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

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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.

Keywords: Social networks – Group structure – Proximity loggers - Dairy cows – Assortment – Welfare

INTRODUCTION

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).

METHODS

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 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 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 first day of each data collection period. We summed the daily milk yield over each data collection period for each individual.

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).

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, Jordan, Hunter, & Gehrt, 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 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.

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 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.

Measuring the relationship between proximity data and social interactions

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 cows (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 DIM (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 individuals interacting with the focal cow. Chasing, head butting, head shaking 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 (Spearman's rank) 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.

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 each 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.

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.

Group-level patterns

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

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).

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.

Individual-level patterns

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 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.

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).

RESULTS

Measuring the relationship between proximity data and social interactions

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 cows (r= 0.07, n=63, p=0.51, fig. 1a). In contrast, we found a significant positive relationship between the association strength recorded by loggers and the number of affiliative (grooming) events between cows (r=0.51, n=63, p<0.0001, fig. 1b).

Group-level patterns

Community structure

There was no evidence of community structure at any contact threshold (fig. 2) in the four deployment networks (fig. 3).

Centralisation

In all four deployments, networks filtered above and including 0.25 times the expected association showed significant centralisation (fig. 4), p=0.0002 in all cases (excluding deployment 2 at a threshold of 2.75 times the expected association).

Network stability

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

Individual-level patterns

Social differentiation

There was significant social differentiation in all four deployment networks (table 3); cows associated with some individuals more and other individuals less, than would be expected by chance (p < 0.001 for all 4 deployments).

Assortment

For all deployments, the model that best predicted the association strength contained all four variables: gregariousness, lactation number, pasture access and breed (table 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).

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)

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.

ETHICAL STATEMENT

This study was non-invasive and the data collection protocol was approved by the School of Psychology's Ethical Review Group at the University of Exeter. Deployment of collars was coordinated with routine management practice when possible, to minimise any stress associated with handling.

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FIGURE CAPTIONS

Figure 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 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. Visualisation of cow social networks 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), for deployments 1-4

