



OPEN Individual and group level health factors influence social networks of dairy calves

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Evidence across species supports a relationship between health and social relationships, which may have important welfare implications for intensively housed animals. We evaluated how individual and group-level health factors are related to social behavior of group-housed dairy calves, using social network analysis. Holstein dairy calves (heifer: $n = 55$; bull: $n = 32$) were grouped (9 groups; 10 calves/group) at 2 weeks of age until after weaning from milk at 8 weeks of age. To generate social networks, calf positions were recorded continuously using an ultra-wideband positioning system generating undirected pairwise proximity estimates. Individual status and group-level prevalence of clinical respiratory disease, gastrointestinal illness, and lung consolidation were characterized weekly using standard approaches. Mixed-model analysis, following an information theoretic-approach to select predictor values, revealed reduced strength and higher closeness in calves in groups with a higher prevalence of respiratory disease or lung consolidation, whereas individual health status was not a significant predictor. However, eigenvector centrality was lower in calves with lung consolidation during weaning, which was predicted by pre-weaning co-occurrence of respiratory disease and lung consolidation. These results suggest nuance in how multiple health factors, at the individual and group level, influence social network structure in dairy calves.

Keywords Dairy calf, Health, Social behavior, Social networks, Welfare

Evidence across species supports a bidirectional relationship between individual health and social behavior, where social relationships can provide health benefits (e.g., social support reduces infection risk by buffering the susceptibility or transmission of infectious disease¹) and risks (e.g., social contact increases infection risk through contact-mediated transmission of pathogens²). Further, changes in social interactions have been observed as a component of sickness behavior across species (e.g., in rats³ and dairy calves⁴). The relationship between social behavior and health is of particular importance in intensively managed populations of animals. In the dairy industry, there may be a perceived conflict between providing benefits of natural social interaction and increasing disease risk of young calves⁵.

Social housing of neonatal dairy calves is gaining popularity given broad benefits for behavioral development and welfare, including reduced stress during weaning⁶, accommodation of motivated social contact⁷, and opportunity to form social bonds⁸. However, health management is a challenge associated with social housing, given a possible increased risk of respiratory illness in larger groups of calves^{9,10} and reduced opportunity for visual monitoring of individual calves by farm personnel. Dairy calves experience high prevalences of gastrointestinal disease/diarrhea (morbidity and mortality rates of 56% and 32%, respectively¹¹) and clinical respiratory disease (e.g., 20% to 40%^{12,13}), with further evidence of widespread subclinical respiratory disease (evident in thoracic ultrasounds revealing lung consolidation¹⁴). Disease in young dairy calves is a costly animal welfare issue with long-term consequences for dairy cattle productivity¹⁵. Understanding the relationship between social behavior and health status in intensively housed livestock may provide a basis for improved management decisions and evaluation of health risk factors related to social contact.

In recent years, social behavior of intensively managed livestock has been increasingly explored through the application of social network analysis, largely drawing on automated measures of collecting positional data^{16–19}. Relationships between health and social network position are evident in wild populations in both experimental studies (e.g., lipopolysaccharide challenge reduces centrality in vampire bats, *Desmodus rotundus*²⁰) and observational studies (e.g., parasite load correlates with social network connectivity and use of shared spaces in lizards, *Tiliqua rugosa*²¹). In cattle and other intensively managed agricultural animals, social interactions may

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have important implications for health^{22,23} and productivity²⁴. In dairy calves, health status has been related to aspects of social behavior, including social proximity^{4,25} and social grooming⁴. While only limited research to date has specifically evaluated how social networks may relate to health factors in dairy calves, reduced network centrality was observed in group-housed dairy calves experimentally infected with *Mannheimia haemolytica* (a pathogen associated with bovine respiratory disease²⁶), and both calf age and health status were related to network centrality in an observational study¹⁸.

