



## Socio-Spatial Relationships in Dairy Cows

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### Abstract

Farm animals may serve as models for evaluating social networks in a controlled environment. We used an automated system to track, at fine temporal and spatial resolution (once per minute,  $\pm 50$  cm) every individual in six herds of dairy cows (*Bos taurus*). We then analysed the data using social network analyses. Relationships were based on non-random attachment and avoidance relationships in respect to synchronous use and distances observed in three different functional areas (activity, feeding and lying). We found that neither synchrony nor distance between cows was strongly predictable among the three functional areas. The emerging social networks were tightly knit for attachment relationships and less dense for avoidance relationships. These networks loosened up from the feeding and lying area to the activity area, and were less dense for relationships based on synchronicity than on median distance with respect to node degree, relative size of the largest cluster, density and diameter of the network. In addition, synchronicity was higher in dyads of dairy cows that had grown up together and shared their last dry period. This last effect disappeared with increasing herd size. Dairy herds can be characterized by one strongly clustered network including most of the herd members with many non-random attachment and avoidance relationships. Closely synchronous dyads were composed of cows with more intense previous contact. The automatic tracking of a large number of individuals proved promising in acquiring the data necessary for tackling social network analyses.

### Introduction

Social relationships in individualized groups have classically been characterized by agonistic interactions and an ensuing dominance hierarchy (e.g. de Vries 1998) in such diverse taxa as Carnivora (e.g. hyenas: Smith et al. 2007; wild dogs: de Villiers et al. 2003), Artiodactyla (e.g. cattle: Bouissou 1974a,b; Sembraus & Osterkorn 1974; Reinhardt & Reinhardt 1975; Beilharz & Zeeb 1982; Wierenga 1990; sheep: Guilhem et al. 2000), Perissodactyla (e.g. horses: Heitor et al. 2006a; Vervaecke et al. 2007) and primates (e.g. Widdig et al. 2002). These descriptions

have been supplemented by accounts of affiliative relationships reflected by direct interactions (e.g. primates: Bentley-Condit & Smith 1999; Widdig et al. 2002; Lehmann et al. 2007; cattle: Sato et al. 1993; Val-Laillet et al. 2009), spatial associations (e.g. horses: Sundaresan et al. 2007; dolphins: Lusseau & Newman 2004) and spatial proximity (e.g. wild dogs: de Villiers et al. 2003; sheep: Guilhem et al. 2000; horses: Heitor et al. 2006b). Social-network analysis has recently been suggested as a tool for understanding such networks in animal behaviour studies, with a main focus on affiliative relationships (Krause et al. 2007; Wey et al. 2008). To date, however, its

applications have been restricted to the study of single groups or populations, and have thus provided valuable case studies (e.g. fish: Croft et al. 2004; dolphins: Lusseau 2003; Lusseau & Newman 2004) rather than following a comparative approach (but see Rubenstein et al. 2007; Sundaresan et al. 2007) or providing an account on species-typical patterns and their variability.

Farm animals are usually kept in groups, and multiple groups are easily accessible. They may thus serve as a model species for evaluating within-species variability of social-network structure in a relatively controlled environment. In addition, such studies complement our basic knowledge on these species. For the current study, we chose herds of adult cows (*Bos taurus*) in cubicle housing systems, a barn environment widely used in dairy production. To date, few systematic and quantitative studies have focused on the day-to-day social life of cattle, though there is a general notion of their social structure summarized by Bouissou et al. (2001): 'The basis of social organization in most ungulates is a matriarchal group, in which aggressive behaviour is rare and dominance relationships difficult to reveal. This suggests that preferential relationships exist between members of these groups and are responsible for their cohesion. In cattle, affinities include spatial proximity, reduced aggressiveness, enhanced positive interactions and tolerance in competitive situations' (p. 129).

Indeed, once a herd is well established, the relevance of agonistic interactions for the description of the cows' social relationships and for the spatial structuring of dairy-cattle herds is open to question, given that said interactions are rare and of low intensity (Gygax et al. 2006), occur among the same individuals that exchange affiliative behaviour (Gygax et al. 2006), and do not seem to be particularly responsible for spatial distance between individual cows (Kiley-Worthington & de la Plain 1983; Neisen et al. 2007). Similarly, Clutton-Brock et al. (1976) discovered proximity and grooming relationships in free-ranging highland cows that were unrelated to the well-defined hierarchy of the group. Thus, in the day-to-day social life of dairy cows, affiliative relationships and avoidance behaviour are potentially more relevant than overtly agonistic interactions.

Social networks in free-ranging cattle can be expected to reflect the aforementioned matrilineal structure. The feral cattle of Amsterdam Island (Daycard 1990) do indeed show clear grouping patterns with sexual segregation, and Reinhardt & Reinhardt (1981) observed close spatial relationships

in a semi-feral zebu herd during grazing and in the exchange of licking between mother-young and siblings. In dairy herds, group composition is artificial in that herds consisting of adult females only, and groups are supplemented by female animals introduced shortly before their first calving. These may be the offspring of cows still in the herd, but from which they had been separated only hours after birth. A matrilineal structure cannot therefore develop 'naturally'. Nevertheless, in a species evolved to cope with a matrilineal society, one might expect individuals to make use of proximate cues correlated with kinship in the wild to identify their matriline. We believe that cues such as time spent in close proximity are used to form affiliative relationships. Thus, a matrilineal structure is potentially mirrored even under artificial farm conditions. Hall (1986) and Lazo (1994), for example, observed systematic associations between social classes of cattle-herd members at supplementary feeding sites which were consistent with this idea.

In addition to the exchange of affiliative interactions within matrilineal groups or their proxies, Reinhardt & Reinhardt (1981) identified relationships among non-related cows. Wasilewski (2003) adopted a systematic approach to the question of close affiliative relationships in ungulates (*Artiodactyla* and *Perissodactyla*). She found indications that presence of horns, age and year of entry into herd played a role in the formation of such relationships in herds of cattle, but did not shed much light on the particular circumstances leading to such markedly close bonds. Stricklin (1983) found that distances in two mixed Angus-Hereford herds with 20 cows largely depended on breed, but that neither matriline nor its potential proxies, pasture group and calving group, contributed much towards explaining distances between cows. Sato (1984) reported that the exchange of affiliative behaviour could be explained by the dominance relationship, but later studies did not confirm this (Kabuga 1992; Sato et al. 1993). Bouissou & Andrieu (1978) showed that calves formed preferential relationships with peers shortly after birth which endured for at least 6 mo after regrouping. Sato et al. (1993) discovered a positive association between allogrooming during periods of housing and proximity on pasture which would seem to confirm that proximity in stable dairy herds reflects aspects of an affiliative relationship.