Figure 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)
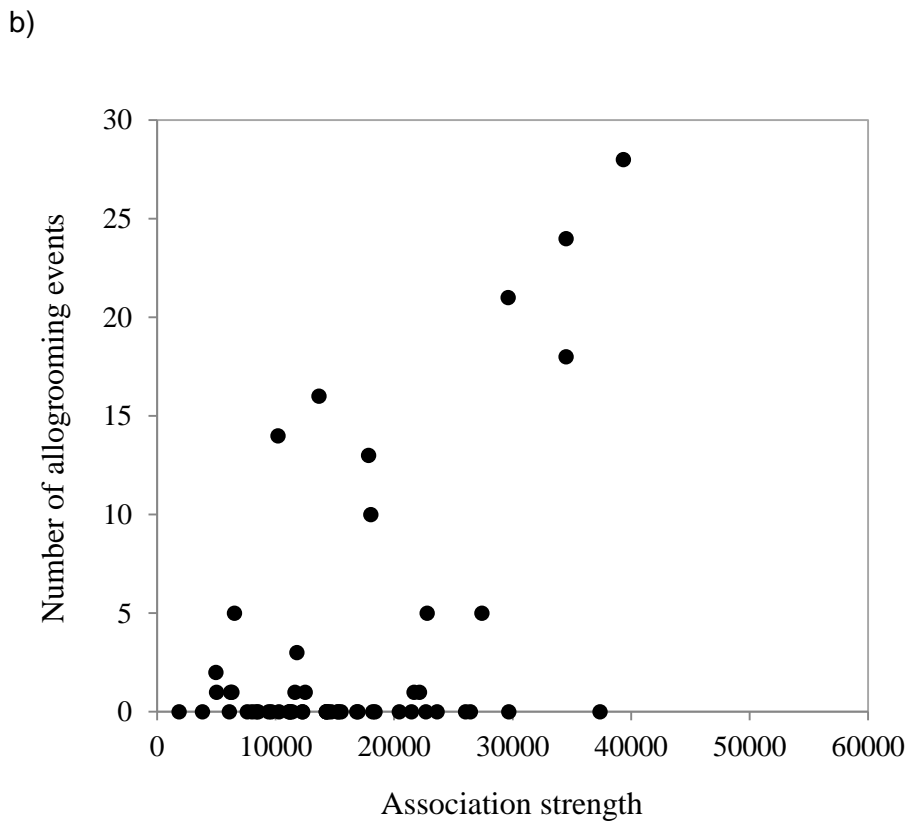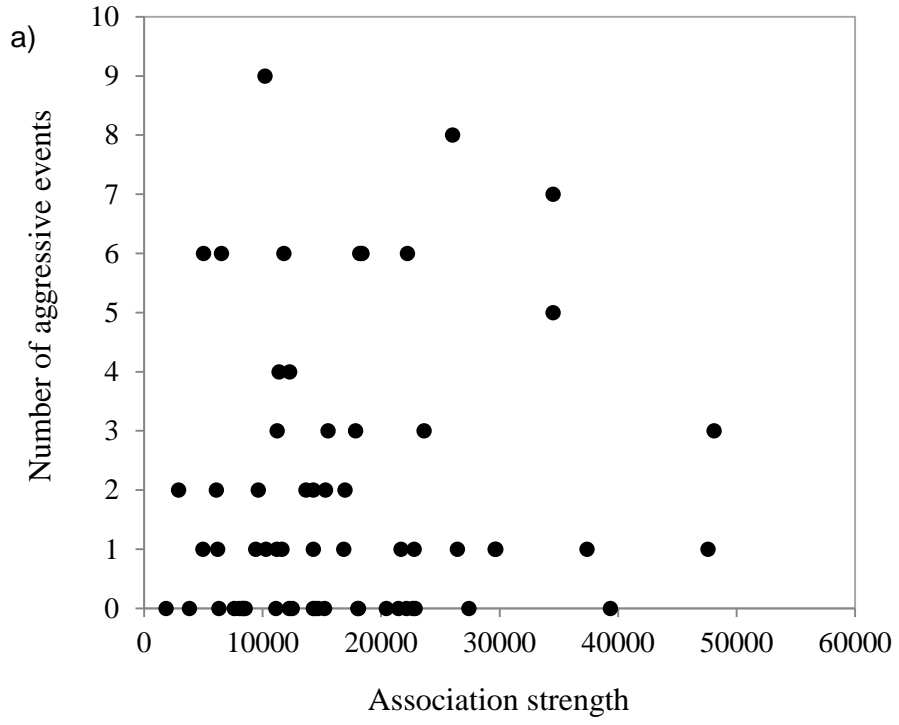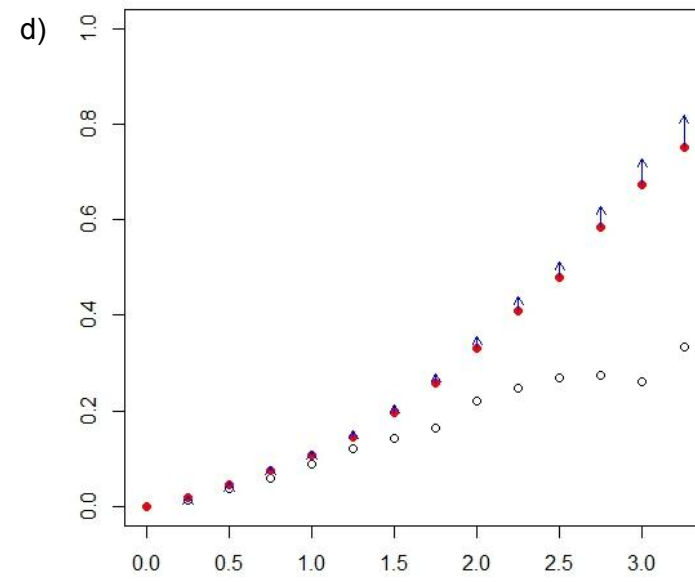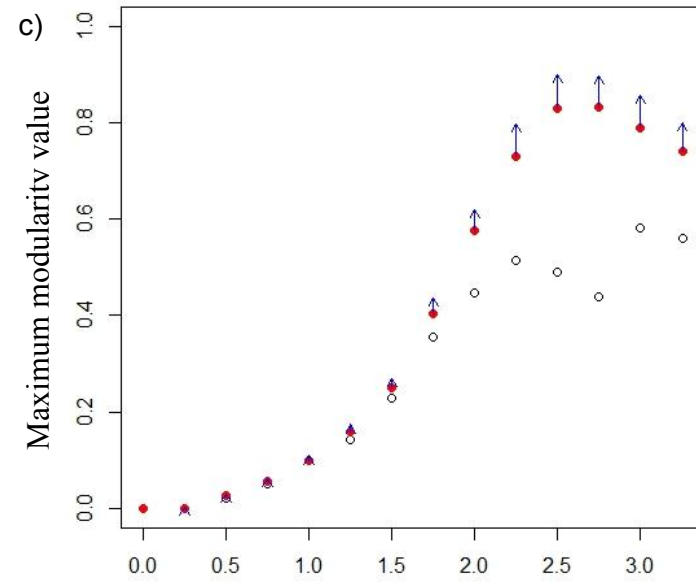
Figure 1

