General Enquiries on the form should be made to:
Defra, Procurements and Commercial Function (Evidence Procurement Team)
E-mail: research.competitions@defra.gsi.gov.uk

Evidence Project Final Report

- **Note**
  In line with the Freedom of Information Act 2000, Defra aims to place the results of its completed research projects in the public domain wherever possible.
  The Evidence Project Final Report is designed to capture the information on the results and outputs of Defra-funded research in a format that is easily publishable through the Defra website
  An Evidence Project Final Report must be completed for all projects.
- This form is in Word format and the boxes may be expanded, as appropriate.
- **ACCESS TO INFORMATION**
  The information collected on this form will be stored electronically and may be sent to any part of Defra, or to individual researchers or organisations outside Defra for the purposes of reviewing the project. Defra may also disclose the information to any outside organisation acting as an agent authorised by Defra to process final research reports on its behalf. Defra intends to publish this form on its website, unless there are strong reasons not to, which fully comply with exemptions under the Environmental Information Regulations or the Freedom of Information Act 2000.
  Defra may be required to release information, including personal data and commercial information, on request under the Environmental Information Regulations or the Freedom of Information Act 2000. However, Defra will not permit any unwarranted breach of confidentiality or act in contravention of its obligations under the Data Protection Act 1998. Defra or its appointed agents may use the name, address or other details on your form to contact you in connection with occasional customer research aimed at improving the processes through which Defra works with its contractors.

Project identification

1. Defra Project code: AW1027
2. Project title: The influence of Social Networks on Welfare and Productivity in Dairy Cattle
3. Contractor organisation(s):
   The University of Exeter
   Northcote House
   The Queen's Drive
   Exeter
4. Total Defra project costs (agreed fixed price): £45,000
5. Project: start date 02/01/2012
   end date .... 31st Dec 2015

6. It is Defra's intention to publish this form.

Please confirm your agreement to do so.. YES ☒ NO ☐

(a) When preparing Evidence Project Final Reports contractors should bear in mind that Defra intends that they be made public. They should be written in a clear and concise manner and represent a full account of the research project which someone not closely associated with the project can follow.

Defra recognises that in a small minority of cases there may be information, such as intellectual property or commercially confidential data, used in or generated by the research project, which should not be disclosed. In these cases, such information should be detailed in a separate annex (not to be published) so that the Evidence Project Final Report can be placed in the public domain. Where it is impossible to complete the Final Report without including references to any sensitive or confidential data, the information should be included and section (b) completed. NB: only in exceptional circumstances will Defra expect contractors to give a "No" answer.

In all cases, reasons for withholding information must be fully in line with exemptions under the Environmental Information Regulations or the Freedom of Information Act 2000.

(b) If you have answered NO, please explain why the Final report should not be released into public domain

Executive Summary

7. The executive summary must not exceed 2 sides in total of A4 and should be understandable to the intelligent non-scientist. It should cover the main objectives, methods and findings of the research, together with any other significant events and options for new work.

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 reproductive success 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.

The aim of this project was to use SNA to investigate the social structure of a dynamic group of dairy cattle, and to quantify the relationship 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 on stress and the formation of social relationships.

Commercial 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 (i.e. cows spent more time with others that were similar to them). 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 housing type (individually or pair-housed) on calves' 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. Future research is needed to quantify the consequences of different management practices on the social structure of cattle and the implications of these effects for welfare and productivity. The recent development of low cost tags for tracking the spatial and social positions of animals opens up unprecedented opportunities for large scale replication of this work across commercial livestock farms. Moreover, because of the dramatic reduction in the cost of technology that can collect real time social and spatial data it is likely that many farmers would find it commercially viable to instrument livestock with tags that can track the social and spatial behaviour of individuals. Doing so would provide unprecedented data which could be used to: provide an early warning system for animal health; improve the control of infectious diseases (through the knowledge of disease transmission pathways), and: manage social stress. The project reported here clearly demonstrates the potential of this approach. However, before the full benefits of this technology and be realised, future work is needed to develop the statistical and mathematical approaches to inform animal management from such data sets.