Affiliative relationships are not necessarily fixed. They have been described as being attuned to context (in e.g. cattle: Reinhardt & Reinhardt 1981; Wasilewski 2003). This may result in different

social-network patterns in functional areas of dairy-cow housing systems such as the activity, feeding and lying areas. Lastly, increasing herd size is likely to affect social networks in that relationships may be diluted by the sheer quantity of potential partners (Kondo et al. 1989) or by the formation of sub-groups (e.g. Rubenstein et al. 2007).

Using an automatic tracking system, we collected socio-spatial data in six herds of dairy cows housed on different farms but under similar conditions. We wanted to investigate the aspects described above using socio-spatial variables, measures of social-network-analysis and quantitative statistical modelling. We addressed these questions by describing the affiliative and avoidance relationships among cows. We analysed whether some affiliative and avoidance relationships are so special that they can be identified as non-random and whether such relationships are context dependent by comparing three functional areas of the housing system (activity, feeding and lying). Finally, we investigated whether the strength of the relationships can be related to the common history of pairs of cows and how two different socio-spatial

dyadic variables, synchronicity and distance, fare in characterizing cattle herds.

## Methods

### Animals and Farms

We conducted our observations on herds at six Swiss working farms (Table 1) comprising a total of 175 dairy cows for a continuous 6 × 24 h per farm. Herd composition did not change any later than 3 d before observations commenced. On all farms, herds were kept in cubicle housing systems. The lying area was thus divided into individual spaces situated side-by-side in one or more rows within the barn. These lying spaces were open towards the back and separated by partitions which consisted of fixed tubing such that cows in adjacent spaces may have touched each other while lying. In the feeding area, cows were fed side-by-side at a feed rack separated into individual feeding places by tubing. Except for short periods of fixation during feeding (see below), cows could freely stick their heads through the feed rack to eat. There was no separation of feeding spaces

**Table 1:** Characteristics of the investigated herds, barns and feeding management (farms ordered by herd size) with information on data availability and time spent in different functional areas

	A	B	C	D	E	F
Herd size and composition	24	24	25	29	30	43
Breeds <sup>a</sup>	BS	Mixed	BS	Mixed	BS	BS
Parity <sup>b</sup>	2.2 ± 0.4	4.2 ± 0.5	2.5 ± 0.4	3.7 ± 0.4	9.9 ± 6.4	3.3 ± 0.3
Days in milk <sup>b</sup>	179 ± 61	174 ± 57	144 ± 62	175 ± 54	236 ± 51	144 ± 47
Barn structure						
Barn area (m <sup>2</sup> )	193	195	243	319	230	340
Floor material <sup>c</sup>	Rubber	Ma	Slatted	Concrete	Slatted	Ma
Management						
Feeding regime <sup>d</sup>	2x	2x	2x	1x	2x	1x
Fixation during feeding (max 30 min)	Yes	Yes	Yes	Yes	No	Yes
Exercise yard	None	Temporary	None	<i>Ad lib</i>	None	<i>Ad lib</i>
Use of pasture <sup>e</sup>	All day	None	All day	Mornings	Mornings	None
Proportion of successful observations (%)						
Median (quartiles)	95 (92–98)	87 (83–89)	76 (72–79)	85 (80–89)	94 (90–97)	63 (56–66)
Range	68–100	72–94	49–85	67–100	83–100	41–74
Proportion of time (%) spent in						
Activity area, median (quartiles)	12 (09–16)	11 (09–12)	16 (14–19)	08 (06–11)	20 (17–24)	19 (18–22)
Feeding area, median (quartiles)	39 (32–42)	29 (27–33)	32 (29–37)	30 (24–32)	29 (25–32)	39 (36–43)
Lying area, median (quartiles)	52 (47–55)	58 (54–63)	51 (45–55)	62 (59–67)	51 (46–55)	40 (35–44)

<sup>a</sup>BS, mainly Brown Swiss; Mixed, mainly Red and Black Holstein on farm C, Brown Swiss and Red Holstein on farm D.

<sup>b</sup>Mean ± SE, parity: number of previous births, i.e. number of current lactation.

<sup>c</sup>Ma, mastic asphalt, slatted concrete floor.

<sup>d</sup>Cows were fed maize silage twice daily and hay was additionally provided *ad libitum* (except farms D where a total mixed ration was fed, and F where silage was fed).

<sup>e</sup>Cows that had access to pasture were let onto pasture after morning milking (approx. 8 h) and were either taken back to the barn at around noon or before the evening milking (approx. 17 h).

that projected into the space where cows moved around. Cows in adjacent feeding places could reach each other with their head and muzzles while feeding. Passageways were situated between rows of lying cubicles and between the feeding rack and the lying cubicles. The feeding-place-to-cow ratio ranged between 1:1 and 1.17:1, and the ratio of lying-cubicles-to-cows from 1.02:1 to 1.28:1. On four farms, cows were fed with fresh feed twice daily, whilst cows received fresh feed just once daily on the remaining two farms. On five of the six farms, the animals' heads were confined between locking bars for a short period of time (up to a maximum of 30 min) in the feed rack during feeding (Table 1). Apart from this time period and when animals were at pasture, they could freely move between the feeding and the lying area 24 h a day.

During the study, cows wore transponders around their necks weighing a total of 2.5 kg (similar to the weight of medium-sized bells). In a previous study (Gygax et al. 2007), no change was observed in the behaviour of the cows and their skin at the neck was not altered. The study was approved and financed by the Federal Veterinary Office (Berne, Switzerland) and a cantonal licence for conducting the experiments had been granted (Thurgau Veterinary Office, Frauenfeld, Switzerland, F2/06). In no other way did we interfere with the day-to-day activities on the farm.