Critically, group level disease prevalence has additional implications for social behavior of dairy calves which remain unexplored to date. Prevalence of both clinical respiratory disease and diarrhea is variable¹⁰ and disease prevalence may affect all calves within a group, given that healthy animals may reduce social behavior if sick group members are less active²⁷. While variability in social network structure between groups of intensively housed livestock has received limited attention to date, group-level factors are well known to influence individual expression of social behavior in other social species²⁸. Our recent findings suggest considerable variability between identically-managed pens of dairy calves in strength, as well as variability between groups in changes over time between rearing stages¹⁹, suggesting that social behavior is highly variable at the group level.

The objective of this study was to explore the relationship between individual and group level health status and the expression of social behaviors in group housed dairy calves using network centrality measures. We hypothesized that individual health status, including clinical respiratory disease, would be negatively associated with centrality in the social network, and that group-level disease prevalence may further influence individual expressions of social behavior.

Results

Prevalence of health conditions at the individual and group level

During the pre-weaning period, 43% of calves were classified with clinical respiratory disease, 41% of calves were classified with lung consolidation, and 21% of calves were classified with gastrointestinal infection. During weaning, 42.2% of calves were classified with clinical respiratory disease and 44.4% of calves were classified with lung consolidation. Average prevalence of each health condition by week at the individual and group level is summarized in Table 1.

Lung consolidation coincided with clinical respiratory disease in approximately one third of individual cases (30.7% in week 2, 36.7% in week 4, 34.8% in week 5, and 34.6% in week 6) and was a weak predictor of respiratory disease status during pre-weaning (estimate = 0.74; SE = 0.42; $p = 0.08$; odds ratio (OR) = 2.1) but not weaning (estimate = 0.22; SE = 0.38; $p = 0.56$; OR = 1.3). During pre-weaning, clinical respiratory disease was more common in calves that also had a gastrointestinal infection (45.2 vs. 21.7%; estimate = 1.1; SE = 0.51; $p = 0.017$; OR = 3.1). Group-level prevalence of lung consolidation and clinical respiratory disease were not correlated during any week ($p > 0.39$).

Pre-weaning co-occurrence of clinical respiratory disease and lung consolidation predicted lung consolidation during weaning; 71.1% of calves classified with both lung consolidation and clinical respiratory disease during pre-weaning had lung consolidation during weaning, which was greater than prevalence of post-weaning lung consolidation in calves with pre-weaning lung consolidation alone, clinical respiratory disease alone, or neither condition during pre-weaning (30.6, 11.7, and 18.3%, respectively; SE = 6.0; $p < 0.01$; OR > 5.6). Occurrence of clinical respiratory disease during weaning was also greater in calves with pre-weaning lung consolidation (37.4 vs. 20%; SE = 9.4; $p = 0.033$; OR = 2.4) but not significantly predicted by pre-weaning respiratory disease status (estimate = 0.55; SE = 0.37; $p = 0.14$; OR = 1.7). At the group-level, prevalence of lung consolidation was correlated between pre-weaning and weaning stages ($R_s = 0.68$; $p = 0.044$) and there was a weak correlation between pre-weaning and weaning group-level prevalence of clinical respiratory disease ($R_s = 0.61$; $p = 0.079$). These trends are visualized in Fig. 1, which indicates classification with clinical respiratory disease and lung consolidation, by group, calf, and week.

Effects of health status on network centrality

During the pre-weaning period, we found that strength centrality was negatively and significantly related to group-level prevalence of clinical respiratory disease (M1: $\beta \pm SE = -1.12 \pm 0.21$, $Z = -5.25$, $p < 0.01$; Table 2; Fig. 2) and presence of lung consolidation (M1: $\beta \pm SE = -0.45 \pm 0.21$, $Z = -2.11$, $p = 0.03$; Table 2) in the top model

Health status	Level	Pre-weaning stage		Weaning stage	
		Week 2	Week 4	Week 5	Week 6
Clinical respiratory	Individual	14.8	34.1	26.1	29.5
	Group	20 (0 – 30)	30 (0 – 70)	20 (0 – 60)	40 (0 – 60)
Lung consolidation	Individual	18.2	29.5	26.1	35.2
	Group	10 (0 – 40)	20 (0 – 80)	20 (0 – 70)	30 (0 – 70)
Gastrointestinal	Individual	8.9	12.2	Not included	
	Group	0 (0 – 30)	0 (0 – 90)		

Table 1. Descriptive summary of prevalence of health conditions (clinical respiratory disease, lung consolidation, and gastrointestinal infection) at the individual level (% of individual calves classified with each condition) and group level (median and range group-level prevalence) during pre-weaning (observation weeks 2 and 4 following grouping) and weaning stages (observation weeks 5 and 6).