Project Report to Defra

8. As a guide this report should be no longer than 20 sides of A4. This report is to provide Defra with details of the outputs of the research project for internal purposes; to meet the terms of the contract; and to allow Defra to publish details of the outputs to meet Environmental Information Regulation or Freedom of Information obligations. This short report to Defra does not preclude contractors from also seeking to publish a full, formal scientific report/paper in an appropriate scientific or other journal/publication. Indeed, Defra actively encourages such publications as part of the contract terms. The report to Defra should include:

- the objectives as set out in the contract;
- the extent to which the objectives set out in the contract have been met;
- details of methods used and the results obtained, including statistical analysis (if appropriate);
- a discussion of the results and their reliability;
- the main implications of the findings;
- possible future work; and
- any action resulting from the research (e.g. IP, Knowledge Exchange).

1. Project overview:

This project involved funding from Defra, DairyCo and the University of Exeter which supported a PhD student for 3 years to undertake the project outlined in the objectives below. The student on the project was awarded a PhD in Jan 2016 and has since secured a permanent job as a Scientific Officer at Compassion in World Farming. To date, the project has produced 2 published papers (Boyland et al. 2013; Boyland et al. 2015) and there are a further 2 manuscripts which are close to submission.

2. The objectives as set out in the contract

Objective 1. Determine how an individual's social network position relates to its welfare and productivity. We will test the hypothesis that an individual's social network position will be a significant predictor of its welfare and productivity. The outputs from this objective will inform farmers of the relationship between the fine social structure of their group and the productivity and welfare of its members, as well as how this structure can be measured.

Objective 2. Determine the consequences of network perturbation for health and productivity. We will use management decisions to add and remove individuals to management groups to test the hypothesis that the removal and replacement of individuals will alter group social structure and that these effects will have welfare and productivity consequences. We will also determine the effects of changing network position (pre vs post perturbation) on individual welfare and productivity. We will compare the effects of removing individuals in different social network positions (central or peripheral within the social network). The outputs of this objective will inform farmers how to minimise the disruptive effects of the removal or introduction of individuals on social network structure (e.g. selection of individuals based on social relationships, timing of introductions and the number of individuals introduced/removed).

Objective 3: Determine the implications of management group size on the structure of social relationships. We will compare social network structure across replicated management groups that differ in size and evaluate the implications of any differences in social network structure for welfare and productivity. The outputs of this objective will inform policy on the implications of increasing management group size for animal welfare and productivity.

3. The extent to which the objectives have been met

At the heart of this project is quantifying the patterns of social behaviour in dairy cattle. To do this we used proximity loggers supplied by SirTrack. Prior to deploying these collars on the cattle it was essential for us to validate the collars and check for any sampling biases. Previous work using this technology has often neglected to undertake appropriate validation trials. We found substantial problems with the collars that had not been reported previously: the collars differed significantly in both their signal strength and detection sensitivity and it was not possible to calibrate the collars prior to deployment. This presented us with a significant challenge because variation in the performance of the loggers introduces sampling bias in the data. We ran numerous pilot tests with the loggers both on the cows and in controlled conditions and we established that the variation in performance was a consistent property of the logger (i.e. it is highly repeatable). Using this knowledge, we developed a method for correcting for the bias in the data collection at the point of analysis, which we published in *Behavioural Ecology and Socio-biology* (Boyland et al. 2013). In this paper we highlight the problem and the consequences of variation in logging performance for making inferences about inter-individual variation in social behaviour. We make recommendations for how to correct for logging biases in the data; this manuscript has already been cited by 7 other studies using proximity loggers.