We differentiated between three functional areas within the barns: cows were defined as being in the feeding area if the transponder at their neck was within 1 m to the feed rack. They were considered to be in the lying area whenever the transponder was inside the area constituted by the rows of lying cubicles. The remainder of the barn area (i.e. passageways) was considered the activity area. No position data from the exercise yards or from the time cows spent on pasture was included in the current study (Table 1).

#### Automatic Position Recording

We used a local-position measurement system to automatically track the individual dairy cows (ABATEC Electronic AG, Regau, Austria; <http://www.lpm-world.com>; Gygax et al. 2007). After setting up the system, a circle of a fixed diameter was paced out at several locations in each barn to determine the accuracy of the measurement. We found measurement accuracy to be similar to that described in Gygax et al. (2007) for an experimental barn, and thus reckon on most two-dimensional position estimates

being within 50 cm to the true location. The system works via a radar signal emitted from the transponder around the cow's neck and received by a set of antennas. The position of each cow is calculated according to the differences in arrival time of the signal at the different antennas. All cows in a herd were tracked simultaneously. The transponders were set to emit a signal for 10 s of every minute. Position estimates were carried out at a rate of 300 Hz and were averaged and rounded to the closest cm for each second in real time. These data were saved. Because transponders were locally activated by switching on their batteries, the 10-s activation interval could not be synchronized among cows. Given the average speed of travel of cows in a barn and the length of our observation period, this temporal variance between the position estimates of different cows was not deemed relevant. Transponder batteries usually lasted for the entire 6-d observation period, but were replaced during the morning feeding whilst the cows' heads were confined between locking bars at the feed rack if the transponders did no longer emit a signal.

The data were further processed offline using self-authored software programmed in R (R Development Core Team 2007). Because the system only reaches full accuracy after 2 s of measurement, the first 3 s of each 10-s activation interval were discarded. The remaining position estimates were averaged for each activation interval and assigned to the nearest full minute. This resulted in a dataset with a position entry (possibly missing) for each cow and minute. For each minute, the distance between the members of each dyad was calculated if the two cows occupied the same functional area and if they were not separated by a barrier.

#### Data Quality

Bearing in mind failures of the position-measurement system (median 0.5 d per farm, range 0–1 d) and the time cows spent on pasture (about 6 h/d on farms using pasture), the proportion of successful recordings was about 85% (median per farm; Table 1). Missing values were the result of problems with specific transmitters as well as the absorption and reflection of the radar signal by metal barn structures such as the feed rack or cubicle partitions. The overall median length of missing-estimate sequences was one interval for the majority of cows, and did not exceed three intervals for any one cow. We think that the small proportion of missing-position estimates can be considered as missing at

random, firstly because they consisted primarily of very short sequences, and secondly because there was no correlation between the quantity of missing data and the time budget of the cows (Table 1).

### Socio-Spatial Variables and Social-Network Analysis

Two socio-spatial variables organized into symmetrical social matrices for each herd were used to describe the relationships between pairs of cows. These variables were (1) *synchronicity*: the number of observations when the two cows of a dyad were in the same given functional area (activity, feeding and lying area) divided by the number of observations when either cow was in that same functional area and data was available for both cows and (2) *median distance*: the median distance observed between the members of a given dyad when the cows were within the same functional area and not separated by an obstacle.

For the two socio-spatial variables, we calculated which dyadic values were higher (attachment relationship) or lower (avoidance relationship) than expected by chance, based on a bootstrap approach similar to the one suggested by Sibbald et al. (2005). For this approach, the social matrices were calculated for each of the six 24-h periods per farm and averaged out over the six periods. The average dyadic values of the six periods were sorted by size, and served as the test statistic. In the bootstrap (sample size 1000), the data in the matrices of the six single days were randomly permuted whilst keeping the columns and rows (i.e. the values for an individual cow) intact. These six permutation matrices were again averaged and sorted by their values. This resulted in a bootstrap dataset with 1000 random estimates of the average dyadic value in the socio-spatial variable for each dyad (sorted by size). The values of the original dataset (test statistic) were compared with the bootstrap sample, and a dyad was considered to have an attachment relationship if the original value was higher than the 0.975 quantile of the bootstrap sample, or an avoidance relationship if the original value was lower than the 0.025 quantile of the bootstrap sample (*synchronicity*) or vice versa (*median distance*), i.e. those relationships among the most extreme 5% of the bootstrap were considered to be non-random.

We used descriptive measures from social network analysis to characterize herds in greater detail as regards their attachment and avoidance relationships (Krause et al. 2007; Wey et al. 2008). Whereas the use of social network analysis for the description of

affiliative relationships (attachment relationships) was a standard application, the use for the avoidance relationships may seem less straight forward. Social network analysis allows us to quantitatively describe relationships among pairs of animals in a group independent of the type of relationship. Avoidance relationships were expected to reflect agonistic relationships with the advantage that we did not need to rely on rare overt agonistic interactions but could instead include those relationships for which spatial and temporal separation was clearly respected. We used the *sna* package in R 2.6.1 (Butts 2008), and considered herd structure based on an undirected binary social matrix.

### Statistical Analyses

We compared measures from the social-network analysis (node degree, relative size of largest clique, density and diameter) using a separate linear mixed-effects model for each measure (Pinheiro & Bates 2000; LME method in R 2.6.1, R Development Core Team 2007). The response variables (proportions) were logit transformed to satisfy statistical assumptions which we checked using graphical analysis of residuals. We analysed these response variables for differences between type of relationship (factor with two levels: attachment and avoidance), type of functional area (factor with three levels: activity, feeding and lying area) and type of socio-spatial variable (factor with two levels: synchronicity and median distance). We included these three factors as well as their two-way and the one three-way interaction as fixed effects. If necessary, we extended the model to account for heterogeneity in variance among the different levels of the fixed effects. We then reduced this full model using a stepwise backwards approach, omitting interactions that did not reach  $p < 0.05$  but retaining all main effects regardless of their significance. We included random effects of cows nested within herds (node degree) and herds (all other response variables) to account for the repeated measurements and hierarchical nesting of the dataset.

