based on milk yield or lactation number. Regrouping has numerous negative consequences, such as increased aggression between cows, and reductions in milk yield, feed intake, rumination and lying times (Hasegawa, Nishiwaki, Sugawara, & Ito, 1997; Hultgren & Svensson, 2009; Raussi et al., 2005; von Keyserlingk, Olenick, & Weary, 2008). Thirdly, on occasion cows may be separated from their social group (e.g. for veterinary treatment) and may be socially isolated for some time. Social isolation acts as a stressor for cattle (McLennan, 2012). Lastly, calves are taken away from cows within the first few days (or often, hours) of birth, which is stressful for both the cow and the calf (Stěhulová, Lidfors, & Špinka, 2008). In addition to the separation from the cow, the calf may also be reared in near social isolation for the first 8 weeks of life, and will be weaned from milk from as early as 5 weeks old. Social isolation is stressful for cattle and rearing calves in individual pens has long-term effects on their behaviour. For example, calves that were reared individually in the first 8 weeks are less confident (Bøe & Færevik, 2003), show more fear (Jensen, Vestergaard, Krohn, & Munksgaard, 1997), play less (Jensen, Munksgaard, Mogensen, & Krohn, 1999) and are involved in more agonistic encounters (Broom & Leaver, 1978) than group-reared calves.

## 1.9 Conclusions

Essentially, social requirements are complex and change over time. Social contact can improve animals' ability to deal with stressors and group stability can allow the development of relationships that enhance this effect. In order to use this as a way to promote positive welfare in farm animals, we need a better understanding of what constitutes a 'good' social environment and should explore new approaches to facilitate this; SNA provides many techniques that could advance this objective.

In the next chapter, I introduce and test the technology that was used to collected social association data in this thesis. Data collection consisted of deploying spatial proximity collars onto cattle to allow remote gathering of detailed association data.

However there were significant challenges while using this technology, predominantly the discovery of a sampling bias, which is demonstrated in *Chapter II*.

# Chapter II

## Spatial proximity loggers for recording animal social networks: consequences of inter-logger variation in performance.

## 2.1 Abstract

Social network analysis has become an increasingly popular method to link individual behaviour to population level patterns (and vice versa). Technological advances of recent years, such as the development of spatial proximity loggers, have enhanced our abilities to record contact patterns between animals. However, loggers are often deployed without calibration which may lead to sampling biases and spurious results. In particular, loggers may differ in their performance (i.e. some loggers may over-sample and other loggers may under-sample social associations). However, the consequences of inter-logger variation in logging performance has not been thoroughly considered or quantified. In this study, proximity loggers made by Sirtrack Ltd. were fitted to 20 dairy cows over a three week period. Contact records resulting from field deployment demonstrated variability in logger performance when recording contact duration, which was highly consistent for each logger over time. Testing loggers under standardised conditions suggested that inter-logger variation observed in the field was due to a combination of intrinsic variation in devices, and environmental/behavioural effects. We demonstrate the potential consequences that inter-logger variation in logging performance can have for social network analysis; particularly how measures of connectivity can be biased by logging performance. Finally, we suggest some approaches to correct data generated by proximity loggers with imperfect performance, that should be used to improve the robustness of future analyses.

## 2.2 Introduction

The study of animal social networks has become increasingly popular in many areas of behavioural research (Krause et al., 2007; Sih et al., 2009; Wey, Blumstein, Shen, & Jordan, 2008); linking individual behaviour to population level patterns and vice versa (Croft et al., 2008). As such, the application of social network analysis to animal populations has advanced our understanding of information and disease transmission, collective group behaviour, habitat use, and the consequences of animal movement (Croft et al., 2008; Krause et al., 2007; Sih et al., 2009; Wey et al., 2008). Animal social networks can be constructed based on pairwise relations between individuals in a group, corresponding to the social interactions that occur between them (Hinde, 1976). However, while providing important contextual information; the frequency and nature of interactions often mean they are difficult to observe or quantify for many animal species living in the wild (Whitehead, 2008). When this is the case, social relationships are often inferred based on patterns of associations between individuals (Whitehead, 2008). A common method to define associations is to use spatial proximity measures (Croft et al., 2008; Whitehead, 2008), from which one can infer relationships or potential interactions provided that proximities are behaviourally relevant to the species (Whitehead & Dufault, 1999).

Collecting data on social associations has traditionally been achieved by direct observation of animals, with group membership being recorded for a given time period at a regular rate (every few minutes, hours or days depending on the study species) (Croft et al., 2008; Whitehead, 2008) and analysed using a ‘gambit of the group’ approach (Whitehead, 2008). Such methods tend to produce sparse data sets and many social associations go unobserved. In contrast recent technological advances have enhanced the sophistication of animal tracking equipment, while simultaneously reducing the size of components. This allows continuous tracking of multiple individuals simultaneously and has introduced tremendous potential for automated data collection, or ‘reality mining’, for animal social networks (Krause, Wilson, & Croft, 2011; Rutz et al., 2012; Ryder, Horton, van den Tillaart, Morales, & Moore, 2012). The use of devices such as GPS logging, PIT tags and radio-telemetry can supplement (or even replace) traditional methods of data collection, and once deployed allow generation of rich data sets with relative ease (Krause et al., 2011). Another advantage is that when 100% of the population are fitted with devices continuous data can be collected, free from the bias of traditional sampling (i.e. direct observation; often being opportunistic and relatively short-term) (Krause et al., 2011). Association data can be gathered remotely for extended time periods while avoiding observer effects. This is particularly beneficial for wild populations that are difficult to observe due to behaviour or habitat.

One technology increasingly being used to collect animal social network data is radio-telemetry, such as the spatial proximity loggers manufactured by Sirtrack Ltd. and Encounternet. Proximity loggers have been used to study: intraspecific (Creech et al., 2012; Hamede, Bashford, McCallum, & Jones, 2009; Ji, White, & Clout, 2005; Marsh, Hutchings, McLeod, & White, 2011); and interspecific (Böhm et al., 2009) contact rates in relation to disease transmission; affiliative interactions (Swain & Bishop-Hurley, 2007); predatory behaviour (Tambling & Belton, 2009); population dynamics (Marsh, McLeod, Hutchings, & White, 2011); and mechanisms for information exchange (Rutz et al., 2012). Whilst this innovative technology has been rapidly embraced by the biological community, devices for recording contact patterns are often deployed without thorough testing or consideration of the potential sampling biases. In particular, an aspect that has largely been overlooked is the degree of inter-logger variation in performance (but see Drewe et al. (2012)) and its potential consequences for data interpretation.

The spatial proximity loggers made by Sirtrack allow users to record the duration and frequency that animals wearing loggers are within a certain distance of each other. Spatial proximity loggers function by simultaneously sending and receiving radio signals, therefore the reciprocity of contacts between two loggers provides a measure of inter-logger consistency. For example, when two loggers are identical in performance, logger *i* will detect logger *j* for the same duration as *j* detects *i*. However, it is clear from the literature that pairs of loggers commonly do not have identical performance, indicated by asymmetries in the reciprocity of data. The response to such a lack of reciprocity is currently unsystematic among authors. Some simply present the overall degree of reciprocity of an association matrix and use either some combined measure of the association strength (such as using duration from the time of contact initiation by the first logger until the termination of contact by both loggers) (e.g. Hamede et al. (2009); Patison et al. (2010); Walrath, Van Deelen, and VerCauteren (2011)) or select the value from the logger in a dyad with the highest number of contacts (e.g. Cross et al. (2012)). Despite acknowledging the issue with contact reciprocity, such approaches assume some degree of general error rather than a sampling bias. They disregard the possibility that loggers may each perform in inherently different ways, and thus biases in the data caused by the technology go unobserved and uncorrected. However it is of concern that when inter-logger performance has been measured; the extent of the variability (in terms of logger dyad reciprocity) is surprisingly large (Drewe et al., 2012).

Variation among individual devices may result from a number of factors influencing signal strength or detection sensitivity. First, their spatial position within the environment can affect their function, as radiation patterns, power and contact detection distance are affected by factors such as: the angle of antennae; distance from the ground; properties of surrounding objects and position relative to the receiving logger (Prange, Jordan, Hunter, & Gehrt, 2006). Second, the size and mass of the collared animal is likely to affect a logger’s signal, as may the orientation and number of collared animals in the immediate area. Third, though some level of error is inevitable when using radio telemetry, intrinsic performance differences among loggers may occur due to differences in device components and/or housing. Any combination of these factors may generate differences in logger performance that could be erroneously interpreted as differences in social behaviour.

As a discipline, behavioural biologists and ethologists have worked hard to standardise sampling techniques when recording patterns of social association in animal groups (Croft et al., 2008; Whitehead, 2008). New remote sensing technology should be given the same judicious consideration with emphasis on quantifying potential biases and errors during data collection, and developing ways to effectively account for these during analysis. For example, we understand that an individual’s social network position can be greatly influenced by sampling frequency, with more central network positions generally being occupied by those most frequently observed (Croft et al., 2008). In response to this, researchers have developed null models that control for sampling frequency of individuals during direct observations (Croft, Madden, Franks, & James, 2011). However, it seems to have been assumed that the use of proximity loggers for recording associations removes sampling problems. We propose that such assumptions require thorough testing and that inter-logger variation in performance is likely to result in fundamental errors in data collected for animal social networks.

Here we investigate the degree of variation in inter-logger performance for 20 proximity loggers purchased from Sirtrack Ltd. This technology has been deployed across various study systems, addressing a range of ecological and behavioural questions (e.g. Hamede et al. (2009); Patison et al. (2010). ‘Performance’ is measured here in terms of individual contact detection distance, and resultant reciprocity in contact detection durations between dyads. Twenty proximity loggers were initially fitted to 20 dairy cows within a commercial milking group of 120 individuals, and were deployed over a three week period. This field deployment provided data on intra-logger consistency and inter-logger variability in recording contacts under field conditions. Subsequently, we tested the loggers under standardised conditions to establish whether the inter-logger variation observed in field deployment was due to intrinsic variation in logger performance. Following this we use an analytical model (validated here using a computational model) to demonstrate the consequences of using data from loggers with inherently biased variation; and the effect of observed sampling biases for conclusions from social network data. Finally, we suggest approaches useful for correcting data generated by loggers with varied performance. Our objective is to draw these issues to the attention of researchers using this technology, with the intention of improving the accuracy of future analyses.

## 2.3 Methods

### 2.3.1 Proximity devices

The proximity loggers used in this study were manufactured by Sirtrack Ltd (New Zealand), with some provided pre-packaged as collars for deployment on cattle (model E2C 181C) and others as base stations (packaged in a cylinder) for deployment in the environment (both have the same internal components, it is only the external packaging that differs). Each proximity logger functions by broadcasting a unique identification code over a ultra-high frequency (UHF) channel, while simultaneously searching for the ID codes of other loggers within a predetermined distance range. A logger can detect up to eight others concurrently; recording the ID of a detected logger, the date, start and end time of the contact, and its duration. Users can adjust the power setting of a UHF coefficient range (0-62) to alter the detection distance (detection distance is negatively correlated to the UHF value), and choose a separation time (the duration any two loggers need to be separated for an encounter to be considered terminated and saved to memory) appropriate to their use, from 1-255 seconds.

### 2.3.2 Field deployment

Twenty proximity collars were deployed for three weeks on 20 dairy cows, within a herd of 120, on a commercial dairy farm in Cullompton, Devon, UK. The herd is housed in a 45x30m (approx.) barn with a straw yard and robotic milking system. Cows in late lactation have access to pastures; however proximity collars were only fitted to early lactation cows that remained in the barn throughout the study. Collars were deployed during routine husbandry procedures, and removed opportunistically during milking following the three week data collection period. Data collected on the day of deployment and days on/following the start of collar removal were excluded from the analysis. Proximity collars were set to a UHF value of 43 (which logged contacts at 1.5-2.5 metres in pilot tests using collared horses) with a separation time of 120 seconds.

In order to measure the inter-logger variability in performance, we constructed an association matrix (Table 2.1). The matrix was based on the total duration of associations between pairs of loggers, summed over the 3 week period. The percentage difference in total contact duration was then calculated for each proximity logger dyad. For example, suppose that the duration that logger $i$ records contact with logger $j$ = $D_{ij}$= 5000 seconds, and the duration that logger $j$ logs collar $i$ = $D_{ji}$ = 4000 seconds. In this scenario, the percentage bias is: $B_{ij} = 100\ \frac{D_{ij} - D_{ji}}{D_{ij} + D_{ji}}$ and thus the bias in logger $i$ recording logger $j$ is $B_{ij}$ = +11.1% and the bias in logger $j$ recording logger $i$ is $B_{ji}$= -11.1%. The mean percentage difference for each proximity logger was used to provide a measure of how each performed comparative to all others, hereafter referred to as the 'logging bias'.

To quantify the repeatability of the observed inter-logger variability (and thus the intra-logger consistency), we repeated the above process after subdividing the data into three one-week periods. Values from this were then used to determine the repeatability of collar logging bias across weeks. This was calculated as: the variance between loggers divided by the sum of the variance between loggers and the residual variance (see Nakagawa and Schielzeth (2010) and Schuett et al. (2011) for details). 95% CIs for repeatability estimates (r) were obtained from parametric bootstrapping (N=1000 simulation iterations) (see Nakagawa and Schielzeth (2010) for details). We tested the correlation between each half of the association matrix (about the diagonal) to assess the reciprocity of total contact duration between dyads using the Mantel test function in Poptools (Hood, 2010).

### 2.3.3. Standardised test

An open-field experiment, adapted from Drewe et al. (2012), was performed in order to determine the degree of inter- and intra-logger variation in detection distance under standard conditions. Twenty proximity collars (those previously used in the field deployment, see methods ii) and one base station were set to a UHF value of 43 (corresponding to the UHF value applied in ii) with a separation time of 10 seconds (the separation time differed from the time used in the field deployment (see ii above) to reduce the time taken to carry out the experiment, however this has no effect on logger performance). Collars were tested individually, each paired with the same base station. Each device was attached (50cm above the ground) to an upturned plastic basket with the antenna positioned vertically. At the start of each trial the base station was positioned out of signal range (6m) to the stationary collar being tested, and then moved towards it at 10cm increments. The base station was paused at each 10cm point for 5 seconds. When a signal was first detected by the collar or base station, the LED on the detecting device began to flash; we defined contact initiation as five short flashes. The base station was then moved towards the collar, again in 10cm increments, until a signal was detected by the second device. The distance at which contact was established, the ‘initiation distance’, was noted for both the base station and the collar. The base station was then moved away from the collar in 10cm increments, until both of the LEDs stopped flashing and the devices logged the contact (indicated by a 10 second interval between the last short flash, and a final long flash). The distance at which contact was lost, the ‘termination distance’, was recorded for both logging devices. This process was carried out eight times (successively) for each collar.

### 2.3.4 Consequences of inter-logger variability for social network analysis

To illustrate the potential consequences that logging bias may have on the social network, we calculated the weighted in and out degree of each individual. In this context the weighted in-degree of an individual is derived from data recorded on its own proximity logger (i.e. the total duration of records of other loggers), while the weighted out degree is the total duration of records of the individual’s logger detected by other loggers on other individuals. Degree is often used as a measure of both the number of social associations an individual has (the un-weighted degree) and the strength of those social associations (weighted degree) (Croft et al., 2008). Using a linear regression, we explored the relationship between the logging bias (see ii, above), and both the weighted in-degree and weighted out-degree.

Table 2.1 Association matrix of total duration (seconds) of associations for 20 individuals during the 3 week field deployment

| | | Individual | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| Individual | 1 | 0 | 99229 | 51960 | 70534 | 48848 | 40738 | 36989 | 52208 | 38344 | 68215 | 45767 | 50838 | 77425 | 32066 | 52840 | 72258 | 64238 | 76297 | 66628 | 44634 |
| | 2 | 75762 | 0 | 56483 | 53305 | 51208 | 34811 | 41478 | 41417 | 38981 | 50884 | 32277 | 46731 | 57700 | 43708 | 47676 | 53163 | 45854 | 56262 | 62589 | 28371 |
| | 3 | 29622 | 44533 | 0 | 39813 | 56573 | 31618 | 29872 | 39247 | 26239 | 46869 | 29927 | 34530 | 57033 | 28672 | 38312 | 48916 | 44964 | 54156 | 47349 | 33765 |
| | 4 | 47534 | 50560 | 46917 | 0 | 39808 | 29437 | 37775 | 58554 | 44273 | 52964 | 41254 | 33592 | 46967 | 14625 | 55289 | 47427 | 51402 | 74536 | 58803 | 36688 |
| | 5 | 24260 | 35845 | 53500 | 31940 | 0 | 15999 | 22742 | 30945 | 16423 | 27712 | 25054 | 19059 | 31672 | 7130 | 37704 | 68853 | 34625 | 37525 | 26436 | 10138 |
| | 6 | 25829 | 33822 | 35501 | 33834 | 22676 | 0 | 23701 | 22081 | 29168 | 27527 | 20707 | 25654 | 34039 | 40167 | 24011 | 38580 | 34225 | 35600 | 34800 | 48505 |
| | 7 | 25643 | 41406 | 37949 | 39266 | 34615 | 24383 | 0 | 31923 | 26947 | 35488 | 40968 | 28247 | 39254 | 15367 | 31441 | 41309 | 32264 | 46986 | 38168 | 30686 |
| | 8 | 38211 | 39012 | 50982 | 64864 | 44909 | 25283 | 34964 | 0 | 47269 | 55432 | 43454 | 25740 | 62795 | 25059 | 57555 | 40749 | 65054 | 66742 | 55728 | 42176 |
| | 9 | 21208 | 26898 | 28483 | 37025 | 20768 | 21765 | 20980 | 34108 | 0 | 48652 | 18250 | 27697 | 39060 | 15444 | 41814 | 28182 | 35996 | 33756 | 41841 | 22246 |
| | 10 | 55910 | 60836 | 65378 | 66836 | 45793 | 36072 | 40745 | 62350 | 71776 | 0 | 57932 | 34619 | 80270 | 26733 | 76973 | 60376 | 62305 | 87674 | 77386 | 37701 |
| | 11 | 24692 | 25506 | 31976 | 33088 | 26954 | 16797 | 33239 | 29667 | 20429 | 33504 | 0 | 17082 | 32078 | 12011 | 36272 | 29686 | 29366 | 58492 | 31080 | 17886 |
| | 12 | 25592 | 33894 | 29368 | 23685 | 21912 | 20220 | 20023 | 16685 | 27094 | 22902 | 15642 | 0 | 37375 | 18762 | 27316 | 31684 | 30235 | 39359 | 26222 | 23884 |
| | 13 | 54248 | 55302 | 71043 | 51092 | 46477 | 34366 | 36596 | 63684 | 45988 | 62239 | 40726 | 50668 | 0 | 41842 | 61483 | 66425 | 52226 | 79219 | 57732 | 40164 |
| | 14 | 19300 | 37177 | 31142 | 15687 | 10721 | 37631 | 12632 | 21024 | 17673 | 19919 | 14585 | 21238 | 39511 | 0 | 13778 | 24530 | 37383 | 19809 | 31375 | 31879 |
| | 15 | 41320 | 52649 | 54529 | 62185 | 58400 | 27476 | 31238 | 65324 | 60516 | 68380 | 54695 | 38168 | 64219 | 18811 | 0 | 55792 | 60074 | 88624 | 56130 | 25602 |
| | 16 | 55087 | 56266 | 61911 | 56411 | 91076 | 45964 | 41773 | 43268 | 41036 | 56198 | 40035 | 42680 | 75752 | 30997 | 49773 | 0 | 61710 | 62198 | 45267 | 40231 |
| | 17 | 45925 | 47270 | 55412 | 59500 | 50243 | 37483 | 35248 | 65556 | 46715 | 59675 | 39051 | 43768 | 54937 | 45486 | 54005 | 57651 | 0 | 54809 | 51687 | 45948 |
| | 18 | 42620 | 41985 | 52510 | 62953 | 41605 | 28565 | 38781 | 48086 | 33419 | 57134 | 58436 | 45660 | 62177 | 17188 | 60661 | 42919 | 38419 | 0 | 41040 | 33810 |
| | 19 | 38345 | 50291 | 47682 | 50213 | 30556 | 28624 | 29795 | 40850 | 40781 | 59093 | 31368 | 30748 | 51152 | 25255 | 38842 | 36515 | 39289 | 43447 | 0 | 36574 |
| | 20 | 25135 | 21777 | 35067 | 34406 | 11988 | 44051 | 25515 | 30112 | 24241 | 26028 | 18853 | 29698 | 34958 | 28948 | 16733 | 29413 | 37632 | 33752 | 34767 | 0 |

### 2.3.5 Analytical model

Using information on the variation in contact initiation distances of loggers collected in the standardised test (see methods iii), we constructed an analytical model to explore the consequences of this variation, for recording patterns of social associations. In this model each logger $i$ has a single distance $r_i$ (set as the logger initiation distance) within which it detects any other logger $j$. The model assumes that individuals use space uniformly, so the time that logger $i$ detects any other logger $j$ is proportional to the square of $i$'s initiation distance: $t_i = \alpha r_i^2$ . The proportionality constant $\alpha$, which depends only on the size of the area used, and the total duration of the observations, is the same for all loggers. As the initiation distance is represented as the square of the observed value, the variation in initiation distance will be magnified in the analytical model. We produced a matrix of expected interaction values from the analytical model, and calculated the percentage difference for each dyad as:

$$B_{ij} = 100 \frac{r_i^2 - r_j^2}{r_i^2 + r_j^2}$$

The mean expected $B_{ij}$ was then calculated for each logger, which is directly comparable to the logging bias calculated during the field deployment (see methods section ii above).

To demonstrate the consequence that variation in contact initiation distance can have for inferences made from social data collected by loggers in the field; we correlated the logging bias matrix calculated from the field data with the logging bias matrix calculated from the analytical model. Given the non-independence of data points in the matrices, we used a Quadratic Assignment Procedure (QAP) correlation (Hanneman & Riddle, 2005), which comprised calculation of Pearson's correlation coefficient for equivalent cells of two data matrices. One matrix was then randomly permuted and Pearson's correlation coefficients were again calculated. This was repeated 10,000 times to determine the proportion of times that coefficients from randomly permuted networks were larger or equal to the observed Pearson's coefficient. From this we were able derive a probability value that the association between the matrices was due to chance.

### 2.3.6 Computational model

In order to validate the analytical model for the current study, and more generally for applicability in future studies using these loggers, we produced a computational model based on the same parameters. The model was constructed with 20 agents (representing cows wearing proximity loggers) able to move around an arena (100m$^2$) for 15,000 time steps. In the model each logger has 2 circles (circle 1 = initiation radius, circle 2 = termination radius); logging starts when logger $j$ is within the initiation radius of logger $i$, and ceases when logger $j$ leaves the logger termination radius. In this way the computational model generates a direct matrix of weighted association strengths that is comparable to the data collected during the field deployment. From this matrix, predicted logging biases were calculated following the same procedure as described in methods section ii. Both the contact initiation and termination radiuses were parameterised using the distances measured for each logger during the standardised tests (see iii above). Whilst this null model is purposefully simplistic it could easily be developed to provide a more realistic null model of social interactions (e.g. non-random space use etc.).

### 2.3.7 Correction method

We suggest a method of correcting accumulated association data by scaling all contact durations in an association matrix to the performance of each logger with the logger with the lowest recorded contact durations. To achieve this we first identified the lowest recorded logger (the logger with the highest mean logging bias) across all dyadic interactions. We then calculated the logging bias of all other loggers when paired with this logger. The total contact duration was then adjusted for all loggers according to their logging bias with the least recorded logger. For example if logger *i* had a logging bias of 12% when compared to the least recorded logger, the contact duration that logger *i* recorded with all other loggers would be reduced by 12%. In this way we were able to standardise all loggers relative to their performance with the least recorded logger. It is important to note that this method requires that all possible pairwise interactions occur (i.e. it is possible to establish the performance of loggers in all possible pairwise combinations).

## 2.4 Results

### 2.4.1 Field deployment

All proximity loggers functioned throughout the study, and data were successfully recovered from each device for the full duration of the deployment period. As in previous studies, all one second contact records were removed prior to data analysis as these are thought to occur sporadically when individuals are at the edge of the detection range, and reduce reliability of dyadic contact records (Drewe et al., 2012).

The mean number of contacts recorded by loggers was 5478.75, and the mean duration of contacts was 141.68 seconds. The logging bias (calculated from the association matrix derived from field data) ranged from -14.8 % to 22.1% across the sample (n=20) (see Figure 2.1). It is important to note that during field deployment all proximity loggers recorded contacts with every other logger, allowing us to compare all dyadic interactions. The proximity loggers showed a very high degree of consistency in logging bias over the three time periods (r=0.992, 95%CI 0.982-0.996). The reciprocity of total contact duration between dyads in the association matrix was 0.76; as calculated across the entire association matrix.

### 2.4.2 Standardised test

The standardised test demonstrated substantial variation in logger performance (measured as the mean contact detection and termination distances), as shown in Figure 2.2a and 2.2b. The logging bias observed in the field study (see results section i) was significantly positively correlated with the mean initiation (Spearman's rank; $r_s$=0.457, n=20, P= 0.043; Figure 2.3a) and termination (Spearman's rank; $r_s$=0.49, n=20, P= 0.028; Figure 2.3b) distances of the base station (distance at which the base station detected each collar, individually). Similarly, the logging bias was significantly positively correlated to the mean initiation distances (Spearman's rank; $r_s$=0.460, n=20, P=0.041; Figure 2.3c) of the collars (distance at which collars detected the base station, individually), however, the mean termination distances of collars was not significantly related to logging bias, though the effect was in the same direction (Spearman's rank; $r_s$=0.368, n=20, P=0.111; Figure 2.3d).

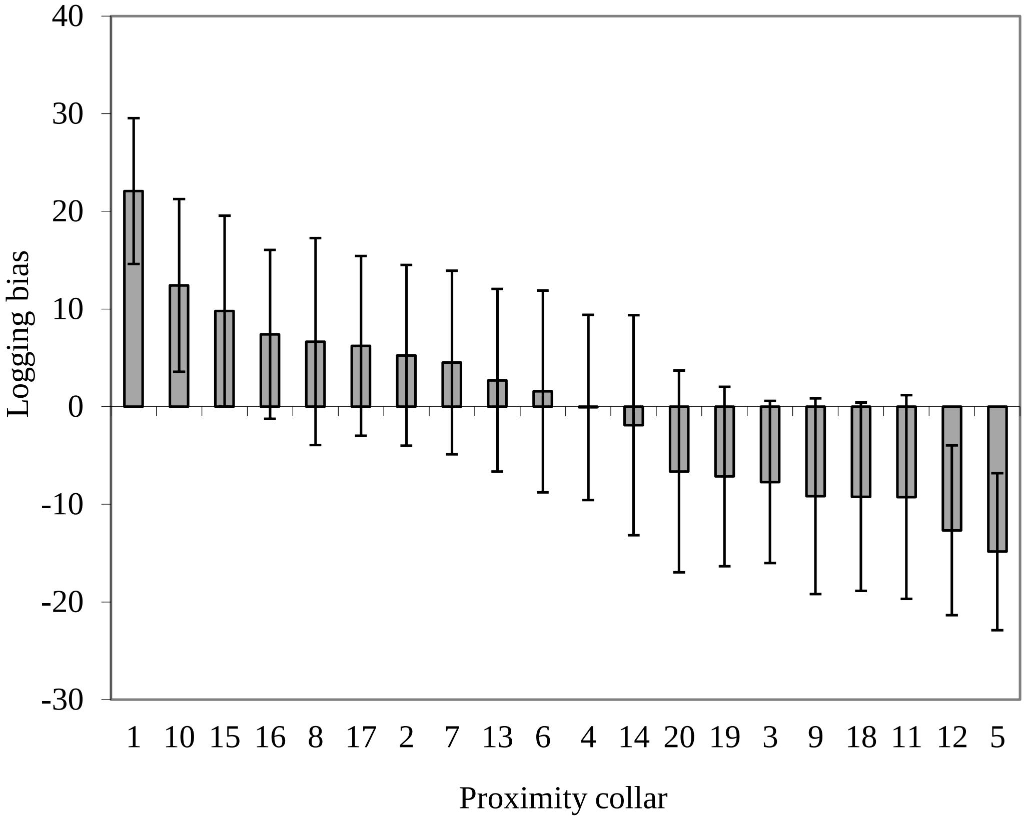
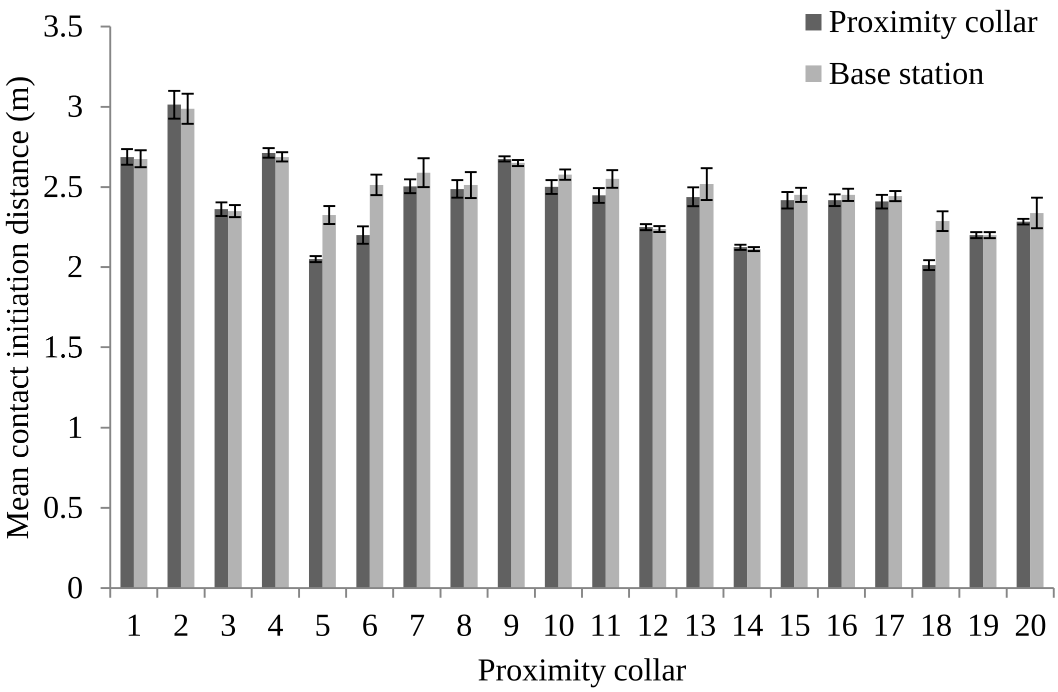


Figure 2.1 Logging bias (mean percentage difference in contact logging) of each proximity logger, based on total duration of associations over a 3 week period (error bars represent standard deviations)

(a)



(b)

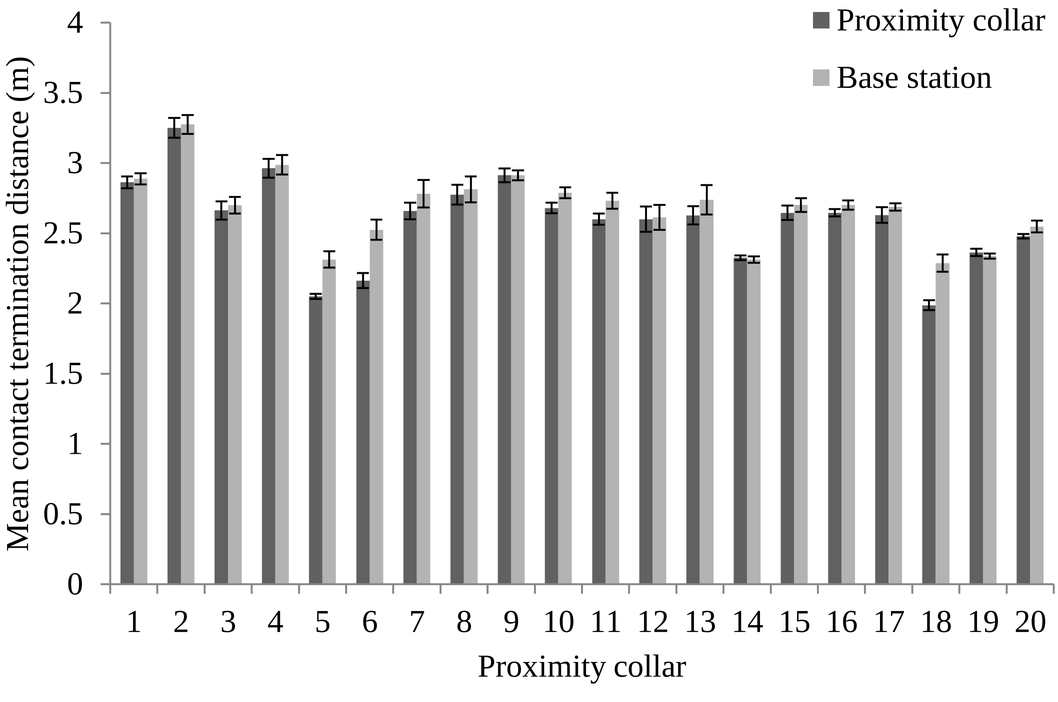


Figure 2.2 Mean contact initiation (a) and termination (b) distances of twenty proximity collars and one base station when paired in the standardised test (error bars represent standard errors)

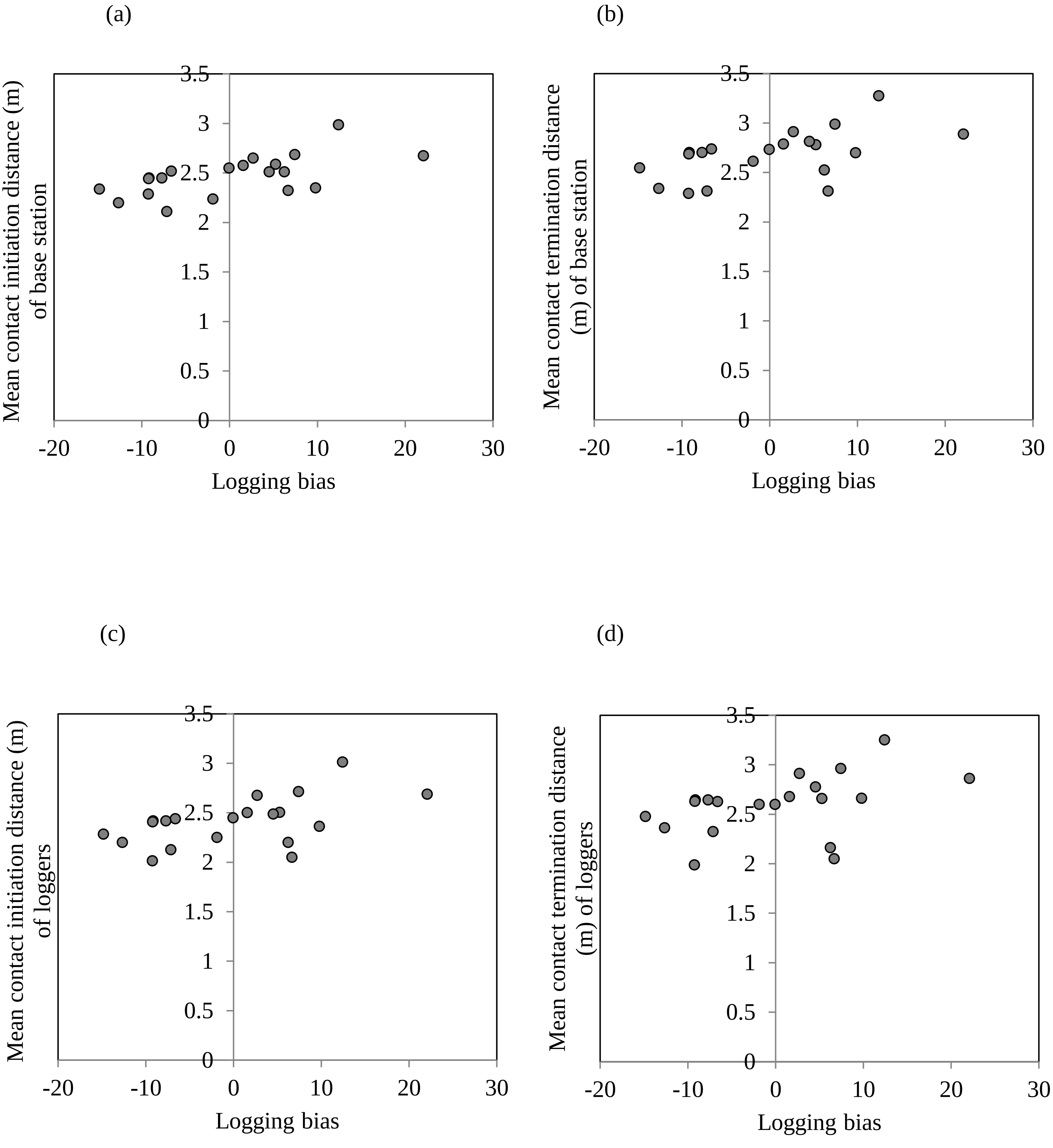


Figure 2.3 Correlation between the logging bias (as calculated from field deployment) and the mean contact initiation and termination distances of the base station (a & b) and twenty proximity collars (c & d) during the standardised test

### 2.4.3 Consequences of inter-logger variability for social network analysis

When constructing a network from the association matrix of total contact durations during field deployment (Table 2.1), all individuals were interconnected; however there was variation in the strength of interactions. There was a significant relationship between the weighted in-degree and the logging bias; meaning that those proximity loggers more likely to record other loggers had a higher in-degree (linear regression with permutation test, n=10,000 permutations, $r^2=0.546$, $F=2.58$, $P<0.001$, Fig. 2.4a). In contrast, we found no significant relationship between the weighted out-degree and the logging bias (linear regression with permutation test, $r^2=-0.095$, $F=0.17$, $P=0.705$; Fig. 2.4b).

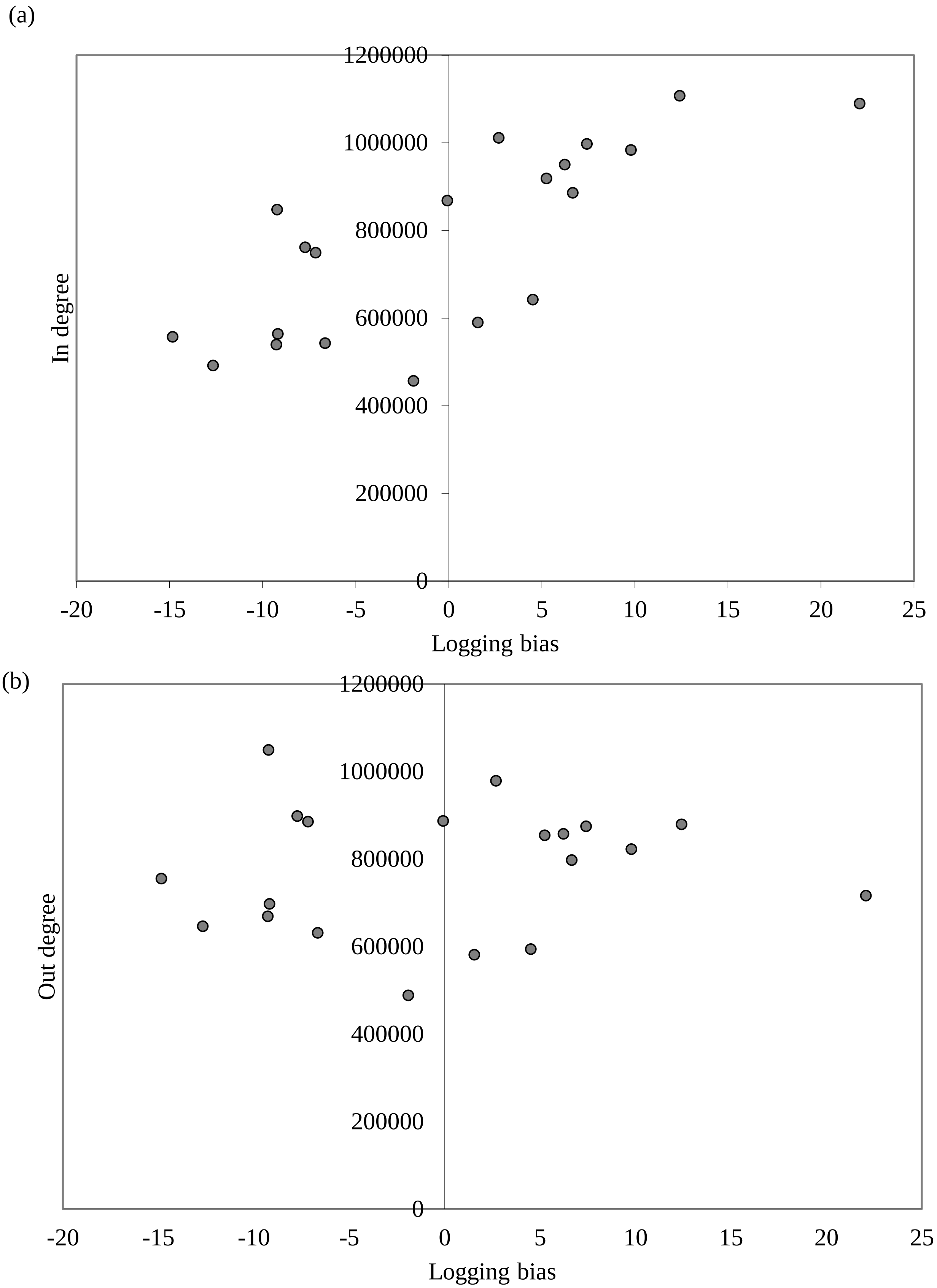


Figure 2.4 Correlation between logging bias (as calculated from field deployment) and in-degree (a) and out-degree (b). The in-degree (total duration of contacts logged by a focal logger) provides a measure of detection sensitivity, while the out degree (total duration of contacts with the focal logger, logged by all other loggers) provides a measure of signal strength

### 2.4.4 Modelling

The analytical model and computational model were highly consistent in the calculation of logging biases (Spearman's rank; $r_s=0.99$, $n=20$, $p<0.0001$). We therefore used the analytical model for all further analysis as it was easier to implement (only needing one calculation rather than intensive simulations, etc.). The logging bias matrix from the field data was significantly correlated with the logging bias matrix from the data produced by the analytical model (Spearman's rank; $r_s=0.52$, $n=20$, $p=0.008$).