It was essential that we invested the time at the start of the project to establish the error and variation in the logger performance. The consequence of these problems with the technology meant that the first year of the project was spent validating and developing the correction method for the proximity loggers which we had not anticipated (given, for example, that they had been deployed on cattle previously (e.g. Bohm et al. 2009). These problems also meant that data processing was more complex than we had envisaged. As a result of these issues we did not have time to complete objectives 2 and 3 within the duration of the project. We did however establish a data set that will allow us to address objective 2 and we are currently working towards analysing the data for this objective.

3. Details of Methods, Analysis and Results

In addressing objective 1 we completed four sub-projects.

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

Boyland, N. K., et al. *Behavioral Ecology and Sociobiology* 67.11 (2013): 1877-1890.

3.1 Summary: 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.

3.1 Methods: 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.

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. 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. 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).

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.

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).

3.1 Results: 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 1). 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.

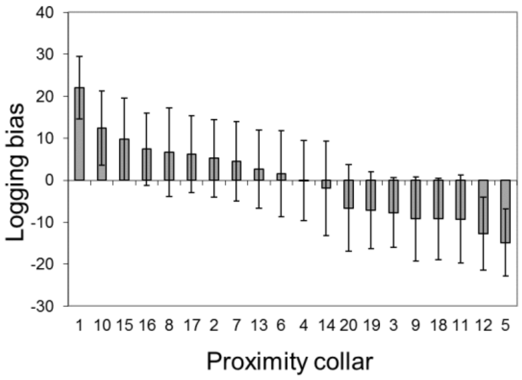

Figure 1 Logging bias (mean percentage difference in contact logging) of each proximity logger, based on total duration of associations over a 3 week period (error bars represent standard deviations).

When constructing a network from the association matrix of total contact durations during field deployment 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, $r2=0.546$, $F=2.58$, $P<0.001$). In contrast, we found no significant relationship between the weighted out-degree and the logging bias (linear regression with permutation test, $r2=-0.095$, $F=0.17$, $P=0.705$).

As all possible pairwise interactions occurred during the field deployment, we were able to apply the correction method to the association data. Collar 1 was identified as the lowest recorded logger, as it had the highest mean logging bias during deployment (as shown in Figure 1).

Therefore, duration data from collars 2-20 were adjusted in accordance with their logging performance the weakest logger. This improved the overall reciprocity of contact between dyads, from 0.76 to 0.99.

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

Boyland, Natasha K., et al. *Applied Animal Behaviour Science* 174 (2016): 1-10.

3.2 Summary: 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 (or sub groups) within the herd. The social networks showed significant centralisation, indicating substantial variation among individuals in how central they were in the herd social network (i.e. some cows had many strong social ties and some had few). 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 Methods: 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. Data was collected using proximity loggers as outlined above (see 3.1) and was corrected for biases in the data using the method we developed (Boyland et al. 2013).

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.

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.

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.

3.2 Results:

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 2a). 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 2b). It is important to note that for many pairwise interactions allogrooming was not observed which is most likely due to the duration of time the dyads were observed and the frequency of allogrooming in the population. Further work is thus required to establish if variation in the frequency of allogrooming between pairs is due to differences in the social relationship or due to sample constraints.

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 (Newman 2006b; Newman 2006a). There was no evidence of community structure in the four deployment networks.

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. To examine centralisation in the networks we filtered they dyadic association scores (ranging between 0 and 1). In all four deployments, all networks filtered above and including 0.25 times the expected association showed significant centralization, $p=0.0002$ in all cases (excluding deployment 2).

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. All week long association matrices (within a given deployment) were significantly (positively) correlated ($p = 0.0002$). Effect size of correlations between consecutive matrices ranged from $R^2 = 0.176$ to $R^2 = 0.576$.

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:

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

There was significant social differentiation in all four deployment networks; cows associated with some individuals more and other individuals less, than would be expected by chance ($p < 0.001$ for all 4 deployments). This result demonstrates that the cows had both preferred and avoided companions in the herd.