Because of the repeated occurrence of each individual in dyads with all the other animals in a group, the analysis of social-interaction matrices poses a special problem (Hemelrijk 1990). Hemelrijk (1990) proposed an approach, the  $\tau_{KR}$  correlation, for calculating correlations among two social matrices from the same group, correcting for the dependence in the data of the same individual. We used this correlation coefficient to estimate the interrelation of social matrices. We were also interested in how the

socio-spatial variables on the farms depended on a set of explanatory variables. We therefore needed an extension to the matrix correlation which allowed for the inclusion of several farms and several explanatory variables. It is possible to view such a data structure as a special case of a linear mixed-effects model with crossed random effects (Gill & Swartz 2001; Li & Loken 2002). For the two socio-spatial variables of synchronicity and median distance and the three functional areas (activity, feeding and lying), a separate linear mixed-effects model was calculated with the LMER method (Bates 2007) in R 2.6.1 (R Development Core Team 2007). Residuals were checked graphically for normal distribution, homoscedasticity and outliers. To satisfy these assumptions, the response variable of median distance had to be log-transformed for all functional areas. The explanatory variables were the fixed effects of whether cows in a given dyad had grown up together (factor with levels no/yes: cows were considered to have grown up together if they were born within a few weeks of each other and raised on the farm in question), whether they had shared their last dry period typically for 7–10 wks (factor with levels no/yes: we considered two cows to have shared this period if they had been kept in same barn compartment, and if their calves were born within 10 d of each other), herd size (continuous), all possible two-way interactions and the one three-way interaction. The crossed random effects of the row individual of a dyad and the column individual within the same dyad nested within farm were included in all models. The crossed random effects reflect the variability attributed to the general sociability of the row individual and the general effect of the column individual as a partner in a dyad.

The models were set up as full models as described above, then reduced by a stepwise backward procedure (threshold  $p < 0.025$ , one-sided). All main effects were retained in the model regardless of their statistical significance. The calculation of p-values in such a model is non-trivial (Bates 2006), and we

followed the recommendations of Bates (2006, 2007) and used a Markov Chain Monte Carlo method to resample the posterior distribution of the parameter estimates (a method borrowed from Bayesian statistics, e.g. Gelman et al. 2004) to provide credibility intervals (similar to confidence intervals) for the model parameters. By calculating the percentile  $X$  at which the credibility interval borders on the value zero (e.g. the 99% credible interval), we attributed a p-value to the parameter as  $p = 1 - (X/100)$  (e.g.  $1 - (99/100) = 0.01$ ).

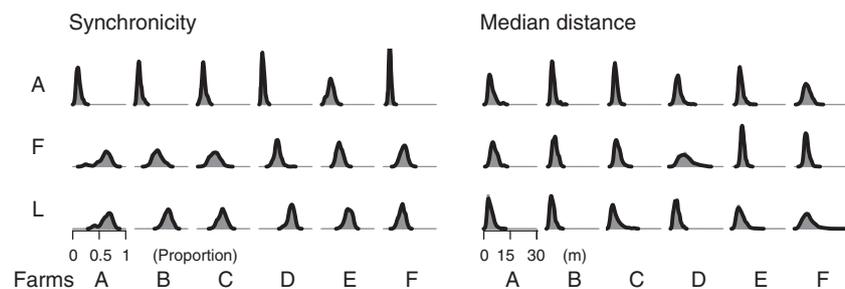
## Results

### Socio-Spatial Variables and Social-Network-Analysis Measures

In general, cows spent about 10–20% of their time in the activity area in the barn, 30–40% at the feed rack, and the remaining 40–60% in the lying cubicles (Table 1). In parallel, the mode of the dyadic synchronicity values observed increased from below 20%, to below 40% and to below 60%, whereas the mode of the median distance showed little variability at around 5 m (Fig. 1).

Matrix correlation coefficients were calculated between the different functional areas for the two socio-spatial variables per farm (Table 2). Although these correlations were consistently positive, the absolute value of the correlation coefficients was low, especially for the median distance. There was little farm-to-farm variability in the correlation coefficients for the median distance (maximum range 0.21), but the range was larger for synchronicity (maximum range 0.47). Hence, neither synchronicity nor distance between cows was strongly predictable among the functional areas.

Visualization of the networks based on attachment and avoidance relationships showed that networks were either very sparsely or very densely populated (Fig. 2a). Avoidance networks tended to be more centralized than attachment networks, with some



**Fig. 1:** Densities of observed dyadic values of the two socio-spatial variables synchronicity and median distance in the three functional areas for activity (A) feeding (F) and lying (L) per observed farm. Axes are identical for all areas and farms.

**Table 2:** Matrix correlation coefficients  $\tau_{kr}$  of the socio-spatial variables synchronicity (below diagonal) and median distance (above diagonal) between the different functional areas (activity, feeding and lying)