Figure 2
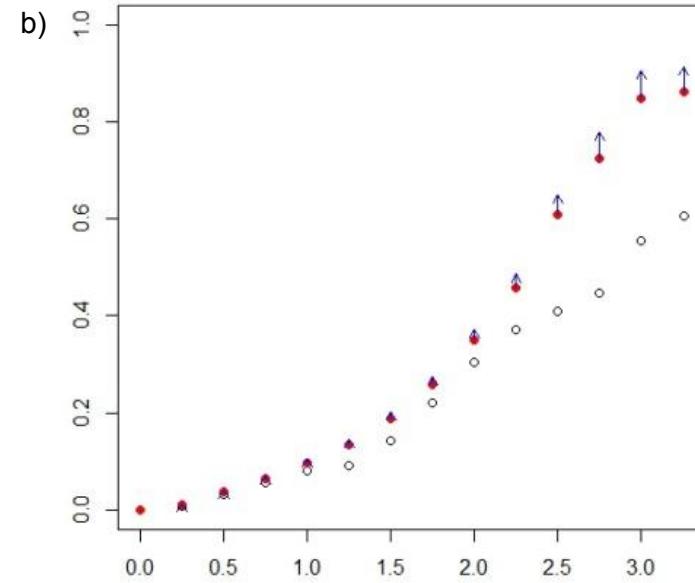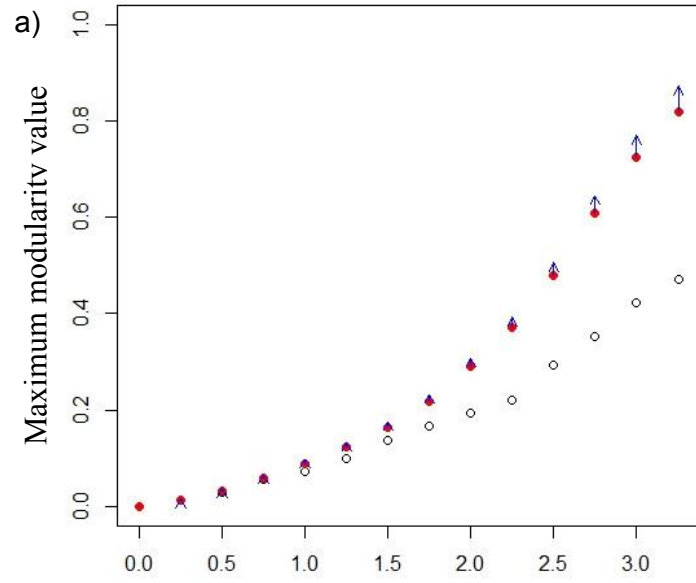
Figure 3