In order to test for assortment of individuals based on known attributes, we used 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. 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. For all deployments, the model that best predicted the association strength contained all four independent variables: gregariousness, lactation number, pasture access and breed. Across all deployments there was significant positive assortment by lactation number (dep 1: post. mean= -0.019, p<0.001; dep 2: post. mean= -0.021, p<0.001; dep3: post. mean= -0.014, p<0.001; dep 4: post. mean= -0.018, p<0.001).Significant positive assortment by breed was found in deployments 1-3 (dep 1: post. mean= -0.048, p<0.001; dep 2: post. mean=-0.031, p=0.002; dep 3: post. mean= -0.024, p=0.036). Cows were significantly positively assorted by gregariousness in deployments 1 (post. mean= -0.0004, p<0.001) and 2 (post. mean= -0.0006, p=0.002), and significantly negatively assorted by gregariousness in deployment 3 (post. mean= 0.0013, p<0.001). 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).

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

Boyland, Natasha K., et al.. *In preparation*

3.3 Summary: 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 reproductive success, 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 required.

3.3. Methods: The social data set collected using proximity loggers in 3.2 was used for the analysis (see 3.2 for details of data collection). Using this data we 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. Mobility was scored once per fortnight by a single scorer, according to the DairyCo Mobility Scoring system (DairyCo, accessed July 2015) whereby a cow's ability to move is 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. 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.

3.3 Results:

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). Age and DIM were not significant predictors of degree centrality in any of the deployment periods (dep 1: age β=1140.499, p=0.145; DIM β=-580.642, p=0.171. Dep 2: age β=10.709, p=0.266; DIM β=-314.588, p=0.162. Dep 3: age β=-251.534, p=0.37; DIM β=-106.104, p=0.202. Dep 4: age β=83.975, p=0.488).

We fitted individual SCC data using node-level permutation-based regressions (30,000 iterations), to investigate whether SCC could be predicted by degree centrality or DIM. SCC was significantly positively correlated to degree centrality in deployments 1 (β=0.0002, p=0.026) and 4 (β=0.0003, p=0.033), and was significantly positively correlated to DIM in deployments 3 (β=2.925, p=0.037) and 4 (β=1.146, p=0.043).

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). There was a significant positive relationship between milk yield and degree centrality in deployments 1, 2 and 4 (dep 1: β=0.0002, p=0.004; dep 2: β=0.0003, p=0.015; dep 4: β=0.00004, p=0.0006), and significant negative correlations between milk yield and DIM in all four deployment periods (dep 1: β= -1.5, p<0.0001; dep 2: β= -1.51, p<0.0001; dep 3: β=-1.603, p<0.0001; dep 4: β=-0.775, p=0.014).(However, we found no relationship between milk yield and age; although there was a trend for a positive relationship in deployment 2 (β=0.068, p=0.053).

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)).

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

Bolt, Sarah .L. *et al. In preparation*

3.4 Summary: 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.

3.4 Methods

Pair Rearing:

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. 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. 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.

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, 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 weigh-scale (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).

Barn Grouping:

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. 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. Straw feed and pellets (BOCM, Super Rearer 18 + deccox) were delivered (into a trough) morning and evening, and water was available *ad libitum*.

Social associations between the calves was recorded using spatial proximity loggers (model E2C181C) made by Sirtrack Ltd. (New Zealand) which were deployed on day 55. Data collected using the collars was corrected for logging biases using the methods outlined above (see 3.1).

3.4 Results

Pair Rearing:

There was no significant effect of treatment on health scores (MANOVA: *V* = 0.12, *F* = (4, 40) = .61, *p* = .657 (Pillai's Trace)). There was no significant differences in concentrate intake between treatments 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). There was no significant difference in specific growth rate between treatments from day 47-55 (ANOVA: $F_{(2, 20)}$ = .184, *p* = .833).