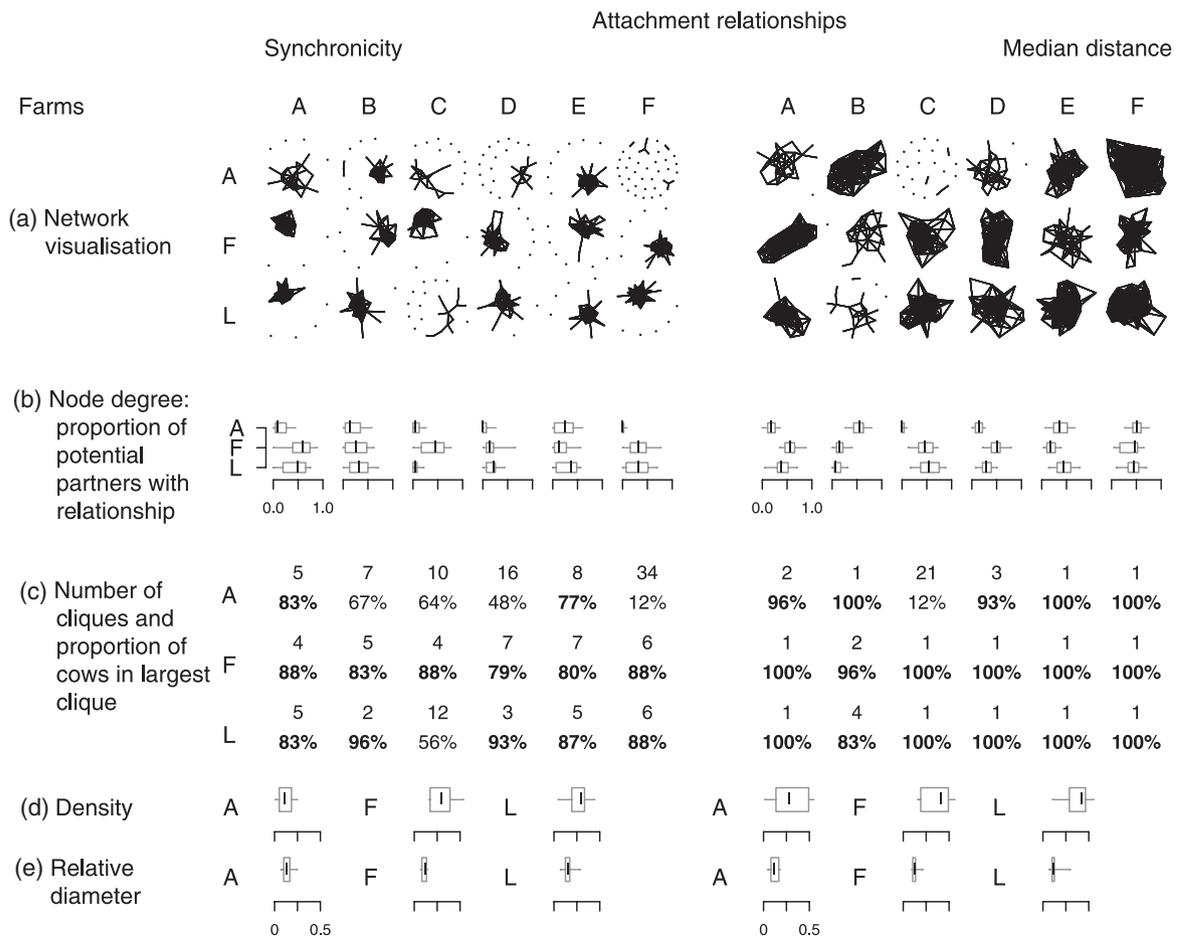
	Activity area	Feeding area	Lying area
Activity area		0.12 (0.07; 0.17)	0.06 (-0.02; 0.19)
Feeding area	0.22 (-0.08; 0.36)		0.02 (-0.04; 0.08)
Lying area	0.17 (-0.21; 0.26)	0.35 (0.19; 0.47)	

Median  $\tau_{kr}$ -values and their range across farms are presented (total  $n = 6$  farms).

individuals occupying central roles and relationships being less equally distributed. None of the networks consisted of more than one densely connected cluster that would only be loosely interconnected. Aspects of the visualized structure can be described

one-by-one using descriptive measures from social-network analysis. Below, we evaluate a selection of these (node degree, relative size of largest clique, density and diameter) in greater detail.

For many of the networks, the distribution of the node degree, i.e. the proportion of potential partners with a relationship, was wide, and covered a large part of the possible range (interval 0, 1). If the value range was restricted, the distribution was often right-skewed (Fig. 2b). The individual values for the node degree increased from the activity to the feeding area. Compared with the feeding area, these values decreased slightly in the lying area for synchronicity, but increased somewhat further for median distance (interaction:  $F_{2,1918} = 41.87$ ,  $p < 0.001$ ; Fig. 3a). The values were higher for attachment relationships than for avoidance relationships,



**Fig. 2:** (a) Visualization of the network based on attachment and avoidance relationships and a selection of measures used in social network analysis, on the level of the individuals: (b) node degree, and on the level of the herds: (c) number of cliques and proportion of animals in largest clique, (d) density (proportion of dyads with relationship) and (e) relative diameter (length of longest chain divided by group size). Small rectangular displays in (a–c) reflect the values for each farm (columns A–F) and each functional area (rows: A, activity; E, feeding; L, lying area). In (c), values >75% are depicted in bold. Axes are identical within rows.