Deployment 1   Deployment 2   Deployment 3   Deployment 4

Figure 4

Table 1. Descriptive statistics of cows included in analyses and others in the milking group during each deployment
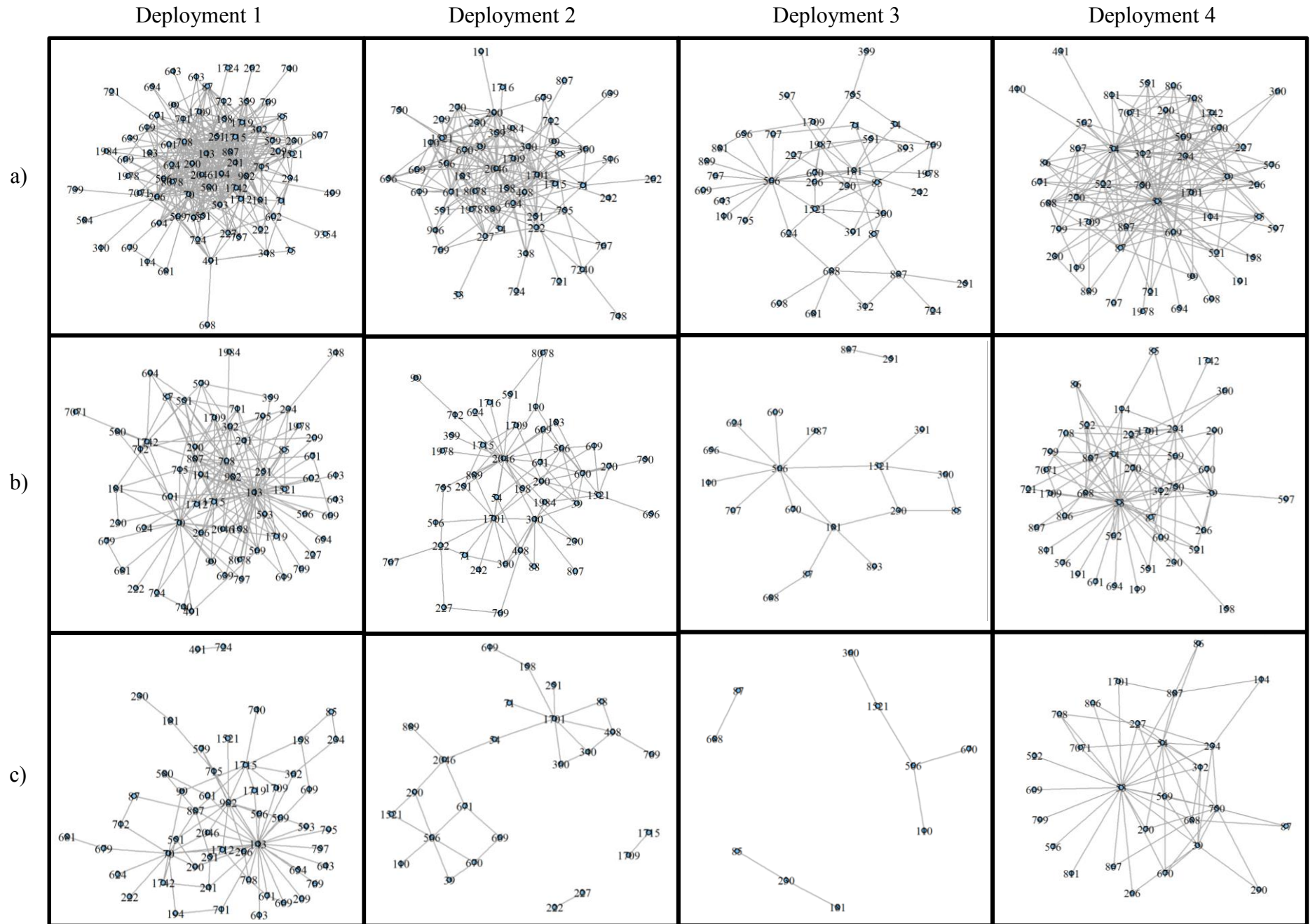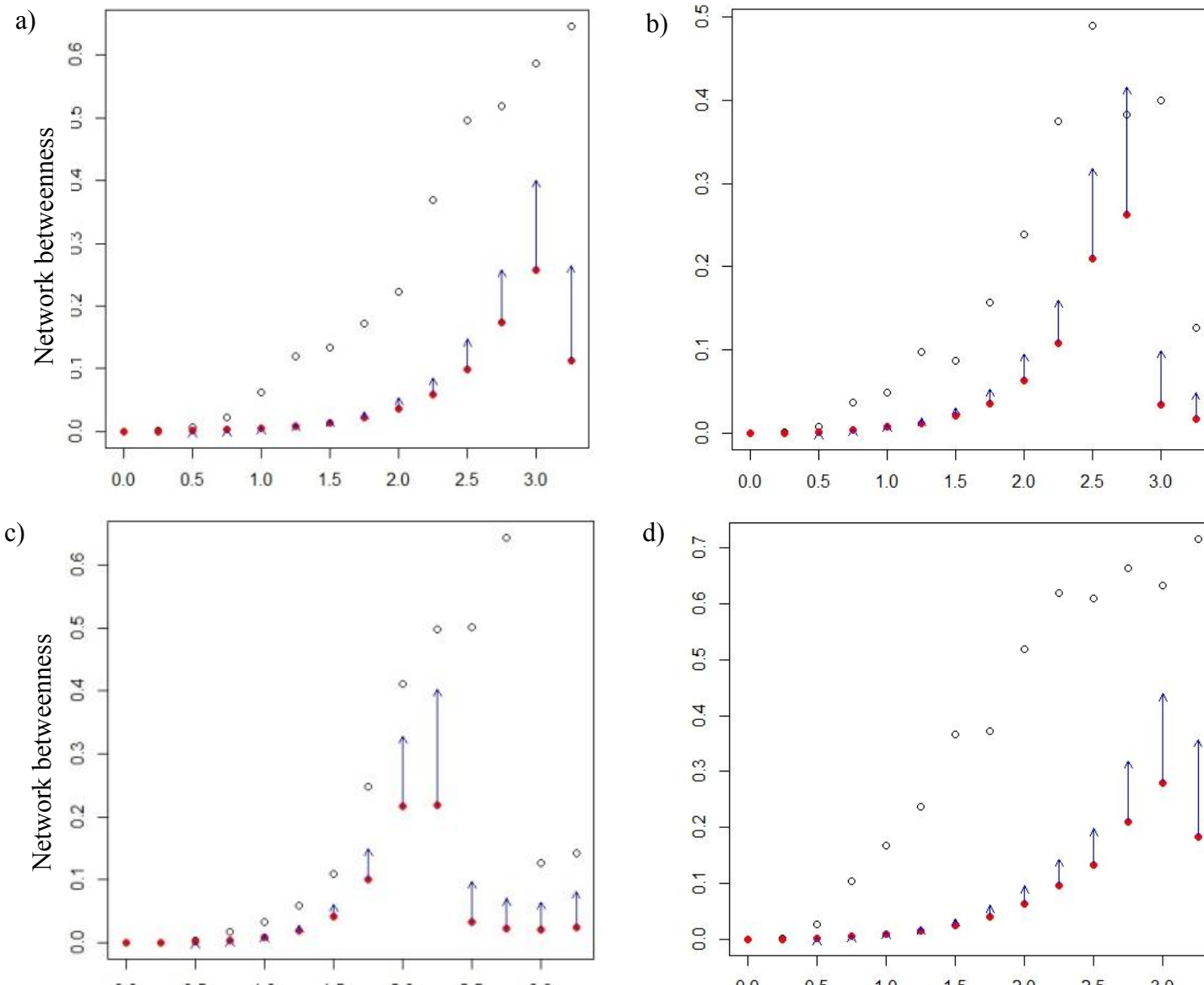
Deployment		1	2	3	4
Data period		08/11/12 to 06/12/12	22/12/12 to 18/01/13	14/03/13 to 09/04/13	13/05/13 to 09/06/13
Cows included in analyses	N	94	73	59	64
	Breed:				
	Ayrshire	20	11	7	8
	British Friesian	3	3	3	3
	Brown Swiss Cross	2	4	3	3
	Holstein Friesian	44	37	34	37
	Holstein Friesian Cross	6	6	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

Table 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				

18   Table 3. The social differentiation measured in deployments 1-4, indicates that cows were significantly

19   more heterogeneous than we would expect given a null hypothesis that all cows associate uniformly

20   (while accounting for pasture access)

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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

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Table 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*
	(Intercept)	3.996	3.938	4.065	<0.001
	Gregariousness	-0.0004	-0.0007	-0.0002	<0.001
1	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
	(Intercept)	3.969	3.912	4.037	<.001
	Gregariousness	-0.0006	-0.001	-0.0002	0.002
2	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
	(Intercept)	4.031	3.965	4.09	<0.001
	Gregariousness	0.0013	0.009	0.0019	<0.001
3	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
	(Intercept)	3.925	3.834	4.02	<0.001
	Gregariousness	0.0004	0.0001	0.0008	0.094
4	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

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