### 2.4.5 Correction method

As all possible pairwise interactions occurred during the field deployment, we were able to apply the correction method to the association data shown in Table 2.1. Collar 1 was identified as the lowest recorded logger, as it had the highest mean logging bias during deployment (as shown in Figure 2.1). Therefore, duration data from collars 2-20 were adjusted in accordance with their logging performance with collar 1, as shown in Table 2.2. This improved the overall reciprocity of contact between dyads, from 0.76 (Table 2.1) to 0.99 (Table 2.2).

Table 2.2 Corrected association matrix of total duration (seconds) of associations for 20 individuals during the 3 week field deployment; data for each logger corrected in accordance to its performance with the lowest recorded logger (collar 1)

| | | Individual | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| Individual | 1 | 0 | 75762 | 29622 | 47435 | 24260 | 25829 | 25643 | 38211 | 21208 | 55910 | 24692 | 25592 | 54248 | 19300 | 41320 | 55087 | 45925 | 42620 | 38345 | 25135 |
| | 2 | 75762 | 0 | 32201 | 35848 | 25432 | 22071 | 28755 | 30313 | 21560 | 41705 | 17414 | 23525 | 40428 | 26307 | 37282 | 40530 | 32782 | 31428 | 36021 | 15977 |
| | 3 | 29622 | 34001 | 0 | 26775 | 28097 | 20047 | 20709 | 28725 | 14513 | 38415 | 16146 | 17383 | 39960 | 17257 | 29959 | 37292 | 32146 | 30252 | 27250 | 19014 |
| | 4 | 47435 | 38523 | 26687 | 0 | 19716 | 18618 | 26116 | 42761 | 24431 | 43290 | 22197 | 16869 | 32823 | 8762.8 | 43138 | 36053 | 36666 | 41546 | 33776 | 20592 |
| | 5 | 24260 | 27368 | 30500 | 21480 | 0 | 10144 | 15766 | 22649 | 9083.5 | 22713 | 13517 | 9594.4 | 22191 | 4291.4 | 29484 | 52491 | 24754 | 20962 | 15214 | 5709.1 |
| | 6 | 25829 | 25823 | 20239 | 22754 | 11262 | 0 | 16431 | 16161 | 16133 | 22562 | 11172 | 12914 | 23850 | 24176 | 18776 | 29412 | 24468 | 19886 | 20028 | 27315 |
| | 7 | 25643 | 31614 | 21634 | 26407 | 17191 | 15459 | 0 | 23364 | 14904 | 29086 | 22103 | 14220 | 27503 | 9249.1 | 24586 | 31493 | 23066 | 26247 | 21966 | 17280 |
| | 8 | 38211 | 29786 | 29064 | 43622 | 22304 | 16030 | 24239 | 0 | 26144 | 45433 | 23444 | 12958 | 43997 | 15083 | 45007 | 31066 | 46508 | 37283 | 32072 | 23751 |
| | 9 | 21208 | 20537 | 16238 | 24900 | 10314 | 13800 | 14545 | 24964 | 0 | 39876 | 9846.2 | 13943 | 27367 | 9295.5 | 32698 | 21485 | 25734 | 18856 | 24080 | 12528 |
| | 10 | 55910 | 46449 | 37271 | 44948 | 22743 | 22871 | 28247 | 45634 | 39699 | 0 | 31255 | 17427 | 56241 | 16090 | 60192 | 46029 | 44543 | 48975 | 44536 | 21231 |
| | 11 | 24692 | 19474 | 18229 | 22252 | 13387 | 10650 | 23043 | 21713 | 11299 | 27460 | 0 | 8599.1 | 22476 | 7229.2 | 28364 | 22632 | 20994 | 32674 | 17887 | 10072 |
| | 12 | 25592 | 25878 | 16742 | 15928 | 10882 | 12820 | 13881 | 12212 | 14986 | 18771 | 8439.1 | 0 | 26187 | 11293 | 21361 | 24155 | 21616 | 21986 | 15091 | 13450 |
| | 13 | 54248 | 42223 | 40501 | 34360 | 23082 | 21789 | 25371 | 46610 | 25436 | 51012 | 21972 | 25506 | 0 | 25184 | 48079 | 50640 | 37337 | 44252 | 33225 | 22618 |
| | 14 | 19300 | 28385 | 17754 | 10550 | 5324.5 | 23859 | 8757.3 | 15387 | 9774.9 | 16326 | 7868.8 | 10691 | 27683 | 0 | 10774 | 18701 | 26726 | 11065 | 18057 | 17952 |
| | 15 | 41320 | 40198 | 31087 | 41820 | 29004 | 17421 | 21656 | 47811 | 33471 | 56045 | 29509 | 19214 | 44995 | 11322 | 0 | 42534 | 42948 | 49506 | 32303 | 14417 |
| | 16 | 55087 | 42959 | 35295 | 37937 | 45232 | 29142 | 28960 | 31668 | 22697 | 46061 | 21599 | 21485 | 53076 | 18657 | 38922 | 0 | 44118 | 34744 | 26052 | 22656 |
| | 17 | 45925 | 36091 | 31590 | 40014 | 24953 | 23765 | 24436 | 47980 | 25838 | 48910 | 21069 | 22033 | 38492 | 27377 | 42231 | 43951 | 0 | 30617 | 29746 | 25875 |
| | 18 | 42620 | 32056 | 29936 | 42337 | 20663 | 18111 | 26885 | 35194 | 18484 | 46828 | 31527 | 22985 | 43564 | 10345 | 47436 | 32720 | 27466 | 0 | 23619 | 19040 |
| | 19 | 38345 | 38398 | 27183 | 33769 | 15175 | 18148 | 20656 | 29898 | 22556 | 48433 | 16924 | 15479 | 35840 | 15201 | 30374 | 27838 | 28088 | 24270 | 0 | 20596 |
| | 20 | 25135 | 16627 | 19991 | 23138 | 5953.8 | 27930 | 17689 | 22039 | 13408 | 21333 | 10171 | 14950 | 24493 | 17423 | 13085 | 22423 | 26904 | 18854 | 20009 | 0 |

## 2.5. Discussion

It is evident that recently improved technology for automated data collection can provide great advantages for behavioural studies. However, their success is ultimately dependent on their accuracy and repeatability, and an understanding of their limitations. We found marked variability in performance of individual Sirtrack proximity loggers, which are popular devices for collecting data on patterns of social associations. Inherent device variation, if uncorrected, has serious consequences for the interpretation and understanding of social networks built on such automated processes. During field deployment of proximity loggers on dairy cows, there was variation in the reciprocity of contacts recorded within logger dyads, indicating that loggers performed differently in detecting and being detected by others. Importantly, we show that rather than loggers exhibiting a general error, they appear to have individual, intrinsic biases in performance. The logging bias, calculated from the reciprocity values to provide a relative performance measure, ranged from -14.8% to +22.1% across the sample of collars and repeatability tests demonstrated this to be a consistent trait of each device over the study period.

The logging bias (from the field) was correlated with moderate effect sizes to the initiation distances for loggers during the standardised test; which supports that they are working similarly (relative to each other) under both conditions. However it is important to note that the standardised test used in the current study is not directly comparable to the field deployment in that loggers were positioned at a different height, and on a substrate very dissimilar to a cow. Also, results from the field test were in the form of duration however in the standardised test we recorded contact detection distance. Despite these differences we demonstrate that recording the performance of the collars in the standardised test can predict their behaviour when deployed under field conditions. It is important to note that not all of the variation in collar performance can be predicted by the standardised tests; suggesting that other factors associated with the field deployment affected logger performance (see below for a discussion). The comparison, albeit indirect, between the tests is useful in determining the consequence of variation in logger detection distance for the performance of the loggers under field conditions.

Comparison of the predicted logging biases calculated from the analytical model and the logging biases observed in the field data, demonstrate that a significant proportion of the observed bias in the field data is due to the inter-logger variation in contact initiation distance. This is in addition to the potentially varying conditions of deployment such as the size or mass of the animals, the fitting of collars, and their orientation to each other in the field. Quantifying these factors were beyond the scope of the current study, but are likely to provide further variation influencing logger performance and thus influencing the form of the interaction network. The effect of collar orientation has been tested by Prange et al. (2006), who found that detection distance was increased when antennas were directed towards each other. Vertical positioning also had a significant effect; signal detection appeared to be facilitated when loggers were vertically aligned. Whilst we did not explicitly measure such effects in the current study, these would likely have been present in our field data.

These biases in performance generate bias in the structure of interaction networks when the loggers are deployed in the field. The positive correlation (Figure 2.3a-d) between logger performance in the standardised test and the logging bias in the field means that loggers that had the largest contact initiation and termination distances in standardised tests consistently logged other loggers for longer overall during the field deployment.

Many past studies appear to have overlooked the issue of consistent inter-logger variation in performance when analysing data; and have assumed that variation in contact records between individuals wearing loggers is due to biological variation in social behaviour. This may be the case. However, our data suggest that at least some variation is due to logging bias, and that without quantifying and accounting for such bias, there is serious danger of misinterpretation of social data. For example, this technology has been used previously to collect data on contact rates in relation to disease transmission, including the identification of 'high contact' individuals in the population thought to play pivotal roles in the spread of disease (Böhm et al., 2009). However when the variation in logger performance is left unmeasured we cannot be certain that an individual who is assigned high contact status does not hold that status simply because it was fitted with a particularly strong logger. Indeed in the current study, the significant relationship between the weighted in-degree and the logging bias illustrates the potential bias that inter-logger variation in detection sensitivity can exert on the interpretation of social network data.

Unfortunately, accounting for differences in logger performance in systems with large numbers of individuals engaging in complex polyadic interaction networks is not trivial. Setting each logger individually may be expected to offer some control over variation in logger performance, yet in practice this proves to be difficult and time-consuming. In the case of the Sirtrack loggers, although the UHF coefficient range (0-62) can be altered, the scale functions so that the lower half (0-31) alters the signal strength while the upper half (32-62) affects the detection sensitivity, meaning only one of these can be controlled at any one time. This is likely to generate significant challenges when trying to tune individual loggers. Some previous studies have individually set the UHF value of loggers with aim to attain more uniform detection distances across devices (e.g. Creech et al. (2012); Cross et al. (2012); Drewe et al. (2012)). However, the actual effectiveness of this approach is only reported in one of these studies (Drewe et al., 2012); which subsequently did not deem it worthwhile.

We propose two general methods to correct data collected from large numbers of loggers based on an adjustment of the data that has been collected, rather than trying to standardise the performance of individual loggers prior to deployment. Given the many factors that may influence logger performance in the field, this post-hoc computational correction is likely to be more efficient in correcting contact records post-deployment. First, assuming that all possible dyadic interactions occur between loggers during deployment, we show that it is possible to use the variation in logging reciprocity observed in the association matrix to correct for variation in logger performance. By calculating a logging bias for all proximity loggers, we achieved a measure of each logger's relative performance. From this we could adjust the contact duration data by correcting values from each logger in accordance to its performance with a focal logger. We suggest correcting all loggers against their performance with the least recorded logger. This is the most conservative approach (i.e. data are removed rather than added), and when carried out on the data from field deployment, resulted in a marked improvement in dyad reciprocity from 0.76 (Table 2.1) to 0.99 (Table 2.2). However, we believe that this requires that all possible dyadic interactions are observed.

Such complete data may not be available in systems with more sparse interaction networks. In such instances we suggest that one approach is to correct for the variation in collar performance by using standardized measures of logger accuracy.  For example, the row sum of the association duration matrix (Table 2.1) may be used as a simple measure of sociality of an individual. In the matrix produced by the analytical model the row sum is proportional to $r_i^2$. Given that any variation in $r_i^2$ in the analytical model is due to variation in contact initiation distance of loggers, we refer to this as 'predicted sociality'.

Observed sociality from the field deployment can then be compared to the predicted sociality of loggers to provide a measure of sociality that is independent of the logging bias. As shown in Figure 2.5a, field data (observed sociality) suggests that cow 10 is the most social followed by cow 1; with both exceeding the sociality values as predicted based on relative logger performance. Conversely individual 2, for example, is ranked quite highly in the observed sociality; yet this is less than its predicted score meaning that this individual may be less social than what we would expect (while accounting for the bias of its collar). One possible approach to control for the variation in logger performance (predicted sociality) in this instance may be to divide the observed sociality by the predicted sociality. This leads us to the conclusion that cow 18 is actually the most social (see Figure 2.5b). Thus by quantifying the variation in logger performance during standardised tests; it may be possible to correct social variables calculated from the association matrix generated by field data. This requires that loggers be individually measured prior to deployment in a standardised manner. In the example above, the $r^2$ value used in the analytical model is derived from the standardised tests. Whilst this value can explain a moderate amount of the variation in logger performance in the field, many other factors may have affected logger performance under field conditions, as discussed above. We suspect that it would be possible to significantly improve the predictive power of the $r^2$, if these measures were taken during deployment of the collars on study animals. In the system studied here, for example, it may have been possible to do this by directing cows through a walkway with base stations positioned at set distances. The distance at which the base stations detected the loggers on the study animals, could then be recorded to provide a $r^2$ value under field conditions.

It is important to acknowledge that although we have accounted for the logging bias in our measure of observed sociality, there may still be ‘noise’ in our data. Another example of discrepancy in the data is observed by ‘broken’ contacts. When loggers are within detection range for a set period of time, contact will often be recorded as a series of shorter interactions for one or both loggers (rather than one continuous record). Some previous studies have combined broken contacts in such instances to improve reciprocity of contact frequency and duration (e.g. Goodman (2007); Drewe et al. (2012)). This method was not used in the current study as it does not account for the logging bias of loggers. Using this method, if logger *i* recorded logger *j* for 10 minutes, and *j* recorded *i* intermittently within that 10 minutes (but with total duration therefore <10 minutes), logger *j*'s contacts could be combined to also result in a full 10 minute record. However, this would likely result in inconsistencies when dealing with logger dyads of varying performance. For example, combining contacts between two 'strong' loggers or two 'weak' loggers would improve the reciprocity of contact frequency and duration within these pairs. However, though both pairs might have been together (within the desired distance range) for 10 minutes, this may only be clear on the strong logger pair. Both weak loggers' records could have been made reciprocal due to the contact combining process, but this may still have resulted in a contact of less than 10 minutes duration. We therefore suggest that in addition to considering combining contacts as described above it is essential to consider how variation in logger performance may affect the reciprocity of interactions and to correct for this variation.

When there is stable variation in the performance of contact loggers it may be possible to undertake a longitudinal analysis of egocentric social networks. With an egocentric network approach, the network is built around a focal individual (see Croft et al. (2008)) and comparisons are made *within* individuals during analysis which would control for variation in logging performance among individuals. This could be used, for example, to investigate how changes in an individual's patterning of social interactions can predict changes in health or welfare. Egocentric network methods are prominent in the social sciences (Marin & Wellman, 2011), however, they have received little application in the context of animal social networks (but see Croft et al. (2011)). It appears that this approach will be valuable for studying association data from spatial proximity loggers in future studies.

### 2.5.1 Conclusions

The automated logging of animal social interactions and the subsequent construction and analysis of social networks based on this logged data is likely to be susceptible to noise and bias caused by technological inconsistencies. This means that the potential benefits afforded by remote data collection are negated by doubts over the reliability of the data. Previous attempts to account for this error have based their efforts on the reciprocity of logger contact durations considered at the population level. This is misleading because although dyad reciprocity may be reasonably high overall, it does not represent how variance in reciprocity is distributed among loggers. When reciprocity is measured for individual loggers it may become apparent that discrepancies are caused by a few strong or weak devices in particular, rather than a degree of general noise in the data produced by all loggers. When reciprocity is not considered at the level of the dyad, there is risk of interpreting anomalies caused by variation in logger performance as significant behavioural differences. Therefore it is imperative for researchers to consider, and if necessary correct for, logging biases when working with this technology in order that it may be used to its full potential.

This first experimental chapter investigated the technology used to collect the social association data underpinning this thesis. The advantages of using automated data collection methods are easily recognisable; however this research has highlighted a potential pitfall that must be avoided when working with technology. By carrying out this research we gained a better understanding of the data and developed methods to evade the problem of sampling bias, using these in the following chapters. The following chapter quantifies the social network structure of cows on a commercial farm, taking an important first step in investigating the social components of welfare and productivity.

# Chapter III

## The social network structure of a dynamic group of dairy cows: from individual to group level patterns.

## 3.1 Abstract

Social relationships have been shown to significantly impact individual and group success in wild animal populations, but are largely ignored in farm animal management. There are substantial gaps in our knowledge of how farm animals respond to their social environment, which varies greatly between farms but is commonly unstable due to regrouping. Fundamental to addressing these gaps is an understanding of the social network structure resulting from the patterning of relationships between individuals in a group. Here, we investigated the social structure of a group of 110 lactating dairy cows during four one-month periods. Spatial proximity loggers collected data on associations between cows, allowing us to construct social networks. First we demonstrate that proximity loggers can be used to measure relationships between cows; proximity data was significantly positively correlated to affiliative interactions but had no relationship with agonistic interactions. We measured group-level patterns by testing for community structure, centralisation and repeatability of network structure over time. We explored individual-level patterns by measuring social differentiation (heterogeneity of social associations) and assortment of cows in the network by lactation number, breed, gregariousness and milk production. There was no evidence that cows were subdivided into social communities; individuals belonged to a single cluster and networks showed significant centralisation. Repeatability of the social network was low, which may have consequences for animal welfare. Individuals formed differentiated social relationships and there was evidence of positive assortment by traits; cows associated more with conspecifics of similar lactation number in all study periods. There was also positive assortment by breed, gregariousness and milk production in some study periods. There is growing interest in the farming industry in the impact of social factors on production and welfare; this study takes an important step towards understanding social dynamics.

## 3.2 Introduction

Sociality is believed to have evolved as a strategy to cope with ecological challenges (Wilson, 1975) and affords individuals the many benefits of group living (Pulliam & Caraco, 1984; West-Eberhard, 1979). Growing research documents the importance of social relationships for health and fitness in wild animal populations (see Brent et al. (2014) for a summary) and this has significant welfare implications for captive populations. The social environment has been identified as a key factor determining health and welfare of farm animals (Keeling & Gonyou, 2001), with social factors acting as a prominent trigger of the stress response in farm animals (e.g. de Groot, Ruis, Scholten, Koolhaas, and Boersma (2001); Riedstra and Groothuis (2002); Ringgenberg, Bergeron, Meunier-Salaün, and Devillers (2012)). The ways in which effective management of social groups could positively impact animal welfare should be explored (Rault, 2012). Social support is a term that broadly refers to the benefits provided by social companions that improve an individual's ability to cope with challenges (Rault, 2012). Such benefits include improved: cardiovascular health (Boissy & Le Neindre, 1997; Ruis et al., 2001; Takeda et al., 2003), immune function (Gust et al., 1994), learning (Boissy & Le Neindre, 1990), and recovery from stressful experiences (Kikusui, Winslow, & Mori, 2006; Ruis et al., 1999). Social support can be gained from the mere presence of another conspecific, although in some cases certain individuals can be more effective in providing support, for example familiar (rather than novel) conspecifics (e.g. Takeda et al. (2003)), mothers or adult 'pair-bond' partners (Hennessy, Kaiser, & Sachser, 2009). Farm animal species are typically gregarious (Estevez et al., 2007) and individuals seek social contact upon exposure to stressors (Ishiwata, Kilgour, Uetake, Eguchi, & Tanaka, 2007; Rault, 2012). This natural tendency could be drawn upon by increasing the ability of individuals to provide each other with social support in order to enhance farm animal welfare.

Individuals often prefer to associate more with conspecifics that are familiar, enabling the use of information from past experience to improve group activities (e.g. foraging and anti-predator responses) and reduce conflict via formation of dominance hierarchies (Krause & Ruxton, 2002). This social familiarity is frequently manifested as preferential social bonds with particular conspecifics, referred to as ‘friendships’ in humans (see Brent et al. (2014) for a comprehensive summary of animal social bonds across taxa). Research by Silk and colleagues (Silk, Altmann, & Alberts, 2006; Silk et al., 2009; Silk et al., 2010) has demonstrated that long-lasting bonds with particular conspecifics can increase individual fitness in baboon society, and studies of other species have shown that more gregarious individuals have greater reproductive success (e.g. rhesus macaques (Brent et al., 2013), horses (Cameron et al., 2009), mice (Weidt, Hofmann, & König, 2008).

Subsequently, social relationships within a group are frequently heterogeneous and influence overall group organisation. In some instances social patterns at the individual level can lead to distinctive structural patterns at the group level. ‘Communities’ are a group level structure commonly observed in animal social networks (Krause et al., 2007; Lusseau & Newman, 2004) and consist of subgroups of individuals that are more associated to each other than they are to the rest of the group (Croft et al., 2008). Community structure can reflect class assortment (Porter, Onnela, & Mucha, 2009), the type of mating system (Wolf, Tautz, & Trillmich, 2007) or space use (du Toit, Ruckstuhl, & Neuhaus, 2005; Wolf, Mawdsley, Trillmich, & James, 2007) and is noteworthy for its influence on information flow and disease transmission. For example disease will often affect individuals within the community from which it originated, more quickly than it would individuals from a neighbouring community (Krause et al., 2007). Measuring substructure is therefore important for understanding disease dynamics, and identifying the characteristics of individuals that link communities could be vital for disease management (Lusseau & Newman, 2004). Furthermore, substructure in networks influences the impact of perturbation events (individuals entering or leaving a group) on social structure, and can determine a population's cohesiveness and robustness to fragmentation (Tina Wey, Blumstein, Shen, & Jordán, 2008). The Group cohesiveness of a group can also be reflected by network centralisation: the extent to which individuals are structured about a central node (Makagon, McCowan, & Mench, 2012). The degree of network centralisation represents the level of influence that the central individual has on leadership, decision making, information and disease flow (Sueur, Deneubourg, & Petit, 2012).

In the UK dairy industry there is considerable diversity in the way animals are grouped and managed; group sizes and stocking density vary greatly across farms, and regrouping cows during lactation (based on yield or parity etc.) is common practice. Numerous studies have demonstrated the negative welfare and productivity consequences of regrouping, including reductions in milk yield, feed intake, rumination and lying times, and increased aggression between cows (Hasegawa, Nishiwaki, Sugawara, & Ito, 1997; Hultgren & Svensson, 2009; Raussi et al., 2005; von Keyserlingk, Olenick, & Weary, 2008). Agonistic interactions such as threat gestures, chasing and head butting, often result in displacements from resources, but can escalate to prolonged (and more injurious) fights. The latter are less frequent in stable social groups (Reinhardt & Reinhardt, 1981) as a well-established dominance hierarchy shortens agonistic events or prevents them through active avoidance, profiting both dominant and subordinate animals (Gurney & Nisbet, 1979).

Within a stable social group many cows form preferential social bonds, which may differ between activities such as feeding or social grooming (Gygax, Neisen, & Wechsler, 2010; Reinhardt & Reinhardt, 1981). Preferred social partners can influence status in the social hierarchy (Reinhardt & Reinhardt, 1981) and their presence or absence can affect stress responses (McLennan, 2012). Social grooming can be used as an indicator of affiliative relationships among social animals (Boissy et al., 2007; Wasilewski, 2003), with the strength of social bonds often reflected by the degree of grooming between individuals. Social grooming is believed to have a calming effect on cows (S. Sato, Sako, & Maeda, 1991; S. Sato & Tarumizu, 1993), and plays a role in reducing social tension and maintaining social stability (Benham, 1984; Boissy et al., 2007; Shusuke Sato, Tarumizu, & Hatae, 1993). Interestingly, social grooming has been linked to production; it has been positively correlated with both milk yield and weight gain in past studies (Arave & Albright, 1981; S. Sato et al., 1991). The social preferences of cattle are also reflected in their spatial proximity to others in the group (Bouissou, Boissy, Le Neindre, & Veissier, 2001), thus the ability to maintain suitable inter-individual space is important to cows (Bøe & Færevik, 2003). In fact, Miller and Wood-Gush (1991) suggest the lower levels of agonistic behaviour exhibited by cows at pasture (compared to indoor-housed cows) is due to a greater opportunity to avoid others.

As the dairy industry becomes more aware of the impact the social environment can have on welfare and production, there is growing demand for information on optimal size, stocking density and composition of dairy cow management groups. In order to begin answering questions on the most effective social conditions for cattle, we first need to accurately measure and understand their social dynamics and group structure. Social network analysis (SNA) has been developed to quantitatively measure and analyse the structure of groups and patterns caused by dyadic social interactions (Croft, James & Krause, 2008). A network is made up of nodes (individuals; cows in this case) and edges (interactions; association time in this case). We can calculate statistics for individuals in the network such as ‘degree’ (number of edges for a given node) and ‘betweenness centrality’ (number of shortest paths between pairs of individuals that pass through a particular individual) (Krause, Lusseau, & James, 2009). These methods allow us to study non-random patterns of association, and detect differences in group structure that may be linked to individual attributes (Croft et al., 2008). SNA is becoming more popular in the field of animal behaviour, however its potential for improving animal welfare in captive populations is currently underappreciated, with only a handful of empirical studies to date (e.g. rhesus macaques; McCowan, Anderson, Heagarty, and Cameron (2008), Atlantic salmon; Cañon Jones et al. (2010), pigtailed macaques; Flack, Girvan, De Waal, and Krakauer (2006), domestic chickens (Abeyesinghe, Drewe, Asher, Wathes, & Collins, 2013)). Though few, these examples establish very promising applications of SNA in animal management and have been centred on reducing aggression and improving social cohesion. They suggest an important future role for SNA in animal welfare science (Koene & Ipema, 2014).

In this study, we quantified the social network structure of a group of lactating dairy cows, collecting association data using spatial proximity loggers. We corroborated this method by determining how well associations measured by the proximity loggers matched agonistic and affiliative interactions recorded during behavioural observations. We predicted that data collected by the proximity loggers would closely resemble affiliative interactions, but would not resemble agonistic interactions. Group-level structure was measured by testing for communities, betweenness centralisation, and assessing network stability over time. We investigated individual-level structure by determining whether individuals formed socially differentiated relationships, and by assessing the extent to which cows were assorted by attributes (lactation number, breed, gregariousness and milk production).

## 3.3 Methods

### 3.3.1 Animals and housing

The study was carried out on a commercial dairy farm in Devon, UK from November 2012 to June 2013, in the form of 4 one-month data collection periods (see Table 3.1). The farm comprises a 1045m$^2$ (approx.) barn with straw yard housing and a voluntary milking system operating two Delaval robotic milking units. A total mixed ration was fed twice daily (approx. 9am and 5pm) at a feed barrier and additional concentrate feed was provided during milking and at an out-of-parlour feeder. At any given time the milking group contained between 106 and 113 lactating cows. Due to year-round calving, group structure was dynamic with cows entering and leaving depending on calving and drying off dates, in addition to sale or culling. The total number of unique cows present throughout the study was 134. The group was of mixed breed though the majority were Holstein–Friesian (see Table 3.1 for more details on cows included in the study). A Charolais bull was added to the milking group on 07-05-13, and was therefore present within the fourth period of data collection only.

Although managed and housed as a single milking group, pasture access was regulated (via electronic collars) based on each cow's stage of lactation. Cows were restricted to the barn in the early part of their lactation, however after both testing positive for pregnancy and when milk yield dropped below a threshold of approximately 26 litres, they were also given free access to pasture. All cows were thus able to mix when inside the barn, but there were physical constraints to group synchrony when any cows with access chose to enter the pasture. As this affected some cows' ability to associate, we incorporated this management factor into all null models used in our analyses.

Individual attribute data (lactation number, breed, last calving date and milk yield) were downloaded from the on-farm computer system (Delpro). The number of days in milk (DIM) for each cow was determined as the number of days from the last calving date  to the date of the first day of each data collection period. We summed the daily milk yield over each data collection period for each individual.

Table 3.1 Descriptive statistics of cows included in analyses and others in the milking group during each deployment

| **Deployment** | | **1** | **2** | **3** | **4** |
|---|---|---|---|---|---|
| Data period | | 08/11/12 to 06/12/12 | 22/12/12 to 18/01/13 | 14/03/13 to 09/04/13 | 13/05/13 to 09/06/13 |
| **Cows included in analyses** | N | 94 | 73 | 59 | 64 |
| | *Breed:* | | | | |
| | Ayrshire | 20 | 11 | 7 | 8 |
| | British Friesian | 3 | 3 | 3 | 3 |
| | Brown Swiss Cross | 2 | 4 | 3 | 3 |
| | Holstein Friesian | 44 | 37 | 34 | 37 |
| | Holstein Friesian Cross | 6 | 6 | 2 | 4 |
| | Holstein | 16 | 10 | 9 | 6 |
| | Holstein Cross | 1 | 1 | 1 | 1 |
| | British Shorthorn | 0 | 1 | 1 | 1 |
| | Pasture access - Y | 59 | 69 | 45 | 48 |
| | Pasture access - N | 35 | 4 | 28 | 16 |
| **All cows in milking group** | Total N | 125 | 114 | 114 | 117 |
| | N calved | 9 | 6 | 8 | 4 |
| | N dried off | 9 | 5 | 3 | 6 |
| | N given pasture access within deployment | 2 | 1 | 6 | 6 |

### 3.3.2 Spatial proximity loggers

The proximity loggers used in this study were manufactured by Sirtrack Ltd (New Zealand), and are supplied as ready-made collars to attach around cows' necks (model E2C181C). These devices broadcast unique identification codes over an ultra-high frequency (UHF) channel while simultaneously searching for the ID codes of others within a pre-set distance range. Each logger is able to detect up to eight others simultaneously; recording its ID, the date, start and end time of the contact and its duration. The detection distance may be altered by users, by adjusting the power setting of a UHF coefficient range (0–62). The duration that any two loggers need be separated for an encounter to terminate ("separation time") can also be adjusted prior to deployment. Here, proximity loggers were set to a UHF value of 47 (which logged contacts at 1.5–2m in pilot tests using collared horses) with a separation time of 120s. Due to memory fill rate we deployed and removed loggers on four occasions so that data could be downloaded, hence we divided our analyses into four data collection periods (hereafter referred to as deployments 1-4).

#### *3.3.2.1 Proximity logger data handling*

Data collected by proximity loggers consisted of dyadic associations over time. We summed the duration of all associations between dyads within each deployment period and these values were used to construct social networks. As advised in previous studies (Drewe et al., 2012; Prange et al., 2006) we removed all 1-second contact records from the database prior to analysis, as these are considered unreliable, occurring sporadically when individuals are at the edge of the detection range (Drewe et al., 2012; Prange et al., 2006). Only loggers that functioned fully (both sending and receiving signals) for the whole deployment period were included in analysis. We therefore omitted data from broken loggers, and from cows that entered or left the milking group (or whose loggers fell off) mid-way through a deployment (see Table 3.1 for the number of individuals included in analyses for each deployment). As a result of this, and the turnover of cows throughout the study period, group membership differed across the deployments. It is important to note that as battery power decreases over time, which is expected to affect logger function (see Drewe et al. (2012)), we analysed each deployment separately and did not make any quantitative comparisons between the deployments.

### *3.3.2.2 Logging bias correction*

Previous work has shown that spatial proximity loggers can exhibit a sampling bias due to inter-logger variation in performance (Boyland, James, Mlynski, Madden, & Croft, 2013). This is made evident by association matrices with highly variable dyadic reciprocity; contact durations between dyads should be mirrored if loggers are functioning uniformly. We therefore adjusted data using correction methods from chapter II (Boyland et al., 2013). This involved scaling all contact durations in an association matrix relative to the performance of each given logger when compared with the most under-recorded logger. This was achieved by calculating the percentage difference in contact durations (e.g. the percentage difference between the total time logger A recorded contact with logger B, and the total time logger B recorded logger A) between all dyads, then identifying the logger that was most under-recorded, overall. The total contact duration (all contacts summed over the deployment period) for each dyad was then reduced according to their logging bias with the most under-recorded logger. For example, if logger A had a logging bias of 10% when compared to the most under-recorded logger, the duration that logger A recorded contact with all other loggers would be reduced by 10%. We thus standardised associations between loggers relative to each other. We used Spearman’s correlations to calculate the reciprocity between each side of the matrix (about the diagonal) both before and after application of this correction to assess its efficacy. This resulted in Spearman's r increasing from 0.72 to 0.93, 0.59 to 0.91, 0.56 to 0.72, and 0.67 to 0.92 ($p < 2.2e-16$ in all cases) for deployments 1-4 respectively. We symmetrised the corrected matrix by averaging values within each dyad (as proximity cannot be directed), before creating social networks.

### 3.3.3 Measuring the relationship between proximity data and social relationships

In order to quantify how proximity logger data relates to social relationships, we compared the association strengths measured by the proximity loggers with measures of observed social interactions between cows. We undertook 160 hours of behavioural observations in which 10 focal individuals (chosen at random) wearing proximity loggers were observed for 4 hours/day on 4 days (therefore a total observation duration of 16 hours for each cow), during deployment 4. Focal cows varied in age (2-10 years old), lactation number (1-7), breed and number of days in milk (30-112). During the behavioural observations, each cow was followed for a total of 4 hours in a day, usually separated by periods of lying (during which observations were paused). We recorded all agonistic and affiliative interactions (continuous sampling), including the identity of cows interacting with the focal individual. Chasing, head butting, headshaking and threat gestures were considered 'agonistic interactions and social grooming was considered an 'affiliative' interaction. When multiple interactions occurred between the same individuals consecutively (e.g. a cow head butts the focal cow three times), interactions were recorded as one event provided the time between each interaction was <10 seconds. Additionally, we recorded the identity of the focal cow's 'nearest neighbour' (or multiple neighbours when there were two or more cows equidistant to the focal) at 2 minute intervals. The nearest neighbour was identified as the cow (any part of body) that was closest to the head of the focal cow; if the closest cow was over 5 cow body lengths away from the focal it was not recorded and the focal cow was considered to have no neighbours. We only included dyads in our analyses that had been recorded as nearest neighbours >10 times, indicating a level of opportunity to interact during the behavioural observations. We calculated the correlation coefficient between the association strength measured by the loggers, and the number of aggressive and affiliative events between dyads. To calculate statistical significance we permuted (10,000 imputations) association strengths among dyads, while constraining the identity of the focal individual.

### 3.3.4 Statistical Analysis

We used R statistical software version 3.1.0 (R Core Team, 2013) to prepare and analyse the proximity logger data. Specifically, we used the packages ‘Matrix’ (Bates & Maechler, 2014), ‘sna’ (Butts, 2014), ‘igraph’ (Csardi & Nepusz, 2006), ‘MCMCglmm’ (Hadfield, 2010) and ‘vegan’ (Oksanen et al., 2013). Principal Components Analysis (PCA) was completed in SPSS v.19, and weighted degree was calculated using UCINET v.6 (Borgatti, Everett, & Freeman, 1999).

Our observed networks were completely saturated (meaning that all possible dyadic interactions occurred in the data). In a binary sense our network data thus has no structural topology, as every cow encountered every other. Because of this we focus much of our analysis of network structure on the edge weights. To reveal social structure at differing edge weights, we use increasing contact thresholds as an alternative to performing a single test on a saturated weighted network. We treat our data as dyadic and use a multilevel mixed-effects model to examine patterns of social assortment.

### 3.3.5 Generating expected duration matrices

To control for the effect of farm management practices on associations, observed contact durations between dyads were compared to 'expected' durations based on whether or not each cow had access to pasture. Expected values were calculated by separately summing the total duration that each cow was in contact with all others *with* and *without* pasture access, then assigning the mean value to each dyad (corresponding to pasture access). This was done for each cow individually to account for the individual differences in total contact time. Therefore each expected matrix estimates the associations between each dyad if cows showed no social preference.

### 3.3.6 Group-level patterns

#### *3.3.6.1 Community structure*

We tested for evidence of community structure, i.e. subsets of individuals that are more closely connected to each other than to the rest of the network, using Newman's modularity clustering algorithm (M. E. J. Newman, 2006a, 2006b). This method finds the most parsimonious partitioning of a network, in which the number and weights of edges are maximised within communities, and minimised between communities. The "best" partitioning of a network is the one that maximises the modularity coefficient, Q, resulting in individuals belonging to one or more clusters (Lusseau, Whitehead, & Gero, 2009). We tested for community structure at increasing contact thresholds as an alternative to performing a single test on a saturated weighted network. We filtered networks to contain only associations that were 0-3.25 (in intervals of .25) times the expected value for each dyad, and then binarised the connections that remained. We compared the maximum modularity value for each of our filtered observed networks with a suite of values generated by 4999 null networks; each null network was made by randomising (within individuals) the filtered and binarised networks. We included the observed maximum Q in the distribution of null networks as it could have arisen by chance, thus n=5000. We used Equation 1 to calculate a p-value (one-tailed).

Equation 1: $$p = \frac{number\ of\ \ Q(null)\ values \geq S(obs)}{n}$$

*3.3.6.2 Centralisation*

We tested for significant centralisation in the networks, using betweenness centralisation as a test statistic (Freeman, 1979), and performed this on the observed and 4999 null networks with isolates removed. Betweenness centralisation is a measure of the individual variation in betweenness centrality within the network; a star network would be an example of perfect centralisation (c=1). We compared the observed betweenness centralisation of our observed networks with betweenness centralisation of null networks (as described above for community structure). Again, networks were tested at increasing filter thresholds (0-3.25 x expected, at .25 intervals).

*3.3.6.3 Network stability*

We examined the stability of associations through time at the group level. Each one-month association matrix was divided into 4 week–long periods, which were compared with each other. To determine the correlation between two given matrices (with the same actors) we calculated a Spearman’s rank correlation coefficient. We generated a *p*-value by comparing the observed coefficient to a distribution of coefficients produced by a null model. Edge-level permutations in the null matrices were stratified according to cows’ pasture access; values were permuted between those dyads that had pasture access, dyads that did not have pasture access, and dyads in which one cow had pasture access and the other did not.

### 3.3.7 Individual-level patterns

#### *3.3.7.1 Social differentiation*

To assess whether associations between cows were more heterogeneous than we would expect given a null hypothesis that all cows associate uniformly (while accounting for pasture access), we calculated the following statistic for social differentiation using Equation 2 (based on that from Whitehead (2008) appendix 9.4]).

Equation 2: $$S = \frac{\sum_i^N \sum_j^N (O_{ij} - E_{ij})^2}{N(N-1)}$$

In this equation the difference between the observed value and the expected value is summed for each dyad, and then divided by the total number of dyads.