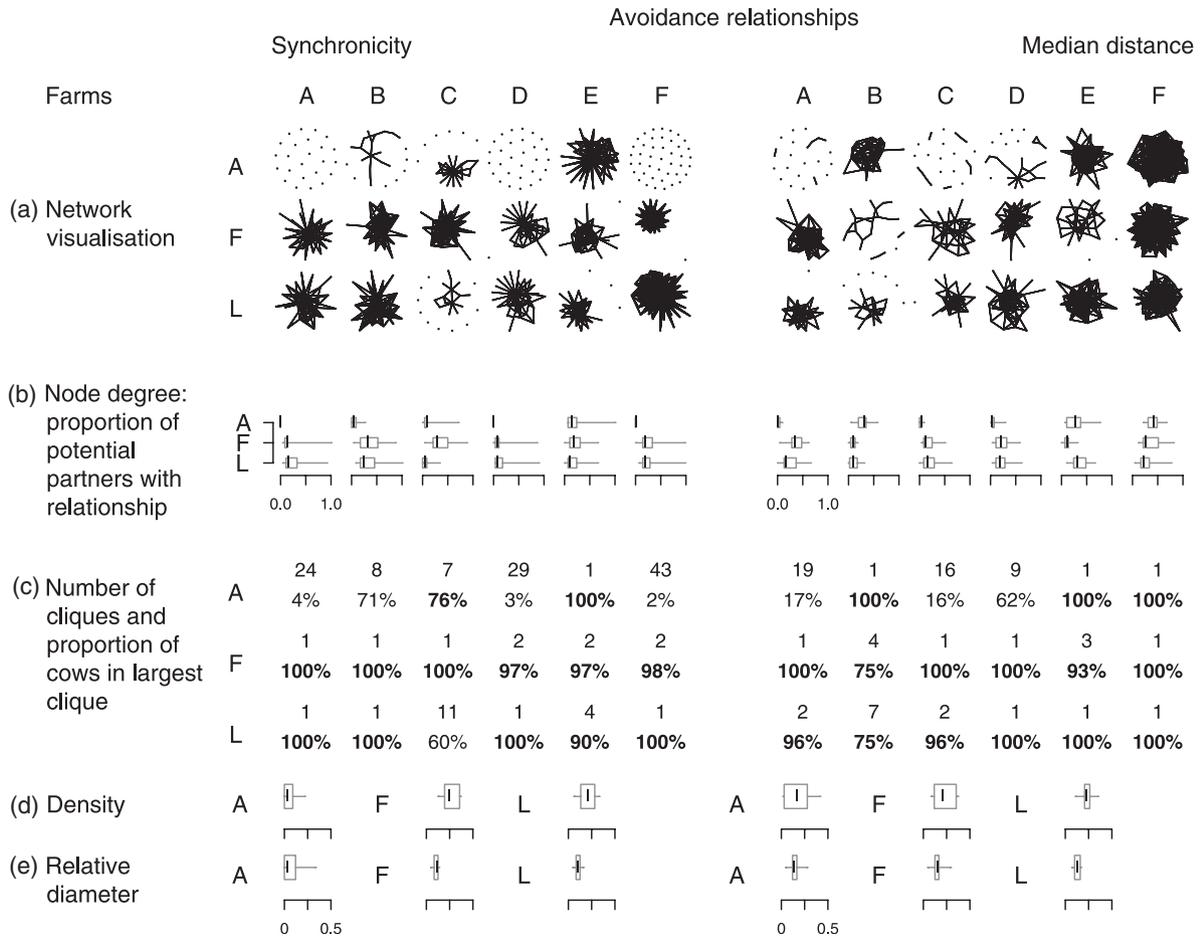


Fig. 2: Continued

but the difference between the two was smaller for synchronicity than for median distance (interaction:  $F_{L,1918} = 20.17, p < 0.001$ ). This implies that networks were more homogeneously connected for the attachment relationships and in the feeding and lying area. The distributions of other measures of connectedness were either similar to the node degree (eigenvector centrality, information central-

ity, stress centrality and clustering coefficient) or showed hardly any variability, with low values for the observed networks (closeness centrality and betweenness centrality; data not shown).

In general, the number of cliques, i.e. clusters of cows connected by either attachment or avoidance relationships, was quite low (Fig. 2c). Accordingly, the largest cluster in the herd was often large,

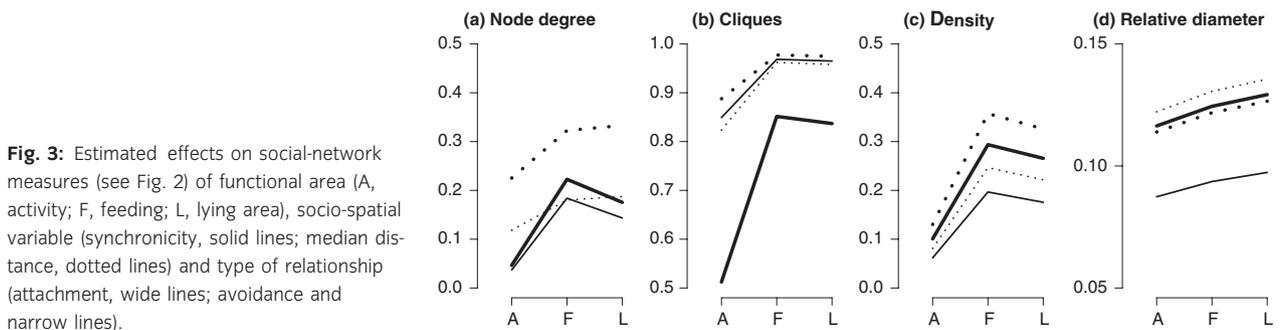


Fig. 3: Estimated effects on social-network measures (see Fig. 2) of functional area (A, activity; F, feeding; L, lying area), socio-spatial variable (synchronicity, solid lines; median distance, dotted lines) and type of relationship (attachment, wide lines; avoidance and narrow lines).

including more than three-fourth of all cows in 58 (81%) of the 72 values shown in Fig. 2c. The proportion of cows in the largest clique increased from the activity area to the feeding and lying areas ( $F_{2,61} = 6.57$ ,  $p = 0.003$ ; Fig. 3b). For synchronicity, the proportion was clearly lower for attachment than for avoidance relationships, whilst values were slightly higher in attachment than in avoidance relationships for the median distance (interaction:  $F_{1,61} = 30.26$ ,  $p < 0.001$ ). Apart from the activity area, most cows were thus part of one single network of attachment and avoidance relationships.

The density, i.e. the proportion of dyads with significant relationships (avoidance and attachment), ranged from approx. 0% up to 50% (Fig. 2d). Density increased from the activity to the feeding and lying areas ( $F_{2,62} = 7.76$ ,  $p = 0.001$ ; Fig. 3c) and from avoidance to attachment relationships ( $F_{1,62} = 7.66$ ,  $p = 0.008$ ). Densities were higher for synchronicity than for median distance, but not significantly so ( $F_{1,62} = 2.31$ ,  $p = 0.13$ ). Density of attachment and avoidance relationships correlated positively for all combinations of socio-spatial variables and functional areas (Kendall rank correlations:  $n = 6$  farms, median  $\tau = 0.60$ , range 0.20–0.73), indicating that some herds showed little non-random structure, and thus few strong and few weak relationships, whilst other herds were more clearly structured, with many strong and weak relationships occurring simultaneously.

The absolute values for the diameter, i.e. the longest chain indirectly connecting a pair of animals in the largest clique of cows, were in the range from 2.5 (lower quartile) to 5 (upper quartile). For comparability we divided these values by herd size (Fig. 2e). This relative measure of diameter increased slightly but non-significantly from the activity area to the feeding and lying areas ( $F_{2,61} = 0.46$ ,  $p = 0.63$ ; Fig. 3d). Diameter values for synchronicity were higher for attachment than avoidance relationships, but showed the inverse pattern with a smaller difference for the median distance (interaction:  $F_{1,61} = 6.28$ ,  $p = 0.015$ ).