The number of vocalisations was significantly affected by stage of weaning (Friedman's ANOVA: χ^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). 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 3) 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 3). *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).

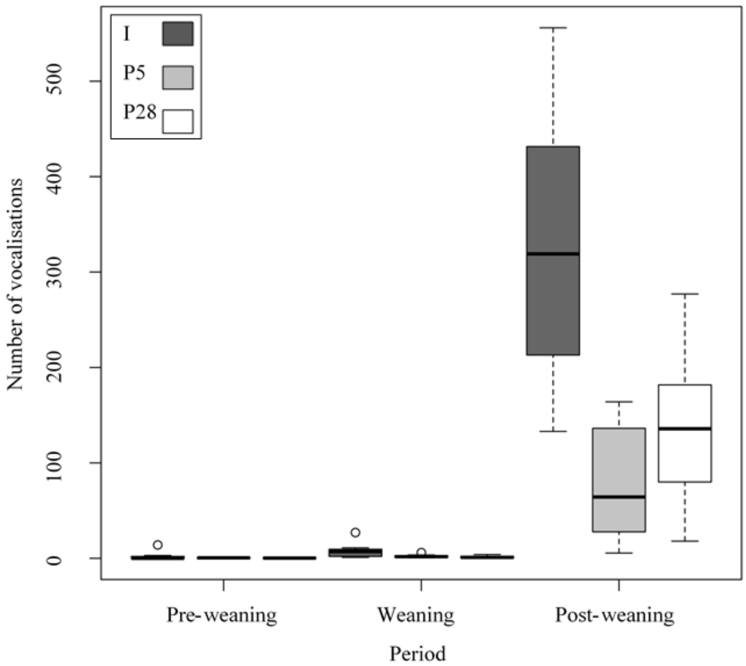

Figure 3. The total number of vocalisations, during 1 hour observations of calves, over each 3-day period (pre-weaning, weaning and post-weaning)

Barn grouping

All week-long association matrices were significantly positively correlated, indicating a degree of stability in the calves' network. 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. In each week–long social network there was significant social differentiation (mean R^2= 0.562, p=0.0002) which demonstrates that calves associated non-uniformly, spending more or less time with others than would be expected by chance.

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).

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). 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). 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) or week 4 ($F_{(2, 34)}$=0.274, p=0.762).

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).

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).

4. Discussion and Implications of the Findings

In this project we used social network analysis to measure the social structure of dairy cattle, and determine the relationship between social structure and welfare and productivity. Social relationships were determined by continuously recording spatial associations between cattle using Sirtrack proximity loggers. 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 is likely to have 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 clearly 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 of social structure is fundamental to ensuring 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 project provided an important step in this direction. The main findings / outputs of this project are summarised below.

1. **The use of proximity loggers for recording social contact and affiliative interactions in dairy cattle was validated**

The first major finding of this work 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 (Swain and Bishop-Hurley 2007; O'Neill et al. 2014), 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.

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. Using direct observations of social interactions we validated spatial proximity loggers for measuring affiliative relationships in dairy cattle. We found that associations recorded by the proximity loggers were positively correlated with social grooming events recorded during behavioural observations.

2. **Dairy cattle form differentiated stable social associations which are influenced by breed and lactation number.**

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 (Reinhardt and Reinhardt 1981; Lazo 1994). Our findings 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 (Gygax et al. 2010; Gutmann et al. 2015). 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 and 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 (Mench et al. 1990; Hasegawa et al. 1997). 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. Cows associated more with others of the same breed, of similar lactation number, and those more similar in milk yield during the study periods. Understanding what phenotypic traits are important in structuring social relationships in dairy cattle may allow for the better management of social groups. For example, an understanding the relationship between phenotypic traits and social structure may allow for informed management decisions that provide beneficial social environments for individuals.