#### *3.3.7.2 Assortment*

In order to test for assortment of individuals based on known attributes, we fit mixed-effect models using a Markov Chain Monte Carlo (MCMC) framework. We tested for significant relationships between the dependent variable, association strength, and the following fixed factors: gregariousness, lactation number, pasture access, breed and milk production. To measure milk production, we quantified DIM and milk yield. Because these variables were highly correlated, we used the principal component between the two as a variable. This component accounted for a considerable proportion of the total variance: 82.4%, 80.4%, 78.2%, and 68.1% for deployments 1-4 respectively. We used the weighted degree of each node in a network, which is the sum of the strength of edges connected to each node (Croft et al., 2008) (in this case, the total duration of time each cow spent in proximity to other cows), as a basic measure of individual gregariousness. We calculated the absolute difference in value between all dyads for each explanatory variable. For example, if cow A was in her 2nd lactation and cow B was in her 5th lactation, the value awarded to that dyad for 'lactation number' was 3. Because breed is a categorical variable, we award dyads a '0' if they were of the same breed and a '1' if they were of different breed.  Similarly, pasture access was coded as '0' if dyads had the same access and

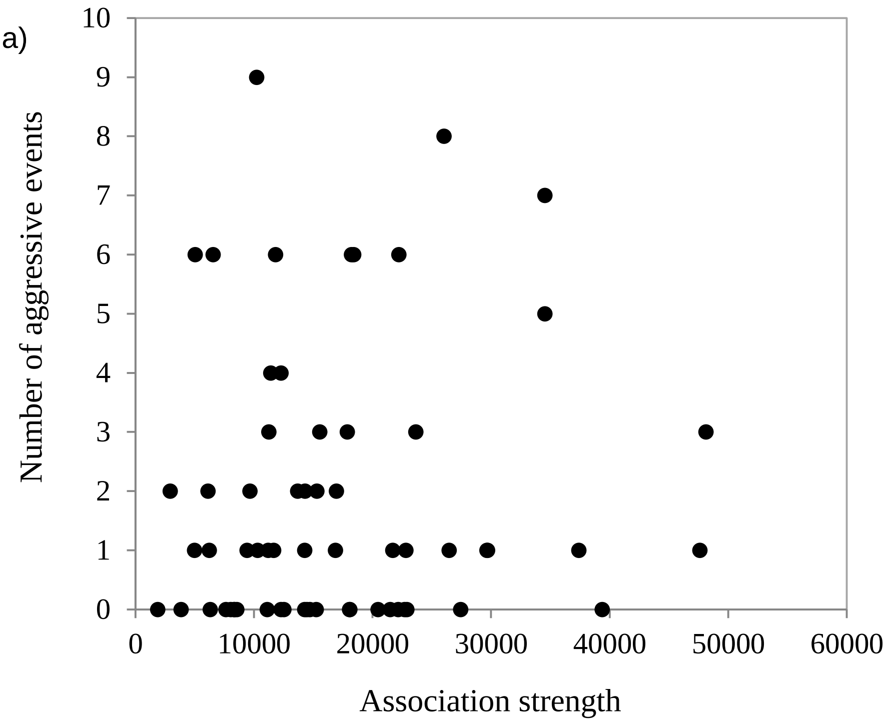
‘1’ if they did not. We included cow ID as a random effect in all models. The multi-membership modelling capacity of the MCMCglmm package (Hadfield, 2010) accounts for the undirected nature of association measures that result in each cow ID appearing as both individual A and individual B in a dyad. To satisfy assumptions of normality, we log-transformed the dependent variable. As our network is completely saturated, we have made the assumption that transitivity (if *A* and *B* are connected and *B* and *C* are connected, then there is a greater chance of *A* and *C* being connected) in our network is negligible (see Snijders (2011)). Using a Bayesian approach, we ran MCMCglmm models with all possible combinations of fixed factors (gregariousness, lactation number, breed, and pasture access), then identified the best fitting model as the one with the lowest deviance information criterion (DIC) (Spiegelhalter, Best, Carlin, & Van Der Linde, 2002). As milk production determines pasture access, fixed factors could not be included together in the models. We therefore ran additional models to test for assortment by milk production, using a subset of cows that did not have pasture access (as a greater proportion of cows did not have pasture access).

## 3.4 Results

### 3.4.1 Measuring the relationship between proximity data and social relationships

As two of the focal cows’ loggers malfunctioned during deployment 4, we were only able to include data from eight of the focal cows in this analysis. There was no relationship between the association strength recorded by the proximity loggers and the number of aggressive events between individuals (r= 0.07, n=63, p=0.51, Figure 3.1a). In contrast, we found a significant positive relationship between the association strength recorded by loggers and the number of affiliative events between individuals (r=0.51, n=63, p<0.0001, Figure 3.1b).

a)



b)

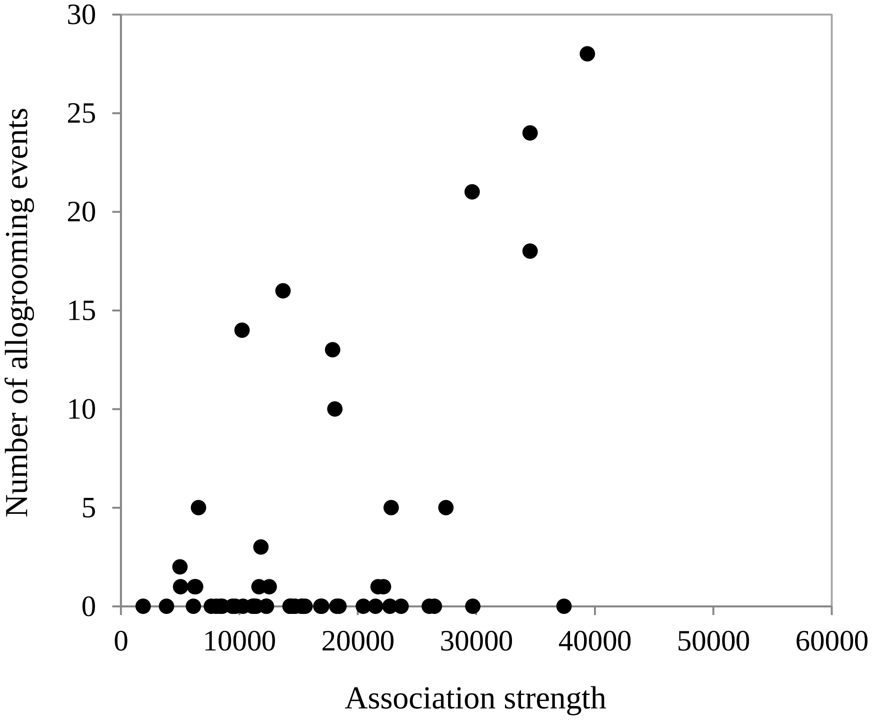


Figure 3.1 Correlation between the association strength recorded by the proximity loggers and the number of (a) aggressive (r= 0.07, n=63, p=0.51) and (b) affiliative (r=0.51, n=63, p<0.0001) events observed between cows during behavioural observations (p-values are based on permutation tests)

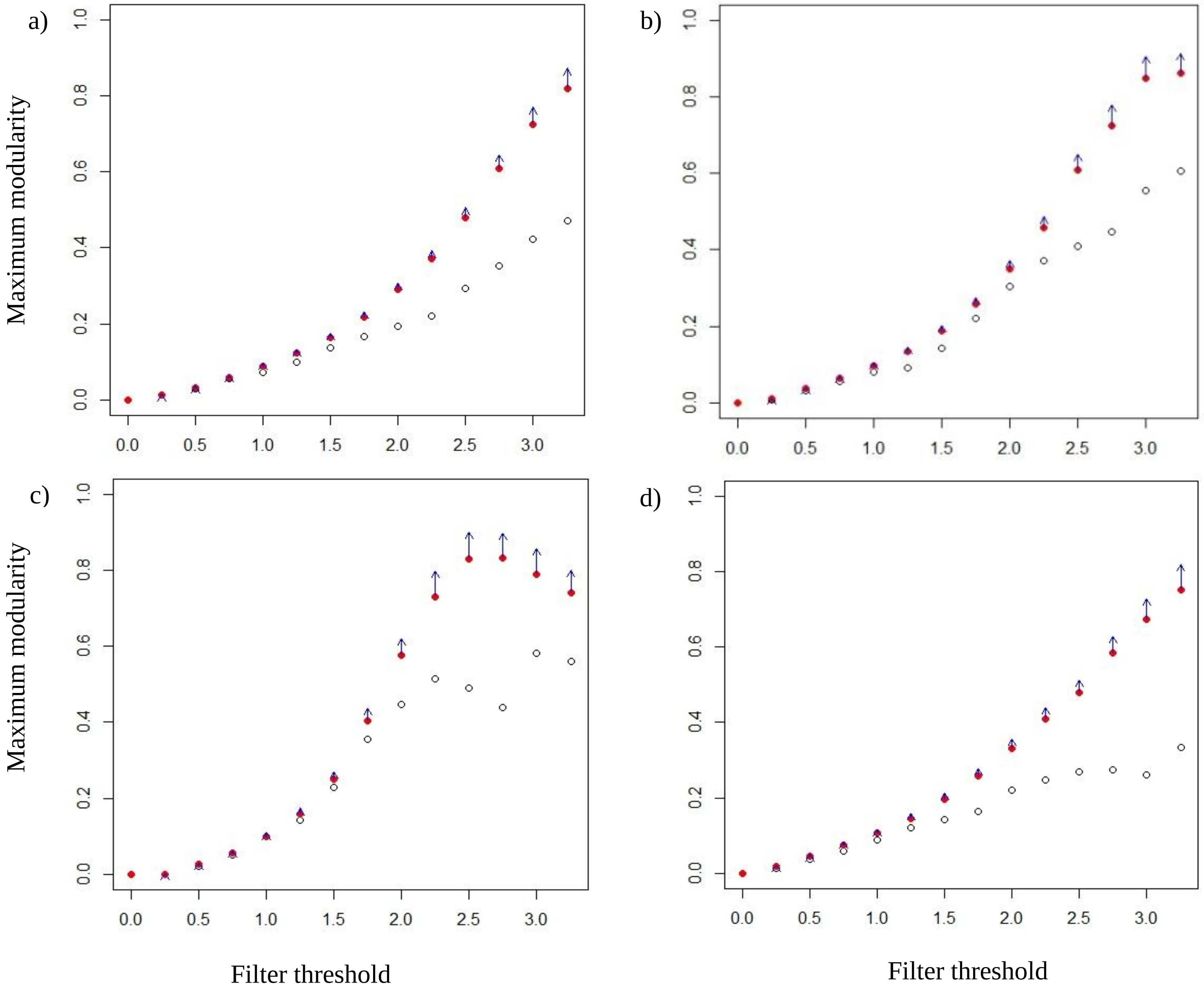


Figure 3.2 Patterns of community structure during the four logger deployments. There was no significant community structure found at any filter threshold for deployments 1-4 (a-d). Empty circles indicate the observed maximum modularity for each network. Solid circles indicate the maximum modularity generated by the null model, with arrows specifying 95% confidence intervals

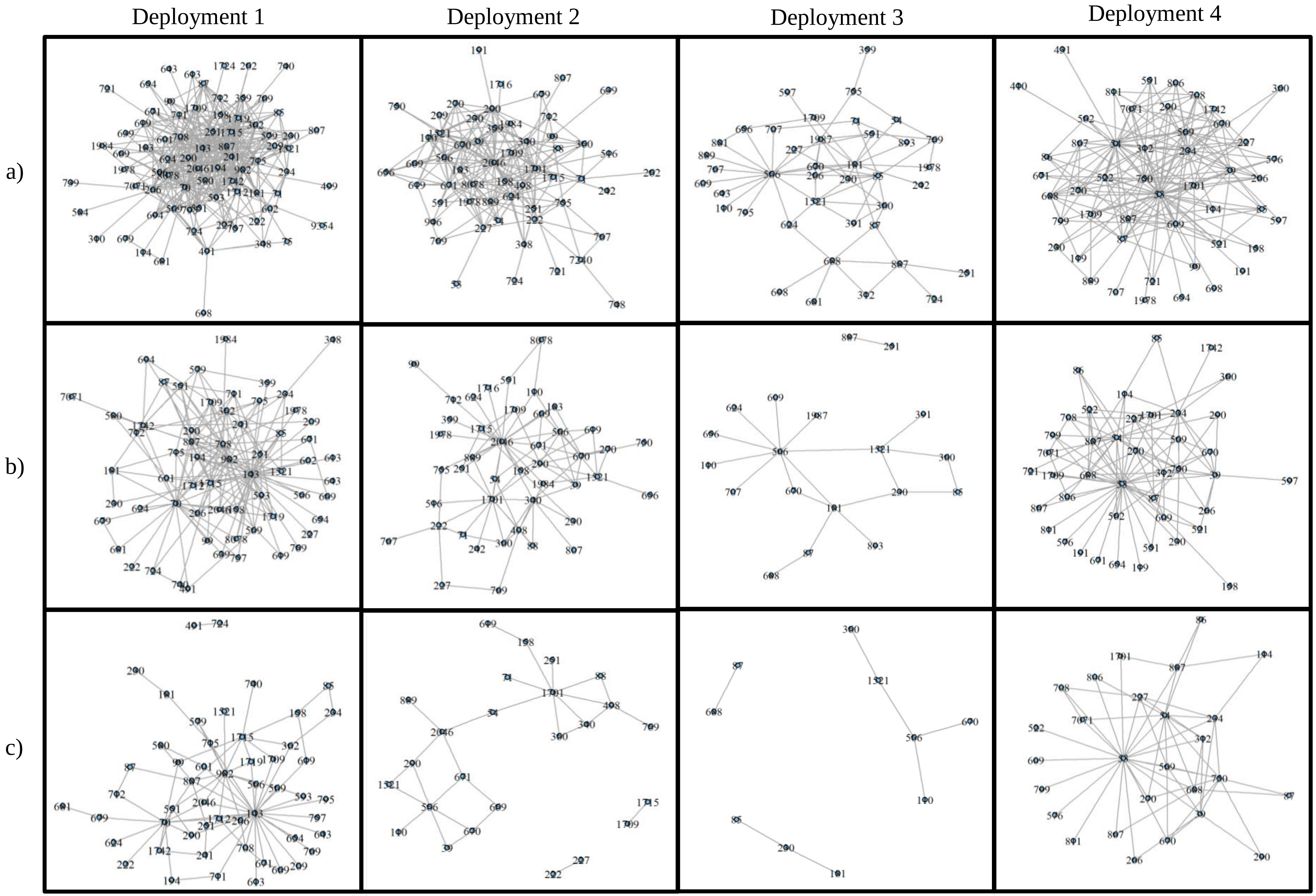


Figure 3.3 Visualisation of cow social networks in deployments 1-4, that have been filtered to only include total associations that were 2 (a), 2.5 (b) or 3 (c) times longer than expected based on networks generated by a null model (controlling for pasture access)

### 3.4.2 Group-level patterns

#### *3.4.2.1 Community structure*

There was no evidence of community structure at any level of association filter (Figure 3.2) in the four deployment networks (Figure. 3.3).

#### *3.4.2.2 Centralization*

In all four deployments, all networks filtered above and including 0.25 times the expected association showed significant centralization (Figure 3.4), p=0.0002 in all cases (excluding deployment 2 at a threshold of 2.75 times the expected association).

#### *3.4.2.3 Network stability*

All week long association matrices (within a given deployment) were significantly (positively) correlated (Table 3.2). Effect size of correlations between consecutive matrices ranged from $R^2$= 0.176 to $R^2$= 0.576.

Table 3.2 Spearman's rank correlations between each week-long matrix, measuring network stability for deployments 1-4. Significance was calculated using a null model with edge-level permutations, stratified according to cows' pasture access

| **Week-long matrices** | **Deployment** | | | |
|---|---|---|---|---|
| | **1** | **2** | **3** | **4** |
| 1 and 2 | $R^2$=.421* | $R^2$=.415* | $R^2$=.26* | $R^2$=.501* |
| 2 and 3 | R2$^2$=.424* | $R^2$=.368* | $R^2$=.198* | $R^2$=.524* |
| 3 and 4 | $R^2$=.462* | $R^2$=.327* | $R^2$=.176* | $R^2$=.576* |
| 1 and 3 | $R^2$=.378* | $R^2$=.332* | $R^2$=.173* | $R^2$=.433* |
| 2 and 4 | $R^2$=.378* | $R^2$=.401* | $R^2$=.112* | $R^2$=.482* |
| 1 and 4 | $R^2$=.377* | $R^2$=.371* | $R^2$=.034** | $R^2$=.416* |

*p=.0002, **p=.031

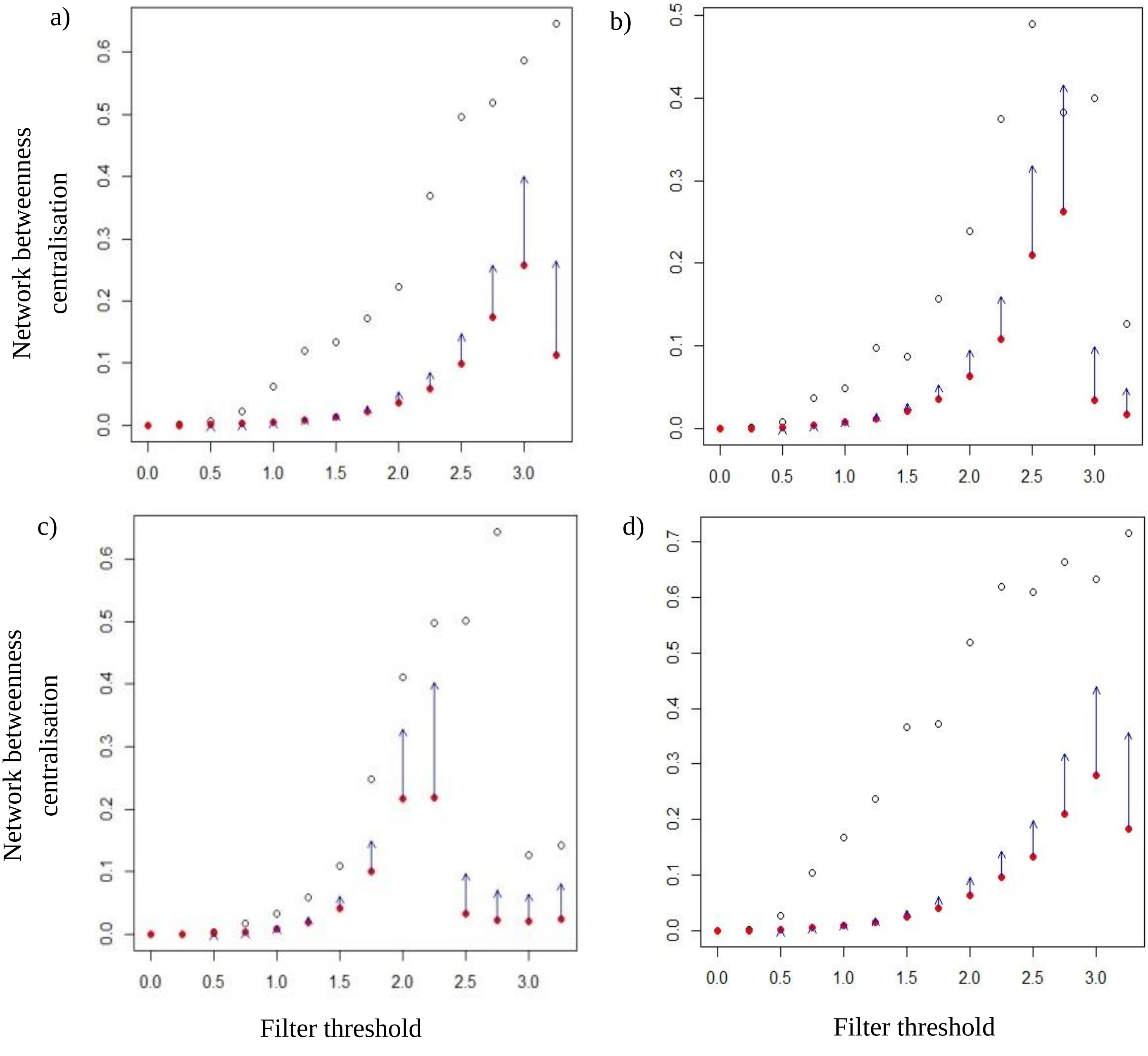


Figure 3.4 Network betweenness centralisation at increasing filter thresholds for deployments 1-4 (a-d). Empty circles indicate the observed mean betweenness centralisation in each network. Solid circles indicate the mean betweenness centralisation generated by the null model, with arrows specifying 95% confidence intervals. Filtered networks showed significant betweenness centralisation, except for deployment 2 at a threshold of 2.75 (p=0.1)

### 3.4.3 Individual-level patterns

#### *3.4.3.1 Social differentiation*

There was significant social differentiation in all four deployment networks (Table 3.3); cows associated with some individuals more and other individuals less, than would be expected by chance (p < 0.001 for all 4 deployments).

Table 3.3 The social differentiation measured in deployments 1-4, indicates that cows were significantly more heterogeneous than we would expect given a null hypothesis that all cows associate uniformly (while accounting for pasture access)

| **Deployment** | **Social differentiation** | | **95% quantile of null distribution** | **p value** |
|---|---|---|---|---|
| | **Observed** | **Median of Nulls** | | |
| 1 | 30274488 | 998195.5 | 1027177 | 0.0002 |
| 2 | 29276011 | 965649.8 | 999924.9 | 0.0002 |
| 3 | 31105959 | 1100702 | 1148958 | 0.0002 |
| 4 | 39014159 | 953668.4 | 995659.7 | 0.0002 |

#### *3.4.3.2 Assortment*

For all deployments, the model that best predicted the association strength contained all four independent variables: gregariousness, lactation number, pasture access and breed (Table 3.4). Across all deployments there was significant positive assortment by lactation number. Significant positive assortment by breed was found in deployments 1-3. Cows were significantly positively assorted by gregariousness in deployments 1 and 2, and significantly negatively assorted by gregariousness in deployment 3. In deployment 4 there was a trend for negative assortment by gregariousness and positive assortment by breed, but these were not significant. A second model showed there was also positive assortment by milk production for cows without pasture access in all deployments; this pattern was significant for deployments 1 (post. mean= -0.016, p= 0.026) and 2 (post. mean= -0.03, p<0.001) but not for deployments 3 (post. mean= -0.012, p= 0.302) and 4 (post. mean= -0.003, p= 0.762).

Table 3.4 Results of best fitting model (indicated by lowest deviance information criterion) from mixed model regression, measuring assortment of cows by traits in deployments 1-4

| **Deployment** | **Factor** | **Posterior mean** | **l-95% CI** | **u-95% CI** | ***p*** |
|---|---|---|---|---|---|
| 1 | (Intercept) | 3.996 | 3.938 | 4.065 | <0.001 |
| | Gregariousness | -0.0004 | -0.0007 | -0.0002 | <0.001 |
| | Lactation number | -0.019 | -0.024 | -0.015 | <0.001 |
| | Pasture access | -0.13 | -0.142 | -0.117 | <0.001 |
| | Breed | -0.048 | -0.034 | -0.061 | <0.001 |
| 2 | (Intercept) | 3.969 | 3.912 | 4.037 | <.001 |
| | Gregariousness | -0.0006 | -0.001 | -0.0002 | 0.002 |
| | Lactation number | -0.021 | -0.026 | -0.016 | <0.001 |
| | Pasture access | -0.087 | -0.146 | -0.022 | 0.004 |
| | Breed | -0.031 | -0.011 | -0.049 | -0.002 |
| 3 | (Intercept) | 4.031 | 3.965 | 4.09 | <0.001 |
| | Gregariousness | 0.0013 | 0.009 | 0.0019 | <0.001 |
| | Lactation number | -0.014 | -0.019 | -0.008 | <0.001 |
| | Pasture access | -0.013 | -0.027 | 0.004 | 0.098 |
| | Breed | -0.024 | -0.004 | -0.048 | 0.036 |
| 4 | (Intercept) | 3.925 | 3.834 | 4.02 | <0.001 |
| | Gregariousness | 0.0004 | 0.0001 | 0.0008 | 0.094 |
| | Lactation number | -0.018 | -0.023 | -0.013 | <0.001 |
| | Pasture access | -0.287 | -0.308 | -0.267 | <0.001 |
| | Breed | -0.022 | -0.002 | -0.048 | 0.11 |

## 3.5 Discussion

In the current study, we investigated the social network structure of a dynamic group of lactating dairy cows at two social scales. At the group level, we found significant network centralisation and no evidence of community sub-structure. At the individual level, we found evidence for differentiated social relationships and association strength between cows being related to attribute similarity. We tested whether our spatial proximity networks were reflective of social interactions between individuals: an important assumption to validate when using this type of data (Farine, 2015). There was a significant positive correlation between the association strength measured by the proximity loggers, and the number of social grooming events recorded during behavioural observations. This supports the use of this method for measuring social preferences and relationships between cattle, and corresponds to findings of previous studies (Val-Laillet, Guesdon, von Keyserlingk, de Passillé, and Rushen (2009).

The absence of substructure in the current study is consistent with findings by Gygax et al. (2010) who analysed six herds of 24-43 individuals and found that each network was connected as a single component. Stocking density in this study was 9.5m$^2$/cow (assuming an average group size of 110 cows and that all cows were inside the barn) which is just over current Red Tractor Assurance guidelines (10m$^2$/cow for a 700-799g cow in a straw bedded system; Red Tractor Farm Assurance Dairy Scheme, 2014). This may have limited the potential for cows to avoid other individuals and for the formation of spatial divisions. In fact, space was further reduced during routine husbandry: cows were restricted to one half of the barn during the distribution of straw bedding (for approximately 45 minutes, twice a day) and when bedding areas were scraped out (for approximately 3 hours on every 10th day). Maintaining suitable inter-individual distance according to partner preferences and social status reduces conflict between cattle, and thus decreases social stress (Miller & Wood-Gush, 1991; O'Connell, Giller, & Meaney, 1989). Further research into the effects of space allowance on social structure would be particularly beneficial.

Significant network centralisation suggests that a few key cows may be particularly influential in terms of social structure, and by consequence these individuals may have disproportionate influence over the rate of disease spread, and the maintenance of group stability. Furthermore, betweenness centralisation can be important for a network's robustness to regrouping (Makagon, McCowan, & Mench, 2012). Assessing social instability and its consequences is crucial to the dairy industry, as group perturbation is known to have negative effects on the welfare and production of cows (Bouissou et al., 2001; Hasegawa et al., 1997; Hultgren & Svensson, 2009; Raussi et al., 2005; von Keyserlingk et al., 2008). At the group level, cows showed some consistency in their social associations. Our results suggest that up to 57% of the social structure in one week is repeated in the following week. However in some cases the amount of repeated structure is as low as 17% for consecutive weeks, indicating a substantial (83%) change in network structure. Though we only analysed a subset of the cows in the milking group (those present for the entirety of a deployment), we remind readers that group composition was dynamic. During deployments, a number of cows that were not included in analyses were moved into and out of the milking group, which likely had some effect on the relationships between cows that were included in the analyses.

Correlations indicating network stability for deployment 3 were markedly lower than that of other deployments; this is not easily accounted for by group movements, which were not noticeably different for deployment 3. A potential explanation is that although the number of individuals moved in deployment 3 does not appear particularly conspicuous, the identity of those individuals differed, which may be significant. Individuals occupying certain network positions can have more influence on network structure than others, and so their introduction or removal from a group can have a greater impact (Makagon et al., 2012). 'Knockout' experiments on a large, captive group of pigtailed macaques (*Macaca nemestrina*) carried out by Flack et al. (2006) revealed that network structure was largely influenced by a small subset of individuals who performed a specific role in conflict management. These 'keystone individuals' (as termed by Pruitt and Keiser (2014)) can be characterised in some animal groups by factors such as dominance (e.g. in lekking species; Robel and Ballard (1974)), status (e.g. in species with a highly developed class system; Aron, Passera, and Keller (1994)) and personality (Pruitt & Keiser, 2014). We encourage further research to investigate this effect in farm animals, including the characteristics and/or roles of individuals that hold positions in the network deemed particularly important for network stability. Conclusions from such studies could be applied in husbandry to increase animal welfare and production.

There was significant social differentiation in the relationships between cows; individuals associated more or less with some individuals than would be expected if social associations occurred at random. This supports previous findings that cows interact non-uniformly, often forming preferential relationships with some while avoiding other individuals (Gygax et al., 2010; Reinhardt & Reinhardt, 1981; Wasilewski, 2003). We explored some factors that could account for the non-random associations observed in the networks, testing for network assortment: a measure of the tendency of individuals to associate with others that share their characteristics (Wolf, Mawdsley, Trillmich, & James, 2007). This is commonly observed in human groups, with association due to similar race, ethnicity, age, religion etc. having a huge impact on social preferences (McPherson, Smith-Lovin, & Cook, 2001). The benefits of assortative mixing can be explained by group synchrony because, in order for a group to function efficiently, activities such as foraging, travelling and resting should be coordinated (Conradt & Roper, 2000). Variation in classes such as age, sex or size may result in differences in energy requirements and motivation (e.g. larger individuals may require longer or more frequent foraging bouts than smaller individuals) and deviation from an individual's optimal activity budget may come at some cost. This may lead to individuals associating more with others that are similar to themselves. Assortativity can lead to group segregation (Conradt & Roper, 2000), as observed in some wild ungulates such as bighorn sheep (*Ovis canadensis*) (Conradt, 1998) and red deer (*Cervus elaphus*) (Ruckstuhl & Neuhaus, 2002) who spend most of their lives in all-male or all-female groups that only re-join periodically, such as during the breeding season. There is also evidence of assortment by kin in some animal societies (Silk, Altmann, & Alberts, 2006; Ward & Hart, 2003; Wiszniewski, Lusseau, & Möller, 2010).

The influence of assortment on network structure has been investigated in previous studies (e.g. trinidadian guppies (Croft et al., 2005); pigtailed macaques (Flack et al., 2006); bottlenose dolphins (Lusseau & Newman, 2004)) but this study is the first (to the authors' knowledge) to investigate these patterns in a farm animal species. Behavioural synchrony has been observed in cattle, and synchronised lying has been used as a welfare indicator (Fregonesi & Leaver, 2001). Stoye, Porter, and Stamp Dawkins (2012) found that cows were more synchronised with their nearest neighbours (than other randomly selected individuals in the group) and suggest that postural synchronisation in cattle is the result of both social facilitation and concurrent activity cycles. In this study, we found significant patterns of assortative mixing by breed, milk production, pasture access, lactation number and gregariousness. Cows associated more with those of the same breed to themselves (significant for deployments 1-3). The different breeds in the study group may be reflective of body mass and energy requirements (and by extension, activity budget). For example, most Holstein-Friesian cows were notably larger than most Ayrshire cows. Cows associated more with those similar in milk production in all deployments, and these patterns were statistically significant for deployments 1 and 2. Assortative mixing by milk production may also be related to energy requirements, which vary with stage of lactation/pregnancy and yield (Coulon & Rémond, 1991). Additionally, DIM is a measure of how long a cow has been present in the milking group and thus is a measure of the opportunity for social contact and bond formation. Cows associated significantly more with others of similar lactation number. This measure reflects age, which may affect energy demands to some extent, but is likely to be more significant in terms of familiarity between individuals; the amount of previous experience of conspecifics may be directly related to strength of bonds. Indeed, familiarity has been identified as an important factor for social relationships in previous studies (Gygax et al., 2010; Takeda, Sato, & Sugawara, 2003; Wikberg, Ting, & Sicotte, 2014). In a study by Gygax et al. (2010), synchronicity was significantly affected by whether or not cows were reared together and/or had been together during the latest dry period.

Individuals were significantly assorted by gregariousness in all four networks. However the direction of the effect differed, highlighting the advantage of repeated data periods in this study. In deployments 1 and 2 cows associated significantly more with those with similar gregariousness values to themselves, while in deployments 3 and 4 cows associated less with others of similar gregariousness (this pattern was significant in deployment 3). Further work is required to determine which factors drive temporal dynamics in the social networks of dairy cattle. Assortment by gregariousness has been reported in other species (Croft et al., 2005; Lusseau et al., 2006) . It infers association with others of access to similar social resources (Flack et al., 2006) and may have implications for the spread of disease and information (Croft et al., 2005). Although significant assortment was found in the networks, these relationships were surprisingly weak; the variables we tested accounted for only a small amount of variation in the observed association patterns. In addition to the removal of cows for culling or selling, cows in this herd calve all year round, resulting in regular change in the milking group's composition. The relationships that form may be dynamic, with more temporary bonds forming due to factors not accounted for here. The dominance hierarchy is likely to influence mixing patterns, as it determines individuals' access to resources, which could have implications for space use and proximity to others. For example, when resources such as lying areas are limited and of unequal quality, more dominant individuals will gain access to more favourable positions, perhaps resulting in these cows lying in closer proximity. At the study farm, cows voluntarily enter a waiting area when they are due to be milked, and then compete for entry to one of two milking units. As cows cannot leave the waiting area until they have been milked, the time spent in this small space is largely determined by dominance, therefore prolonged proximity between subordinates may be inevitable in some cases. As such, mixing patterns can help identify problems in farm animal groups, such as when high avoidance patterns lead to uneven distribution of resources (Koene & Ipema, 2014).

### 3.5.1 Conclusions

Fundamental to investigations into the social components of welfare and productivity, is a thorough understanding of the structure in which social mechanisms occur. Our results shed light on the factors affecting the social network structure of dairy cows in a commercial farm setting.

Networks did not indicate any community structure; however we found significant centralisation in all deployment periods. Relationships between individuals were differentiated, with cows associating non-randomly, and there was assortative mixing based on lactation number, breed, gregariousness and milk production. Analyses revealed relatively low network stability which may have implications for welfare and productivity via social stress. This study demonstrates the use of innovative automated tools and social network analysis for understanding social relationships in farm animal groups, both of which are likely to play an important role in the future of animal welfare science.

In this chapter I have explored the social structure of a dynamic group of cattle, and found interesting patterns of heterogeneous relationships and network assortment. The following chapter investigates whether differences in individual social network position are associated with measures of health and productivity.

# Chapter IV

## The relationship between social network position and health and productivity in dairy cattle

## 4.1 Abstract

Complex social structures often arise in animal groups due to the heterogeneity of social relationships between individuals. There is emerging evidence that social relationships and the resultant social network position of individuals can influence performance and fitness, which has implications for animals under human management. Dairy cattle are gregarious and sensitive to social instability, with decreases in feed intake and milk production associated with regrouping. Insights from a network approach could be important for understanding the relationship between social dynamics and health and productivity. In this study, we used spatial proximity loggers to measure social relationships within a group of dairy cattle on a commercial farm, over four one month deployment periods; spatial proximity can be used as a measure of affiliation between individuals and overall sociability in cattle. We used multiple regressions to test for relationships between weighted degree centrality and the health and productivity of individuals. There was no relationship between degree centrality and age or stage in lactation. Higher degree centrality was significantly correlated with higher somatic cell count (in deployments 1 and 4) and higher milk yield (in deployments 1, 2 and 4). We did not find any differences in degree centrality between cows with good or poor mobility. These results may represent a trade-off between the benefits of social contact and group cohesiveness, and increased exposure to pathogens; further investigation into these effects is encouraged.

## **4.2 Introduction**

Studies on wild animal populations demonstrate the benefits of group living, such as improved foraging, predator defence and mate choice (Pulliam & Caraco, 1984; Shrader, Kerley, Kotler, & Brown, 2007; West-Eberhard, 1979). Research has shown that complex group structures arise due to the heterogeneity of social relationships between individuals, and that social relationships influence individual performance and fitness in a number of species (L. J. N. Brent et al., 2014; Wolf, Brodie, & Moore, 1999). Depending on their nature and context, social interactions can become a source of stress or provide a buffer against it, and thus influence animals' health (Rault, 2012). Fundamentally, 'stress' is an adaptive response allowing for behavioural and physiological adjustments to unpredictable events in the environment (McEwen & Wingfield, 2010). Yet its effects on the welfare and productivity of individuals make it a key concern for those working with farm animals (Keeling & Gonyou, 2001). Social instability is often associated with stress, and has been shown to suppress immune responses (e.g. pigs: de Groot et al. (2001), chickens: Gross (1984)), impair reproduction (e.g. pigs: Knox, Salak-Johnson, Hopgood, Greiner, and Connor (2014)), induce depressive-like states (e.g. rats: Herzog et al. (2009)), impact stress physiology (e.g. horses: Nuñez, Adelman, Smith, Gesquiere, and Rubenstein (2014)) and slow growth (e.g. pigs: Stookey and Gonyou (1994)). Stress levels are also related to dominance status (Sapolsky, 2004). Alternatively, the effects of positive social contact can be profound. They can improve wound healing (e.g. hamsters: Detillion, Craft, Glasper, Prendergast, and DeVries (2004)), reduce distress in novel environments (e.g. sheep: Porter, Nowak, and Orgeur (1995), rhesus monkeys: Gust et al. (1994)), enhance recovery after social defeat (e.g. pigs: Ruis et al. (2001), rats: Ruis et al.

(1999)) and improve reproductive success (horses; Cameron et al. (2009), baboons; (J. B Silk et al., 2003).

However, even in an ideal social environment, the relationship between health and sociality is complex. The proximity and social interactions between individuals that are intrinsic to group living can directly impact health in the form of infectious disease transmission (Nunn, Craft, Gillespie, Schaller, & Kappeler, 2015). Simply increasing group size is expected to increase social transmission, with greater opportunities for social contact, yet often this factor does not explain the disease patterns observed (Nunn, Jordán, McCabe, Verdolin, & Fewell, 2015). Additional features of a social network, such as the rate (e.g. Hamede et al. (2009)), type and direction (e.g. Drewe et al. (2011); Rimbach et al. (2015); Theis, Ugelvig, Marr, and Cremer (2015)) of interactions are also very important determinants of disease spread. The social structure that emerges from the non-uniform patterns of interactions and relationships is therefore important for the health of an animal group (Altizer et al., 2003). It leads to differences in social network positions (e.g. variations in network centrality) for individuals, and differences in whole network structure between groups (or indeed within the same group at different times). Numerous factors can affect an individual’s position in the network, including early social conditions (Naguib, Flörcke, & van Oers, 2011), developmental stress (Boogert, Farine, & Spencer, 2014) and personality (Aplin et al., 2013; Pike, Samanta, Lindström, & Royle, 2008), and there may be multiple factors working simultaneously. Evidence for a connection between social network positions and fitness is emerging. For example, Oh and Badyaev (2010) found that less elaborate (in plumage ornamentation) male house finches, *Carpodacus mexicanus*, were more socially labile (measured by betweenness centrality) than more elaborate males, which proved beneficial for mating success; Ryder, Parker, Blake, and Loiselle (2009) showed that network connectivity was related to male fitness in wire-tailed manakins (*Pipra filicauda*); and the sociality of female baboons was shown to influence offspring's survival by Silk et al. (2003; 2009).

In the farm environment, management often dictates that animals experience frequent social instability (e.g. regrouping based on production status) and trends are moving towards larger herd sizes (Baker, 2015). In addition to this, increasing global production demands (Godfray et al., 2010)mean that investigation into the links between health, productivity and sociality are more pertinent than ever. We already understand that when group membership is stable dairy cows form stable social relationships, and expect that individual social network position is likely to vary based on a number of factors. Using a social network approach, we can begin to understand how these factors interact, and work towards providing the optimal social conditions for cattle on farm. Individual differences in social behaviour have previously been demonstrated in differences in sociability (Boissy & Le Neindre, 1997; Gibbons, Lawrence, & Haskell, 2010), defined as the motivation of individuals to remain close to conspecifics (Sibbald, Erhard, Hooper, Dumont, & Boissy, 2006). Further, variation has been seen in the social differentiation of individuals, with some cows having non-random relationships with others in the group and others acting more homogeneously (Gygax et al., 2010; Phillips & Rind, 2001; Reinhardt & Reinhardt, 1981). These factors may affect the social network position of cows, along with other features such as dominance and familiarity between individuals; the latter has proved to be significant for dyadic relationships between cows in a study by Gutmann, Špinka, and Winckler (2015).

The importance of understanding how individual differences in social behaviour can affect cow health can be highlighted in relation to two major welfare concerns in the dairy industry: lameness and mastitis. Lameness is the behavioural expression of pain (Rutherford et al., 2009), elicited by a foot/leg abnormality caused by various disease, environmental or management factors. Social behaviour should be considered in both prevention and treatment of lameness. For example, social rank can affect the development of foot problems when housing design leads to competition for higher quality (more comfortable, clean, dry, etc.) cubicles or loafing areas (F Galindo & Broom, 2000). Greater incidence of lameness has been found in lower ranking cows, accounted for by decreased lying times and increased time standing in dirty areas (F Galindo & Broom, 2000). Similarly, there may be secondary effects if poor mobility reduces an individual's ability to compete for important resources such as food, water and lying areas, potentially impairing recovery and affecting other aspects of health and welfare (Wierenga & Metz, 1986; Wierenga, 1991). Mastitis is an inflammation of the mammary gland and udder tissue due to bacterial infection, which is typically painful and may lead to premature culling. Depending on the strain of bacteria, transmission can be environmental (i.e. via dirty bedding) or contagious, (transmitted between cows via milking equipment, etc.). Udder health is routinely assessed in the UK by recording the somatic cell count (SCC) in milk. Somatic cells (including leukocytes and epithelial cells) originate in the udder and high numbers indicate an immune response has been triggered by a mastitis-causing pathogen (Sharma, Singh, & Bhadwal, 2011). In a study by Kay, Collis, Anderson, and Grant (1977), increased SCC was linked to group movements, and dominance status appeared influential on the effects; the addition of dominant cows, but not subordinate cows, was associated with increased SCC for the group. However, this study only measured bulk milk SCC and there has been little further work carried out on this topic. Social instability due to regrouping has also been linked to decreased production, including reductions in milk yield, feed intake, rumination and lying times (Brakel & Leis, 1976; Brouček et al., 2013; Hasegawa et al., 1997; Hultgren & Svensson, 2009; Raussi et al., 2005; Sowerby & Polan, 1978; von Keyserlingk et al., 2008). It is currently unknown whether milk yield is connected to individual differences in social behaviour or network positions.

In this study, we explored the relationship between social network position, and health and productivity measures from a group of lactating dairy cows, over four one-month periods. We recorded associations between cows using spatial proximity loggers, and used the data to calculate a measure of individual social network position: weighted degree centrality (hereafter referred to as degree centrality). We then tested for a relationship between degree centrality and 1) age or DIM (number of days since most recent calving date), 2) somatic cell count, 3) milk yield, and 4) mobility.