#### Effects of Previous Contact on Socio-Spatial Variables

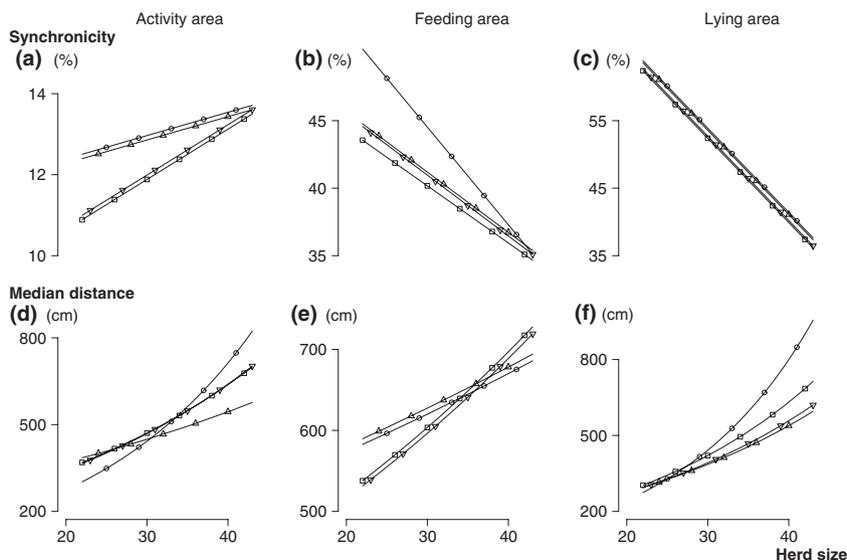
We investigated the effect of two cows having grown up together, of having shared their last dry period, and of herd size on the socio-spatial variables synchronicity and median distance. Of the total of 2596 dyads (range across farms: 276–903), 2401 (259–832) had neither grown up together nor shared their

last dry period. A total of 85 (6–25) and 98 (3–43) dyads had grown up together or shared their last dry period respectively. Twelve dyads had both grown up together and shared their last dry period (1–4). On each farm, there was at least one dyad in each category.

Synchronicity in the activity area generally increased along with herd size, and was higher when cows in a dyad had grown up together (regardless of whether they had shared their last dry period:  $p > 0.10$ ) than when they had only shared their last dry period, or had not spent time together either whilst growing up or during their last dry period. This difference disappeared with increasing herd size (interaction:  $p < 0.01$ ; Fig. 4a). In the feeding area, synchronicity generally decreased with increasing herd size, and was significantly higher for the animals that had both grown up together and shared their last dry period. The difference between cows of such dyads and cows of other types of dyads disappeared with increasing herd size. Across all herd sizes, animals that had either grown up together or shared their last dry period had slightly elevated synchronicity values compared with cows in dyads that had neither spent time together whilst growing up nor during their last dry period (three-way interaction,  $p < 0.05$ ; Fig. 4b). In the lying area, dyads that had grown up together were more synchronous ( $p < 0.001$ ), regardless of whether they had shared their last dry period ( $p > 0.10$ ). Synchronicity generally decreased with herd size ( $p < 0.001$ , Fig. 4c).

In the activity area, dyads that had grown up together observed smaller median distances than did other types of dyads, especially in the case of large group sizes. Dyads that had both grown up together and shared their last dry period observed smaller distances in small groups and larger distances in large groups (three-way interaction,  $p < 0.001$ ; Fig. 4d). The median distance in the feeding area for dyads that had grown up together, regardless of whether their last dry period had been shared ( $p > 0.10$ ), was larger for small herds and smaller for large herds than for other types of dyads (interaction:  $p < 0.01$ ; Fig. 4e). The median distance in the lying area was comparable for all types of dyads in small herds. With increasing herd size, the distance was lower for dyads that had either grown up together or shared their last dry period, but not as low as for dyads that had both grown up together and shared their last dry period (three-way interaction,  $p < 0.01$ ; Fig. 4f).

The largest absolute-average differences between the different types of dyads were in the range of



**Fig. 4:** Estimated effects on synchronicity (top row) and median distance (bottom row) of having shared their last dry period ( $\nabla$ ), grown up together ( $\Delta$ ), both ( $\circ$ ) or neither ( $\square$ ), and group size in the three functional areas (activity, feeding and lying).

1–5% for synchronicity and 0.5–3 m for median distance (Fig. 4, differences between pairs of curves).

## Discussion

### Do Cows Exercise Any Choices in Terms of Barn Areas or Social Partners?

Two general questions regarding the social relationships of dairy cows kept in barns may be posed: (1) Are cows constrained appreciably in their movements by management procedures such as milking and feeding? And if not, (2) do cows actually choose specific social partners, rather than merely choosing consistent locations in the barn?

We found considerable variability in individual cows' time budgets for the different functional areas, which implies some free choice as to when to switch between areas. Furthermore, we would assume that synchronicity and distances between pairs of animals would vary randomly and within a small range if caused primarily by management procedures. This was not the case, however, as we could identify non-random relationships. The systematic differences in our socio-spatial and social-network-analysis measures can also be interpreted easily according to the notion that temporal (synchronicity) and spatial (median distance) proximity reflect affiliative relationships, and these measures therefore seem to be meaningful.

Assuming that cows can indeed exercise a choice as to their whereabouts, they might still consistently

choose locations rather than social partners, which might give a mistaken impression of systematic social relationships. We do not believe that this is the case. Firstly, specific locations in the feeding and lying areas are likely to be especially attractive for all cows such as the feeding places where food delivery starts or cubicles that have a favourable microclimate. We might then assume that higher-ranking cows would attempt to monopolize these attractive locations. We would thus expect cows close in rank to be found in close proximity. This was not observed in an earlier study (Neisen et al. 2007). Secondly, the choice of partners at the feed rack and in the lying cubicles seems especially important, given that cows spend much of their time feeding and lying; they can feed more tranquilly with tolerant and lie more undisturbedly with vigilant neighbours. Thirdly, many studies of free-living species also assume that proximity and association are valid measures for affiliative relationships (e.g. horses: Heitor et al. 2006b; Sundaresan et al. 2007; dolphins: Lusseau & Newman 2004; wild dogs: de Villiers et al. 2003; sheep: Guilhem et al. 2000), although these animals might as well be under ecological pressure influencing their choice of position. Dairy cows supplied with abundant resources might actually be freer to choose their social partners. Lastly, close affiliative relationships may well develop among individuals with similar requirements and preferences, as they would often meet. Thus, choosing locations according to one's need and forming affiliative relationships may well be viewed as an interdependent process rather than as two distinct mechanisms.