3. **The social network position of a cow is related to its health and productivity**

We found significant relationships between our measures of social structure and health and productivity. 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. An alternative explanation is that cattle with higher milk yield are healthier and thus more central / dominant in the network. Further work is needed to understand the causal nature of this relationship. 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. We also found that cows that associated together more, had more similar SCC. It is important to highlight that whilst these results were statistically significant the effect sizes were small. Further work is needed to determine if these effects are widespread in the dairy industry and the economic and welfare costs and benefits of differing social structures in dairy cattle.

4. **Social support in calves can reduce stress during weaning.**

We found that familiarity was a substantial determinant of social bond strength in cattle. 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. Our work on the stress calves experience during weaning provides further evidence that pair housing can provide calves with social support effective in reducing the stress response (De Paula Vieira et al. 2010). 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. 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.

In the studies presented here we observed patterns of social contact over relatively short time periods (in the case of the lactating cattle for example this was done using four, one-month sampling periods). These time periods are biologically relevant for changes in the health status and productivity of the animals in the study. However such short term studies to not provide insight into the ontogeny of social structure through development or how early life social position can influence late life health and productivity. Future work examining the relationship between social structure health and welfare over longer time periods are essential to understand the consequences of structured social relationships for health and welfare in dairy cattle.

5. Possible future work

The output of this project clearly demonstrates a link between social structure and measures of health (SCC), productivity (milk yield) and welfare (stress). The majority of the work to date has focused on single farms and future work is needed to determine the consequences of farm animal management for the social structure of dairy herds and the implications of this structure for health and productivity. Management systems in the industry differ substantially between farms in key factors that are likely to influence social structure, e.g. management group size, regrouping practices, year round vs block calving, space allowance, cubicle vs straw yard housing. Thus it is likely that there are substantial differences in social structure between farms which may have consequences for animal health, welfare and productivity. Future work comparing social structure across replicated herds would allow for the relationship between animal management and herd structure to be determined which could provide substantial welfare and productivity benefits to the UK dairy industry.

Thanks to the recent development of low cost technology there is an ideal opportunity to scale up studies from social behaviour on single farms to large scale replicated studies. For example the technology that we deployed in the current study cost approximately £350 per unit. We have just established a collaboration with SocioPatterns (http://www.sociopatterns.org/) who have developed a tag that will provide high resolution social and spatial information for approximately £20 per unit. The dramatic reduction in price means that it is both possible to instrument large numbers of animals but also that it is likely to be economically viable for farmers to instrument animals to track social connectivity as a management tool.

A major focus of our work was to describe the social structure of cattle and the relationship between socials structure and animal welfare and productivity. Future work should examine how changes in animal welfare result in and from changes in social structure. By tracking an animal's social environment as a measure of its welfare and health it may be possible to provide an early warning system for animal disease and further work is needed to investigate this.

Finally, knowledge of the fine scale social structure of livestock on farms has the potential to provide substantial improvements to the control of infectious diseases. In classical epidemiological models, disease hosts are assumed to interact randomly. In reality, however, pathogens are transmitted according to structured patterns of interaction among individual hosts. As shown in this project such variation in the frequency, content and context of contacts can be mapped into social networks, the structure of which can relate to the risks of hosts acquiring and transmitting pathogens. The effect of host social network structure on pathogen transmission is well described for some infections of humans, e.g. HIV and measles, but much less so for other animals. There is clear potential to use the real time monitoring of animal social interactions to improve the control of key disease in the UK cattle industry such as bovine TB.