## 4.3 Methods

### 4.3.1 Animals and housing

The study was carried out on a commercial dairy farm in Devon, UK from November 2012 to June 2013, in the form of 4 one-month data collection periods. The farm has a 1045m$^2$ (approx.) barn with straw yard housing and a voluntary milking system operating two Delaval robotic milking units. A total mixed ration was fed twice daily (approx. 9am and 5pm) at a feed barrier and additional concentrate feed was provided during milking and at an out-of-parlour feeder. At any given time the milking group contained between 106 and 113 lactating cows. Due to year-round calving, group structure was dynamic with cows entering and leaving depending on calving and drying off dates, in addition to sale or culling. There was a total of 134 unique cows present throughout the study. The group was of mixed breed though the majority were Holstein–Friesian. A Charolais bull was added to the milking group on 07-05-13, and was therefore present within the fourth period of data collection only.

### *4.3.1.1 Access to pasture*

Although managed and housed as a single milking group, pasture access was regulated (via electronic collars) based on each cow’s stage of lactation. Cows were restricted to the barn in the early part of their lactation, however after both testing positive for pregnancy and when daily milk yield dropped below a threshold of approximately 26 litres, they were also given free access to pasture. All cows were thus able to mix when inside the barn, but there were physical constraints to group synchrony when any cows with access chose to enter the pasture. As this affected some cows’ ability to associate, we incorporated this management factor into all null models used in our analyses.

### *4.3.1.2 Mobility Scoring*

Mobility scoring of cows in the milking group was carried out on a single day once per fortnight by a single scorer, according to the DairyCo Mobility Scoring system (DairyCo, accessed July 2015). In the DairyCo Mobility Scoring system the cow's ability to move easily is assessed (without accounting for issues affected by breeding or conformation), and recorded by a four point score ranging from 0 to 3. Cows scoring 0 are considered to have good mobility, cows scoring 1 are considered to have imperfect mobility, score 2 describes cows with impaired mobility, and score 3 is given to those with severely impaired mobility. As a voluntary milking system (VMS) was in place on this farm, there was no daily movement of cows that could provide a convenient opportunity to carry out mobility scoring; additionally some cows were at pasture during mobility scoring. Therefore, not all cows could be scored on every occasion.

### 4.3.2 Spatial proximity loggers

The proximity loggers used in this study were manufactured by Sirtrack Ltd (New Zealand), and are supplied as ready-made collars to attach around the neck of each cow (model E2C181C). These devices broadcast unique identification codes over an ultra-high frequency (UHF) channel while simultaneously searching for the ID codes of others within a pre-set distance range. Each logger is able to detect up to eight others simultaneously; recording its ID, the date, start and end time of the contact and its duration. The detection distance may be altered by users, by adjusting the power setting of a UHF coefficient range (0–62). The duration that any two loggers need be separated for an encounter to terminate ("separation time") can also be adjusted prior to deployment. Here, proximity loggers were set to a UHF value of 47 (which logged contacts at 1.5–2m in pilot tests using collared horses) with a separation time of 120s. Due to memory fill rate we deployed and removed loggers on four occasions so that data could be downloaded, hence we divided our analyses into four one-month data collection periods (hereafter referred to as deployments 1-4).

#### *4.3.2.1 Proximity logger data handling*

Data collected by proximity loggers consisted of dyadic associations over time. We summed the duration of all associations between dyads within each deployment period and these values were used to construct social networks. Data was manipulated for analysis using the R packages 'Matrix' (Bates & Maechler, 2014) and 'chron' (James & Hornik, 2014). As advised in previous studies (Drewe et al. (2012); Prange et al. (2006), we removed all 1-second contact records from the database prior to analysis, as these are considered unreliable, occurring sporadically when individuals are at the edge of the detection range (Drewe et al., 2012; Prange et al., 2006). Only loggers that functioned fully (both sending and receiving signals) for the whole deployment period were included in analysis. We therefore omitted data from broken loggers, and from cows that entered or left the milking group (or whose loggers fell off) mid-way through a deployment. As a result of this, and the turnover of cows throughout the study period, group membership differed across the deployments. As logger batteries were not changed throughout the study, battery power is likely to have decreased over time, consequently affecting logger function (see Drewe et al. (2012)) from deployments 1-4. Therefore it is important to note that we analysed each deployment separately and deployments should not be quantitatively compared.

### *4.3.2.2 Logging bias correction*

Previous work has shown that spatial proximity loggers can exhibit a sampling bias due to inter-logger variation in performance (Boyland et al., 2013). This is made evident by association matrices with highly variable dyadic reciprocity; contact durations between dyads should be mirrored if loggers are functioning uniformly. We therefore adjusted data using correction methods from Boyland et al. (2013). This involved scaling all contact durations in an association matrix relative to the performance of each given logger when compared with the most under-recorded logger. This was achieved by calculating the percentage difference in contact durations (e.g. the percentage difference between the total time logger A recorded contact with logger B, and the total time logger B recorded logger A) between all dyads, then identifying the logger that was most under-recorded, overall. The total contact duration (all contacts summed over the deployment period) for each dyad was then reduced according to their logging bias with the most under-recorded logger, e.g. if logger A had a logging bias of 10% when compared to the most under-recorded logger, the duration that logger A recorded contact with all other loggers would be reduced by 10%. We thus standardised associations between loggers relative to each other. We used Spearman's correlations to calculate the reciprocity between each side of the matrix (about the diagonal) both before and after application of this correction to assess its efficacy. This resulted in Spearman's rho increasing from 0.72 to 0.93, 0.59 to 0.91, 0.56 to 0.72, and 0.67 to 0.92 ($p$ < 2.2e-16 in all cases) for deployments 1-4 respectively. We symmetrised the corrected matrix by averaging values within each dyad of cows (as proximity cannot be directed), before creating social networks.

### 4.3.3 Statistical Analysis

R Statistical Software (R Core Team, 2014) was used to run multiple regressions with node-level permutations (described below), using code adapted from Rushmore et al. (2013). ANOVA (described below) were carried out in IBM SPSS Statistics 21 (Corp, 2012). Using UCINET v.6 (Borgatti et al., 1999), we generated four social network measures for individuals in each deployment: clustering coefficient, eigenvector centrality, weighted degree centrality and flow betweenness. We assessed whether these variables raised problems of collinearity, firstly by testing for correlations between all social network measures in each of the deployments. Pearson's correlations were used to test for relationships between variables that were normally distributed, and Spearman's were used where this was not the case, determined by Shapiro-Wilk tests of normality. Each of the social network measures were strongly correlated with each other (see Table 4.1) therefore, weighed degree centrality was used in all analyses and the other variables were disregarded. Weighted degree centrality (hereafter referred to as degree centrality) is the sum of each node's edge weights (Newman, 2010). Secondly, we tested for relationships between age, DIM and degree centrality. Spearman's correlations indicated that there were some significant relationships between degree centrality and DIM (in deployments 1 and 4 only; see Figure 4.1) however, the effect sizes of these correlations were less than -0.5 (see Table 4.2) and so do not indicate a problematic collinearity

(Dormann et al., 2013). We also calculated the variance inflation factor (VIF), using the 'fmsb' package (Nakazawa, 2014) in R, for variables (age, degree centrality and DIM) in deployments 1-4 which, all being <2 (see Table 4.3), also suggest there are no multicollinearity issues (Hair, Black, Babin, & Anderson, 2009).

Table 4.1. Correlations between all social network measures in deployments 1-4. Spearman's correlations are used where one of the variables is not normally distributed; for those where both variables are normally distributed, tests use the Pearson method. All correlations are significant to <0.0001

| Deployment | | 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| *Variable 1* | *Variable 2* | *Correlation coefficients* | | | |
| Degree | Clustering coefficient | -0.999 | -0.999 | -0.999 | -0.999 |
| Degree | Eigenvector centrality | 0.998 | 0.998 | 0.997 | 0.998 |
| Degree | Flow Betweenness | 0.962 | 0.862 | 0.773 | 0.965 |
| Clustering coefficient | Eigenvector centrality | -0.998 | -0.998 | -0.995 | -0.996 |
| Clustering coefficient | Flow Betweenness | -0.962 | -0.862 | -0.787 | -0.965 |
| Eigenvector centrality | Flow Betweenness | 0.957 | 0.865 | 0.754 | 0.965 |

Table 4.2 Spearman's correlations were used to test for relationships between variables; significant relationships are highlighted in bold

| Deployment | *Variable 1* | *Variable 2* | *Correlation coefficient* | *p* |
|---|---|---|---|---|
| 1 | Age | DIM | 0.162 | 0.119 |
| | Degree | DIM | -0.237 | **0.021** |
| | Degree | Age | 0.073 | 0.482 |
| 2 | Age | DIM | -0.019 | 0.871 |
| | Degree | DIM | -0.146 | 0.218 |
| | Degree | Age | 0.029 | 0.805 |
| 3 | Age | DIM | 0.059 | 0.661 |
| | Degree | DIM | -0.031 | 0.815 |
| | Degree | Age | -0.042 | 0.753 |
| 4 | Age | DIM | 0.042 | 0.732 |
| | Degree | DIM | -0.473 | **<0.0001** |
| | Degree | Age | 0.055 | 0.657 |

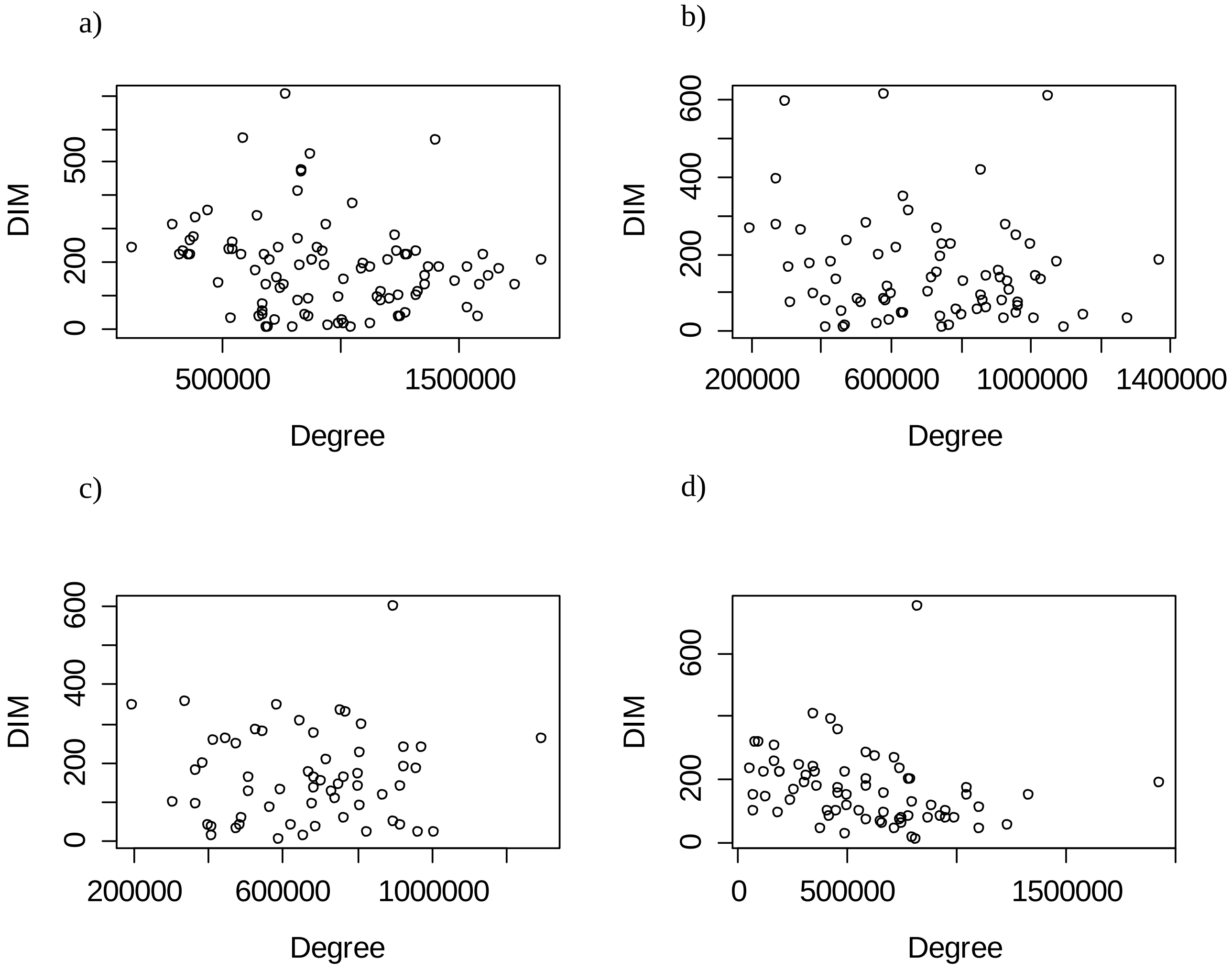


Figure 4.1 Relationship between DIM (number of days in milk) and weighted degree centrality of cows during deployments 1-4 (a-d respectively)

Table 4.3 To test for multicollinearity of variables used in our multiple regression models, the variance inflation factor (VIF) from the result of linear models were calculated. If VIF is more than 10, multicollinearity is strongly suggested; the results therefore do not suggest multicollinearity issues

| Deployment | | 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| *Test variable* | *Other variables* | *VIF* | *VIF* | *VIF* | *VIF* |
| Degree | DIM + Age | 1.046 | 1.028 | 1.005 | 1.170 |
| DIM | Degree + Age | 1.099 | 1.05 | 1.003 | 1.172 |
| Age | DIM + Degree | 1.063 | 1.023 | 1.003 | 1.002 |

#### *4.3.3.1 Is degree centrality associated with individual traits?*

The traits of individuals, age (in months) and DIM, were recorded from the start date of each deployment period. We tested for a relationship between degree centrality and the predictor variables (age and DIM), using node-level permutation-based regressions (30,000 iterations). In order to control for the physical constraints to group synchrony due to some cows having pasture access, and the resultant effect on degree centrality, nodes were only permuted between those that had the same access (i.e. nodes with pasture access were permuted, and nodes without pasture access were permutated separately).

#### *4.3.3.2 Is individual somatic cell count related to degree centrality or DIM?*

We fit individual SCC data using node-level permutation-based regressions (30,000 iterations), to investigate whether SCC could be predicted by degree centrality or DIM. Individual somatic cell count (SCC) was tested monthly by National Milk Records, as part of routine management on the study farm. For each deployment we compared the SCC records closest in date; SCC was recorded on day 17 of deployment 1, on day 9 of deployment 3 and on day 20 of deployment 4. Deployment 2 was omitted from this analysis as SCC was not recorded during this study period.

#### *4.3.3.3 Is individual milk yield related to degree centrality, age or DIM?*

We tested for a relationship between the total milk yield of individuals (summed over each deployment) and the predictor variables degree centrality, age and DIM, using node-level permutation-based regressions (30,000 iterations).

#### *4.3.3.4 Are there differences in degree centrality between cows with good or impaired mobility?*

ANOVA with 10,000 bootstrap permutations (stratified by group) were carried out to compare the degree centrality scores of cows with good (and imperfect) mobility, defined as cows scoring 0 or 1 on the DairyCo Mobility Scoring system, and cows with impaired (and severely impaired) mobility, defined as cows scoring >1 on the DairyCo Mobility Scoring system. Impaired mobility was observed in 10 out of 84 cows scored during deployment 1, 11 out of 63 cows scored during deployment 2, eight out of 35 cows scored during deployment 3, and 13 out of 65 cows scored during deployment 4.

## 4.4 Results

### 4.4.1 Is degree centrality associated with individual traits?

Age and DIM were not significant predictors of degree centrality in any of the deployment periods (Table 4.4).

### 4.4.2 Is the somatic cell count of individuals related to their degree centrality or DIM?

SCC was significantly positively correlated to degree centrality in deployments 1 and 4 (note that deployment 2 could not be tested), and was significantly positively correlated to DIM in deployments 3 and 4 (Table 4.4; Figure 4.2).

### 4.4.3 Is individual milk yield related to degree centrality, DIM or age?

There was a significant positive relationship between milk yield and degree centrality in deployments 1, 2 and 4, and significant negative correlation between milk yield and DIM in all four deployment periods (Table 4.4; Figure 4.3). However, we found no relationship between milk yield and age; although there was a trend for a positive relationship in deployment 2 (Table 4.4).

### 4.4.4 Are there differences in degree centrality between cows with good or impaired mobility?

ANOVA (with 10,000 bootstrap permutations stratified by pasture access) showed that there were no significant difference in degree centrality among cows with good or impaired mobility in any of the deployments (deployment 1 ($F_{(1,84)}$=0.023, p=0.880); deployment 2 ($F_{(1,73)}$=01.26, $p$=0.265); deployment 3 ($F_{(1,35)}$=0.819, $p$=0.372); deployment 4 ($F_{(1,65)}$=0.989, $p$=0.324)).

Table 4.4 Multiple regressions with node-level permutations (30,000 iterations per test) were carried out to test relationships between predictor variables. Nodes were only permuted between individuals that had the same pasture access, in order to control for the effect of management on social associations.

***Model 1**: DV - Weighted degree centrality*

| | Deployment 1, n=94 | | Deployment 2, n=73 | | Deployment 3, n=59 | | Deployment 4, n=69 | |
|---|---|---|---|---|---|---|---|---|
| | β | *P* | β | *P* | β | *P* | β | *P* |
| Intercept | 980499.457 | 0.057 | 738446.586 | 0.451 | 696828.949 | 0.424 | 811228.447 | 0.382 |
| Age | 1140.499 | 0.145 | 10.709 | 0.266 | -251.534 | 0.37 | 83.975 | 0.488 |
| DIM | -580.642 | 0.171 | -314.588 | 0.162 | -106.104 | 0.202 | -1468.128 | 0.324 |

***Model 2**: DV - Somatic cell count*

| | Deployment 1, n=92 | | Deployment 3, n=51 | | Deployment 4, n=60 | |
|---|---|---|---|---|---|---|
| | β | *P* | β | *P* | β | *P* |
| Intercept | -96.145 | **0.014** | -636.733 | **0.032** | -0.014 | **0.021** |
| Degree | 0.0002 | **0.026** | 0.0009 | 0.117 | 0.0003 | **0.033** |
| DIM | 0.436 | 0.086 | 2.925 | **0.037** | 1.146 | **0.043** |

***Model 3**: DV - Milk yield*

| | Deployment 1, n=94 | | Deployment 2, n=73 | | Deployment 3, n=59 | | Deployment 4, n=69 | |
|---|---|---|---|---|---|---|---|---|
| | β | *P* | β | *P* | β | *P* | β | *P* |
| Intercept | 750.162 | 0.442 | 763.857 | 0.145 | 838.119 | 0.365 | 811.9 | 0.216 |
| Degree | 0.0002 | **0.004** | 0.0003 | **0.015** | 0.0002 | 0.185 | 0.00004 | **0.0006** |
| Age | 0.989 | 0.189 | 0.068 | 0.053 | 1.129 | 0.189 | 0.003 | 0.486 |
| DIM | -1.5 | **<0.0001** | -1.51 | **<0.0001** | -1.603 | **<0.0001** | -0.775 | **0.014** |

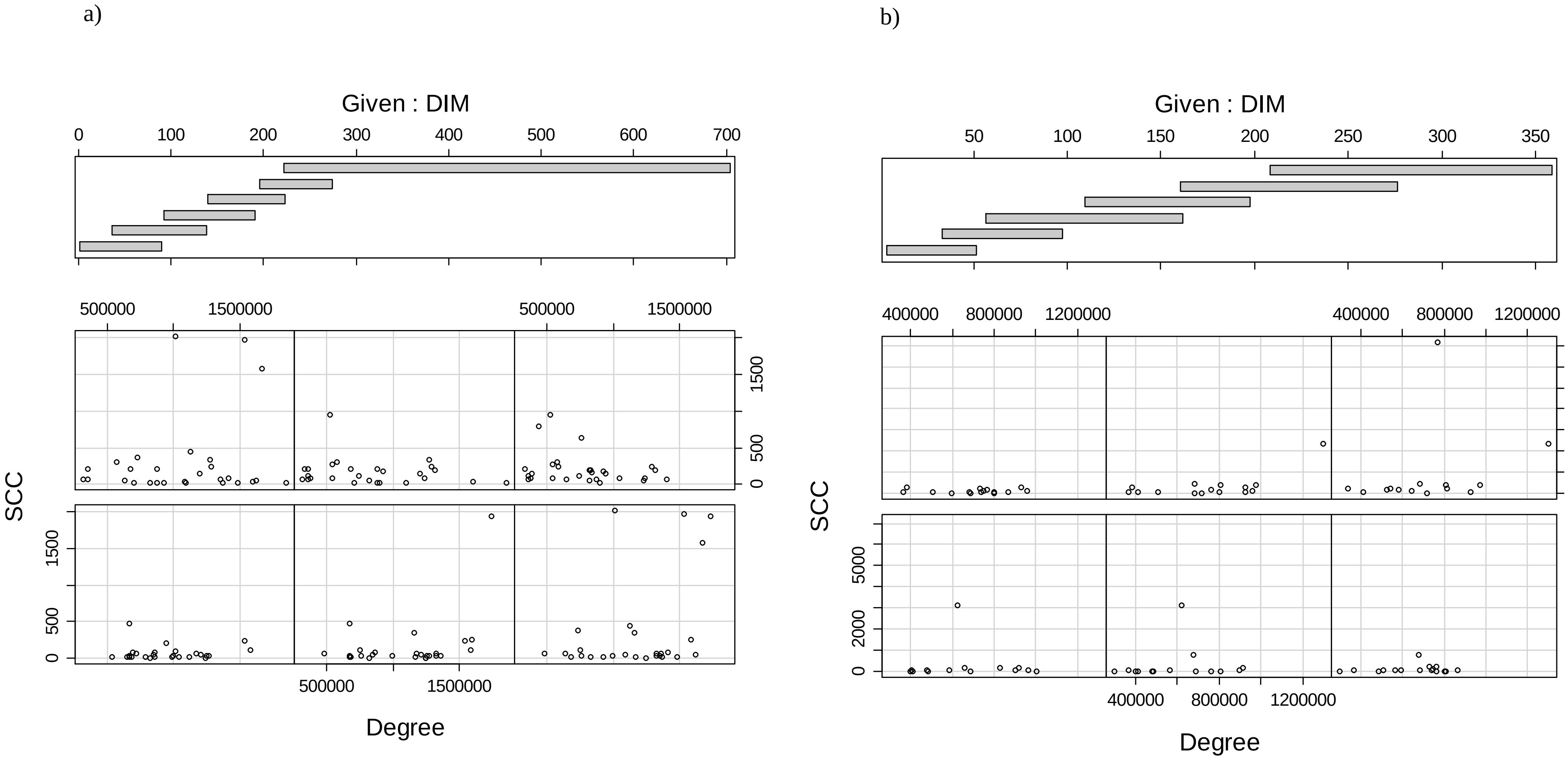


Figure 4.2 Coplots show the relationship between somatic cell count (SCC) and predictor variables: weighted degree centrality and DIM (number of days in milk), during deployments 1, 3 and 4 (a-c respectively). In each graph, each of the six conditioning variable (DIM) bars corresponds to one scatterplot. This correlation begins on the left-hand side for DIM, and this first bar (approx. 0-80 DIM in 2c.) corresponds to the scatterplot on the bottom row, left-hand corner. The scatterplots are then read from left to right, and from bottom to top

c)

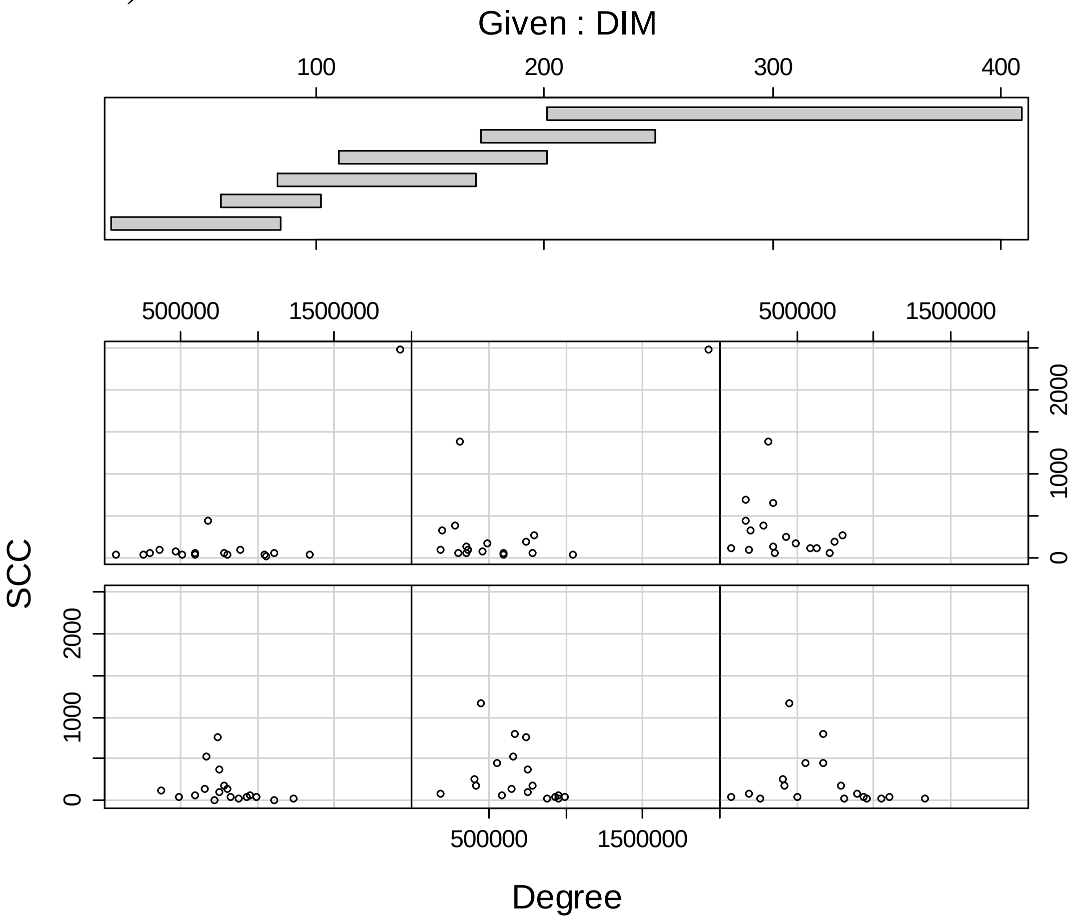


Figure 4.2 Coplots show the relationship between somatic cell count (SCC) and predictor variables: weighted degree centrality and DIM (number of days in milk), during deployments 1, 3 and 4 (a-c respectively). In each graph, each of the six conditioning variable (DIM) bars corresponds to one scatterplot. This correlation begins on the left-hand side for DIM, and this first bar (approx. 0-80 DIM in 2c.) corresponds to the scatterplot on the bottom row, left-hand corner. The scatterplots are then read from left to right, and from bottom to top

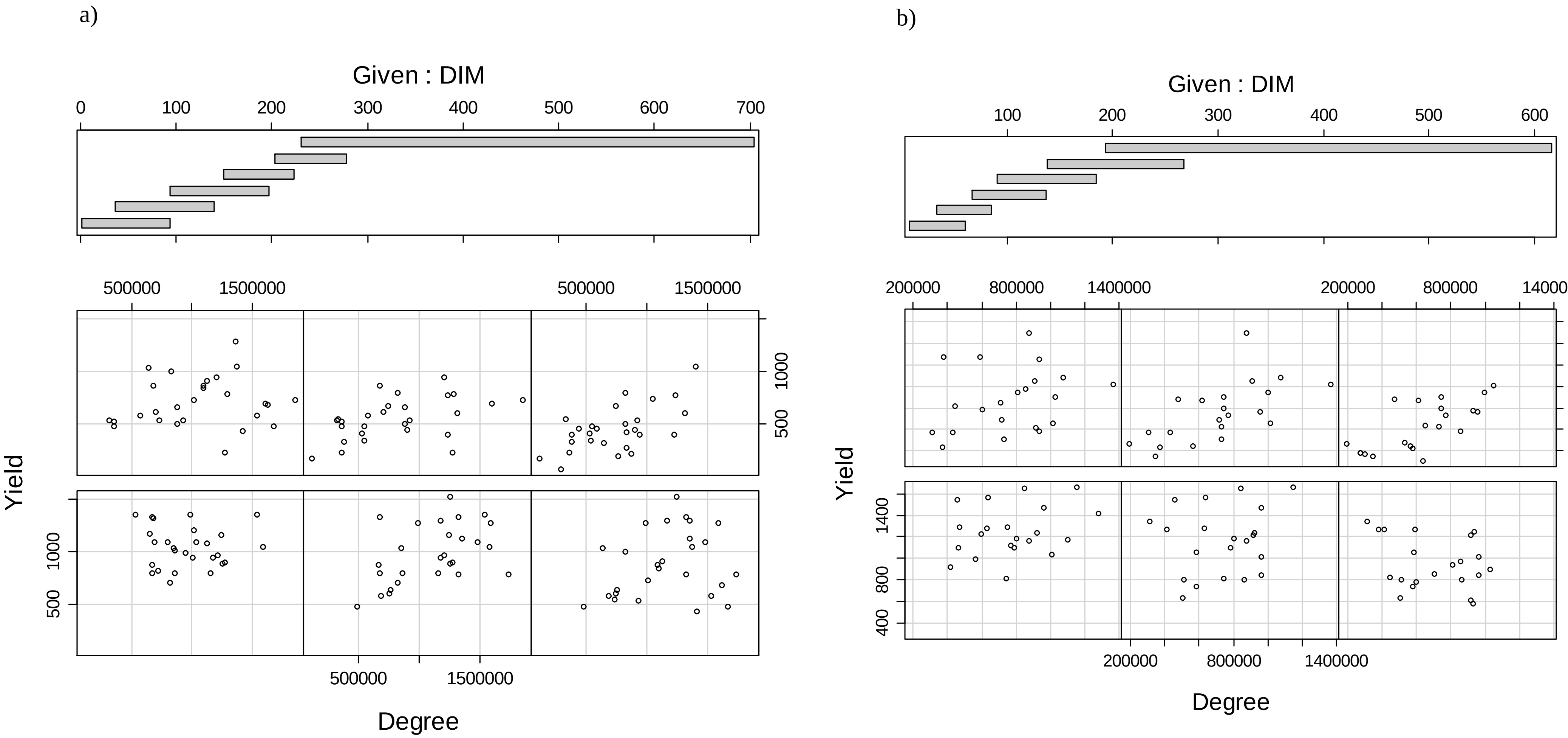


Figure 4.3 Coplots show the relationship between total milk yield and predictor variables: weighted degree centrality and DIM (number of days in milk), during deployments 1-4 (a-d respectively). In each graph, each of the six conditioning variable (DIM) bars correspond to one scatterplot. This correlation begins on the left-hand side for DIM, and this first bar (approx. 0-90 DIM for 3a.) corresponds to the scatterplot on the bottom row, left-hand corner. The scatterplots are then read from left to right, and from bottom to top

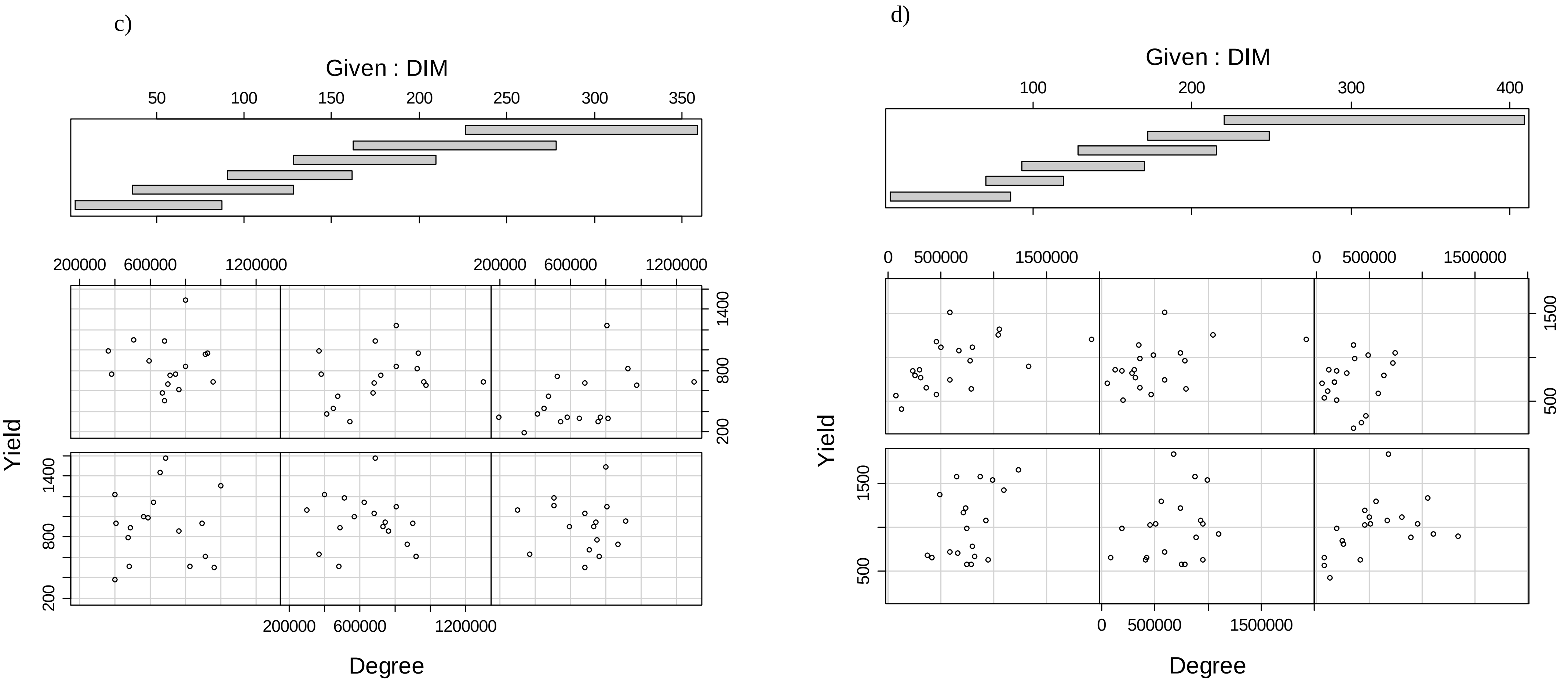


Figure 4.3 Coplots show the relationship between total milk yield and predictor variables: weighted degree centrality and DIM (number of days in milk), during deployments 1-4 (a-d respectively). In each graph, each of the six conditioning variable (DIM) bars correspond to one scatterplot. This correlation begins on the left-hand side for DIM, and this first bar (approx. 0-90 DIM for 3a.) corresponds to the scatterplot on the bottom row, left-hand corner. The scatterplots are then read from left to right, and from bottom to top

## **4.5 Discussion**

In this study, we investigated the relationship between a measure of social individual network position, degree centrality, and the traits, health and productivity measures of individual cows. We used spatial proximity loggers to measure social relationships between cows on a commercial dairy farm over four one month periods, as spatial proximity reflects affiliation between cows (Bouissou et al., 2001) and sociability of individuals (Gibbons et al., 2010). We did not find any differences in degree centrality between cows with good or poor mobility in the current study. There were also no relationships between degree centrality and age or DIM. However we found relationships between degree centrality and SCC, and between degree centrality and milk yield of cows across multiple deployments. As higher degree centrality was related to both higher milk yield and higher somatic cell counts, the findings of this study may demonstrate a cost-benefit trade-off.

Our results demonstrate inter-individual variation in degree centrality, which is likely to be driven by differences in individual gregariousness/sociability of cows as found in previous studies (Boissy & Le Neindre, 1997; Fisher, Morris, & Matthew, 2000; Gibbons et al., 2010). We explored possible explanations for differences in degree centrality, by testing for relationships with age and DIM. These factors represent, to some degree, familiarity with others in the group; as the majority of cows were bred and reared on farm, long-term familiarity is approximately reflected by age, and recent familiarity reflected by DIM. Therefore cows that were older or had been in the milking group for longer during the current lactation would have more opportunity to build social bonds with others. Familiarity has shown to be important for bond formation and strength in previous studies (e.g. Gygax et al. (2010)). In a study by Gutmann, Špinka, and Winckler

(2015) social relationships between dairy cows were significantly strengthened by long-term familiarity, and this was shown to be more influential on bond strength than very recent shared experience. However we did not find any relationship between degree centrality and age or DIM of cows in this study. Alternatively, gregariousness may be a stable feature of individuals. Consistent individual differences (repeatable across time and in different contexts) in behavioural response to relevant stimuli are generally referred to as ‘personality’ in ecology (Wilson & Krause, 2015). However within the farm industry the term ‘temperament’ has been used in parallel (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Some degree of consistency in aggressive feeding behaviour (Gibbons, Lawrence, & Haskell, 2009), behavioural response to temporary social isolation (Hopster & Blokhuis; Müller & Schrader, 2005) and sociability (Gibbons et al., 2010), has previously been observed in cattle. Gibbons et al. (2010) demonstrated that proximity to conspecifics could be used to measure sociability on commercial dairy farms by comparing these observations with results from a standardised runway test (assessing social motivation). This suggests that our measure of degree centrality could inform us of the sociability of individual cows.

Some work has been carried out on the heritability of social network position in humans (Fowler & Christakis, 2010); however this area has received very little attention in non-human animals. Temperament traits associated with handling by humans have recently been shown to be moderately heritable in cattle (Haskell, Simm, & Turner, 2014), however the heritability of social traits is largely unknown for cattle, and indeed across taxa (but see Faure and Mills (1998)). Research into the heritability of social traits could be fruitful, as breeding cows that are better able to cope in the social environment determined by modern farming (often large, high density groups with frequent regrouping) could enhance welfare and productivity.

In this study we tested for a link between social network position and udder health using somatic cell counts recorded during the deployment periods. This measure aids the diagnosis of mastitis which is considered one of the most economically important diseases for the dairy industry in developed countries (Petrovski, Trajcev, & Buneski, 2006), and costs the UK industry approximately £170 million per year (Bradley, 2002). As mastitis-causing pathogens can be transmitted between cows via milking equipment, and contracted from the environment via bedding, it was interesting to explore whether the duration of time spent associating with others was related to the SCC of individuals. In our model to predict SCC, we found that higher degree centrality was associated with higher SCC in two out of three of the deployments tested. There was also a significant positive relationship between SCC and DIM in deployments 3 and 4; supporting findings of previous studies (O'Brien, Berry, Kelly, Meaney, & O'Callaghan, 2009). Grouping of unfamiliar animals has been associated with an increase in SCC in the bulk milk tank (Kay et al., 1977) which could reflect reduced immune function due to stress surrounding regrouping. However in the present study, we found a relationship between a cow's position in the social network and her SCC. Causes of this relationship cannot currently be determined however higher associations between animals indicate greater sharing of environment. Future investigation into the space use (particularly lying areas) and social associations of cows would be useful to expand on this study. Additionally, information on the bacterial pathogens found on the udder of individual cows would benefit any development of this research.

In order to test for a relationship between the social network position and productivity of cows, we modelled milk yield with degree centrality, age and DIM as the predictor variables. As would be expected (as milk production is highest following calving and decreases throughout the lactation) there was a significant negative relationship between milk yield and DIM in all four deployments. We found no relationships between age and milk yield in any of the deployment periods. However, there was a significant positive relationship between degree centrality and milk yield in deployments 1, 2 and 4; cows that were more socially central during this time produced more milk. Several studies report a decline in milk yield following regrouping of cows (Brakel & Leis, 1976; Brouček et al., 2013; Hasegawa et al., 1997; Sowerby & Polan, 1978; von Keyserlingk et al., 2008), suggesting that social stress has an effect on milk production. However this is the first study, to the authors' knowledge, to demonstrate a connection between individual gregariousness (as measured by degree centrality) and milk yield. It could be that highly gregarious and socially central individuals may benefit more from the stress buffering effects of social support; indeed cows produce less milk when they are exposed to stress glucocorticoids (Varner & Johnson, 1983). Alternatively, cows that were producing more milk may have behaved in a way that resulted in higher degree centrality, e.g. spent more time feeding at peak times which may have resulted in more encounters recorded by the proximity loggers. Similarly, the relationship may be driven by cows that had poorer health during the study, and consequently produced less milk, investing less time in social behaviour or choosing to avoid high competition (e.g. at the feed face). The latter seems less likely however, when we consider the final result from this study.

There were no significant differences in degree centrality between cows with good mobility and cows with impaired mobility. Self-isolation and activity reduction are typical responses to disease, however self-isolation is dependent on available space (Proudfoot et al., 2012). It may be that opportunities for isolation were limited in the barn environment and it is likely that, of the cows that had pasture access (and thus access to more space), those with poor mobility were reluctant to walk outside, preferring to remain close to essential resources in the barn. Additionally, although lame cows typically reduce other important behaviours (e.g. feeding (Norring et al., 2014)) they may benefit from positive social interactions when experiencing pain. One study showed that lame cows were less likely (than non-lame cows) to initiate an aggressive encounter but were more often receivers of allogrooming, (Galindo & Broom, 2002) which is believed to have a comforting effect on cows (Sato et al., 1991; Sato & Tarumizu, 1993). Due to a lame cow's inability to keep up with the movement of the herd, in addition to increased opportunity for self-isolation behaviour, differences in degree centrality between cows that have good or poor mobility may be more evident in groups kept at pasture.