### Socio-Spatial Variables and Social-Network-Analysis Measures

The two socio-spatial variables 'synchronicity' and 'median distance' contain different information, as e.g. visible in the social networks (Fig. 2a). They thus reflect different aspects of the social relationships. A given cow may have sought a high amount of synchronicity with another cow that is either a preferred partner or 'known' (through experience) to make good choices in activity switches. It might also be a cow with similar requirements, and thus a similar time budget. Short median distances are likely to be linked to tolerance, i.e. the ability to use neighbouring feeding places and lying cubicles.

The two socio-spatial variables correlated only weakly between functional areas, indicating that the cows had different partners for different activities (Table 2) as has been previously observed (Reinhardt & Reinhardt 1981; Wasilewski 2003). Cows may develop these relationships according to different criteria. In the feeding area, a tolerant partner might be preferable, allowing feeding at a close distance where feed quality is good. While resting, the proximity of vigilant cows might be attractive, allowing the cow in question to reduce her own vigilance behaviour. In the activity area, cows that are likely to exchange affiliative interactions might be sought out. Proximity in the activity area might therefore reflect individual choices of the animals most closely.

Our statistical comparisons of node degree and density showed that attachment relationships were more equally distributed in the network than avoidance relationships (Fig. 3a, c). Attachment relationships based on synchronicity were also characterized by a smaller relative size of the largest clique and a larger relative diameter compared with avoidance relationships (Fig. 3b, d). This indicates that affiliative relationships (attachment) were more common and connected smaller cliques all the better, and may thus be more important in shaping socio-spatial processes than avoidance relationships. All measures indicated that social networks were denser and more tightly connected in the feeding and lying area than in the activity area. In addition, the median distance lead to denser networks as compared with synchronicity. Thus, the socio-spatial variable of synchronicity and data collected in the activity area might be more sensitive to measure changes in the social networks of dairy-cow herds. The measure 'synchronicity' was in fact similar to association measures used in previous studies (e.g. Lusseau & Newman 2004;

Sundaesan et al. 2007) reflecting co-occurrence in the same area compared with co-occurrence in the same group.

Sundaesan et al. (2007) found networks that were largely comparable to those of our dairy cows in similarly sized Grevy's zebra and onager populations, in that the latter two species formed 2–11 cliques depending on how associations were defined, and in that the largest clique encompassed a high proportion of the animals. The diameter in our networks was around 10%, i.e. each cow was indirectly connected to all the other cows via an average of 2.5–5 intermediate cows for our given herd sizes.

Farms investigated in the current study differed in terms of detailed arrangement of the functional areas, size and management. Surprisingly few systematic differences were apparent between the farms (Fig. 2a). Social networks of dairy cow herds of between 20 and 50 animals can thus be generally characterized as follows:

1. Networks were either tightly connected or almost unstructured, i.e. a high number of attachment relationships coincided with a high number of avoidance relationships.
2. A large proportion of herd members belonged to the largest cluster of cows. There was no further subdivision of these clusters.
3. Attachment relationships weaved a network that was more strongly connected than the network of avoidance relationships, where more individuals with few relationships became apparent.
4. Variability between cows within groups was significant, i.e. there were some cows with non-random (attachment or avoidance) relationships with almost all other cows, and other cows with hardly any such relationships in most networks.

### Effects of Previous Contact on Socio-Spatial Variables

Cows which had grown up together and – to a lesser extent – cows which had shared their last dry period have closer relationships (Fig. 4) which are statistically detectable. Our study therefore supports the presence of an early creation of preferential relationships among cattle, as suggested by Bouissou & Andrieu (1978), and indicated that these preferences endured for several years. Similarly, Reinhardt et al. (1978) reported that Zebu calves formed long-term attachments. This is in contrast to the results of Stricklin (1983) who found no influence of pasture and calving group on distances between mixed Angus and Hereford cows. This may have been a

result of the mixing of the two breeds, which was the main factor explaining distances chosen to other cows, and may have overshadowed subtler choices though in other studies the common social history seemed to be more important than breed (Murphey 1990; Murphey & de Moura Duarte 1990). Sato et al. (1993) found that cows close in birth date exchanged more allogrooming when indoors, and were observed closer together on pasture. The median distance showed a less clear pattern but in general, there seemed to be a similar effect as with synchronicity, but only for a portion of the group-size spectrum.

The absolute differences between types of dyads differing in the amount of time they had previously spent together were of the order of 1–5% for synchronicity and 0.5–3 m for median distance, and must therefore be regarded as small. Similarly, in the study by Stricklin (1983), kinship information only contributed to a minor extent to the explanation of distances observed between cattle. Specific preferences among cows may be shaped most strongly by the detailed history of interactions among pairs of cows (Wasilewski 2003) and systematic effects as those investigated will thus only account for a small proportion of the variability in preferences.

With larger herd sizes differences between types of dyads decreased, and lead to lower synchronicity and larger distances (Fig. 4). Whether this is a result of dilution effects caused by herd size, i.e. herd members cannot distribute their time among all other members of the herd infinitely, or an effect of increased space, i.e. herd members can observe distances to one another in larger barns that are impossible in smaller barns, can not be answered, given the current study with herd size and barn area being confounded.

#### Use of Automatic Tracking System

The use of an automatic tracking system allowed the collection of detailed data on the synchronicity and proximity of all pairs of dairy cows in several herds in a quasi-continuous fashion and over a short period of time. Neither the installation of the system in the various barns nor the programming work required to deal with the data was particularly labour-intensive. Finally, this system allowed the collection of several datasets which were independent, and hence open to statistical analysis, and which permitted a view on the variability across different dairy herds.

#### Conclusions

Most of the observed dairy herds showed one strongly clustered network encompassing the majority of individual cows, with many non-random attachment and avoidance relationships. This network was strongly interconnected for attachment compared with avoidance relationships. Though variability among the cows of a herd was quite large, there were no cows whose removal would have led to the formation of unrelated sub-clusters. The measure of synchronicity and data collected in the activity area showed fewer dyadic relationships and more variability in the proportion of herd members involved in such relationships, and may thus be sensitive if a change in the social network owing to changes in the housing conditions or management is the subject of investigation. Synchronicity was influenced by whether or not the two cows in question had grown up together and/or had spent the dry period before their latest calving together. Even with the data gathered from our in-depth study, the exact causes for the structuring of dairy herds remain largely unknown; however the method applied, viz. the automatic tracking of a large number of individuals, proved promising in acquiring the necessary data for tackling research questions of this type.

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