6. References

Bohm M, Hutchings MR, White PC (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:e5016

Bouissou MF, Boissy A, Le Neindre P, Veissier I (2001) The social behaviour of cattle. In: Keeling LJ, Gonyou HW (eds) Social Behaviour in Farm Animals. CABI Publishing, Wallingford, Oxon, UK, pp 113-145

Boyland NK, James R, Mlynski DT, Madden JR, Croft DP (2013) Spatial proximity loggers for recording animal social networks: consequences of inter-logger variation in performance. Behav. Ecol. Sociobiol.:1-14

Boyland NK, Mlynski DT, James R, Brent LJN, Croft DP (2015) The social network structure of a dynamic group of dairy cows: From individual to group level patterns. Appl. Anim. Behav. Sci. 174:1-10

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:1359-1363

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

Croft DP, James R, Krause J (2008) Exploring Animal Social Networks. Princeton University Press, Princeton

DairyCo MOBILITY SCORING. In:

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 93:3079-3085

Drewe JA, Weber N, Carter SP, Bearhop S, Harrison XA, Dall SRX, McDonald RA, Delahay RJ (2012) Performance of proximity loggers in recording intra- and inter-species interactions: a laboratory and field-based validation study. PLoS ONE 7:e39068

Færevik G, Jensen MB, Bøe KE (2006) Dairy calves social preferences and the significance of a companion animal during separation from the group. Applied Animal Behaviour Science 99:205-221

Freeman LC (1979) Centrality in social networks conceptual clarification. Social networks 1:215-239

Gutmann AK, Špinka M, Winckler C (2015) Long-term familiarity creates preferred social partners in dairy cows. Applied Animal Behaviour Science 169:1-8

Gygax L, Neisen G, Wechsler B (2010) Socio-Spatial Relationships in Dairy Cows. Ethology 116:10-23

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 51:15-27

Hood GM (2010) PopTools version 3.2.5. In:

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

Krause J, Wilson A, Croft DP (2011) New technology facilitates the study of social networks. Trends Ecol. Evol. 26:5

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

McLennan KM (2012) Farmyard Friends. The Biologist 59:19-22

Mench JA, Swanson JC, Stricklin WR (1990) SOCIAL STRESS AND DOMINANCE AMONG GROUP MEMBERS AFTER MIXING BEEF COWS. Canadian Journal of Animal Science 70:345-354

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

Newman MEJ (2006a) Finding community structure in networks using the eigenvectors of matrices. Physical Review E 74:036104

Newman MEJ (2006b) Modularity and community structure in networks. Proceedings of the National Academy of Sciences 103:8577-8582

O'Neill CJ, Bishop-Hurley GJ, Williams PJ, Reid DJ, Swain DL (2014) Using UHF proximity loggers to quantify male–female interactions: A scoping study of estrous activity in cattle. Animal Reproduction Science 151:1-8

Prange S, Jordan T, Hunter C, Gehrt SD (2006) New Radiocollars for the Detection of Proximity among

Individuals. Wildlife Society Bulletin 34:1333-1344
Reinhardt V, Reinhardt A (1981) Cohesive Relationships in a Cattle Herd (Bos indicus). Behaviour 77:121-151
Rutz C, Burns ZT, James R, Ismar SMH, Burt J, Otis B, Bowen J, St Clair JJH (2012) Automated mapping of social networks in wild birds. Curr. Biol. 22:R669-R671
Ryder TB, Horton BM, van den Tillaart M, Morales JDD, Moore IT (2012) Proximity data-loggers increase the quantity and quality of social network data. Biology Letters 8:917-920
Schuett W, Dall SRX, Baeumer J, Kloesener MH, Nakagawa S, Beinlich F, Eggers T (2011) Personality variation in a clonal insect: the pea aphid, *Acyrthosiphon pisum*. Developmental Psychobiology 53:631-640
Swain DL, Bishop-Hurley GJ (2007) Using contact logging devices to explore animal affiliations: Quantifying cow–calf interactions. Applied Animal Behaviour Science 102:1-11
Val-Laillet D, Guesdon V, von Keyserlingk MAG, de Passillé AM, Rushen J (2009) Allogrooming in cattle: Relationships between social preferences, feeding displacements and social dominance. Appl. Anim. Behav. Sci. 116:141-149
Wolf JB, 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 74:1293-1302

References to published material

9. This section should be used to record links (hypertext links where possible) or references to other published material generated by, or relating to this project.