With regard to the relationships we found between degree centrality and both milk yield and SCC, we must acknowledge that the effect sizes for these relationships are small. It could be that additional social factors added noise to this data. For example, although we only included cows in the analyses that were present in the milking group for the entirety of a deployment, there were additional cows in the group that had been added or removed during the data collection periods. The influence that social perturbation had on the stress of individuals (and subsequently on health and production) was not quantified, but it is likely to have had some effect. Nonetheless the null model shows that the relationships are significant, and when considered at the scale of the dairy industry, small effects could have huge economical and welfare consequences.

### 4.5.1 Conclusions

This study demonstrates a link between social network position and health and production in dairy cows. A multitude of factors are likely to determine both udder health and milk yield at any one time, but here we present evidence that gregariousness could play a role. High degree centrality in this study was related to higher milk yields but also higher somatic cell counts, which may exemplify a cost-benefit trade-off. Social contact and cohesiveness can be beneficial in terms of stress reduction but increase individuals' exposure to pathogens (Kappeler, Cremer, & Nunn, 2015), and this may be particularly evident in the farm environment. The links between social behaviour and other important infectious diseases, such as bovine tuberculosis, should be investigated in future research, as understanding more about transmission dynamics could have a huge impact on preventative measures.

In this chapter, individual social network position was shown to be linked with health and productivity. In *Chapter V*, I explore one way in which individual differences in social network position could occur: through different early social experience. The influence of calf-calf social bond strength, on the effectiveness of stress reduction during weaning is also investigated.

# Chapter V

## Pair housing dairy calves and age at pairing: effects on weaning stress, health, production and social networks.

## 5.1 Abstract

The early social environment can influence the health and behaviour of animals, with effects lasting into adulthood. In the UK dairy industry, calves are separated from their dam almost immediately and 60% are subsequently reared individually during their first eight weeks of life. This study assessed the effects of housing calves in pairs (and age at pairing) on weaning stress, health and production during pen rearing, and on the social networks that calves later formed when grouped. Forty female Holstein-Friesian calves were allocated to one of three treatments: individually housed (*I*, n = 8), pair-housed from day 5 (*P5*, n = 8 pairs), and pair-housed from day 28 (*P28*, n = 8 pairs). From day 48, calves were weaned by gradual reduction of milk over three days, and vocalisations were recorded as a measure of stress for three days before, during and after weaning. Health and production were not affected by treatment over the whole study, or during the weaning period. Vocalisations were higheset post-weaning, and were significantly higher in *I* calves than pair-reared calves. Furthermore, *P28* calves vocalised significantly more than *P5* calves. The social network of calves was measured for one month after all calves were grouped in a barn, using association data from spatial proximity loggers. We tested for week-week stability, social differentiation and assortment in the calf network. Additionally, we tested for treatment differences in: coefficient of variation (CV) in association strength, percentage of time spent with paired calf and weighted degree centrality. The network was relatively stable from weeks 1 to 4 and was significantly differentiated, with individuals assorting based on prior familiarity. *I* calves had significantly higher CV in association strength than *P5* calves in week 1 but there were no significant treatment differences in week 4. The mean percentage of time that individuals spent with their paired calf after regrouping decreased from weeks 1-4, though treatment did not affect this. There were also no significant differences in weighted degree

centrality between calves in each rearing treatment. These results suggest that early pair-rearing can allow calves the benefits of social support (and that this is more effective when calves are paired earlier) without compromising health or production, and sheds light on the early development of social behaviour in cattle.

## 5.2 Introduction

Research shows that early social conditions influence many key factors in an animal's life, including the development of personality (Bergmüller & Taborsky, 2010), abnormal behaviours (Mason & Rushen, 2008), stress response (Meaney et al., 1996), susceptibility to infection (Tuchscherer, Kanitz, Puppe, & Tuchscherer, 2006) and wound healing (Detillion et al., 2004). For many young mammals, the social environment effectively consists of the mother-infant bond, and disrupting this relationship induces a range of biological consequences (Newberry & Swanson, 2008) which can result in persistent changes in neurobiology and behaviour (Braun, Lange, Metzger, & Poeggel, 1999). Such consequences can be seen in a diverse range of taxa (e.g. primates (Hawkley, Cole, Capitanio, Norman, & Cacioppo, 2012), pigs (Kanitz et al., 2004), rodents (Weiss, Pryce, Jongen-Rêlo, Nanz-Bahr, & Feldon, 2004). Individual differences in early social experiences and developmental environment, can also lead to consistent individual differences in adult social behaviour (Boogert et al., 2014; Sachser, 1993). This can be expressed as differences in the way individuals form and maintain social relationships (Aplin et al., 2013), which can affect social network position and overall social group structure (Boogert et al., 2014). Significant connections between social relationships and fitness have emerged in numerous animal studies  (see Brent et al. (2014)), therefore understanding how human management of the early social environment affects captive individuals, such as farm animals, is vital for maximising welfare and productivity.

In the UK dairy industry there is variation in the way young calves are housed; however, an estimated 60% of calves experience social isolation soon after birth, being reared in individual pens during the milk feeding period (Marcé, Guatteo, Bareille, & Fourichon, 2010). The EU directive on calves (Council Directive 97/2/EC) acknowledges that social contact is important for calves, stating that those over 8 weeks old must be housed in groups. However, for calves under 8 weeks old, regulations only stipulate a requirement for visual and tactile contact e.g. (nose-to-nose contact through pen divides) with others of a similar age. The consequences of restricting social contact during early rearing of calves is not fully understood. Motivations for individual housing are centred on reducing disease transmission: increased contact between animals can increase risk of disease spread. Cross-sucking (sucking objects or body parts of pen mates) and inter-sucking (sucking the udder of pen mates) can lead to inflammation and enhance disease transmission (Ude, Georg, & Schwalm, 2011) and these behaviours are widespread in calf production. However, there are methods that can be used to decrease these undesirable behaviours in group-housed calves, e.g. the provision of a non-nutritive artificial teat, slower milk flow and post-meal hay feeding (de Passillé, 2001). A higher incidence of disease in group-housed calves (compared with pair-housed calves) has been reported in some studies (e.g. Maatje, Verhoeff, Kremer, Cruijsen, and van den Ingh (1993)), however others have demonstrated the opposite result (Hänninen et al., 2003; Kung et al., 1997) or show no differences in health and disease of calves within each type of rearing system (Chua, Coenen, Van Delen, & Weary, 2002).

Early development of social bonds with conspecifics is common in domestic herbivores and preferential bonds between unrelated individuals are often formed, particularly in the absence of the dams (Veissier et al., 1998). Group housing calves may alleviate the stress caused by separation from the dam, via ‘social support’; this term refers generally to the range of  benefits provided by social companions that improve an individual’s ability to cope with challenges (Rault, 2012). Social contact is important to calves, indicated by a willingness to ‘work’ for access to other calves in preference choice tests (Holm et al., 2002). In fact, group housing can better simulate an age-appropriate social environment. In studies of free-range cattle, calves are observed to spend much of their time resting together  in small groups away from their dams (Sato, Wood-Gush, & Wetherill, 1987; Vitale, Tenucci, Papini, & Lovari, 1986).

Natural weaning of cattle appears to begin when the calf is around 10 months old (Reinhardt & Reinhardt, 1981). However on commercial dairy farms, weaning from milk begins as early as 5 weeks, making this a particularly stressful time for calves (Weary, Jasper, & Hötzel, 2008). Generally, when cattle are stressed they vocalise more (Watts & Stookey, 2000).  Increased vocalisation is a common response to weaning and one that has been used as a non-invasive measure of stress in previous research (e.g Budzynska & Weary, 2008; De Paula Vieira, Von Keyserlingk, & Weary, 2010; Thomas, Weary, & Appleby, 2001). When housed in pairs during weaning, calves have been shown to vocalise less and  have higher growth rates than calves housed individually (Chua et al., 2002; De Paula Vieira et al., 2010). Although there is evidence demonstrating that social companions can buffer stress at weaning, the effect that the strength of the social bond has on the provision of social support in calves is not fully understood.

In addition to the diet chance, following weaning dairy calves experience a new physical and social environment. Calves of a similar age and weight are typically grouped together and moved into new housing facilities, which contain a number of novel items such as feeding and drinking apparatus. For those previously housed individually, this is the first time they experience full social contact with conspecifics. In contrast, group-reared calves have prior social experience and likely have pre-established social bonds with some group members. Rearing method is thus expected to impact stress levels during the process of regrouping. Furthermore, interactions with the physical environment could be affected as early social conditions impact exploratory behaviour (Jensen et al., 1997; Naguib et al., 2011), social facilitation (De Paula Vieira et al., 2010) and food neophobia (Costa, Daros, von Keyserlingk, & Weary, 2014).

Not only does early social contact affect important components of calves' welfare during rearing, it has also been shown to influence adult behaviour. Research demonstrates that cattle that were group housed as calves: are more confident (Bøe & Færevik, 2003), show less fear (Jensen et al., 1997), are more cooperative with humans (Price & Wallach, 1990), play more (Jensen, Vestergaard, & Krohn, 1998), are involved in less agonistic encounters (Veissier, Gesmier, Le Neindre, Gautier, & Bertrand, 1994), and achieve higher social rank (Broom & Leaver, 1978; Warnick, Arave, & Mickelsen, 1977) than individually housed calves. Additionally, early familiarity between calves is associated with more positive social behaviour later in life. For example, heifers that were reared together were less aggressive and engaged in more non-agonistic interactions (with each other), fed and rested closer together, and were more tolerant in a food-competitive situation, compared to those they were not reared with (Bouissou & Hövels, 1976). Therefore management practises which encourage the development and stability of social bonds are beneficial and should be explored.

The aim of this study was to investigate the effect of the early social environment, on the performance and social behaviour of calves. Firstly, we measured the growth, feed intake, health and weaning stress (measured by number of vocalisations) of calves in three rearing treatments: individually housed, pair-housed from day 5 and pair-housed from day 28. Secondly, we measured the social network of the calves over a one-month period when all were grouped together post-weaning, using spatial proximity loggers to measure social associations. We quantified the stability of social relationships in the group and investigated whether the network was socially differentiated (heterogeneous). We investigated whether relationships were affected by prior opportunity to socialise (familiarity between calves, and treatment) during pen rearing. The coefficient of variation (CV) in association strength was calculated for each calf, and we tested for treatment differences in week 1 and 4. We explored whether the percentage of time individuals spent with their paired calf differed between the treatments, and whether it decreased over time after regrouping. Lastly, we tested for differences in social network position between the calves in the three rearing treatments.

## 5.3 Methods

### 5.3.1 Animals, housing and diet

This study was conducted using forty female Holstein-Friesian calves on a commercial farm in Somerset, UK, from April to July 2013. Calves were separated from their dams at calving and individually housed, until randomly assigned to one of three treatments on day 5: individually housed (*I*; n = 8), pair housed from day 5 (*P5*; n = 8 pairs), or pair housed from day 28 (*P28*; n =8 pairs). One replicate of each treatment made up a block and there were eight blocks in total (hence total n = 40), with calves born earliest in block 1 and latest in block 8 (see Figure 5.1). As calves were not all born on the same day, a block entered the trial when the mean age of calves was five days. The age difference between the oldest and youngest calves in any one block was (mean ±SD) 2.5 ±1.19 days. All calves had visual access to others via the front opening of pens and some contact to neighbouring pens via four ventilation slots (23cm high, 8.5cm wide) on the pen walls (Figure 5.1c&d). All pens were bedded with straw, and space per calf (1.22m x 2.13m) was consistent across all treatments. Calves were bucket fed pellets (BOCM, Super Rearer 18 + deccox) from day 4 and water was available *ad libitum* from day 1. Milk replacer (150g BOCM Omega Gold per litre of warm water) was provided by bucket twice daily. The quantity of milk given to calves was increased gradually from four litres/day on day 1, to six litres/day on day 21; this amount was then maintained until day 48. Milk weaning was carried out over three days by reducing milk volume over six feeds (2.5, 2.0, 1.75, 1.5, 1.0 and 0.5 litres) from day 48), and on day 51, three litres of warm water was provided as this can reduce stress at weaning (Jasper, Budzynska, & Weary, 2008).

On day 55 each block of five calves were grouped together by removing the pen walls that separated them, to leave one larger pen made from the original perimeter walls (Figure 5.1f). Each block of calves was then moved to a barn on day 60, so that every 3-5 days the group size increased by five individuals. When the *barn grouping* part of the study began, calves were housed in a 220m$^2$ pen within a 1012m$^2$ barn (Figure 5.2). Straw feed and pellets (BOCM, Super Rearer 18 + deccox) were delivered (into a trough) morning and evening, and water was available *ad libitum*.

### 5.3.2 Statistical methods

Statistical analysis was conducted using IBM SPSS software vs.19 and R statistical software (R Core Team, 2014) . Data for pair-reared calves were averaged to give one value per pen. Where presented as a percentage or proportion, data were transformed using the arcsine square-root transformation. When analysing data around weaning, means were calculated for days 45-47 (pre-weaning), 48-50 (weaning) and 51-53 (post-weaning). Where multiple tests were carried out on one dataset, false discovery rate (FDR) adjusted *p*-values were calculated. These were quoted as a *q*-value using the two-stage sharpened method (Pike, 2011).

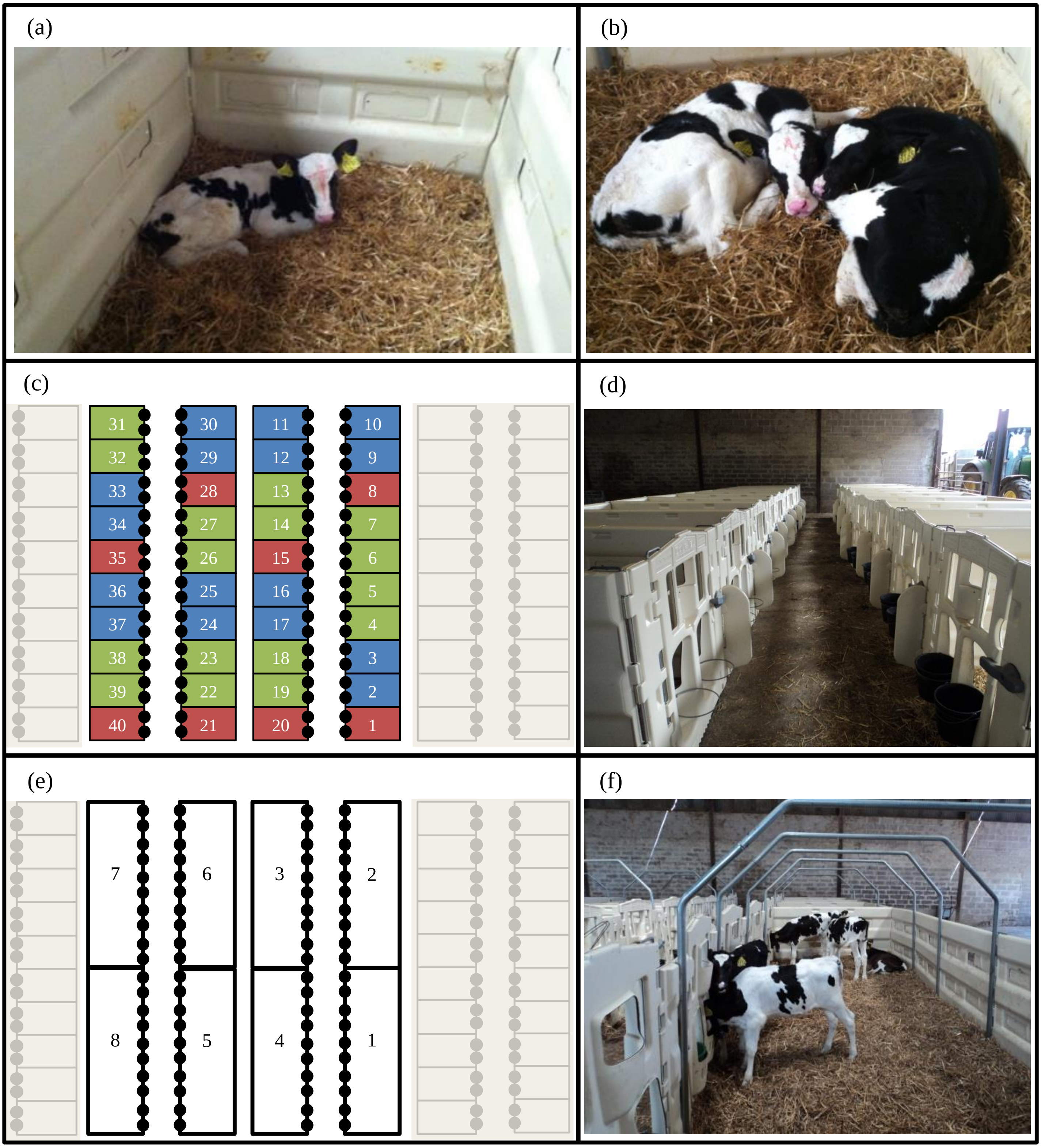


Figure 5.1 Calves were either housed individually (a) for the duration of pen rearing (treatment *I*), housed as a pair (b) from day 5 of pen rearing (treatment *P5*) or housed individually then as a pair from day 28 (treatment *P28*). Layout of pens is shown (c, d): *I* pens are coloured green, P5 pens are blue and I pens are red; greyed out pens show pens of calves that were not involved in the study. Layout of blocks (e) and an example of a block when dividing partitions were removed on day 55 (f).

Figure 5.2 Photograph of study calves in the barn where they were housed from day 60.

### 5.3.3 Pen rearing

#### *5.3.3.1 Measures of health, production and weaning stress*

Health checks of individuals were carried out daily by the experimenter on days 5 to 54, according to the University of Wisconsin-Madison Health Scoring Criteria (Figure 5.3), that was developed by veterinarians to identify calves that should be treated for bovine respiratory disease (McGuirk, 2008). Fecal scores were recorded, and cough score, nasal discharge score, eye score, and ear score were added together to give an overall respiratory score. Daily concentrate intakes (per pen) were determined on days 5 to 54 following morning milk feeding, by weighing feed remaining in the feed bucket and deducting it from the amount provided on the previous day. Vocalisations (per pen) were counted by the experimenter for one hour at approximately 8am (following morning milk feeding on the days this was given) for three days pre-weaning, weaning and post weaning. Body weight was recorded on entry to the study and on day 55 using a weighscale (Iconix FX1, NZ.) and a weigh-band (developed for Holstein-Friesian heifers by the Agri-Food and Biosciences Institute, Belfast, in conjunction with the Royal Veterinary College, AFBI, 2011). An additional measurement was taken on day 47 using the weigh-band only. Specific growth rate (SGR) was used to calculate weight gain, using the following formula:

Equation 1: $$Specific\ growth\ rate\ [\%] = 100\left(\frac{(\ln W_2 - \ln W_1)}{t}\right)$$

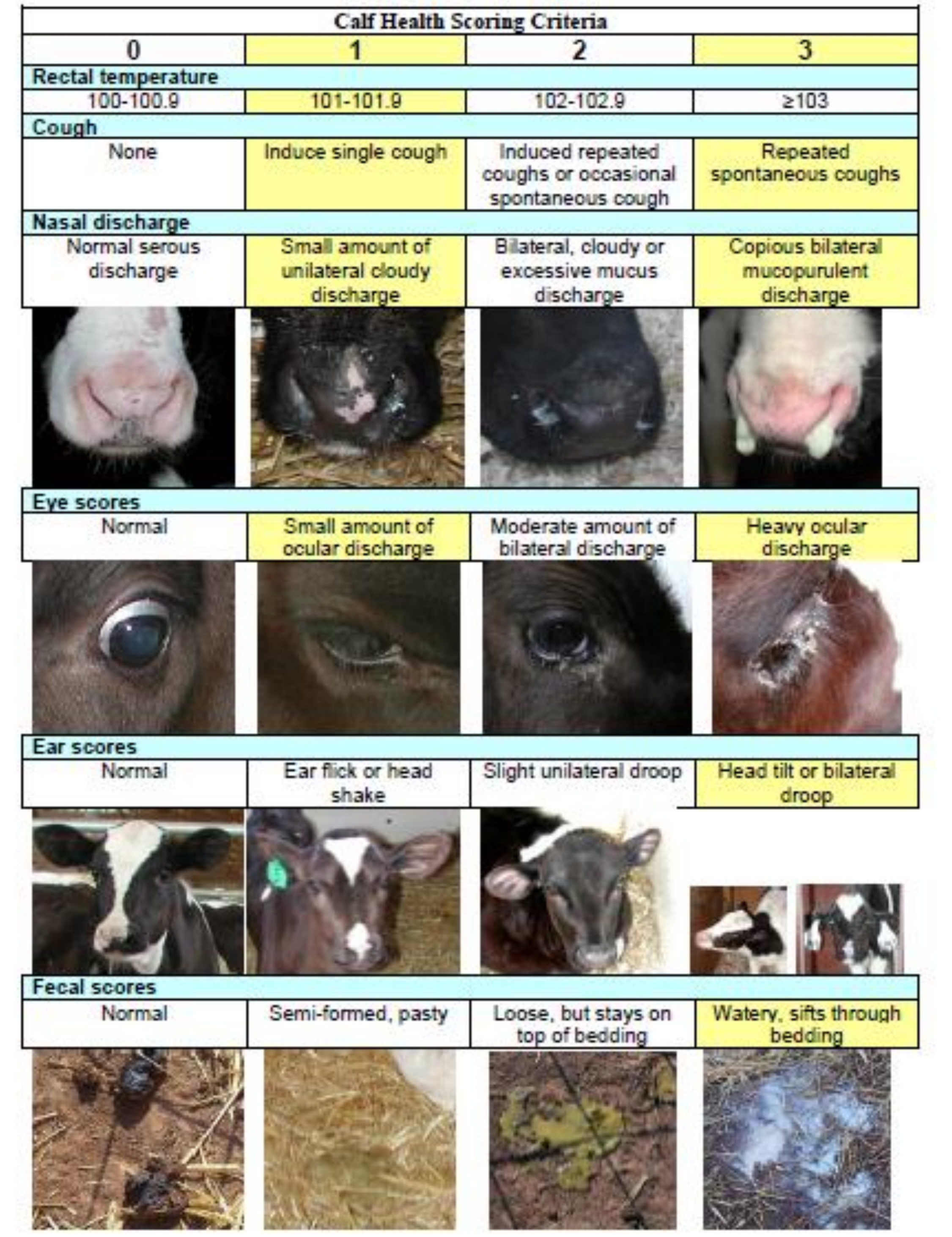
Where $W_1$ is the weight at sample point one, $W_2$ is the weight at sample point two and $t$ is the time in days between sample points one and two.

### *5.3.3.2 Between-treatment differences in overall health, growth and intakes*

We tested for treatment differences in health scores over the whole pen rearing period using a one-way MANOVA. One-way ANOVA were used to test for treatment differences in: concentrate intake over the whole trial, weight at the start of the trial, mean specific growth rates over the whole trial period.

### *5.3.3.3 Between-treatment differences in vocalisations, growth and intakes during weaning*

Friedman’s AVOVA was used to test whether the number of vocalisations differed between the pre-weaning, weaning and post-weaning 3-day periods. Kruskal-Wallis tests were used to assess for any significant differences in the number of vocalisations between treatments during each period. ANOVA were performed to test for treatment differences in: specific growth rate from days 47-55, concentrate intake during the pre-weaning, weaning and post-weaning 3-day periods, concentrate intake from days 48-53 (pre-weaning, weaning and post weaning); and to test whether any differences found were dependent on weaning stage.



**Calf Health Scoring Criteria**

| 0 | 1 | 2 | 3 |
|---|---|---|---|
| **Rectal temperature** | | | |
| 100-100.9 | 101-101.9 | 102-102.9 | ≥103 |
| **Cough** | | | |
| None | Induce single cough | Induced repeated coughs or occasional spontaneous cough | Repeated spontaneous coughs |
| **Nasal discharge** | | | |
| Normal serous discharge | Small amount of unilateral cloudy discharge | Bilateral, cloudy or excessive mucus discharge | Copious bilateral mucopurulent discharge |
| **Eye scores** | | | |
| Normal | Small amount of ocular discharge | Moderate amount of bilateral discharge | Heavy ocular discharge |
| **Ear scores** | | | |
| Normal | Ear flick or head shake | Slight unilateral droop | Head tilt or bilateral droop |
| **Fecal scores** | | | |
| Normal | Semi-formed, pasty | Loose, but stays on top of bedding | Watery, sifts through bedding |

Figure 5.3 University of Wisconsin-Madison Calf Health Scoring Criteria. Copied without permission; sourced from: http://www.vetmed.wisc.edu/dms/fapm/fapmtools/8calf/calf_health_scoring_chart.pdf

### 5.3.4 Barn grouping

#### *5.3.4.1 Spatial proximity loggers*

In order to remotely measure social associations between the calves, spatial proximity loggers (model E2C181C) made by Sirtrack Ltd. (New Zealand) were deployed on day 55. These devices are attached to collars that are worn around the animal's neck, and give users information on frequency and duration of close proximity between individuals. They function by both broadcasting unique identification codes over an ultra-high frequency (UHF) channel, and searching for the ID codes of others. When loggers enter a pre-determined distance range (set by the user via alteration of the power setting of a UHF coefficient range), both record the encountered logger's ID, the date, the start and end time of the encounter, and its duration. Users can also determine the duration that loggers need to be out of contact range for an encounter to terminate (the "separation time") prior to deployment. Here, proximity loggers were set to a UHF value of 45 with a separation time of 120s, which equated to detecting contact between calves when they were within 1.5m (approximately) of each other.

Data were downloaded from proximity loggers and prepared for analysis using the R packages 'Matrix' (Bates & Maechler, 2014) and 'chron' (James & Hornik, 2014). Four week-long association matrices were constructed separately for weeks 1-4 by summing the duration of all associations between each dyad during each week. All 1-second contact records were omitted from the analysis, as these are not deemed reliable (Drewe et al., 2012; Prange et al., 2006). Data was then manipulated. Data were corrected according to methods from Boyland et al. (2013), to account for the sampling bias that can arise when loggers vary in their performance.

### *5.3.4.2 Network stability*

We examined the stability of associations at the group level, during the month that all calves were grouped together in the barn. The four week-long association matrices were compared with each other using the ‘mantel’ function (method= Spearman’s rank correlation) of the ‘vegan’ package (Oksanen et al., 2013) in R. This function finds the Mantel statistic as a matrix correlation between two dissimilarity matrices; a null model with node-label permutations (n=4999, in a Quadratic Assignment Procedure) was used to assess the significance of test statistics.

### *5.3.4.3 Social differentiation*

We calculated social differentiation (heterogeneity of associations at the group level) in each of the four week-long networks, to determine whether associations between calves were more varied than would be expected given a null hypothesis that individuals associate uniformly. The following statistic was used, adapted from Whitehead (2008) appendix 9.4.

Equation 2:

$$S = \frac{\sum_i^N \sum_j^N (O_{ij} - E_{ij})^2}{N(N-1)}$$

In this equation the difference between the observed value and the expected value is summed for each dyad, and then divided by the total number of dyads.

### *5.3.4.4 Assortment*

To test if pen rearing affected patterns of association during barn grouping, we tested for assortment by treatment and familiarity in week 1 and week 4 after regrouping. We used a Markov Chain Monte Carlo (MCMC) framework to measure the relationship between the dependent variable, association strength, and the fixed factors (familiarity and treatment). Familiarity was measured for each calf dyad as the number of days that they had been in full social contact on day 1 of barn grouping; therefore familiarity between individuals ranged from 0 (i.e. no prior full social contact between calves in block 8 and calves in blocks 1-7) to 76 (i.e. calves that were paired at 5 days old in block 1). To test for assortment by treatment, dyads were awarded a ‘0’ if they were of the same treatment and a ‘1’ if they were of different treatment.  Calf ID was included as a random effect in all models. The undirected nature of association measures  (all calves act as individual A and B of a dyad in the dataset) are accounted for within the ‘MCMCglmm’ package (Hadfield, 2010). To satisfy assumptions of normality, we log-transformed the dependent variable, association strength. As our networks were completely saturated (all calves interact), we have made the assumption that transitivity (if *A* and *B* are connected and *B* and *C* are connected, then there is a greater chance of *A* and *C* being connected) in our networks is negligible (see Snijders (2011). Using a Bayesian approach, we ran MCMCglmm models with all possible combinations of fixed factors (familiarity and treatment) and identified the best fitting model as the one with the lowest deviance information criterion (DIC) (Spiegelhalter et al., 2002).

#### *5.3.4.5 Between-treatment differences in coefficient of variation (CV) in association strength*

We calculated the CV in total association strength for calves in week 1 and week 4. ANOVA (with 5000 bootstrap permutations) were then used to test for significant differences in CV between calves of different treatments. Additionally, we re-ran the tests after omitting contact durations between calves that were pair-reared together, in order to determine whether there were treatment differences CV in total association strength, independent of the bond between individuals that were paired during pen rearing.

#### *5.3.4.6 Between-treatment differences in percentage of time spent with paired calf*

We calculated the percentage of social association time that individuals spent with the calf they were paired with during pen rearing and tested for differences between *P5* and *P28* calves in week 1 and week 4, using a one-way ANOVA.

#### *5.3.4.7 Between-treatment differences in social network measures*

Weighted degree centrality (hereafter referred to as degree centrality) and eigenvector centrality scores were calculated for each calf, in UCINET 6 (Borgatti et al., 1999), for week 1 and week 4 of barn grouping. However these measures were highly correlated (Spearman's rho= 0.992 (week 1) and 0.997 (week 4), significant to <0.0001), therefore we only used degree centrality in the analyses. We ran one-way ANOVA with bootstrap permutations (n samples= 5000) to test for differences between *I*, *P5* and *P28* calves in degree centrality in both week 1 and week 4.

## 5.4 Results

### 5.4.1 Pen rearing

#### *5.4.1.1 Overall health, growth and intakes*

It should be noted that one calf, allocated to treatment *I*, died on day 12, and the cause of death was unknown. All data for this calf was omitted from the analysis. The mean percentage of days with a faecal score above zero (indicating impaired health) was 10.77 (±8.22)%, and a respiratory score above zero (indicating impaired health) was 5.00 (±4.32)%. There was no significant effect of treatment on health scores (MANOVA: $V = 0.12$, $F = (4, 40) = .61$, $p = .657$ (Pillai's Trace)).

The mean concentrate intake over the whole trial period was 448.41 (±171.43)g/day. Mean concentrate intake was highest for *P5* calves, however there were no significant treatments differences in concentrate intake over the whole trial (*I*: 425.17 (±192.63)g, *P5*: 536.55 (±175.29)g, *P28*: 380.61 (±123.11)g; ANOVA: $F_{(2,\ 20)} = 1.89$, $p = 0.177$).

Calves weighed, on average 37.39 (±5.55)kg on arrival at the rearing unit and there was no significant difference in arrival weights between the treatments (*I*: 35.11 (±7.06)kg, *P5*: 39.39 (±3.59)kg, *P28*: 36.39 (±6.11)kg, $F_{(2,\ 36)} = 1.99$, $p = 0.152$). There was also no significant difference in growth between the treatments (ANOVA: $F_{(2,\ 20)} = 0.70$, $p = 0.510$). The mean specific growth rate across the whole trial period was 1.06(± 0.14)%

*5.4.1.2 Vocalisations, growth and intakes during weaning*

The number of vocalisations was significantly affected by stage of weaning (Friedman's ANOVA: $\chi^2\,(2) = 41.42$, $p<.001$). Calves vocalised significantly more during the weaning period (1.25 ±1.93 calls/h) than during the pre-weaning period (0.34 ±0.97 calls/h; Wilcoxon: $Z = -3.180$, $p = 0.001$, $q = 0.001$) and significantly more during the post-weaning period compared to the weaning period ($Z = -4.197$, $p <0.001$, $q <0.001$). There was no significant difference in the number of vocalisations between treatments during the pre-weaning period (*I*: 0.86 ±1.72 calls/h, *P5*: 0.10 ±0.9 calls/h, *P28*: 0.10 ±0.13 calls/h; Kruskal-Wallis: $H(2) = 0.19$, $p =.701$; Figure 5.4). However, treatment had a significant effect on the number of vocalisations during the weaning period (*I*: 2.76 ± 1.14 calls/h, *P5*: 0.73 ± 0.21 calls/h, *P28*: 0.46 ±0.16 calls/h; Kruskal-Wallis: $H(2) = 6.46$, $p =.008$; Figure 5.4) and post-weaning period (*I*: 109.38 ±51.40 calls/h, *P5*: 26.08 ±20.16 calls/h; *P28*: 45.42 ±26.77 calls/h; Kruskal-Wallis: $H(2) = 11.44$, $p <.001$; Figure 5.4). *I* calves vocalised four times more than *P5* calves during the post-weaning period (Mann-Whitney: $U = 2.00$, $p = 0.001$, $q = 0.001$) and over twice as much as *P28* calves ($U = 7.00$, $p = .014$, $q = .007$). During the post-weaning period *P28* calves vocalised significantly more than *P5* calves ($U = 17.50$, $p = 0.137$, $q = 0.048$).

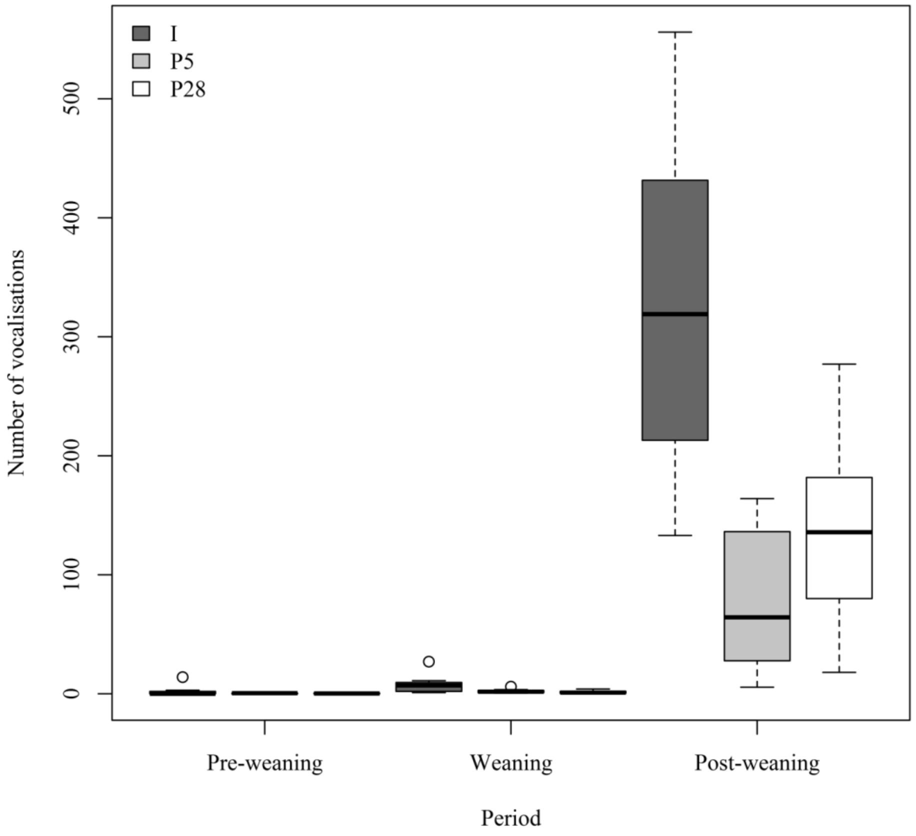


Figure 5.4 The total number of vocalisations, during 1 hour observations of calves, over each 3-day period (pre-weaning, weaning and post-weaning)

There was no significant difference in specific growth rate between treatments from day 47-55 (ANOVA: $F(_{2,\,20}) = .184$, $p = .833$). Stage of weaning had a significant effect on concentrate intakes (ANOVA: $F(_{2,\,40}) = 428.39$, $p < 0.001$); gradually reducing the volume of milk fed to calves over a 3 day weaning period (day 48-50) significantly affected the concentrate intake, which increased from 575.86 (±263.62) g/d pre-weaning to 973.37 (±374.10) g/d during weaning ($p<0.001$), and 1683.40 (±452.49) g/d, ($p<0.001$) post weaning. However, concentrate intake from days 48-53 (pre-weaning, weaning and post-weaning) did not significantly differ between treatments (ANOVA: $F(_{2,\,20}) = 1.67$, $p = 0.212$) nor did it differ between treatments depending on weaning stage ($F(_{4,\,40}) = 0.62$, $p = 0.654$).

### 5.4.2 Barn regrouping

#### *5.4.2.1 Network stability*

All week-long association matrices were significantly positively correlated, indicating a degree of stability in the calves' network (Table 5.1). The R squared value for the correlation between weeks 1 and 4 suggests around 50% of the network was stable from the start to the end of the month.

Table 5.1 Correlations between each week-long matrix, measuring network stability across weeks 1-4. Significance values were generated by comparing the observed values with those from 4999 null networks

| **Weeks** | **$R^2$** | ***p* value** |
|---|---|---|
| 1 and 2 | .572 | 0.0002 |
| 1 and 3 | .527 | 0.0002 |
| 1 and 4 | .505 | 0.0002 |
| 2 and 3 | .576 | 0.0002 |
| 2 and 4 | .554 | 0.0002 |
| 3 and 4 | .637 | 0.0002 |

#### *5.4.2.2 Social differentiation*

In each week–long social network there was significant social differentiation (table 5.2) which demonstrates that calves associated non-uniformly, spending more or less time with others than would be expected by chance.

Table 5.2 There was significant social differentiation for each week–long social network; calves spent more or less time associating with other individuals than would be expected by chance

| **Network** | **Social differentiation** | | **95% quantile of null distribution** | ***p* value** |
|---|---|---|---|---|
| | **Observed** | **Median of Nulls** | | |
| Week 1 | 20187018 | 606831.1 | 651672.5 | 0.0002 |
| Week 2 | 10949424 | 453363.6 | 489180 | 0.0002 |
| Week 3 | 10563239 | 516759.3 | 555467.9 | 0.0002 |
| Week 4 | 36357611 | 1005410 | 1085073 | 0.0002 |

#### *5.4.2.3 Assortment*

There was significant assortment by familiarity in week 1 (post. mean=1.417, p<0.001, DIC=4490.49) and week 4 (post. mean= 1.037, p<0.001, DIC=4664.901); calves spent more time with those they were more familiar with (in terms of duration of full social contact). Calves were not significantly assorted by treatment in week 1 (post. mean=-2.97, p=0.076, DIC=4876.727) or week 4 (post. Mean=-2.124, p=0.2, DIC=4876.406).

#### *5.4.2.4 Between-treatment differences in coefficient of variation (CV) in association strength*

ANOVA (with 5,000 bootstrap permutations) showed there was a significant difference in CV in association strength between treatments during week 1 ($F_{(2,34)}$=5.238, p=0.011; Figure 5.5a). A Bonferroni post hoc test revealed that *P5* calves had significantly higher CV than *I* calves. However, there were no significant differences in CV in association strength between treatments during week 4 ($F_{(2,34)}$=1.883, p=0.169; Figure 5.5b). After omitting the duration that calves spent with their paired calf from the analyses, there were no significant differences in CV in association strength between treatments in week 1 (F($_{2, 34}$)=0.504, p=0.609; Figure 5.5a) or week 4 (F($_{2, 34}$)=0.274, p=0.762; Figure 5.5b).

### *5.4.2.5 Between-treatment differences in percentage of time spent with paired calf*

The percentage of social association time individuals spent with the calf they were paired with during pen rearing (‘percentage pair-time’) was not significantly different for *P5* and *P28* calves in week 1 (F($_{1,24}$)= 0.831, p=0.371) or in week 4 (F($_{1,24}$)=0.583, p=0.453). Overall there was a significant decrease in percentage pair-time from week 1 (11.015±6.049) to week 4 (6.827±3.95) (paired samples t-test; t(25)=7.2. p<0.001).

### *5.4.2.6 Between-treatment differences in social network measures*

There were no significant differences between treatments in the weighted degree centrality of calves in week 1 (F($_{2,34}$)=2.402, p=0.107) or in week 4 (F($_{2,34}$)=0.763, p=0.475).

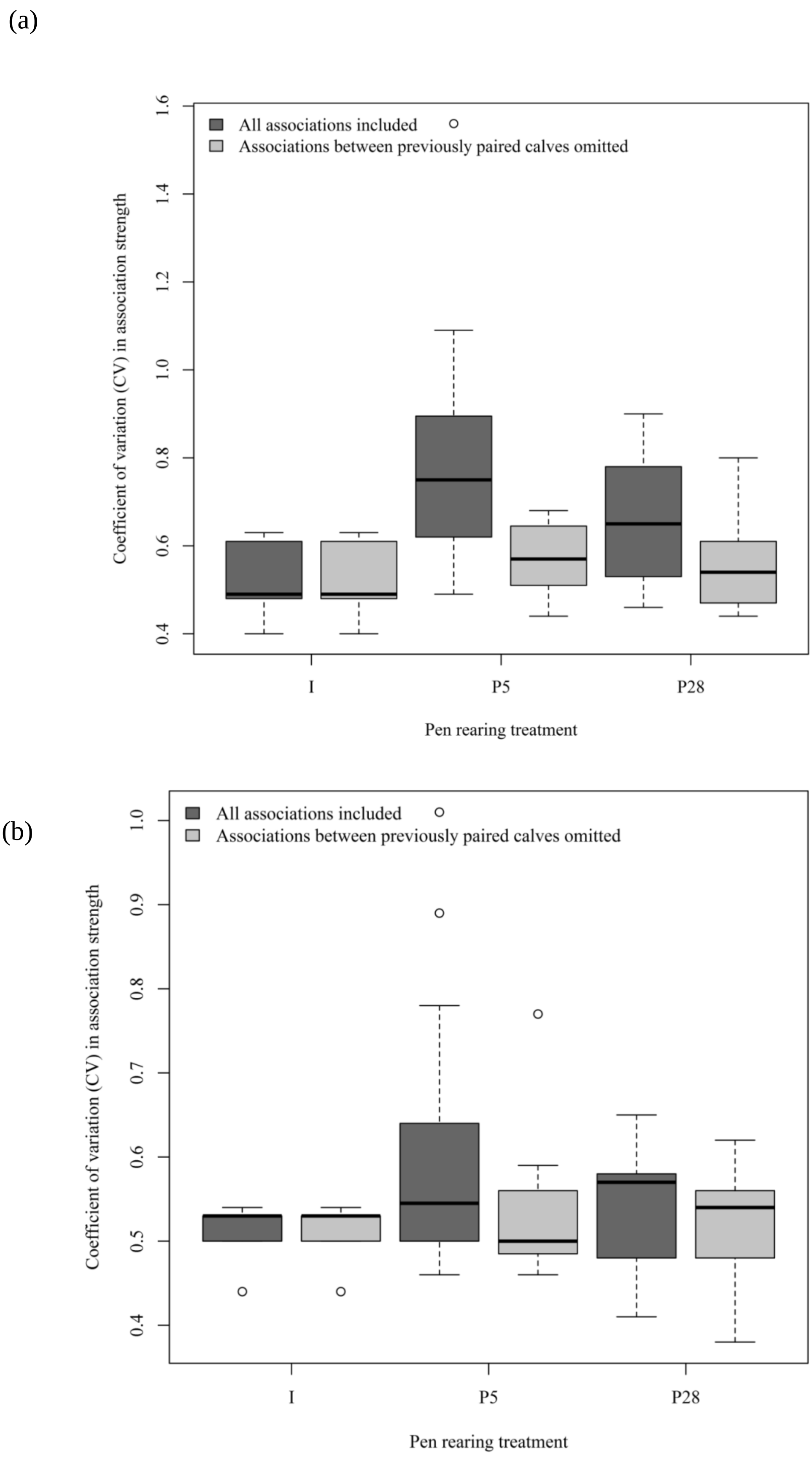


**Figure 5.5** The coefficient of variation (CV) in association strength for calves in each rearing treatment during week 1 (a) and week 4 (b). Light grey boxes show data when associations between previously paired calves was omitted.

## 5.5 Discussion

This study investigated the effects of early rearing methods on the health, productivity and welfare of dairy calves, on a UK commercial farm. Individual and paired pen rearing were compared and the effect of age at pairing was explored, with particular interest in how this influenced social support at weaning. Following pen rearing, calves were grouped and moved to a barn, and the social network that formed was measured using data from spatial proximity collars.

Dairy farmers often avoid grouping calves in early life due to the anticipated negative consequences for health and production. However in the current study, there was no evidence of health or productivity differences between calves that were housed in pairs or in individual pens. As required by UK legislation (Council Directive 97/2/EC), individually reared calves were still able to make direct (oral and nasal) contact through the slots in the partitions between pens, thus pathogen transmission may still have been possible. Past studies have reported a higher incidence of diarrhoea and respiratory diseases for group-reared calves (e.g. Maatje et al. (1993)), though the difficulties of early disease detection in larger groups (Svensson & Liberg, 2006) are thought to contribute to these findings. It is believed however, that calf immunity in conjunction with good hygiene, ventilation and adequate feeding can have a greater impact on susceptibility to disease than housing type (Chua et al., 2002).

Pair rearing or age at pairing did not influence the concentrate intake of calves during pen rearing in this study. Previous studies have described diverse findings. For example Maatje et al. (1993) observed reduced feed intake in group-reared calves and suggested this was due to competition for feed. In contrast, De Paula Vieira et al. (2010) and Warnick et al. (1977) found significantly higher concentrate intake for group-reared calves. Interestingly, these studies reported no significant increases in weight gain as result of the increased concentrate intake. In this study, weight gain over the whole trial period did not appear influenced by pair-rearing or by age of pairing. Our results support comparable studies evaluating weight gain of group-reared and individually reared calves (e.g. Arave, Mickelsen, and Walters (1985), Broom and Leaver (1978), De Paula Vieira et al. (2010), Duve, Weary, Halekoh, and Jensen (2012), Warnick et al. (1977)). However, a significantly higher  (Tapki, 2007) and a significantly lower Maatje et al. (1993) weight gain for group-reared calves compared to individually reared calves has been found in other studies.  Experimental methodology or management practices may account for these variations.

Vocalisations are a common behavioural response to the stress of milk withdrawal from calves (Jasper et al., 2008). Therefore unsurprisingly, we found a significant increase in the number of vocalisations during weaning and in the days post-weaning. The greatest effect was seen during the post-weaning period, when individually reared calves vocalised significantly more than pair-reared calves. In addition to the presence of a conspecific, the efficacy of social support may be influenced by several factors, including the strength of the affiliation between the individuals (Kikusui et al., 2006). Indeed in the current study, the significantly lower number of vocalisations exhibited by *P5* calves compared to *P28* calves suggests a greater affiliation between those paired at an earlier age and, resultantly, more effective social support.  There is often growth check in calves at weaning (Weary et al., 2008), and in this study growth rates over the weaning period were lower than the average across the whole trial period. The mean SGR was highest in the *P5* calves, however it was not significantly different to that of *P28* or *I* calves. Chua et al. (2002) reported lower growth rates in individually-housed calves when compared to pair-housed calves during the weaning period. The disparity between our findings and the findings of Chua et al. (2002) may be related to the increased concentrate intake by pair-housed calves which were not observed in this study.

After (all) calves had been grouped in the straw barn, we quantified their social relationships and network structure by measuring time in close proximity. We found significant positive correlations between all week-long matrices, indicating that over the one month data collection period calves were stable, to some degree, in their social associations. Correlations indicated a very similar level of consistency from weeks 1-2 and weeks 1-4. Therefore, network stability did not appear to lessen over this time. We also found that calves were socially differentiated; there was heterogeneity in the connections between individuals. In combination, these results suggest that there was stable inter-individual variation in social associations, and thus social preferences of calves were detected. In a recent study by Koene and Ipema (2014), calf social networks were created from nearest neighbour data but the authors found no evidence that calves had preferred partners or that social relationships were stable; daily matrices were not significantly correlated (apart from 1 out of 12 matrix pairs which were negatively correlated). Disparity between our results and those of Koene and Ipema (2014) may be due to differences in methodology; they used a smaller group (n=10) of older (3-4 month old) calves, and do not provide information on the history or familiarity of the focal individuals.

Calf networks were assorted by prior familiarity (number of days of full social contact prior to grouping in the barn) however there was no evidence for assortment by treatment type. Assortative mixing refers to the tendency for individuals to associate more with those that are similar to them in some way, and has been found in networks of adult cattle (*Chapter III*). The degree of familiarity is likely to have reflected the strength of social bonds, therefore our results support previous findings of cattle associations (e.g. Raussi et al. (2010), Sato et al. (1987), Færevik et al. (2006), Færevik, Andersen, Jensen, and Bøe (2007)). Assorting with familiar conspecifics can provide adaptive benefits, such as the use of information from prior experiences to improve group activities, and reduction of conflict via predetermined dominance relationships (Krause & Ruxton, 2002). In the farm environment, familiarity may also be particularly significant in terms of improving social support. The enhanced social support observed in *P5* calves at weaning, along with the preference of calves for familiars when grouped in the barn, supports other studies (e.g. Bøe and Færevik (2003); Rault (2012); Raussi et al. (2010)) suggesting that human-managed animals should be encouraged to form stable social bonds over time, due to the welfare benefits.

Although familiarity between individuals may vary considerably when a group first forms, over time this variation decreases, suggesting the effect of familiarity on social bond strength would eventually become insignificant. However research suggests that early preferences persist into adulthood, which may indicate a sensitive period for social bond formation in cattle (Raussi et al., 2010). Vitale et al. (1986) observed calves in a free-ranging context, and found that time associating with peers was highest from 11 to 40 days of age. Indeed a number of studies show that early social relationships remain for substantial time periods (e.g. Sato et al. (1987), Reinhardt and Reinhardt (1981), Bouissou and Hövels (1976), Bouissou and Andrieu (1978), Raussi et al. (2010)). For example, Bouissou and Andrieu (1978) found that heifers grouped at birth formed more preferential associations than those grouped at six or 12 months, and in a study by Gygax et al. (2010) cattle that had been reared together were more synchronised. Both pair-housed treatments (*P5* and *P28*) involved full social contact for calves within this potential sensitive period, and although differences based on age at pairing were seen during weaning (in the stress response to weaning), in the month following regrouping there were no substantial differences in the amount of time calf pairs spent in close association. In week 1, the CV in association strength between calves was significantly higher for *P5* calves than *I* calves, indicating that their (*P5* calves) associations were more heterogeneous. This effect appears to have been driven by the time *P5* calves spent with their pair from pen rearing, as there were no significant differences when these associations were omitted. Further, by week 4 these treatment differences in association patterns were no longer significant. Heterogeneous social associations could be beneficial in the farm environment if, for example, an individual contracted an infectious disease. If the infected calf mostly associated with only a few individuals, it may allow farmers more time to detect the sick calf before pathogens are spread to the rest of the group. This could be particularly important for grouping of young calves, when immunity is less developed.

The early social environment has been shown to affect calves' development. For example individually housed calves were more reactive to environmental and social novelty (indicated by increased rates of defecation, kicking and vocalisations) than pair-housed calves (De Paula Vieira, de Passillé, & Weary, 2012) and did not perform as well in cognitive tasks (Gaillard, Meagher, von Keyserlingk, & Weary, 2014). Social rank later in life can also be affected; group-housed calves achieved higher dominance rank than individually reared calves (Warnick et al., 1977). Developmental conditions have also been linked to social network position (Boogert et al., 2014), which has implications for access to resources (e.g. Aplin, Farine, Morand-Ferron, and Sheldon (2012)) and exposure to pathogens (e.g. Bull, Godfrey, and Gordon (2012)) etc. In this study, there were no significant differences based on pen rearing treatments in weighted degree centrality, however further work is required to explore this fully. This research was carried out on a commercial farm, where management determined that calves entered the barn, by block, on different days (five calves entered the group every three days). As we only measured networks after all calves had entered the group, we may have missed initial treatment differences in social behaviour, particularly as *I* calves were experiencing full social contact for the first time. Similarly, we only quantified the social network structure for one month, and differences in network position may appear later in life, when social behaviour develops and dominance hierarchies form. Future work should be aimed at understanding the temporal dynamics of dairy cattle from early rearing through to lactation and beyond.

### 5.5.1 Conclusions

The health and productivity of calves was not affected by rearing treatment during the study, but social pairing appeared to reduce stress at weaning via social support. Calves paired at 28 days provided noticeable social support to each other at weaning; however more effective social support was achieved by pairing calves at five days old. Therefore allowing full social contact with other calves as early as possible should be encouraged. The calf social network structure demonstrated stability in the associations between individuals following barn grouping, with relationships reflecting prior familiarity. The percentage of time that calves spent with their paired calf did not differ based on age at pairing, but did decrease over time. Quantifying social group structure and stability is important for minimising stress and improving welfare in the dairy industry.

# Chapter VII

## General Discussion

## 6. 1 Main findings

The intensification of UK dairy systems, in response to increased demand and competition from abroad, has resulted in cows being housed in large, dynamic groups (McLennan, 2013). The consequences of modern dairy farm conditions for social group structure and relationships between cows are now being explored. Improving our understanding of the social requirements of dairy cattle, and indeed other farm animals, will allow us to provide appropriate group housing that leads to positive social relationships which can enhance welfare and productivity. The overall aim of this thesis was to investigate the social network structure of dairy cattle (*Bos taurus*) and to test for relationships between network measures and welfare and productivity. I measured social relationships between a dynamic group of lactating cows, and also between young calves, on commercial dairy farms. In this discussion chapter I summarise and discuss the main findings from my thesis and suggest avenues for future research in these areas, and lastly propose some additional directions for research.

### 6.1.1 An automated data collection method can measure animal social networks but comes with challenges

#### *6.1.1.1 Sampling bias*

The first major finding of this thesis was that technology developed to improve the efficiency of behavioural data collection, and remove human sampling biases, generated a sampling bias of its own. Automated data collection is increasing in popularity as technological advances provide devices that can generate rich datasets and are small enough for easy deployment on animals (Krause et al., 2011; Rutz et al., 2012; Ryder et al., 2012). Spatial proximity loggers have been used to collect social data on a variety of animals in other studies, including cattle (O'Neill, Bishop-Hurley, Williams, Reid, & Swain, 2014; Swain & Bishop-Hurley, 2007), and can enable interesting ethological questions to be asked and answered. Some research into the reliability of Sirtrack proximity loggers had been conducted prior to this project (e.g. Prange et al. (2006) and Drewe et al. (2012)) and other researchers (e.g. Hamede et al. (2009); Patison et al. (2010); Walrath et al. (2011); Cross et al. (2012)) had previously noted that association matrices produced by logger data were asymmetrical (indicating differences within a dyad in proximity contacts, a measure that is inherently non-directional). However the implications of non-reciprocity in contact data were not fully realised. These were demonstrated in *Chapter II*, where we showed that performance variation existed between loggers, which resulted in inaccurate datasets and unreliable social networks.

We investigated the source of variation in contact records, finding that they were not only due to general error resulting from variation in size and position of the animal or properties of surrounding objects (Prange et al., 2006), but that loggers were inherently different in the extent to which they recorded others. Differences between dyads varied but could be very substantial, with almost 30% differences in some cases. When social networks were constructed from this data, many cows wearing loggers that were found to over-record (having a positive mean logging bias) appeared to be more gregarious than others, demonstrating that networks created from raw logger data cannot be relied upon (providing the set of loggers exhibit a logging bias). Fortunately we found within-logger consistency in the logging biases, which led to the development of a method that can be used to correct the data. Due to the correction procedure there were some restrictions on how we could use the data. For example, calculating the mean logging bias required that all cows encountered all (or most) others. This requires data be collected over a period long enough that all cows encountered all others. We were able to make week-long matrices, but this involved removing some of the cows from the dataset if they did not have records with the majority of others. The correction method results in association matrices of accumulated contact durations over a given time period; however it does not allow for fine scale temporal data analysis. Future application of this method may require further, context-specific validation.

#### *6.1.1.2 Additional challenges with Sirtrack proximity loggers*

In addition to the logging bias, the proximity loggers presented other problems related to the practicalities sides of data collection and for data handling prior to analysis. Some of the difficulties were unavoidable and expected, while others were unpredicted. Therefore, I will describe these issues (listed in Table 6) in order to highlight these to other researchers who may use this technology in the future. As loggers were deployed on a (mostly) indoor group of cattle, and thus the high density of animals meant that memory capacity (each logger can store up to 32,767 contact records) was reached fairly quickly. Data were only recorded for around 4 weeks, and then had to be manually downloaded for each logger individually. This required the removal of loggers from cows, and led to gaps of at least 4 days in the data. This was not of major concern for the type of analysis carried out in this thesis, however it maybe more problematic for other studies assessing social associations on a finer scale and over a longer time period.

As described in previous studies (Drewe et al., 2012; Prange et al., 2006; Watson-Haigh, O'Neill, & Kadarmideen, 2012) we also found many 1-second records in our dataset and logger clocks drifted by varying amounts. These 1-second records are considered to be unreliable, occurring sporadically when individuals are at the edge of their detection range; we therefore removed these records from the dataset as advised (Drewe et al., 2012; Prange et al., 2006). ‘Clock drift’ refers to instances where the logger’s internal clock is set to the correct time before the deployment, but is inaccurate by a number of seconds when the logger is later downloaded. This varies between loggers even when these are set and switched on and off within a few hours of each other, and are left to collect data for the same time period. For example after a ten day deployment of 103 loggers (unpublished date) clock drift ranged from -111 seconds to +117 seconds, and the clocks of three loggers were "not set" when data was downloaded. In a later deployment of 86 loggers (unpublished data), clock drift ranged from -488.85 hours to +133.24 hours. Another known issue that was in a study by Drewe et al. (2012), was that as battery power decreases over time, logger function is declines, therefore we chose to analyse each deployment separately. Similar to a study by Watson-Haigh et al. (2012) we also found records referring to loggers that did not exist. The number of logs recorded for these non-existent loggers were considerably lower than the number of logs recorded for actual loggers, and removing the data was fast and easy. Yet this does raises the concern that if fake contacts could be spontaneously recorded for non-existent loggers, there may also be fake contacts created for existing loggers, which would likely go unnoticed if they were not particularly unusual (e.g. of unusually long duration, or between cows that were known to be out of detection range at the time that contact was recorded). However, these would be accounted for during the logging bias correction to some extent, and we do not expect there would be many instances of this occurring.

During downloads I also found that some loggers had incorrect settings (e.g. the UHF value had changed), or had been switched off during the deployment; but note that these cases were rare. As loggers do not have an external power switch (loggers are switched on/off by holding a magnet against the logger) that could have been knocked by the cow, we are unsure why this happened. It may have been the result of the logger experiencing a substantial blow against a hard surface, etc. or a fault in the internal hardware.

Lastly, we found that some loggers stopped logging contacts or being logged by others prematurely; for example loggers sometimes stopped logging contacts before they had reached their memory storage capacity, but continued to be logged by others showing that they were still producing a signal and thus the batteries were not exhausted. This happened to only a few loggers during each deployment however there was no obvious explanation for this. We omitted the data from these loggers from the dataset as, unsurprisingly, this created significant dyadic reciprocity issues and affected the logging biases that were calculated during the correction process.

Table 6.1 Summary of problems encountered when using Sirtrack proximity loggers, and our response to these.

| Problem | Response |
|---|---|
| 1. Logging bias | Altered data using the correction method (*Chapter II*) |
| 2. Memory fill and manual download | Removed loggers after one month, redeployed multiple times |
| 3. Sporadic 1-second contact records | Removed these contacts from the dataset |
| 4. Clock drift | Used accumulated data (but see *6.1.1.4*) |
| 5. Battery power decline decreases signal | Analysed each deployment separately and did not quantitatively compared these. |
| 6. Recorded contacts for non-existent loggers | Removed these records from the dataset |
| 7. Incorrect settings or switched off before end of deployment period | Omitted records from the dataset |
| 8. Stopped logging or being logged before memory capacity was reached | Omitted logger data from dataset if this occurred mid-deployment |

Due to the issues described above, a proportion of the data collected was omitted and some cows were therefore removed from the final dataset used in analyses. This was unfortunate, however this cautious approach means the remaining data can be considered more trustworthy. We were still able to analyse social structure using this ‘incomplete’ dataset; in fact, in many studies of wild animal groups researchers are only able to collect data on a proportion of the group/population (Croft et al., 2008). With the increasing use of automated data collection methods in animal studies, research into the reliability and accuracy of the technology is essential. Though there may be numerous challenges to overcome when using new technologies, they can lead to rich datasets which would be almost impossible to collect using more traditional methods.

#### *6.1.1.3 Spatial proximity data reflects affiliative interactions between cows*

Allogrooming and spatial proximity between cattle are believed to reflect social relationships (Bouissou et al., 2001). We found that associations recorded by the proximity loggers were positively correlated with social grooming events recorded during behavioural observations. A relationship between spatial proximity and allogrooming was also confirmed by Val-Laillet et al. (2009) however it was important to test for this relationship using the data collected by the proximity loggers.

#### *6.1.1.4 Future directions*

Another correction method is currently being developed (led by collaborator DM), which will become part of DM’s thesis. This correction method aims to increase the reliability of contact records from proximity loggers without reducing the temporal resolution of the data, and involves editing contacts based on their reliability weighting, which is determined based on the five principles outlined in Table 6.2. All contact records that are considered less reliable than a given threshold are filtered out of the dataset. This correction method corrects each contact record individually, and thus we do not lose resolution and the data can be used to explore patterns in social interactions through time.

Table 6.2 Five principles underlying a new logger data correction method

| Principles determining reliability of contact records |
|---|
| **1.** Contact records from the logger with least clock drift are more accurate. |
| **2.** Contact records that are longer in duration, are more reliable than shorter contact records. |
| **3.** Contact records that occur close (in time) to other records with the same encountering logger, are more accurate than contact records that are isolated in time. |
| **4.** Contact records logged by ‘under-sampling loggers’ are more accurate than the contact records logged by ‘over-sampling loggers’. |
| **5.** Reciprocated contact records (i.e. both loggers concurrently record contacts) contact records are more reliable than non-reciprocal contact records. |

The new correction method would be particularly useful in improving data when studying effects of social disruption (i.e. when an unfamiliar cow is introduced into the milking group) or social instability (i.e. when cows are regrouped). In a study by von Keyserlingk et al. (2008) when a single unfamiliar cow was added to an existing group of 11 cows (the study included 4 replicates of this set up, and control groups) competitive displacements were elevated for up to 3 days, lying time decreased on the day of social disruption and a reduction in allogrooming was observed for two days after the disruption. These effects were found after one cow was added to an otherwise small, stable group; although experimentally useful, this does not replicate the type of social change that happens on farm, where group sizes are larger (average herd size was 133 in 2014 (DairyCo, 2015)) and multiple cows are interchanged between groups and pens simultaneously. Hasegawa et al. (1997) swapped half the cows between two groups of 51 primiparous heifers and found that social behaviour did not return to baseline levels until day 15 after regrouping. Other studies report various durations for groups to stabilize, such as 10 days (Tennessen, Price, & Berg, 1985) and 30-45 days (S Sato, Sassa, & Sonoda, 1990), though there is considerable variation in study design and type of cattle across these examples. Automated data collection would offer huge advantages for measuring temporal social dynamics in large groups. Further, using SNA to investigate these detailed contact records, collected continuously and automatically, would be ideal for exploring the effects of social disruption. Studies using more traditional methods may measure changes in the number of interactions, or the duration of different activities, however they are not able to quantify the effects on group structure. For example, following a disruption event the number of social interactions may eventually return to baseline, however they may have been redirected to different individuals. Unless the identity of individuals involved in the social interaction is incorporated into analysis, we cannot fully understand the social group structure or the effects of the social stressor.

### 6.1.2 Social structure in dairy cattle

The first objective of this project was to measure the social network structure of dairy cattle. Studies of feral, semi-wild and extensively grazed cattle have explored the social structure of cattle in the absence of human intervention and have found that cows tend to form long-term stable social relationships and social structure appears to be based on matriarchal families that are interconnected by non-kin social bonds (Lazo, 1994; Reinhardt & Reinhardt, 1981). Lazo (1994) studied the social group structure of “mostrenca” cattle in Spain (a population that has undergone very little human management since the 13th century). There were approximately 140 individuals living in an area of 67km$^2$, and these were organised into highly stable sub-herds of around 20 adult females, 3 adult males, 6 young females, 7 young males, and 13 calves. Examples of groups that have formed under more natural conditions are quite different to group compositions that are typical of the current dairy industry: typically larger, all-female (though there may be one bull in the group), all-adult groups that experience frequent social instability.

Results from *Chapter III* and *Chapter V* show that, under commercial conditions, the relationships between cattle were more heterogeneous than would be expected by chance, and thus non-random social structure was observed. All cattle social networks measured in this thesis were highly centralised and showed no evidence of community structure. These findings are comparable to  other studies on social associations in dairy cattle on commercial farms (Gutmann, Špinka, & Winckler, 2015; Gygax et al., 2010). The lack of communities, or sub-groups, is perhaps unsurprising given the space restriction of the farm environment, and also due to the daily routine of food delivery etc., encouraging cows in the group to synchronise activity to some level; activity budgets and group synchrony are believed to be important factors for subgrouping in wild animal populations (Conradt, 1998; Conradt & Roper, 2000).

Group-level stability (repeatability) of social relationships was low for both adult cows and calves, although networks were significantly correlated from week-week, and consequently there did appear to be some consistency in whom cattle associated with. These results have welfare implications, as social disruption imposed by husbandry can act as a stressor (Hasegawa et al., 1997; Mench et al., 1990). Thus long-term social instability may lead to animals experiencing chronic stress which is detrimental to both welfare and productivity.

We did find evidence for assortativity in the networks, a measure of the tendency of individuals to associate with others that share their characteristics (Wolf, Mawdsley, et al., 2007). Cows associated more with others of the same breed, of similar lactation number, and those more similar in milk yield during the study periods. Cows were also assorted by gregariousness (see 6.1.3).

#### *6.1.2.1 Future directions*

Maintaining suitable inter-individual distances according to partner preferences and social status reduces conflict between individuals, and thus decreases social stress (Miller & Wood-Gush, 1991; O'Connell et al., 1989). However it is unknown to what extent stocking density affects group social structure and social stress, and this should be tested empirically in future work. Over 500 faecal samples were collected from the adult cattle studied in this thesis, during the four logger deployment periods. Faecal GC metabolite concentrations can provide a measure of an animal’s average GC levels, and thus can be used as an indicator of stress levels (Möstl & Palme, 2002). Unfortunately, due to multiple delays in processing the samples, the data could not be included in this thesis. In future research, this data can allow us to ask a number of interesting questions about the relationship between stress and social factors. For example, we could test whether the gregariousness of individuals is related to the amount of stress they experience during group instability. Other methods are available for measuring stress in cattle, e.g. GC levels in saliva samples (Chacón Pérez, García-Belenguer Laita, Illera del Portal, & Palacio Liesa, 2004) or heart rate monitors (McLennan, 2013); these may be good options to consider when measuring the stress response to social dynamics on a finer scale, and could work well with social data collected automatically.

### 6.1.3 Gregariousness

Due to the nature of the networks in this thesis, many of the social network measures that were calculated for individuals were highly correlated with each other, and thus it did not enhance our studies to use more than one. Therefore, weighted degree centrality was used as a simple measure of gregariousness. In *Chapter III*, we demonstrate that there was weak assortment of cows by gregariousness, though the direction of the effect was inconsistent. In deployments 1 and 2, cows associated more with those similar in gregariousness to themselves, while in deployment 3 they associated more with those that differed in gregariousness, highlighting the need for repeated studies across other groups of cattle. Assortment by gregariousness has also been demonstrated in guppies, *Poecilia reticulata* (Croft et al., 2005), bottlenose dolphins, *Tursiops truncates* (Lusseau et al., 2006) and humans (Newman, 2003).

Increased gregariousness has occurred during domestication in various livestock (Price, 1997); as gregarious individuals are likely to cope better in captive groups and may therefore be more productive. In fact in *Chapter IV*, analysis revealed a relationship between gregariousness and health and productivity measures. Cows that were more gregarious during the study also had higher milk yields. This suggests there are benefits associated with being gregarious that could be related to a reduction in stress, however this needs to be tested (see *6.1.2.1*). We also found a positive relationship with gregariousness and SCC, which may illustrate a cost to being in close proximity to others and thus there may be a trade-off between disease transmission and social cohesiveness. As mastitis-causing pathogens are not believed to be directly transmitted from cow to cow, it is likely that this effect is driven by a greater level of environment sharing by gregarious cows; those that spent longer in close proximity to others may have been exposed to more pathogens in their shared environment. In *Chapter III* we also found that cows that associated together more, had more similar SCC.

In the calf networks (*Chapter V)* we did not find any significant differences in gregariousness between calves from different rearing treatments. Broom and Leaver (1978) found that higher social rank was achieved at 8 months old by calves that were reared in small groups compared to those reared individually, suggesting there may be an effect on social structure. However as it is required by law for calves in the European Union to be housed in groups after 8 weeks old, the differences in social development may not appear as strongly, or may not have appeared yet.

#### *6.1.3.1 Future directions*

In light of the relationship we found between gregariousness and SCC (described in **6.1.3**) it would be very interesting to test for a relationship between gregariousness and diseases that are directly transmitted from one cow to another. Disease remains a major problem in animal agriculture today, and is closely linked to the social environment via social stressors that impact health (Proudfoot et al., 2012). Patterns of social interactions, in the context of the group's social organisation, are also significant for studying disease transmission. For example in a study by Drewe et al. (2011), meerkats that groomed others more were at greatest risk of TB infection, a finding that could be valuable for disease control programmes. Learning more about these links may enable us to reduce pathogen transmission between animals in a group, or indeed between groups in a population, which could have huge impacts on farm animal health and management.

Further research into individual gregariousness as a consistent trait in cattle could be beneficial. Consistent social behaviour responses have been found in a few other studies (Gibbons et al., 2009; Gibbons et al., 2010; Hopster & Blokhuis; Müller & Schrader, 2005) suggesting this could be possible. Moreover, if gregariousness proved to be a heritable social trait, this could allow the breeding of cows that are better able to cope in the social environment of the modern farm, thus enhancing welfare.

### 6. 1.4 Familiarity, social bond strength and implications for social support

Research into the stress calves experience during weaning in *Chapter V*, supports previous work showing that the withdrawal of milk acts as a stressor for calves (Jasper et al., 2008), and that pair housing can provide calves with social support effective in reducing the stress response (De Paula Vieira et al., 2010). This effect has also been found in another context; when calves were provided with a companion calf during group separation (rather than separation from the main group alone), their stress response was lower (Færevik et al., 2006) and when the companion was a *familiar* calf, the stress response was further reduced. Results from *Chapter V* show that the stress response to weaning was significantly lower in calves that had been pair-housed from 5 days old compared to those housed individually. In addition, we found that calves paired from 5 days old also have a significantly lower stress response to weaning than those that were paired at 28 days, thus suggesting that the strength of the social bond between the pair influenced the amount of social support received. It is likely that the effectiveness of social support is also affected by social bond strength in adult cattle. McLennan (2012) demonstrated that when dairy cows were separated from their social group, their heart rates were lower when they were given a familiar cow as a companion, and when that companion was also a preferred partner (i.e. a cow with whom the focal animal had a stronger social bond) heart rates were further reduced.

Familiarity appears to be a substantial determinant of social bond strength in cattle. In *Chapter V* we found that when calves were moved into a barn and grouped together, the social network was significantly positively assorted by familiarity, meaning that calves spent more time associating with those they had known for longer. Similarly, in *Chapter III* we show that cows were significantly positively assorted by lactation number, which reflects life-time familiarity; the strength of dairy cattle social relationships was also connected to long-term familiarity in a recent study by Gutmann et al. (2015). The growing evidence for links between familiarity, social bond strength and implications for social support provide further evidence that allowing cattle to maintain stable social bonds can increase welfare.

#### *6.1.4.1 Future directions*

Future research would benefit from repeating the study in *Chapter V* but on a larger scale and over a longer timeframe. We were only able to measure calf networks for a one month period following barn grouping, but it may be that differences in social network measures manifest later in life. A longitudinal study of the social network in a stable group from calf to death would be very interesting.

Continuing research into the connection between social bond strength and social support would also be beneficial, including identifying the most efficient way for farmers to detect strong social bonds and take advantage of these. For example, strong social relationships could be used as a stress buffer during typically stressful events such as regrouping or during veterinary procedures.

## 6.2 Additional directions for future research

### 6.2.1 Integrating social behaviour and technology on farm

As more and more aspects of farm management become computerised and automated, there are increasing opportunities to improve efficiency in animal monitoring and husbandry. In this section, I suggest areas that could be enhanced by incorporating social behaviour and relationships into management systems and social network analysis would be advantageous here (*6.2.1.1*). Additionally, data from technology on farm could be used to collect data for the study of animal behaviour.

#### *6.2.1.1 Oestrous detection*

There are various methods available to try to predict oestrous (with aims to improve reproductive efficiency), including visual observation, biosensors, milk temperature, mount detectors, pedometers and activity loggers (Firk, Stamer, Junge, & Krieter, 2002). However, the occurrence of silent ovulation is significant (Ranasinghe, Nakao, Yamada, & Koike, 2010) and the incidence of oestrus going undetected is increasing (Dobson, Walker, Morris, Routly, & Smith, 2008; Walsh, Williams, & Evans, 2011). None of the aforementioned methods are 100% accurate, for example oestrous detection via activity levels may often be confounded by lameness (Walker et al., 2010), and systems may rely on using more than one method simultaneously.

Sirtrack loggers have recently been used to measure cow-bull associations in order to detect oestrous in beef cattle at pasture in Australia (O’Neill et al., 2014). However, for many dairy farms that do not run a bull with the dairy herd, we may be able to use such technology to detect the onset of oestrous via changes in social networks. Around oestrous the behaviour of cattle changes significantly - mounting behaviour occurs between females and when more than one cow is in oestrous they form, and spend much of their time in, what are referred to as sexually active groups (SAG) (Albright & Arave, 1997). Sveberg et al. (2013) found that SAG (and related behavioural changes) could be used as indicators of oestrous. The use of SNA to quantify changes in individual social behaviour and social associations that occur during oestrous should be explored, and automated data collection methods would be well suited. This could allow detection of oestrous even in cows that do not express typical oestrous ‘mounting’ behaviour, and therefore has huge potential in improving artificial insemination efficiency.

#### *6.2.1.2 Improving voluntary milking systems*

Social dominance has substantial effects in livestock systems when it leads to unequal access to important resources (Grant & Albright, 2001). For dairy cattle this could include difficulty for subordinates in accessing food, water, cubicles, gateways or the milking parlour. Voluntary milking systems (VMS) reduce labour, can generate a vast amount of information on individual cows’ health and productivity, and give cows some control over when they are milked, being more adaptive to individuals’ daily activity patterns (Jacobs & Siegford, 2012). However, as with any system, there are welfare implications to consider.

When carrying out behavioural observations, on the farm studied in *Chapters III* and *IV*, I observed considerably higher agonistic encounters when cows were in the waiting area for the VMS (unpublished data). After entering the waiting area (see Figure 6), cows compete for access to the two milking units (MU), and once inside this waiting area cows cannot leave until they have been milked. Social dominance thus plays a major role in determining how long an individual waits in this area; when there is high demand for the MU, waiting time for a subordinate cow may be very long. During behavioural observations, I observed some cows waiting for access to the MU for over four hours (unpublished data). This has major implications for welfare and production, as the longer cows wait, the longer they are prevented from feeding and resting, which may be even more significant for lame cows.

As the VMS stores detailed information about milking events on a central computer, I was able to download data such as: Cow ID, date/time of entry to the waiting area, date/time of start and finish of milking in the MU, date/time of exit from the waiting area. The resultant dataset contained information on all milking events for 127 cows over two months. I conducted preliminary analyses, along with DM, and we developed a method to calculate CO from this dataset (unpublished data). Dominance is classically assessed via behavioural observations such as continuous sampling of all occurring agonistic interactions to establish relationships between individuals; and creation of a competitive scenario to encourage agonistic behaviour e.g. presenting food to two animals in a bucket only large enough for one to feed from. The second method results in a CO which indicates dominance in a specific context and is influenced by motivation for the resource (G. Syme, 1974). Traditional methods to measure dominance become more difficult and time consuming as group size increases.

The basic idea behind our CO method was that each time ‘cow A’, for example, enters the waiting area, she competes against all others for the MU. From that point forward, every cow that is milked before cow A scores a ‘win’ against her. When cow A succeeds in entering the MU she is considered to be out of the competition and scores a ‘win’ against all those that are left in the waiting area. When this is done over a substantial time period, cows will compete against each other multiple times allowing calculation of CO scores. Within our two month dataset 97% of all possible cow dyads were observed in the waiting area together at least once.

There are multiple potential applications for this research after further development: 1) It provides a measure of dominance that could be useful for researchers;

2) It could be used as an indicator of health decline, as unexpected changes in CO may occur due to illness; 3) By integrating CO into the VMS system, it could be used to grant different access to cows to reduce overall waiting times for the MU. For example, if there were multiple MU on farm, subordinate cows could be directed to the MU with least number of cows waiting; or when there are equal numbers of cows in all MUs, directed to the unit with cows of lowest overall CO.  It would be advantageous to reduce waiting times of subordinate individuals in the group; time spent standing is a significant risk factor for lameness (Fregonesi, Flower, Vittie, Tucker, & Weary, 2002; Francisco Galindo & Broom, 2002; Leonard, O'Connell, & O'Farrell, 1996).  It could also be used to give priority access to lame cows (with a higher requirement for rest and potentially a reduced ability to compete), by directing a lame cow to a MU and not directing any non-lame cows there until she has been milked. This could substantially improve welfare for such individuals.

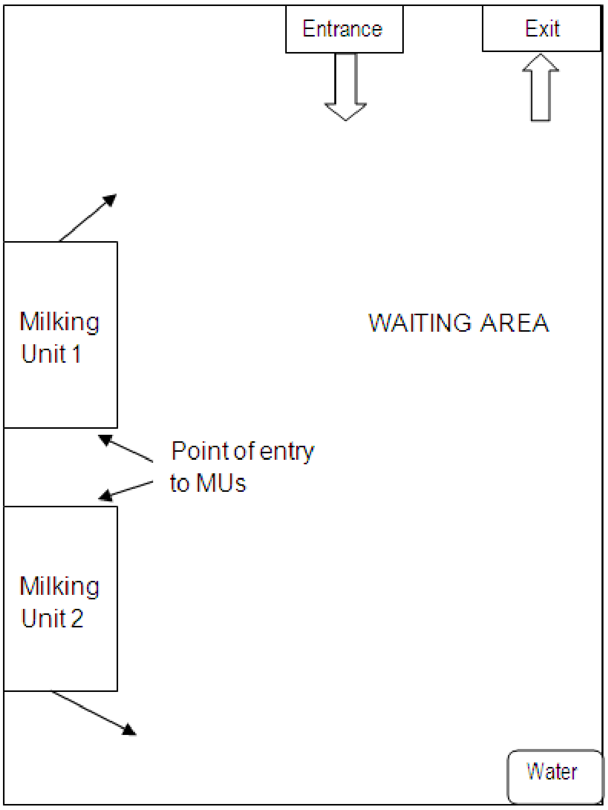


**Figure 6** Schematic representation of the VMS waiting area. Cows due to be milked are allowed access to the waiting area via the entrance gate, activated by collar transponders. Cows are not allowed to exit the milking area and return to the barn until they have been milked by one of two milking units (MU)

## 6.3 Conclusions

In this thesis, I used social network analysis to measure the social structure of dairy cattle, and explore the connection between social relationships and welfare and productivity. Social relationships were determined by continuously recording spatial associations between cattle using Sirtrack proximity loggers. This resulted in a rich dataset but also an important lesson in treating novel technologies with caution and investing time in validation. In a commercial farm environment, relationships between cattle were heterogeneous and network assortment offered some explanation for differential associations. However, social group structure was not particularly stable for cows or calves, which has negative implications for welfare and productivity. Familiarity between cattle appeared to be a significant factor determining the strength of social bonds, and the importance of social bond strength was nicely demonstrated by calves' enhanced benefit from social support during weaning, due to stronger social bonds. Gregariousness was associated with higher milk yield but also with poorer udder health, suggesting costs and benefits to associating with others. With the expansion and intensification of dairy systems, and use of large, unstable management groups, an understanding of the consequences is fundamental to the welfare of cattle. The application of SNA to quantify social dynamics is likely to play an important role in the future of farm animal welfare science, and this thesis takes an important step in this direction.

# References

Adkins-Regan, E. (2002). Development of sexual partner preference in the zebra finch: a socially monogamous, pair-bonding animal. *Archives of sexual behavior, 31*(1), 27-33.

Albright, J. L., & Arave, C. W. (1997). Reproductive behaviour *The Behaviour of Cattle* (pp. 82-89). CAB International, New York.

Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., . . . Jones, K. E. (2003). Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, 517-547.

Andersen, I. L., Nævdal, E., Bakken, M., & Bøe, K. (2004). Aggression and group size in domesticated pigs, Sus scrofa:'when the winner takes it all and the loser is standing small'. *Animal Behaviour, 68*(4), 965-975.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (Parus major). *Ecology Letters, 16*(11), 1365-1372. doi: 10.1111/ele.12181

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). *Social networks predict patch discovery in a wild population of songbirds* (Vol. 279).

Appleby, M. C., Hughes, B. O., & Elson, H. A. (1992). *Poultry production systems: behaviour, management and welfare*: CAB international.

Appleby, M. C., Hughes, B. O., & Mench, J. A. (2011). *Animal Welfare*: CABI.

Arave, C., Mickelsen, C., & Walters, J. (1985). Effect of early rearing experience on subsequent behavior and production of Holstein heifers. *Journal of dairy science, 68*(4), 923-929.

Arave, C. W., & Albright, J. L. (1981). Cattle behavior. *Journal of Dairy Science, 64*(6), 1318-1329. doi: http://dx.doi.org/10.3168/jds.S0022-0302(81)82705-1

Aron, S., Passera, L., & Keller, L. (1994). Queen-worker conflict over sex ratio: A comparison of primary and secondary sex ratios in the Argentine ant, Iridomyrmex humilis. *Journal of Evolutionary Biology, 7*(4), 403-418.

Asher, L., Collins, L. M., Ortiz-Pelaez, A., Drewe, J. A., Nicol, C. J., & Pfeiffer, D. U. (2009). Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. *Journal of The Royal Society Interface, 6*(41), 1103-1119. doi: 10.1098/rsif.2009.0221

Baker, C. (2015). Dairy industry in the UK: statistics. *House of Commons Library, UK.*

Bassett, L., & Buchanan-Smith, H. M. (2007). Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science, 102*(3–4), 223-245. doi: http://dx.doi.org/10.1016/j.applanim.2006.05.029

Bates, D., & Maechler, M. (2014). Matrix: Sparse and Dense Matrix Classes and Methods, from http://CRAN.R-project.org/package=Matrix

Beisner, B. A., & McCowan, B. (2014). Social networks and animal welfare. In J. Krause, R. James, D. W. Franks & D. P. Croft (Eds.), *Animal social networks* (pp. 111-121): Oxford University Press.

Benham, P. F. J. (1984). *Social organisation in groups of cattle and the interrelationship between social and grazing behaviours under different grazing management systems.* (Ph.D), University of Reading.

Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution, 25*(9), 504-511. doi: http://dx.doi.org/10.1016/j.tree.2010.06.012

Biondi, M., & Picardi, A. (1999). Psychological stress and neuroendocrine function in humans: the last two decades of research. *Psychotherapy and psychosomatics, 68*(3), 114-150.

Blokhuis, H. J., & Wiepkema, P. R. (1998). Studies of feather pecking in poultry. *Veterinary Quarterly, 20*(1), 6-9. doi: 10.1080/01652176.1998.9694825

Boccia, M. L., Laudenslager, M. L., & Reite, M. L. (1995). Individual differences in Macaques' responses to stressors based on social and physiological factors: Implications for primate welfare and research outcomes. *Laboratory Animals, 29*(3), 250-257.

Bøe, K. E., & Færevik, G. (2003). Grouping and social preferences in calves, heifers and cows. *Applied Animal Behaviour Science, 80*(3), 175-190. doi: 10.1016/s0168-1591(02)00217-4

Böhm, M., Hutchings, M. R., & White, P. C. L. (2009). Contact networks in a wildlife-livestock host community: identifying high-risk individuals in the transmission of bovine TB among badgers and cattle. *PLoS ONE, 4*(4), e5016. doi: 10.1371/journal.pone.0005016

Boissy, A., & Le Neindre, P. (1990). Social influences on the reactivity of heifers: Implications for learning abilities in operant conditioning. *Applied Animal Behaviour Science, 25*(1–2), 149-165. doi: 10.1016/0168-1591(90)90077-q

Boissy, A., & Le Neindre, P. (1997). Behavioral, Cardiac and Cortisol Responses to Brief Peer Separation and Reunion in Cattle. *Physiology &amp; Behavior, 61*(5), 693-699. doi: 10.1016/s0031-9384(96)00521-5

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., . . . Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology &amp; Behavior, 92*(3), 375-397. doi: 10.1016/j.physbeh.2007.02.003

Bolhuis, J. E., Schouten, W. G. P., Schrama, J. W., & Wiegant, V. M. (2005). Behavioural development of pigs with different coping characteristics in barren and substrate-enriched housing conditions. *Applied Animal Behaviour Science, 93*(3–4), 213-228. doi: 10.1016/j.applanim.2005.01.006

Boogert, N. J., Farine, D. R., & Spencer, K. A. (2014). Developmental stress predicts social network position. *Biology letters, 10*(10), 20140561.

Borgatti, S. P., Everett, M. G., & Freeman, L. C. (1999). *UCINET 6.0 Version 1.00*: Analytic Technologies.

Bouissou, M.-F., & Andrieu, S. (1978). Etablissement Des Relations Preferentielles Chez Les Bovins Domestiques. *Behaviour, 64*(1), 148-157. doi: doi:10.1163/156853978X00486

Bouissou, M., & Hövels, J. (1976). Effet d'un contact précoce sur quelques aspects du comportement social des bovins domestiques. *Biol. Behav, 1*, 17-36.

Bouissou, M. F., & Boissy, A. (2005). The social behaviour of cattle and its consequences on breeding. *Productions Animales, 18*(2), 87-99.

Bouissou, M. F., Boissy, A., Le Neindre, P., & Veissier, I. (2001). The social behaviour of cattle. In L. J. Keeling & H. W. Gonyou (Eds.), *Social Behaviour in Farm Animals* (pp. 113-145). Wallingford, Oxon, UK: CABI Publishing.

Boyland, N. K., James, R., Mlynski, D. T., Madden, J. R., & Croft, D. P. (2013). Spatial proximity loggers for recording animal social networks: consequences of inter-logger variation in performance. *Behavioral Ecology and Sociobiology, 67*(11), 1877-1890. doi: 10.1007/s00265-013-1622-6

Bracke, M., & Hopster, H. (2006). Assessing the Importance of Natural Behavior for Animal Welfare. *Journal of Agricultural and Environmental Ethics, 19*(1), 77-89. doi: 10.1007/s10806-005-4493-7

Bradley, A. J. (2002). Bovine Mastitis: An Evolving Disease. *The Veterinary Journal, 164*(2), 116-128. doi: http://dx.doi.org/10.1053/tvjl.2002.0724

Brakel, W. J., & Leis, R. A. (1976). Impact of Social Disorganization on Behavior, Milk Yield, and Body Weight of Dairy Cows. *Journal of Dairy Science, 59*(4), 716-721. doi: http://dx.doi.org/10.3168/jds.S0022-0302(76)84263-4

Braun, K., Lange, E., Metzger, M., & Poeggel, G. (1999). Maternal separation followed by early social deprivation affects the development of monoaminergic fiber systems in the medial prefrontal cortex of Octodon degus. *Neuroscience, 95*(1), 309-318.

Brent, L. J., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A. G., . . . Platt, M. L. (2013). Genetic origins of social networks in rhesus macaques. *Scientific reports, 3*.

Brent, L. J. N., Chang, S. W. C., Gariépy, J.-F., & Platt, M. L. (2014). The neuroethology of friendship. *Annals of the New York Academy of Sciences, 1316*(1), 1-17. doi: 10.1111/nyas.12315

Broom, D., & Leaver, J. (1978). Effects of group-rearing or partial isolation on later social behaviour of calves. *Animal Behaviour, 26*, 1255-1263.

Broom, D. M. (1988). The scientific assessment of animal welfare. *Applied Animal Behaviour Science, 20*(1–2), 5-19. doi: 10.1016/0168-1591(88)90122-0

Brouček, J., Uhrinčať, M., Tančin, V., Hanus, A., Tongeľ, P., Botto, Ľ., & Bôžik, I. (2013). Performance and behaviour at milking after relocation and housing change of dairy cows. *Czech Journal of Animal Science, 58*(9), 389-395.

Bshary, R., & Lamprecht, J. (1994). Reduction of Aggression Among Domestic Hens (Gallus Domesticus) in the Presence of a Dominant Third Party. *Behaviour, 128*(3), 311-324. doi: doi:10.1163/156853994X00316

Budzynska, M., & Weary, D. M. (2008). Weaning distress in dairy calves: Effects of alternative weaning procedures. *Applied Animal Behaviour Science, 112*(1–2), 33-39. doi: http://dx.doi.org/10.1016/j.applanim.2007.08.004

Bull, C. M., Godfrey, S. S., & Gordon, D. M. (2012). Social networks and the spread of Salmonella in a sleepy lizard population. *Molecular Ecology, 21*(17), 4386-4392. doi: 10.1111/j.1365-294X.2012.05653.x

Cameron, E. Z., Setaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of the United States of America 106*(33), 13850-13853.

Cañon Jones, H. A., Hansen, L. A., Noble, C., Damsgård, B., Broom, D. M., & Pearce, G. P. (2010). Social network analysis of behavioural interactions influencing fin damage development in Atlantic salmon (Salmo salar) during feed-restriction. *Applied Animal Behaviour Science, 127*(3–4), 139-151. doi: 10.1016/j.applanim.2010.09.004

Capitanio, J. P., Mendoza, S. P., & Baroncelli, S. (1999). The relationship of personality dimensions in adult male rhesus macaques to progression of simian immunodeficiency virus disease. *Brain, Behavior, and Immunity, 13*(2), 138-154. doi: 10.1006/brbi.1998.0540

Pérez, G. C., Laita, S. G. B., del Portal, J. I., & Liesa, J. P. (2004). Validation of an EIA [enzyme immunoassay] technique for the determination of salivary cortisol in cattle. *Spanish Journal of Agricultural Research*, *2*(1), 45-51.

Chua, B., Coenen, E., Van Delen, J., & Weary, D. (2002). Effects of pair versus individual housing on the behavior and performance of dairy calves. *Journal of dairy science, 85*(2), 360-364.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: behaviourand ecology of two sexes*. Chicago: Universityof Chicago Press.

Cohen, S. (1988). Psychosocial models of the role of social support in the etiology of physical disease. *Health psychology, 7*(3), 269.

Collias, N. E., & Collias, E. C. (1967). A field study of the red jungle fowl in north-central India. *Condor*, 360-386.

Conradt, L. (1998). Could asynchrony in activity between the sexes cause inter-sexual social segregation in ruminants? *Proceedings of the Royal Society of London B*(265), 1359-1363.

Conradt, L., & Roper, T. J. (2000). Activity synchrony and social cohesion: A fission-fusion model. *Proceedings of the Royal Society B: Biological Sciences, 267*(1458), 2213-2218.

Corner, L. A. L., Pfeiffer, D. U., & Morris, R. S. (2003). Social-network analysis of Mycobacterium bovis transmission among captive brushtail possums (Trichosurus vulpecula). *Preventive Veterinary Medicine, 59*(3), 147-167. doi: 10.1016/s0167-5877(03)00075-8

Corp, I. (2012). IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY: IBM Corp.

Costa, J. H. C., Daros, R. R., von Keyserlingk, M. A. G., & Weary, D. M. (2014). Complex social housing reduces food neophobia in dairy calves. *Journal of Dairy Science, 97*(12), 7804-7810. doi: http://dx.doi.org/10.3168/jds.2014-8392

Cote, J., Fogarty, S., & Sih, A. (2012). Individual sociability and choosiness between shoal types. *Animal Behaviour, 83*(6), 1469-1476.

Coulon, J. B., & Rémond, B. (1991). Variations in milk output and milk protein content in response to the level of energy supply to the dairy cow: A review. *Livestock Production Science, 29*(1), 31-47. doi: http://dx.doi.org/10.1016/0301-6226(91)90118-A

Council Directive 97/2/EC of 20 January 1997 amending Directive 91/629/EEC laying minimum standards for the protection of calves.

Coyne, J. C., & Downey, G. (1991). Social factors and psychopathology: Stress, social support, and coping processes. *Annual review of psychology, 42*(1), 401-425.

Craig, J. V. (1981). *Domestic animal behaviour: causes and implications for animal care and management*: Prentice-Hall.

Creech, T. G., Cross, P. C., Scurlock, B. M., Maichak, E. J., Rogerson, J. D., Henningsen, J. C., & Creel, S. (2012). Effects of low-density feeding on elk–fetus contact rates on Wyoming feedgrounds. *The Journal of Wildlife Management, 76*(5), 877-886. doi: 10.1002/jwmg.331

Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, Lycaon pictus. *Animal Behaviour, 50*(5), 1325-1339. doi: http://dx.doi.org/10.1016/0003-3472(95)80048-4

Croft, D., James, R., Thomas, P., Hathaway, C., Mawdsley, D., Laland, K., & Krause, J. (2006). Social structure and co-operative interactions in a wild population of guppies (Poecilia reticulata ). *Behavioral Ecology and Sociobiology, 59*(5), 644-650. doi: 10.1007/s00265-005-0091-y

Croft, D. P., James, R., & Krause, J. (2008). *Exploring Animal Social Networks*. Princeton: Princeton University Press.

Croft, D. P., James, R., Ward, A., Botham, M., Mawdsley, D., & Krause, J. (2005). Assortative interactions and social networks in fish. *Oecologia, 143*(2), 211-219.

Croft, D. P., Krause, J., & James, R. (2004). Social networks in the guppy (Poecilia reticulata). *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*(Suppl 6), S516-S519. doi: 10.1098/rsbl.2004.0206

Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal social networks. *Trends in Ecology & Evolution, 26*(10), 502-507.

Cross, P., Creech, T., Ebinger, M., Heisey, D., Irvine, K., & Creel, S. (2012). Wildlife contact analysis: emerging methods, questions, and challenges. *Behavioral Ecology and Sociobiology, 66*(10), 1437-1447. doi: 10.1007/s00265-012-1376-6

da Costa, A. P., Leigh, A. E., Man, M.-S., & Kendrick, K. M. (2004). *Face pictures reduce behavioural, autonomic, endocrine and neural indices of stress and fear in sheep* (Vol. 271).

DairyCo MOBILITY SCORING. Retrieved 01-10-2012, from: http://dairy.ahdb.org.uk/technical-information/animal-health-welfare/lameness/husbandry-prevention/mobility-scoring/#.VbJZg_lVhBc

DairyCo AVERAGE HERD SIZE. Retrieved 15-08-2015, from: http://dairy.ahdb.org.uk/resources-library/market-information/farming-data/average-herd-size/#.Vc92NvlVhBc

Dantzer, R., & Kelley, K. W. (2007). Twenty years of research on cytokine-induced sickness behavior. *Brain, behavior, and immunity, 21*(2), 153-160.

Dawkins, R. (1976). Hierarchical organisation: A candidate principle for ethology. In P.P.G. Bateson & R.A. Hinde (Eds.), *Growing points in ethology* (pp. 7-54). Cambridge: Cambridge Univeristy Press.

de Groot, J., Ruis, M. A. W., Scholten, J. W., Koolhaas, J. M., & Boersma, W. J. A. (2001). Long-term effects of social stress on antiviral immunity in pigs. *Physiology &amp; Behavior, 73*(1–2), 145-158. doi: 10.1016/s0031-9384(01)00472-3

de Passillé, A. M. (2001). Sucking motivation and related problems in calves. *Applied Animal Behaviour Science, 72*(3), 175-187. doi: 10.1016/s0168-1591(01)00108-3

De Paula Vieira, A., de Passillé, A. M., & Weary, D. M. (2012). Effects of the early social environment on behavioral responses of dairy calves to novel events. *Journal of Dairy Science, 95*(9), 5149-5155. doi: http://dx.doi.org/10.3168/jds.2011-5073

De Paula Vieira, A., Von Keyserlingk, M., & Weary, D. (2010). Effects of pair versus single housing on performance and behavior of dairy calves before and after weaning from milk. *Journal of dairy science, 93*(7), 3079-3085.

Detillion, C. E., Craft, T. K. S., Glasper, E. R., Prendergast, B. J., & DeVries, A. C. (2004). Social facilitation of wound healing. *Psychoneuroendocrinology, 29*(8), 1004-1011. doi: http://dx.doi.org/10.1016/j.psyneuen.2003.10.003

DeVries, A. C., Glasper, E. R., & Detillion, C. E. (2003). Social modulation of stress responses. *Physiology &amp; Behavior, 79*(3), 399-407. doi: 10.1016/s0031-9384(03)00152-5

Directive, E. U. (1999). Council Directive 99/74/EC of 19 July 1999 laying down minimum standards for the protection of laying hens. *Official Journal of the European Communities*, 53-57.

Dobson, H., Walker, S. L., Morris, M. J., Routly, J. E., & Smith, R. F. (2008). Why is it getting more difficult to successfully artificially inseminate dairy cows? *Animal, 2*(8), 1104-1111. doi: 10.1017/S175173110800236X

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., . . . Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*(1), 27-46. doi: 10.1111/j.1600-0587.2012.07348.x

Drewe, J. A., Eames, K. T. D., Madden, J. R., & Pearce, G. P. (2011). Integrating contact network structure into tuberculosis epidemiology in meerkats in South Africa: Implications for control. *Preventive Veterinary Medicine, 101*(1–2), 113-120. doi: 10.1016/j.prevetmed.2011.05.006

Drewe, J. A., Weber, N., Carter, S. P., Bearhop, S., Harrison, X. A., Dall, S. R. X., . . . Delahay, R. J. (2012). Performance of proximity loggers in recording intra- and inter-species interactions: a laboratory and field-based validation study. *PLoS ONE, 7*(6), e39068. doi: 10.1371/journal.pone.0039068

Drews, C. (1993). The concept and definition of dominance in animal behaviour. *Behaviour Research and Therapy, 125*, 283-313.

du Toit, J. T., Ruckstuhl, K., & Neuhaus, P. (2005). Sex differences in the foraging ecology of large mammalian herbivores. *Sexual segregation in vertebrates: ecology of the two sexes. Cambridge: Cambridge University Press. p*, 35-52.

Dubé, C., Ribble, C., Kelton, D., & McNab, B. (2008). Comparing network analysis measures to determine potential epidemic size of highly contagious exotic diseases in fragmented monthly networks of dairy cattle movements in Ontario, Canada. *Transboundary and emerging diseases, 55*(9-10), 382-392.

Dunbar, R. I. M. (1991). Functional Significance of Social Grooming in Primates. *Folia Primatologica, 57*(3), 121-131.

Duve, L. R., Weary, D., Halekoh, U., & Jensen, M. B. (2012). The effects of social contact and milk allowance on responses to handling, play, and social behavior in young dairy calves. *Journal of dairy science, 95*(11), 6571-6581.

Edenbrow, M., Darden, S. K., Ramnarine, I. W., Evans, J. P., James, R., & Croft, D. P. (2011). Environmental effects on social interaction networks and male reproductive behaviour in guppies, Poecilia reticulata. *Animal Behaviour, 81*(3), 551-558. doi: 10.1016/j.anbehav.2010.11.026

Estevez, I., Andersen, I.-L., & Nævdal, E. (2007). Group size, density and social dynamics in farm animals. *Applied Animal Behaviour Science, 103*(3–4), 185-204. doi: 10.1016/j.applanim.2006.05.025

Estevez, I., Keeling, L. J., & Newberry, R. C. (2003). Decreasing aggression with increasing group size in young domestic fowl. *Applied Animal Behaviour Science, 84*(3), 213-218. doi: 10.1016/j.applanim.2003.08.006

Estevez, I., Newberry, R. C., & Keeling, L. J. (2002). Dynamics of aggression in the domestic fowl. *Applied Animal Behaviour Science, 76*(4), 307-325. doi: 10.1016/s0168-1591(02)00013-8

Færevik, G., Andersen, I. L., Jensen, M. B., & Bøe, K. E. (2007). Increased group size reduces conflicts and strengthens the preference for familiar group mates after regrouping of weaned dairy calves (Bos taurus). *Applied Animal Behaviour Science, 108*(3–4), 215-228. doi: 10.1016/j.applanim.2007.01.010

Færevik, G., Jensen, M. B., & Bøe, K. E. (2006). Dairy calves social preferences and the significance of a companion animal during separation from the group. *Applied Animal Behaviour Science, 99*(3–4), 205-221. doi: 10.1016/j.applanim.2005.10.012

Farine, D. R. (2015). Proximity as a proxy for interactions: issues of scale in social network analysis. *Animal Behaviour, 104*, e1-e5. doi: http://dx.doi.org/10.1016/j.anbehav.2014.11.019

Faure, J. M., & Mills, A. D. (1998). Improving the adaptability of animals by selection *Genetics and the behavior of domestic animals* (pp. 235-264): Academic Press San Diego.

Faust, K. (2011). Animal Social Networks In J. Scott & P. J. Carrington (Eds.), *The SAGE handbook of Social Network Analysis*. Great Britain: MPG Books Group.

FAWC (2007). Opinion on beak trimming of laying hens. *Farm Animal Welfare Council, London, UK*, 12.

Firk, R., Stamer, E., Junge, W., & Krieter, J. (2002). Automation of oestrus detection in dairy cows: a review. *Livestock Production Science, 75*(3), 219-232. doi: http://dx.doi.org/10.1016/S0301-6226(01)00323-2

Fischhoff, I., Dushoff, J., Sundaresan, S., Cordingley, J., & Rubenstein, D. (2009). Reproductive status influences group size and persistence of bonds in male plains zebra (&lt;i&gt;Equus burchelli ). *Behavioral Ecology and Sociobiology, 63*(7), 1035-1043. doi: 10.1007/s00265-009-0723-8

Fisher, A. D., Morris, C. A., & Matthew, L. R. (2000). Cattle behaviour: comparison of measures of temperament in beef cattle. *Proceedings of the New Zealand Society of Animal Production, 60*, 214-217.

Flack, J. C., Girvan, M., De Waal, F. B., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439*(7075), 426-429.

Fortuna, M. A., Popa-Lisseanu, A. G., Ibáñez, C., & Bascompte, J. (2009). The Roosting Spatial Network of a Bird-Predator Bat. *Ecology, 90*(4), 934-944.

Fowler, J. H., & Christakis, N. A. (2010). Cooperative behavior cascades in human social networks. *Proceedings of the National Academy of Sciences, 107*(12), 5334-5338.

Fraser, A. F., & Broom, D. M. (1990). *Farm Animal Behaviour and Welfare*. London: Bailliere Tindall.

Fraser, D. (2008). Toward a global perspective on farm animal welfare. *Applied Animal Behaviour Science, 113*(4), 330-339. doi: 10.1016/j.applanim.2008.01.011

Freeman, L. C. (1979). Centrality in social networks conceptual clarification. *Social networks, 1*(3), 215-239.

Fregonesi, J., Flower, F., Vittie, T., Tucker, C. B., & Weary, D. M. (2002). Rubber flooring affects behavior of dairy cows, especially animals with hoof injuries. *Journal of Dairy Science, 85*.

Fregonesi, J. A., & Leaver, J. D. (2001). Behaviour, performance and health indicators of welfare for dairy cows housed in strawyard or cubicle systems. *Livestock production science, 68*(2), 205-216.

Fregonesi, J. A., & Leaver, J. D. (2002). Influence of space allowance and milk yield level on behaviour, performance and health of dairy cows housed in strawyard and cubicle systems. *Livestock Production Science, 78*(3), 245-257. doi: 10.1016/S0301-6226(02)00097-0

Gaillard, C., Meagher, R. K., von Keyserlingk, M. A. G., & Weary, D. M. (2014). Social Housing Improves Dairy Calves' Performance in Two Cognitive Tests. *PLoS ONE, 9*(2), e90205. doi: 10.1371/journal.pone.0090205

Galindo, F., & Broom, D. (2000). The relationships between social behaviour of dairy cows and the occurrence of lameness in three herds. *Research in Veterinary Science, 69*(1), 75-79.

Galindo, F., & Broom, D. M. (2002). The effects of lameness on social and individual behavior of dairy cows. *Journal of Applied Animal Welfare Science, 5*(3), 193-201.

Garner, J. P., & Mason, G. J. (2002). Evidence for a relationship between cage stereotypies and behavioural disinhibition in laboratory rodents. *Behavioural brain research, 136*(1), 83-92.

Gentle, M. J. (2011). Pain issues in poultry. *Applied Animal Behaviour Science, 135*(3), 252-258.

Geverink, N. A., Schouten, W. G. P., Gort, G., & Wiegant, V. M. (2003). Individual differences in behaviour, physiology and pathology in breeding gilts housed in groups or stalls. *Applied Animal Behaviour Science, 81*(1), 29-41. doi: 10.1016/s0168-1591(02)00253-8

Gibbons, J. M., Lawrence, A. B., & Haskell, M. J. (2009). Consistency of aggressive feeding behaviour in dairy cows. *Applied Animal Behaviour Science, 121*(1), 1-7.

Gibbons, J. M., Lawrence, A. B., & Haskell, M. J. (2010). Measuring sociability in dairy cows. *Applied Animal Behaviour Science, 122*(2–4), 84-91. doi: http://dx.doi.org/10.1016/j.applanim.2009.11.011

Goddard, M. (2009). Genomic selection: prediction of accuracy and maximisation of long term response. *Genetica, 136*(2), 245-257. doi: 10.1007/s10709-008-9308-0

Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., . . . Toulmin, C. (2010). Food security: the challenge of feeding 9 billion people. *science, 327*(5967), 812-818.

Godfrey, S. S., Bradley, J. K., Sih, A., & Bull, C. M. (2012). Lovers and fighters in sleepy lizard land: where do aggressive males fit in a social network? *Animal Behaviour, 83*(1), 209-215. doi: 10.1016/j.anbehav.2011.10.028

Goodman, E. L. (2007). *Quantifying interactions in a high-density badger (Meles meles) population.* University of York, York.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin, 127*(1), 45-86. doi: 10.1037/0033-2909.127.1.45

Goymann, W., & Wingfield, J. C. (2004). Allostatic load, social status and stress hormones: the costs of social status matter. *Animal Behaviour, 67*(3), 591-602. doi: 10.1016/j.anbehav.2003.08.007

Grant, R. J., & Albright, J. L. (2001). Effect of Animal Grouping on Feeding Behavior and Intake of Dairy Cattle. *Journal of Dairy Science, 84, Supplement*(0), E156-E163. doi: http://dx.doi.org/10.3168/jds.S0022-0302(01)70210-X

Grignard, L., Boissy, A., Boivin, X., Garel, J. P., & Le Neindre, P. (2000). The social environment influences the behavioural responses of beef cattle to handling. *Applied Animal Behaviour Science, 68*(1), 1-11. doi: 10.1016/s0168-1591(00)00085-x

Gross, W. (1984). Effect of a range of social stress severity on Escherichia coli challenge infection. *American journal of veterinary research, 45*(10), 2074-2076.

Gurney, W. S. C., & Nisbet, R. M. (1979). Ecological stability and social hierarchy. *Theoretical Population Biology, 16*(1), 48-80. doi: http://dx.doi.org/10.1016/0040-5809(79)90006-6

Gust, D. A., Gordon, T. P., Brodie, A. R., & McClure, H. M. (1994). Effect of a preferred companion in modulating stress in adult female rhesus monkeys. *Physiology &amp; Behavior, 55*(4), 681-684. doi: 10.1016/0031-9384(94)90044-2

Gutmann, A. K., Špinka, M., & Winckler, C. (2015). Long-term familiarity creates preferred social partners in dairy cows. *Applied Animal Behaviour Science, 169*, 1-8. doi: 10.1016/j.applanim.2015.05.007

Gygax, L., Neisen, G., & Wechsler, B. (2010). Socio-Spatial Relationships in Dairy Cows. *Ethology, 116*(1), 10-23. doi: 10.1111/j.1439-0310.2009.01708.x

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software, 33*(2), 1-22.

Hadley, C., Hadley, B., Ephraim, S., Yang, M., & Lewis, M. H. (2006). Spontaneous stereotypy and environmental enrichment in deer mice (Peromyscus maniculatus): reversibility of experience. *Applied Animal Behaviour Science, 97*(2), 312-322.

Hair, J. F., Black, W. C., Babin, B. J., & Anderson, R. E. (2009). *Multivariate Data Analysis* (7 ed.): Prentice Hall.

Hamede, R. K., Bashford, J., McCallum, H., & Jones, M. (2009). Contact networks in a wild Tasmanian devil (Sarcophilus harrisii) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecology Letters, 12*(11), 1147-1157. doi: 10.1111/j.1461-0248.2009.01370.x

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology, 31*(2), 295-311. doi: 10.1016/0022-5193(71)90189-5

Hanneman, R. A., & Riddle, M. (2005). Introduction to social network methods, from http://faculty.ucr.edu/~hanneman/

Hänninen, L., Hepola, H., Rushen, J., De Passille, A. M., Pursiainen, P., Tuure, V.-M., . . . Saloniemi, H. (2003). Resting behaviour, growth and diarrhoea incidence rate of young dairy calves housed individually or in groups in warm or cold buildings. *Acta Agriculturae Scandinavica, Section A-Animal Science, 53*(1), 21-28.

Hasegawa, N., Nishiwaki, A., Sugawara, K., & Ito, I. (1997). The effects of social exchange between two groups of lactating primiparous heifers on milk production, dominance order, behavior and adrenocortical response. *Applied Animal Behaviour Science, 51*(1–2), 15-27. doi: http://dx.doi.org/10.1016/S0168-1591(96)01082-9

Haskell, M. J., Simm, G., & Turner, S. P. (2014). Genetic selection for temperament traits in dairy and beef cattle. *Frontiers in genetics, 5*.

Hawkley, L. C., Cole, S. W., Capitanio, J. P., Norman, G. J., & Cacioppo, J. T. (2012). Effects of social isolation on glucocorticoid regulation in social mammals. *Hormones and behavior, 62*(3), 314-323.

Hennessy, M. B., Deak, T., & Schiml-Webb, P. A. (2001). Stress-induced sickness behaviors: An alternative hypothesis for responses during maternal separation. *Developmental Psychobiology, 39*(2), 76-83. doi: 10.1002/dev.1031

Hennessy, M. B., Kaiser, S., & Sachser, N. (2009). Social buffering of the stress response: diversity, mechanisms, and functions. *Frontiers in neuroendocrinology, 30*(4), 470-482.

Herzog, C. J., Czéh, B., Corbach, S., Wuttke, W., Schulte-Herbrüggen, O., Hellweg, R., . . . Fuchs, E. (2009). Chronic social instability stress in female rats: A potential animal model for female depression. *Neuroscience, 159*(3), 982-992. doi: http://dx.doi.org/10.1016/j.neuroscience.2009.01.059

Hessing, M. J. C., Hagelsø, A. M., Schouten, W. G. P., Wiepkema, P. R., & Van Beek, J. A. M. (1994). Individual behavioral and physiological strategies in pigs. *Physiology &amp; Behavior, 55*(1), 39-46. doi: 10.1016/0031-9384(94)90007-8

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man, 11*, 1-17.

Holm, L., Jensen, M. B., & Jeppesen, L. L. (2002). Calves' motivation for access to two different types of social contact measured by operant conditioning. *Applied Animal Behaviour Science, 79*(3), 175-194. doi: 10.1016/s0168-1591(02)00137-5

Hood, G. M. (2010). PopTools version 3.2.5 Retrieved 1 May, 2013, from http://www.poptools.org

Hopster, H., & Blokhuis, H. J. Consistent individual stress responses of dairy cows during social isolation. *Applied Animal Behaviour Science, 40*(1), 83-84. doi: 10.1016/0168-1591(94)90109-0

Hosey, G., Melfi, V., & Pankhurst, S. (2009). *Zoo animals: behaviour, management and welfare* New York: Oxford University Press Inc.

House, J. S., Landis, K. R., & Umberson, D. (1988). Social relationships and health. *Science, 241*(4865), 540-545.

Huber-Eicher, B., & Sebö, F. (2001). Reducing feather pecking when raising laying hen chicks in aviary systems. *Applied Animal Behaviour Science, 73*(1), 59-68. doi: 10.1016/s0168-1591(01)00121-6

Hultgren, J., & Svensson, C. (2009). Heifer rearing conditions affect length of productive life in Swedish dairy cows. *Preventive Veterinary Medicine, 89*(3–4), 255-264. doi: 10.1016/j.prevetmed.2009.02.012

Huntingford, F. A. (1976). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, Gasterosteus aculeatus. *Animal Behaviour, 24*(2), 245-260.

Ishiwata, T., Kilgour, R., Uetake, K., Eguchi, Y., & Tanaka, T. (2007). Choice of attractive conditions by beef cattle in a Y-maze just after release from restraint. *American Society of Animal Science, 85*, 1080-1085.

Jacobs, J. A., & Siegford, J. M. (2012). Invited review: The impact of automatic milking systems on dairy cow management, behavior, health, and welfare. *Journal of Dairy Science, 95*(5), 2227-2247. doi: http://dx.doi.org/10.3168/jds.2011-4943

James, D., & Hornik, K. (2014). chron: Chronological Objects which Can Handle Dates and Times, from http://CRAN.R-project.org/package=chron

Jasper, J., Budzynska, M., & Weary, D. M. (2008). Weaning distress in dairy calves: Acute behavioural responses by limit-fed calves. *Applied Animal Behaviour Science, 110*(1), 136-143.

Jensen, M. B., Munksgaard, L., Mogensen, L., & Krohn, C. C. (1999). Effects of housing in different social environments on open-field and social responses of female dairy calves. *Acta Agriculturae Scandinavica, Section A-Animal Science, 49*(2), 113-120.

Jensen, M. B., Vestergaard, K. S., & Krohn, C. C. (1998). Play behaviour in dairy calves kept in pens: the effect of social contact and space allowance. *Applied Animal Behaviour Science, 56*(2), 97-108.

Jensen, M. B., Vestergaard, K. S., Krohn, C. C., & Munksgaard, L. (1997). Effect of single versus group housing and space allowance on responses of calves during open-field tests. *Applied Animal Behaviour Science, 54*(2–3), 109-121. doi: 10.1016/s0168-1591(96)01183-5

Ji, W., White, P. C. L., & Clout, M. N. (2005). Contact rates between possums revealed by proximity data loggers. *Journal of Applied Ecology, 42*(3), 595-604. doi: 10.1111/j.1365-2664.2005.01026.x

Johnsson, J. I., Petersson, E., Jonsson, E., Bjornsson, B. T., & Jarvi, T. (1996). Domestication and growth hormone alter anti-predator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences 53,* 1546-1554.

Kanitz, E., Tuchscherer, M., Puppe, B., Tuchscherer, A., & Stabenow, B. (2004). Consequences of repeated early isolation in domestic piglets (Sus scrofa) on their behavioural, neuroendocrine, and immunological responses. *Brain, Behavior, and Immunity, 18*(1), 35-45. doi: 10.1016/s0889-1591(03)00085-0

Kappeler, P. M., Cremer, S., & Nunn, C. L. (2015). *Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies* (Vol. 370).

Kay, S. J., Collis, K., Anderson, J., & Grant, A. (1977). The effect of intergroup movement of dairy cows on bulk-milk somatic cell numbers. *Journal of Dairy Research, 44*(03), 589-593.

Keeling, L. J., & Gonyou, H. W. (2001). *Social behaviour in farm animals*: CABI.

Kennes, D., Ödberg, F. O., Bouquet, Y., & De Rycke, P. H. (1988). Changes in naloxone and haloperidol effects during the development of captivity-induced jumping stereotypy in bank voles. *European journal of pharmacology, 153*(1), 19-24.

Kiecolt-Glaser, J. K., & Newton, T. L. (2001). Marriage and health: His and hers. *Psychological Bulletin, 127*(4), 472-503.

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1476), 2215-2228.

Kiss, I. Z., Green, D. M., & Kao, R. R. (2006). The network of sheep movements within Great Britain: network properties and their implications for infectious disease spread. *Journal of the Royal Society Interface, 3*(10), 669-677.

Knox, R., Salak-Johnson, J., Hopgood, M., Greiner, L., & Connor, J. (2014). Effect of day of mixing gestating sows on measures of reproductive performance and animal welfare. *Journal of Animal Science, 92*(4), 1698-1707. doi: 10.2527/jas.2013-6432

Koene, P., & Ipema, B. (2014). Social Networks and Welfare in Future Animal Management. *Animals, 4*(1), 93-118.

Kooij, E. v. E.-v. d., Kuijpers, A. H., Schrama, J. W., van Eerdenburg, F. J. C. M., Schouten, W. G. P., & Tielen, M. J. M. (2002). Can we predict behaviour in pigs?: Searching for consistency in behaviour over time and across situations. *Applied Animal Behaviour Science, 75*(4), 293-305. doi: http://dx.doi.org/10.1016/S0168-1591(01)00203-9

Koolhaas, J., De Boer, S., Buwalda, B., Van der Vegt, B., Carere, C., & Groothuis, A. (2001). How and why coping systems vary among individuals. *Coping With Challenges: Welfare in Animals Including Humans (Broom, DM, ed.)*, 197-209.

Koolhaas, J., Korte, S., De Boer, S., Van Der Vegt, B., Van Reenen, C., Hopster, H., . . . Blokhuis, H. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews, 23*(7), 925-935.

Korte, S. M., Olivier, B., & Koolhaas, J. M. (2007). A new animal welfare concept based on allostasis. *Physiology & Behavior, 92*(3), 422-428. doi: http://dx.doi.org/10.1016/j.physbeh.2006.10.018

Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences: potential applications. [Review]. *Behavioral Ecology and Sociobiology, 62*(1), 15-27.

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford: Oxford University Press.

Krause, J., Wilson, A., & Croft, D. P. (2011). New technology facilitates the study of social networks. *Trends in Ecology & Evolution, 26*(1), 5.

Kung, L., Demarco, S., Siebenson, L., Joyner, E., Haenlein, G., & Morris, R. (1997). An evaluation of two management systems for rearing calves fed milk replacer. *Journal of dairy science, 80*(10), 2529-2533.

Lamb, R. (1976). Relationship between cow behavior patterns and management systems to reduce stress. *Journal of dairy science, 59*(9), 1630-1636.

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (Pan troglodytes). *American Journal of Primatology, 71*(10), 840-851. doi: 10.1002/ajp.20711

Latham, N. R., & Mason, G. J. (2008). Maternal deprivation and the development of stereotypic behaviour. *Applied Animal Behaviour Science, 110*(1–2), 84-108. doi: http://dx.doi.org/10.1016/j.applanim.2007.03.026

Lazo, A. (1994). Social segregation and the maintenance of social stability in a feral cattle population. *Animal Behaviour, 48*(5), 1133-1141.

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour, 74*(6), 1617-1629. doi: http://dx.doi.org/10.1016/j.anbehav.2006.10.025

Lensink, B. J., Fernandez, X., Cozzi, G., Florand, L., & Veissier, I. (2001). The influence of farmers' behavior on calves' reactions to transport and quality of veal meat. *Journal of Animal Science, 79*(3), 642-652.

Leonard, F. C., O'Connell, J. M., & O'Farrell, K. J. (1996). Effect of overcrowding on claw health in first-calved friesian heifers. *British Veterinary Journal, 152*(4), 459-472. doi: http://dx.doi.org/10.1016/S0007-1935(96)80040-6

Lindberg, A. C., & Nicol, C. J. (1996). Effects of social and environmental familiarity on group preferences and spacing behaviour in laying hens. *Applied Animal Behaviour Science, 49*(2), 109-123. doi: 10.1016/0168-1591(96)01046-5

Lusseau, D., & Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*(Suppl 6), S477-S481. doi: 10.1098/rsbl.2004.0225

Lusseau, D., Whitehead, H., & Gero, S. (2009). Incorporating uncertainty into the study of animal social networks. *arXiv preprint arXiv:0903.1519*.

Lusseau, D., Wilson, B. E. N., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., . . . Thompson, P. M. (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology, 75*(1), 14-24. doi: 10.1111/j.1365-2656.2005.01013.x

Maatje, K., Verhoeff, J., Kremer, W. D., Cruijsen, A. L., & van den Ingh, T. S. (1993). Automated feeding of milk replacer and health control of group-housed veal calves. *Veterinary Record, 133*(11), 266-270.

MacDonald, J. M., & McBride, W. D. (2009). The transformation of U.S. livestock agriculture: scale, efficiency, and risks. *United States Department of Agriculture Economic Information Bulletin, 43*.

Makagon, M. M., McCowan, B., & Mench, J. A. (2012). How can social network analysis contribute to social behavior research in applied ethology? *Applied Animal Behaviour Science, 138*(3–4), 152-161. doi: http://dx.doi.org/10.1016/j.applanim.2012.02.003

Marcé, C., Guatteo, R., Bareille, N., & Fourichon, C. (2010). Dairy calf housing systems across Europe and risk for calf infectious diseases. *animal, 4*(09), 1588-1596.

Marin, A., & Wellman, B. (2011). Social network analysis: An introduction *The SAGE Handbook of Social Network Analysis.* Thousand Oaks, CA: SAGE Publications.

Marsh, M., Hutchings, M., McLeod, S., & White, P. (2011). Spatial and temporal heterogeneities in the contact behaviour of rabbits. *Behavioral Ecology and Sociobiology, 65*(2), 183-195. doi: 10.1007/s00265-010-1024-y

Marsh, M. K., McLeod, S. R., Hutchings, M. R., & White, P. C. L. (2011). Use of proximity loggers and network analysis to quantify social interactions in free-ranging wild rabbit populations. *Wildlife Research, 38*(1), 1-12. doi: http://dx.doi.org/10.1071/WR10150

Mason, G., & Rushen, J. (2008). *Stereotypic animal behaviour: fundamentals and applications to welfare*: CABI.

Mason, G. J. (1991a). Stereotypies and suffering. *Behavioural Processes, 25*(2–3), 103-115. doi: 10.1016/0376-6357(91)90013-p

Mason, G. J. (1991b). Stereotypies: a critical review. *Animal Behaviour, 41*(6), 1015-1037. doi: 10.1016/s0003-3472(05)80640-2

Matthews, L. R., & Ladewig, J. (1994). Environmental requirements of pigs measured by behavioural demand functions. *Animal Behaviour, 47*(3), 713-719. doi: 10.1006/anbe.1994.1096

McBride, G., James, J. W., & Shoffner, R. N. (1963). Social Forces Determining Spacing and Head Orientation in a Flock of Domestic Hens. [10.1038/1971272a0]. *Nature, 197*(4874), 1272-1273.

McCowan, B., Anderson, K., Heagarty, A., & Cameron, A. (2008). Utility of social network analysis for primate behavioral management and well-being. *Applied Animal Behaviour Science, 109*(2–4), 396-405. doi: 10.1016/j.applanim.2007.02.009

McEwen, B. S. (1998). Protective and Damaging Effects of Stress Mediators. *New England Journal of Medicine, 338*(3), 171-179. doi: doi:10.1056/NEJM199801153380307

McEwen, B. S., & Wingfield, J. C. (2003). The concept of allostasis in biology and biomedicine. *Hormones and Behavior, 43*(1), 2-15. doi: http://dx.doi.org/10.1016/S0018-506X(02)00024-7

McEwen, B. S., & Wingfield, J. C. (2010). What is in a name? Integrating homeostasis, allostasis and stress. *Hormones and Behavior, 57*(2), 105-111. doi: 10.1016/j.yhbeh.2009.09.011

McGuirk, S. M. (2008). Disease management of dairy calves and heifers. *Veterinary Clinics of North America: Food Animal Practice, 24*(1), 139-153.

McLennan, K. M. (2012). Farmyard Friends. *The Biologist, 59*, 19-22.

McLennan, K. M. (2013). *Social bonds in dairy cattle: the effect of dynamic group systems on welfare and productivity*. The University of Northampton. Retrieved from http://nectar.northampton.ac.uk/6466/

McPherson, M., Smith-Lovin, L., & Cook, J. M. (2001). Birds of a Feather: Homophily in Social Networks. *Annual Review of Sociology, 27*(ArticleType: research-article / Full publication date: 2001 / Copyright © 2001 Annual Reviews), 415-444. doi: 10.2307/2678628

Meaney, M. J., Diorio, J., Francis, D., Widdowson, J., LaPlante, P., Caldji, C., . . . Plotsky, P. M. (1996). Early Environmental Regulation of Forebrain Glucocorticoid Receptor Gene Expression: Implications for Adrenocortical Responses to Stress; pp. 61–72. *Developmental Neuroscience, 18*(1-2), 61-72.

Mench, J. A., Swanson, J. C., & Stricklin, W. R. (1990). Social stress and dominance among group members after mixing beef cows. *Canadian Journal of Animal Science, 70*(2), 345-354. doi: 10.4141/cjas90-046

Mendl, M., & Newberry, R. (1997). Social conditions. In Appleby, M.C. & Hughes, B.O. (Eds.), *Animal Welfare*, CAB International, Wallingford, UK (1997), pp. 191–203.

Michelena, P., Gautrais, J., Gérard, J.-F., Bon, R., & Deneubourg, J.-L. (2008). Social cohesion in groups of sheep: Effect of activity level, sex composition and group size. *Applied Animal Behaviour Science, 112*(1–2), 81-93. doi: 10.1016/j.applanim.2007.06.020

Michelena, P., Sibbald, A. M., Erhard, H. W., & McLeod, J. E. (2009). Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behavioral Ecology, 20*(1), 145-152. doi: 10.1093/beheco/arn126

Miller, K., & Wood-Gush, D. G. M. (1991). Some effects of housing on the social behaviour of dairy cows. *Animal Science, 53*(03), 271-278. doi: doi:10.1017/S0003356100020262

Miller, P. M., & Surtees, P. (1995). Partners in adversity V: support, personality and coping behaviour at the time of crisis. *European archives of psychiatry and clinical neuroscience, 245*(4-5), 245-254.

Mills, A. D., Jones, R. B., Faure, J.-M., & Williams, J. B. (1993). Responses to isolation in Japanese quail genetically selected for high or low sociality. *Physiology & Behavior, 53*(1), 183-189. doi: http://dx.doi.org/10.1016/0031-9384(93)90029-F

Moinard, C., Morisse, J., & Faure, J. (1998). Effect of cage area, cage height and perches on feather condition, bone breakage and mortality of laying hens. *British Poultry Science, 39*(2), 198-202.

Monroe, S. M., Bromet, E. J., Connell, M. M., & Steiner, S. C. (1986). Social support, life events, and depressive symptoms: A 1-year prospective study. *Journal of Consulting and Clinical Psychology, 54*(4), 424-431.

Moore, A. S., Gonyou, H. W., Stookey, J. M., & McLaren, D. G. (1994). Effect of group composition and pen size on behavior, productivity and immune response of growing pigs. *Applied Animal Behaviour Science, 40*(1), 13-30. doi: 10.1016/0168-1591(94)90084-1

Möstl, E., & Palme, R. (2002). Hormones as indicators of stress. *Domestic Animal Endocrinology, 23*(1–2), 67-74. doi: 10.1016/s0739-7240(02)00146-7

Müller, R., & Schrader, L. (2005). Behavioural consistency during social separation and personality in dairy cows. *Behaviour, 142*(9-10), 1289-1306.

Naguib, M., Flörcke, C., & van Oers, K. (2011). Effects of social conditions during early development on stress response and personality traits in great tits (Parus major). *Developmental Psychobiology, 53*(6), 592-600. doi: 10.1002/dev.20533

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews of the Cambridge Philosophical Society, 85*, 935-956.

Nakanishi, Y., Kawamura, T., Goto, T., & Umetsu, R. (1993). Comparative aspects of behavioural activities of beef cows before and after introducing a stranger at night. *九州大学農学部紀要, 37*(3), 227-238.

Nakazawa, M. (2014). fmsb: Functions for medical statistics book with some demographic data, from http://CRAN.R-project.org/package=fmsb

Newberry, R. C., & Swanson, J. C. (2008). Implications of breaking mother–young social bonds. *Applied Animal Behaviour Science, 110*(1–2), 3-23. doi: http://dx.doi.org/10.1016/j.applanim.2007.03.021

Newman, M. (2010). *Networks: an introduction*: Oxford University Press.

Newman, M. E. (2003). The structure and function of complex networks. *SIAM review, 45*(2), 167-256.

Newman, M. E. J. (2006a). Finding community structure in networks using the eigenvectors of matrices. *Physical Review E, 74*(3), 036104.

Newman, M. E. J. (2006b). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences, 103*(23), 8577-8582. doi: 10.1073/pnas.0601602103

Nicol, C. J. (1995). The social transmission of information and behaviour. *Applied Animal Behaviour Science, 44*(2–4), 79-98. doi: 10.1016/0168-1591(95)00607-t

Norring, M., Häggman, J., Simojoki, H., Tamminen, P., Winckler, C., & Pastell, M. (2014). Short communication: Lameness impairs feeding behavior of dairy cows. *Journal of Dairy Science, 97*(7), 4317-4321. doi: http://dx.doi.org/10.3168/jds.2013-7512

Nuñez, C. M. V., Adelman, J. S., Smith, J., Gesquiere, L. R., & Rubenstein, D. I. (2014). Linking social environment and stress physiology in feral mares (Equus caballus): Group transfers elevate fecal cortisol levels. *General and Comparative Endocrinology, 196*(0), 26-33. doi: http://dx.doi.org/10.1016/j.ygcen.2013.11.012

Nunn, C. L., Craft, M. E., Gillespie, T. R., Schaller, M., & Kappeler, P. M. (2015). The sociality–health–fitness nexus: synthesis, conclusions and future directions. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 370*(1669), 20140115.

Nunn, C. L., Jordán, F., McCabe, C. M., Verdolin, J. L., & Fewell, J. H. (2015). *Infectious disease and group size: more than just a numbers game* (Vol. 370).

O'Connell, J., Giller, P. S., & Meaney, W. (1989). A Comparison of Dairy Cattle Behavioural Patterns at Pasture and during Confinement. *Irish Journal of Agricultural Research, 28*(1), 65-72.

O'Connell, N. E., Beattie, V. E., & Moss, B. W. (2004). Influence of replacement rate on the welfare of sows introduced to a large dynamic group. *Applied Animal Behaviour Science, 85*(1-2), 43-56. doi: 10.1016/j.applanim.2003.09.003

O’Brien, B., Berry, D. P., Kelly, P., Meaney, W. J., & O’Callaghan, E. J. (2009). A study of the somatic cell count (SCC) of Irish milk from herd management and environmental perspectives. *Moorepark Dairy Production Research Centre*, 4-6.

O’Connell, N. E., Wicks, H. C. F., Carson, A. F., & McCoy, M. A. (2008). Influence of post-calving regrouping strategy on welfare and performance parameters in dairy heifers. *Applied Animal Behaviour Science, 114*(3–4), 319-329. doi: http://dx.doi.org/10.1016/j.applanim.2008.03.004

O’Neill, C. J., Bishop-Hurley, G. J., Williams, P. J., Reid, D. J., & Swain, D. L. (2014). Using UHF proximity loggers to quantify male–female interactions: A scoping study of estrous activity in cattle. *Animal Reproduction Science, 151*(1–2), 1-8. doi: http://dx.doi.org/10.1016/j.anireprosci.2014.09.017

Odén, K., Gunnarsson, S., Berg, C., & Algers, B. (2005). Effects of sex composition on fear measured as tonic immobility and vigilance behaviour in large flocks of laying hens. *Applied Animal Behaviour Science, 95*(1–2), 89-102. doi: 10.1016/j.applanim.2005.03.003

Odén, K., Vestergaard, K. S., & Algers, B. (2000). Space use and agonistic behaviour in relation to sex composition in large flocks of laying hens. *Applied Animal Behaviour Science, 67*(4), 307-320. doi: 10.1016/s0168-1591(99)00123-9

Oh, K. P., & Badyaev, A., V. (2010). Structure of Social Networks in a Passerine Bird: Consequences for Sexual Selection and the Evolution of Mating Strategies. *The American Naturalist, 176*(3), E80-E89. doi: 10.1086/655216

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., . . . Wagner, H. (2013). vegan: Community Ecology Package, from http://CRAN.R-project.org/package=vegan

Patison, K. P., Swain, D. L., Bishop-Hurley, G. J., Robins, G., Pattison, P., & Reid, D. J. (2010). Changes in temporal and spatial associations between pairs of cattle during the process of familiarisation. *Applied Animal Behaviour Science, 128*(1), 10-17.

Petrovski, K., Trajcev, M., & Buneski, G. (2006). A review of the factors affecting the costs of bovine mastitis: review article. *Journal of the South African Veterinary Association, 77*(2), p. 52-60.

Phillips, C. J. C., & Rind, M. I. (2001). The Effects on Production and Behavior of Mixing Uniparous and Multiparous Cows. *Journal of Dairy Science, 84*(11), 2424-2429. doi: 10.3168/jds.S0022-0302(01)74692-9

Pike, N. (2011). Using false discovery rates for multiple comparisons in ecology and evolution. *Methods in Ecology and Evolution, 2*(3), 278-282. doi: 10.1111/j.2041-210X.2010.00061.x

Pike, T. W., Samanta, M., Lindström, J., & Royle, N. J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B: Biological Sciences, 275*(1650), 2515-2520.

Pollard, K. A., & Blumstein, D. T. (2008). Time allocation and the evolution of group size. *Animal Behaviour, 76*(5), 1683-1699.

Porter, M. A., Onnela, J.-P., & Mucha, P. J. (2009). Communities in networks. *Notices of the AMS, 56*(9), 1082-1097.

Porter, R. H., Désiré, L., Bon, R., & Orgeur, P. (2001). The role of familiarity in the development of social recognition by Lambs. *Behaviour, 138*(2), 207-219.

Porter, R. H., Nowak, R., & Orgeur, P. (1995). Influence of a conspecific agemate on distress bleating by lambs. *Applied Animal Behaviour Science, 45*(3–4), 239-244. doi: http://dx.doi.org/10.1016/0168-1591(95)00630-B

Prange, S., Jordan, T., Hunter, C., & Gehrt, S. D. (2006). New Radiocollars for the Detection of Proximity among Individuals. *Wildlife Society Bulletin, 34*(5), 1333-1344.

Preuschoft, S., & van Schaik, C. P. (2000). Dominance and communication. *Conflict management in various social settings*, 77-105.

Price, E. O. (1997). Behavioural genetics and the process of animal domestication. In T. Grandin (Ed.), *Genetics and the Behaviour of Domestic Animals* (pp. 31-65). London, UK: Academic Press.

Price, E. O., & Wallach, S. J. R. (1990). Physical isolation of hand-reared Hereford bulls increases their aggressiveness toward humans. *27*(3), 263-267.

Proudfoot, K. L., Weary, D. M., & von Keyserlingk, M. A. G. (2012). Linking the social environment to illness in farm animals. *Applied Animal Behaviour Science, 138*(3–4), 203-215. doi: 10.1016/j.applanim.2012.02.008

Pruitt, J. N., & Keiser, C. N. (2014). The personality types of key catalytic individuals shape colonies' collective behaviour and success. *Animal Behaviour, 93*(0), 87-95. doi: http://dx.doi.org/10.1016/j.anbehav.2014.04.017

Pryce, J., Royal, M., Garnsworthy, P., & Mao, I. L. (2004). Fertility in the high-producing dairy cow. *Livestock Production Science, 86*(1), 125-135.

Pulliam, H. R., & Caraco, T. (1984). Living in groups: is there an optimal group size? In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology:An Evolutionary Approach* (2 ed., pp. pp. 122–147.). London Blackwell Scientific Publications Ltd.

Radford, M. (2001). *Animal Welfare Law in Britain*. Oxford: Oxford University Press.

Ranasinghe, R. M. S. B. K., Nakao, T., Yamada, K., & Koike, K. (2010). Silent ovulation, based on walking activity and milk progesterone concentrations, in Holstein cows housed in a free-stall barn. *Theriogenology, 73*(7), 942-949. doi: http://dx.doi.org/10.1016/j.theriogenology.2009.11.021

Rault, J.-L. (2012). Friends with benefits: Social support and its relevance for farm animal welfare. *Applied Animal Behaviour Science, 136*(1), 1-14. doi: 10.1016/j.applanim.2011.10.002

Raussi, S., Boissy, A., Delval, E., Pradel, P., Kaihilahti, J., & Veissier, I. (2005). Does repeated regrouping alter the social behaviour of heifers? *Applied Animal Behaviour Science, 93*(1–2), 1-12. doi: 10.1016/j.applanim.2004.12.001

Raussi, S., Niskanen, S., Siivonen, J., Hänninen, L., Hepola, H., Jauhiainen, L., & Veissier, I. (2010). The formation of preferential relationships at early age in cattle. *Behavioural Processes, 84*(3), 726-731. doi: 10.1016/j.beproc.2010.05.005

Rauw, W. M., Kanis, E., Noordhuizen-Stassen, E. N., & Grommers, F. J. (1998). Undesirable side effects of selection for high production efficiency in farm animals: a review. *Livestock Production Science, 56*(1), 15-33. doi: 10.1016/s0301-6226(98)00147-x

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological reviews, 82*(2), 291-318.

Reebs, S. G. (2000). Can a minority of informed leaders determine the foraging movements of a fish shoal? *Animal behaviour, 59*(2), 403-409.

Reinhardt, V., & Reinhardt, A. (1981). Cohesive Relationships in a Cattle Herd (Bos indicus). *Behaviour, 77*(3), 121-151. doi: 10.2307/4534115

Reinhardt, V., & Reinhardt, A. (1981). Natural sucking performance and age of weaning in zebu cattle (Bos indicus). *The Journal of Agricultural Science, 96*(02), 309-312.

Riedstra, B., & Groothuis, T. G. G. (2002). Early feather pecking as a form of social exploration: the effect of group stability on feather pecking and tonic immobility in domestic chicks. *Applied Animal Behaviour Science, 77*(2), 127-138. doi: http://dx.doi.org/10.1016/S0168-1591(02)00031-X

Rimbach, R., Bisanzio, D., Galvis, N., Link, A., Di Fiore, A., & Gillespie, T. R. (2015). *Brown spider monkeys (Ateles hybridus): a model for differentiating the role of social networks and physical contact on parasite transmission dynamics* (Vol. 370).

Ringgenberg, N., Bergeron, R., Meunier-Salaün, M.-C., & Devillers, N. (2012). Impact of social stress during gestation and environmental enrichment during lactation on the maternal behavior of sows. *Applied Animal Behaviour Science, 136*(2–4), 126-135. doi: http://dx.doi.org/10.1016/j.applanim.2011.12.012

Rivera, E., Benjamin, S., Nielsen, B., Shelle, J., & Zanella, A. J. (2002). Behavioral and physiological responses of horses to initial training: the comparison between pastured versus stalled horses. *Applied Animal Behaviour Science, 78*(2–4), 235-252. doi: 10.1016/s0168-1591(02)00091-6

Robel, R. J., & Ballard, W. B. (1974). Lek Social Organization and Reproductive Success in the Greater Prairie Chicken. *American Zoologist, 14*(1), 121-128. doi: 10.1093/icb/14.1.121

Rodenburg, T. B., Buitenhuis, A. J., Ask, B., Uitdehaag, K. A., Koene, P., Van Der Poel, J. J., & Bovenhuis, H. (2003). Heritability of feather pecking and open-field response of laying hens at two different ages. *Poultry Science, 82*(6), 861-867.

Rodenburg, T. B., & Koene, P. (2007). The impact of group size on damaging behaviours, aggression, fear and stress in farm animals. *Applied Animal Behaviour Science, 103*(3–4), 205-214. doi: 10.1016/j.applanim.2006.05.024

Rose, P., & Croft, D. (2015). The potential of Social Network Analysis as a tool for the management of zoo animals. *Animal Welfare, 24*(2), 123-138.

Ruckstuhl, K., & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews, 77*(1), 77-96.

Ruis, M. A. W., de Groot, J., te Brake, J. H. A., Dinand Ekkel, E., van de Burgwal, J. A., Erkens, J. H. F., . . . Koolhaas, J. M. (2001). Behavioural and physiological consequences of acute social defeat in growing gilts: effects of the social environment. *Applied Animal Behaviour Science, 70*(3), 201-225. doi: 10.1016/s0168-1591(00)00150-7

Ruis, M. A. W., te Brake, J. H. A., Buwalda, B., De Boer, S. F., Meerlo, P., Korte, S. M., . . . Koolhaas, J. M. (1999). Housing familiar male wildtype rats together reduces the long-term adverse behavioural and physiological effects of social defeat. *Psychoneuroendocrinology, 24*(3), 285-300. doi: 10.1016/s0306-4530(98)00050-x

Rushen, J., & Passillé, A. M. B. d. (1992). The scientific assessment of the impact of housing on animal welfare: A critical review. *Canadian Journal of Animal Science, 72*(4), 721-743. doi: 10.4141/cjas92-085

Rushmore, J., Caillaud, D., Matamba, L., Stumpf, R. M., Borgatti, S. P., & Altizer, S. (2013). Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. *Journal of Animal Ecology, 82*(5), 976-986.

Rutherford, K. M. D., Langford, F. M., Jack, M. C., Sherwood, L., Lawrence, A. B., & Haskell, M. J. (2009). Lameness prevalence and risk factors in organic and non-organic dairy herds in the United Kingdom. *The Veterinary Journal, 180*(1), 95-105. doi: http://dx.doi.org/10.1016/j.tvjl.2008.03.015

Rutz, C., Burns, Z. T., James, R., Ismar, S. M. H., Burt, J., Otis, B., . . . St Clair, J. J. H. (2012). Automated mapping of social networks in wild birds. *Current Biology, 22*(17), R669-R671.

Ryder, T. B., Horton, B. M., van den Tillaart, M., Morales, J. D. D., & Moore, I. T. (2012). Proximity data-loggers increase the quantity and quality of social network data. *Biology Letters, 8*, 917-920.

Ryder, T. B., Parker, P. G., Blake, J. G., & Loiselle, B. A. (2009). It takes two to tango: reproductive skew and social correlates of male mating success in a lek-breeding bird. *Proceedings of the Royal Society of London B: Biological Sciences, 276*(1666), 2377-2384.

Sachser, N. (1993). The ability to arrange with conspecifics depends on social experiences around puberty. *Physiology &amp; Behavior, 53*(3), 539-544. doi: 10.1016/0031-9384(93)90151-5

Sachser, N. (1994). Social stratification and health in non-human mammals—a case study in guinea pigs. In L. Ellis (Ed.), *Social Stratification and Socioeconomic Inequality*. Westport 2Praeger.

Sachser, N., Dürschlag, M., & Hirzel, D. (1998). Social relationships and the management of stress. *Psychoneuroendocrinology, 23*(8), 891-904. doi: 10.1016/s0306-4530(98)00059-6

Sachser, N., & Lick, C. (1991). Social experience, behavior, and stress in guinea pigs. *Physiology &amp; Behavior, 50*(1), 83-90. doi: 10.1016/0031-9384(91)90502-f

Sachser, N., & Renninger, S. V. (1993). Coping with social conflict: the role of rearing conditions in guinea pigs. *Ethology Ecology and Evolution, 5*, 65-74.

Salak-Johnson, J. L., & McGlone, J. J. (2007). Making sense of apparently conflicting data: Stress and immunity in swine and cattle. *Journal of Animal Science, 85*(13 suppl), E81-E88. doi: 10.2527/jas.2006-538

Sapolsky, R. M. (2004). Social Status and Health in Humans and Other Animals. *Annual Review of Anthropology, 33*, 393-418. doi: 10.2307/25064859

Sato, S., Sako, S., & Maeda, A. (1991). Social licking patterns in cattle (Bos taurus): influence of environmental and social factors. *Applied Animal Behaviour Science, 32*(1), 3-12. doi: http://dx.doi.org/10.1016/S0168-1591(05)80158-3

Sato, S., Sassa, H., & Sonoda, T. (1990). Effect of the dominance rank of partner cows on social behaviour of newly introduced heifers. *Japanese Journal of Livestock Management (Japan)*.

Sato, S., & Tarumizu, K. (1993). Heart rates before, during and after allo-grooming in cattle (Bos taurus). *Journal of Ethology, 11*(2), 149-150. doi: 10.1007/BF02350048

Sato, S., Tarumizu, K., & Hatae, K. (1993). The influence of social factors on allogrooming in cows. *Applied Animal Behaviour Science, 38*(3–4), 235-244. doi: http://dx.doi.org/10.1016/0168-1591(93)90022-H

Sato, S., Wood-Gush, D., & Wetherill, G. (1987). Observations on creche behaviour in suckler calves. *Behavioural processes, 15*(2), 333-343.

Scheme, R. T. F. A. D. (2011) (Vol. 2): Red Tractor Assurance Dairy, Hestan House, The Crichton, Dumfries, DG1 4TA

Schrøder-Petersen, D. L., & Simonsen, H. B. (2001). Tail Biting in Pigs. *The Veterinary Journal, 162*(3), 196-210. doi: 10.1053/tvjl.2001.0605

Schuett, W., Dall, S. R. X., Baeumer, J., Kloesener, M. H., Nakagawa, S., Beinlich, F., & Eggers, T. (2011). Personality variation in a clonal insect: the pea aphid, *Acyrthosiphon pisum*. *Developmental Psychobiology, 53*, 631-640.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social Bonds Enhance Reproductive Success in Male Macaques. *Current Biology, 20*(24), 2207-2210. doi: http://dx.doi.org/10.1016/j.cub.2010.10.058

Schweitzer, C., Houdelier, C., Lumineau, S., Lévy, F., & Arnould, C. (2010). Social motivation does not go hand in hand with social bonding between two familiar Japanese quail chicks, Coturnix japonica. *Animal Behaviour, 79*(3), 571-578.

Schweitzer, C., Lévy, F., & Arnould, C. (2011). Increasing group size decreases social bonding in young Japanese quail, Coturnix japonica. *Animal Behaviour, 81*(3), 535-542. doi: 10.1016/j.anbehav.2010.11.017

Sharma, N., Singh, N., & Bhadwal, M. (2011). Relationship of somatic cell count and mastitis: An overview. *Asian-Australasian Journal of Animal Sciences, 24*(3), 429-438.

Sherwin, C. M. (1996). Laboratory mice persist in gaining access to resources: a method of assessing the importance of environmental features. *Applied Animal Behaviour Science, 48*(3–4), 203-213. doi: 10.1016/0168-1591(96)01027-1

Shrader, A. M., Kerley, G. I. H., Kotler, B. P., & Brown, J. S. (2007). Social information, social feeding, and competition in group-living goats (Capra hircus). *Behavioral Ecology, 18*(1), 103-107. doi: 10.1093/beheco/arl057

Sibbald, A. M., Erhard, H. W., Hooper, R. J., Dumont, B., & Boissy, A. (2006). A test for measuring individual variation in how far grazing animals will move away from a social group to feed. *Applied Animal Behaviour Science, 98*(1-2), 89-99.

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists *Behavioral Ecology and Sociobiology, 63*, 975-988.

Silk, J. B. (2007). Social components of fitness in primate groups. *Science, 317*(5843), 1347-1351. doi: 10.1126/science.1140734

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science, 302*(5648), 1231-1234.

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 183-195.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . . Cheney, D. L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences, 276*(1670), 3099-3104. doi: 10.1098/rspb.2009.0681

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . . Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology, 20*(15), 1359-1361.

Smith, K., Alberts, S. C., & Altmann, J. (2003). Wild female baboons bias their social behaviour towards paternal half-sisters. *Proceedings of the Royal Society B: Biological Sciences, 270*(1514), 503-510.

Snijders, T. A. B. (2011). Statistical Models for Social Networks. *Annual Review of Sociology, 37*(1), 131-153. doi: doi:10.1146/annurev.soc.012809.102709

Søndergaard, E., & Ladewig, J. (2004). Group housing exerts a positive effect on the behaviour of young horses during training. *Applied Animal Behaviour Science, 87*(1–2), 105-118. doi: 10.1016/j.applanim.2003.12.010

Sowerby, M. E., & Polan, C. E. (1978). Milk Production Response to Shifting Cows Between Intraherd Groups. *Journal of Dairy Science, 61*(4), 455-460. doi: http://dx.doi.org/10.3168/jds.S0022-0302(78)83620-0

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology), 64*(4), 583-639.

Spoolder, H. A. M., Geudeke, M. J., Van der Peet-Schwering, C. M. C., & Soede, N. M. (2009). Group housing of sows in early pregnancy: A review of success and risk factors. *Livestock Science, 125*(1), 1-14. doi: http://dx.doi.org/10.1016/j.livsci.2009.03.009

Stěhulová, I., Lidfors, L., & Špinka, M. (2008). Response of dairy cows and calves to early separation: Effect of calf age and visual and auditory contact after separation. *Applied Animal Behaviour Science, 110*(1), 144-165.

Stookey, J., & Gonyou, H. (1994). The effects of regrouping on behavioral and production parameters in finishing swine. *Journal of animal science, 72*(11), 2804-2811.

Stoye, S., Porter, M. A., & Stamp Dawkins, M. (2012). Synchronized lying in cattle in relation to time of day. *Livestock Science, 149*(1), 70-73.

Sueur, C., Deneubourg, J.-L., & Petit, O. (2012). From Social Network (Centralized vs. Decentralized) to Collective Decision-Making (Unshared vs. Shared Consensus). *PLoS ONE, 7*(2), e32566. doi: 10.1371/journal.pone.0032566

Sveberg, G., Refsdal, A. O., Erhard, H. W., Kommisrud, E., Aldrin, M., Tvete, I. F., . . . Ropstad, E. (2013). Sexually active groups in cattle—A novel estrus sign. *Journal of Dairy Science, 96*(7), 4375-4386. doi: http://dx.doi.org/10.3168/jds.2012-6407

Svensson, C., & Liberg, P. (2006). The effect of group size on health and growth rate of Swedish dairy calves housed in pens with automatic milk-feeders. *Preventive Veterinary Medicine, 73*(1), 43-53. doi: 10.1016/j.prevetmed.2005.08.021

Swain, D. L., & Bishop-Hurley, G. J. (2007). Using contact logging devices to explore animal affiliations: Quantifying cow–calf interactions. *Applied Animal Behaviour Science, 102*(1–2), 1-11. doi: 10.1016/j.applanim.2006.03.008

Syarifuddin, S., & Kramer, D. L. (1996). The effect of group size on space use and aggression at a concentrated food source in blue gouramis, Trichogaster trichopterus (Pisces: Belontiidae). *Environmental Biology of Fishes, 46*(3), 289-296.

Syme, G. (1974). Competitive orders as measures of social dominance. *Animal Behaviour, 22*, 931-940.

Syme, G. J. (1974). Competitive orders as measures of social dominance. *Animal Behaviour, 22, Part 4*(0), 931-940. doi: http://dx.doi.org/10.1016/0003-3472(74)90016-5

Takeda, K.-i., Sato, S., & Sugawara, K. (2003). Familiarity and group size affect emotional stress in Japanese Black heifers. *Applied Animal Behaviour Science, 82*(1), 1-11. doi: 10.1016/s0168-1591(03)00039-x

Tambling, C. J., & Belton, L. E. (2009). Feasibility of using proximity tags to locate female lion *panthera leo* kills. *Wildlife Biology, 15*(4), 435-441. doi: 10.2981/09-029

Tapki, İ. (2007). Effects of individual or combined housing systems on behavioural and growth responses of dairy calves. *Acta Agriculturae Scand Section A, 57*(2), 55-60.

Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A., & Updegraff, J. A. (2000). Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. *Psychological review, 107*(3), 411.

Team, R. C. (2014). R: A language and environment for statistical computing, from http://www.R-project.org/

Tennessen, T., Price, M. A., & Berg, R. T. (1985). The social interactions of young bulls and steers after re-grouping. *Applied Animal Behaviour Science, 14*(1), 37-47. doi: http://dx.doi.org/10.1016/0168-1591(85)90036-X

Theis, F. J., Ugelvig, L. V., Marr, C., & Cremer, S. (2015). *Opposing effects of allogrooming on disease transmission in ant societies* (Vol. 370).

Thomas, T. J., Weary, D. M., & Appleby, M. C. (2001). Newborn and 5-week-old calves vocalize in response to milk deprivation. *Applied Animal Behaviour Science, 74*(3), 165-173. doi: http://dx.doi.org/10.1016/S0168-1591(01)00164-2

Tuchscherer, M., Kanitz, E., Puppe, B., & Tuchscherer, A. (2006). Early social isolation alters behavioral and physiological responses to an endotoxin challenge in piglets. *Hormones and Behavior, 50*(5), 753-761. doi: http://dx.doi.org/10.1016/j.yhbeh.2006.06.026

Turner, S., Ewen, M., Rooke, J., & Edwards, S. (2000). The effect of space allowance on performance, aggression and immune competence of growing pigs housed on straw deep-litter at different group sizes. *Livestock Production Science, 66*(1), 47-55.

Turner, S. P., & Edwards, S. A. (2004). Housing immature domestic pigs in large social groups: implications for social organisation in a hierarchical society. *Applied Animal Behaviour Science, 87*(3–4), 239-253. doi: 10.1016/j.applanim.2004.01.010

Ude, G., Georg, H., & Schwalm, A. (2011). Reducing milk induced cross-sucking of group housed calves by an environmentally enriched post feeding area. *Livestock Science, 138*(1), 293-298.

Val-Laillet, D., Guesdon, V., von Keyserlingk, M. A. G., de Passillé, A. M., & Rushen, J. (2009). Allogrooming in cattle: Relationships between social preferences, feeding displacements and social dominance. *Applied Animal Behaviour Science, 116*(2–4), 141-149. doi: 10.1016/j.applanim.2008.08.005

Van Nieuwamerongen, S. E., Bolhuis, J. E., Van Der Peet-Schwering, C. M. C., & Soede, N. M. (2014). A review of sow and piglet behaviour and performance in group housing systems for lactating sows. *Animal, 8*(3), 448-460. doi: 10.1017/S1751731113002280

Van Putten, G., & Van De Burgwal, J. A. (1990). Vulva biting in group-housed sows: Preliminary report. *Applied Animal Behaviour Science, 26*(1–2), 181-186. doi: 10.1016/0168-1591(90)90097-w

Vanhonacker, F., Verbeke, W., Van Poucke, E., Buijs, S., & Tuyttens, F. A. M. (2009). Societal concern related to stocking density, pen size and group size in farm animal production. *Livestock Science, 123*(1), 16-22. doi: http://dx.doi.org/10.1016/j.livsci.2008.09.023

Varner, M. A., & Johnson, B. H. (1983). Influence of adrenocorticotropin upon milk production, milk constituents, and endocrine measures of dairy cows. *Journal of dairy science, 66*(3), 458-465.

Veissier, I., Boissy, A., dePassillé, A. M., Rushen, J., van Reenen, C. G., Roussel, S., . . . Pradel, P. (2001). Calves' responses to repeated social regrouping and relocation. *Journal of Animal Science, 79*(10), 2580-2593.

Veissier, I., Boissy, A., Nowak, R., Orgeur, P., & Poindron, P. (1998). Ontogeny of social awareness in domestic herbivores. *Applied Animal Behaviour Science, 57*(3–4), 233-245. doi: 10.1016/s0168-1591(98)00099-9

Veissier, I., Gesmier, V., Le Neindre, P., Gautier, J., & Bertrand, G. (1994). The effects of rearing in individual crates on subsequent social behaviour of veal calves. *Applied Animal Behaviour Science, 41*(3), 199-210.

Verbeek, M. E., Boon, A., & Drent, P. J. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour, 133*(11), 945-963.

Vitale, A. F., Tenucci, M., Papini, M., & Lovari, S. (1986). Social behaviour of the calves of semi-wild Maremma cattle, Bos primigenius taurus. *Applied Animal Behaviour Science, 16*(3), 217-231. doi: http://dx.doi.org/10.1016/0168-1591(86)90115-2

von Keyserlingk, M. A. G., Olenick, D., & Weary, D. M. (2008). Acute Behavioral Effects of Regrouping Dairy Cows. *Journal of Dairy Science, 91*(3), 1011-1016. doi: 10.3168/jds.2007-0532

Walker, S., Smith, R., Jones, D., Routly, J., Morris, M., & Dobson, H. (2010). The effect of a chronic stressor, lameness, on detailed sexual behaviour and hormonal profiles in milk and plasma of dairy cattle. *Reproduction in domestic animals, 45*(1), 109-117.

Walrath, R., Van Deelen, T. R., & VerCauteren, K. C. (2011). Efficacy of proximity loggers for detection of contacts between maternal pairs of white-tailed deer. *Wildlife Society Bulletin, 35*(4), 452-460. doi: 10.1002/wsb.76

Walsh, S. W., Williams, E. J., & Evans, A. C. O. (2011). A review of the causes of poor fertility in high milk producing dairy cows. *Animal Reproduction Science, 123*(3–4), 127-138. doi: http://dx.doi.org/10.1016/j.anireprosci.2010.12.001

Ward, A. J. W., & Hart, P. J. B. (2003). The effects of kin and familiarity on interactions between fish. *Fish and Fisheries, 4*(4), 348-358. doi: 10.1046/j.1467-2979.2003.00135.x

Warnick, V., Arave, C. W., & Mickelsen, C. (1977). Effects of group, individual, and isolated rearing of calves on weight gain and behavior. *Journal of Dairy Science, 60*(6), 947-953.

Wasilewski, A. (2003). *“Freundschaft” bei Huftieren? A-Soziopositive Beziehungen zwischen nicht-verwandten artgleichen Herdenmitgliedern.* Philipps University Marburg.

Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications* (Vol. 8): Cambridge university press.

Watson-Haigh, N. S., O'Neill, C. J., & Kadarmideen, H. N. (2012). Proximity loggers: data handling and classification for quality control. *Sensors Journal, IEEE, 12*(5), 1611-1617.

Watts, J. M., & Stookey, J. M. (2000). Vocal behaviour in cattle: the animal's commentary on its biological processes and welfare. *Applied Animal Behaviour Science, 67*(1), 15-33.

Weary, D. M., Jasper, J., & Hötzel, M. J. (2008). Understanding weaning distress. *Applied Animal Behaviour Science, 110*(1), 24-41.

Weary, D. M., Pajor, E. A., Bonenfant, M., Fraser, D., & Kramer, D. L. (2002). Alternative housing for sows and litters Part 4. Effects of sow-controlled housing combined with a communal piglet area on pre- and post-weaning behaviour and performance. *Applied Animal Behaviour Science, 76*(4), 279-290.

Wechsler, B. (1995). Coping and coping strategies: a behavioural view. *Applied Animal Behaviour Science, 43*(2), 123-134. doi: 10.1016/0168-1591(95)00557-9

Wechsler, B., Huber-Eicher, B., & Nash, D. R. (1998). Feather pecking in growers: A study with individually marked birds. *British Poultry Science, 39*(2), 178-185. doi: 10.1080/00071669889097

Weidt, A., Hofmann, S. E., & König, B. (2008). Not only mate choice matters: fitness consequences of social partner choice in female house mice. *Animal Behaviour, 75*(3), 801-808. doi: 10.1016/j.anbehav.2007.06.017

Weiss, I. C., Pryce, C. R., Jongen-Rêlo, A. L., Nanz-Bahr, N. I., & Feldon, J. (2004). Effect of social isolation on stress-related behavioural and neuroendocrine state in the rat. *Behavioural brain research, 152*(2), 279-295.

West-Eberhard, M. J. (1979). Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society, 123*(4), 222-234.

West, B., & Zhou, B. (1989). Did chickens go north? New evidence for domestication. *World’s. Poult. Sci. J. , 45,* 205—218.

Wey, T., Blumstein, D. T., Shen, W., & Jordan, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour, 75,* 333-344. doi: 10.1016/j.anbehav.2007.06.020|ISSN 0003-3472

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour, 75*(2), 333-344. doi: 10.1016/j.anbehav.2007.06.020

Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social analysis*: University of Chicago Press.

Whitehead, H., & Dufault, S. (1999). Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior, 28,* 33-74.

Wiepkema, P. R. (1993). On the significance of ethological criteria for the assessment of animal welfare In D. Smidt (Ed.), *Indicators Relevant to Farm Animal Welfare* (pp. 71-79). The Hague: Martinus Nijhoff.

Wierenga, H., & Metz, J. (1986). Lying behaviour of dairy cows influenced by crowding.

Wierenga, H. K. (1991). Behaviour of dairy cows under modern housing and management.

Wikberg, E. C., Ting, N., & Sicotte, P. (2014). Familiarity is more important than phenotypic similarity in shaping social relationships in a facultative female dispersed primate, *Colobus vellerosus*. *Behavioural processes, 106,* 27-35.

Wilson, A. D. M., & Krause, J. (2015). Personality and social network analysis in animals In J. Krause, R. James, D. W. Franks & D. P. Croft (Eds.), *Animal Social Networks* (pp. 53-60). USA: Oxford University Press.

Wilson, E. O. (1975). *Sociobiology: The New Synthesis*. Cambridge: Cambridge Press.

Wingfield, J. C., Maney, D. L., Breuner, C. W., Jacobs, J. D., Lynn, S., Ramenofsky, M., & Richardson, R. D. (1998). Ecological Bases of Hormone—Behavior Interactions: The “Emergency Life History Stage”. *American Zoologist, 38*(1), 191-206. doi: 10.1093/icb/38.1.191

Wiszniewski, J., Lusseau, D., & Möller, L. M. (2010). Female bisexual kinship ties maintain social cohesion in a dolphin network. *Animal Behaviour, 80*(5), 895-904. doi: http://dx.doi.org/10.1016/j.anbehav.2010.08.013

Wittig, R. A., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior, 54*(1), 170-177. doi: 10.1016/j.yhbeh.2008.02.009

Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior, 54*(1), 170-177. doi: 10.1016/j.yhbeh.2008.02.009

Wolf, J. B., Brodie, E. D., & Moore, A. J. (1999). Interacting Phenotypes and the Evolutionary Process. II. Selection Resulting from Social Interactions. *The American Naturalist, 153*(3), 254-266.

Wolf, J. B., Mawdsley, D., Trillmich, F., & James, R. (2007). Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Animal Behaviour, 74*(5), 1293-1302. doi: http://dx.doi.org/10.1016/j.anbehav.2007.02.024

Wolf, J. B., Tautz, D., & Trillmich, F. (2007). Galápagos and Californian sea lions are separate species: genetic analysis of the genus Zalophus and its implications for conservation management. *Frontiers in Zoology, 4*(1), 20.

Woods, A. (2012). From cruelty to welfare: the emergence of farm animal welfare in Britain, 1964–71. *Endeavour, 36*(1), 14-22. doi: 10.1016/j.endeavour.2011.10.003

Yamashita, H., Okamoto, S., Maeda, Y., & Hashiguchi, T. (1994). Genetic relationships among domestic and jungle fowls revealed by DNA fingerprinting analysis. *Jpn. Poult. Sci, 31*, 335—344.

Ylander, D. M., & Craig, J. V. (1980). Inhibition of agonistic acts between domestic hens by a dominant third party. *Applied Animal Ethology, 6*(1), 63-69. doi: 10.1016/0304-3762(80)90094-2

Zeltner, E., Klein, T., & Huber-Eicher, B. (2000). Is there social transmission of feather pecking in groups of laying hen chicks? *Animal Behaviour, 60*(2), 211-216. doi: 10.1006/anbe.2000.1453

Zuk, M., Thornhill, R., Ligon, J. D., & Johnson, K. (1990). Parasites and Mate Choice in Red Jungle Fowl. *American Zoologist, 30*(2), 235-244.