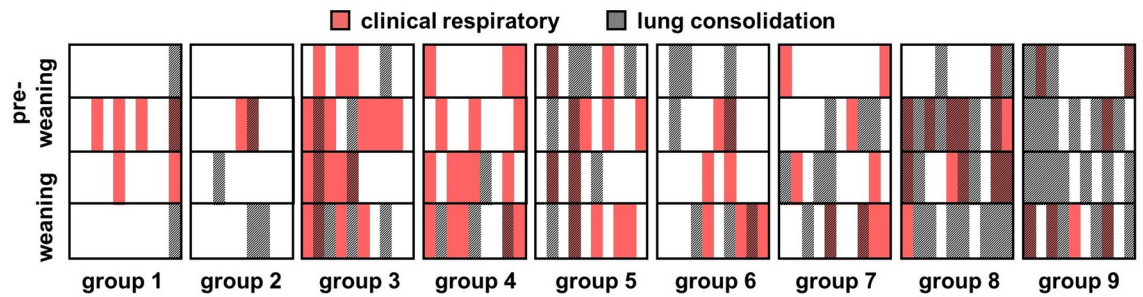


Fig. 1. Classification of calves with clinical respiratory disease (red), lung consolidation (shaded), or both conditions (shaded red), shown by group (groups 1–9; 10 calves/pen), with vertical columns illustrating individual calves within each group, and horizontal rows indicating each of 4 observation weeks in chronological order descending from top to bottom (pre-weaning period: weeks 2 and 4 post-grouping, weaning period: weeks 5 and 6 post-grouping).

(AIC = 129.20; models developed using an information theoretic-approach to select predictor values). Closeness centrality was positively and significantly related to group-level prevalence of clinical respiratory disease (M1: $\beta \pm SE = 0.64 \pm 0.09$, $Z = 6.79$, $p < 0.01$) and presence of lung consolidation (M1: $\beta \pm SE = 0.35 \pm 0.09$, $Z = 3.72$, $p < 0.01$) in the top model (AIC = -136.60; Table 2). In addition, calves experiencing a bout of gastrointestinal illness (M4: $\beta \pm SE = -0.16 \pm 0.08$, $Z = -1.96$, $p = 0.05$) and those in groups with a higher prevalence of gastrointestinal disease (M2: $\beta \pm SE = -0.26 \pm 0.15$, $Z = -1.77$, $p = 0.07$) had marginally lower strength centrality (Table 2). We found no significant effect of individual disease status or group-level disease prevalence on eigenvector centrality during the pre-weaning period.

During the weaning period, calves with lung consolidation had lower eigenvector centrality (M1: $\beta \pm SE = -0.03 \pm 0.01$, $Z = -1.98$, $p = 0.05$; Fig. 3) in the top model (AIC = -288.30; Table 3), with no other significant predictors. We found no significant relationships between group-level disease prevalence and social network measures during the weaning period in any of the top models for eigenvector, strength, and closeness centrality (Table 3).

Discussion

In this observational study, we examined the relationship between social behavior and both individual and group-level health status in dairy calves using social network analysis. In general, our results provide evidence that sickness negatively affects network strength among group-housed calves. This finding aligns with reduced connectedness associated with calves inoculated with *Mannheimia haemolytica*, a main component of bovine respiratory disease, in both directed and undirected networks²⁶ as well as findings that both younger and clinically sick calves had reduced connectedness¹⁸. However, our findings suggest that as disease prevalence varies between groups and over time, associations between health status and network centrality are likely to vary with calf age and depend on group-level factors. The present study is the first to describe how multiple health factors, at both the individual and group level, may influence social network structure in group-housed dairy calves.

In this study, we focused on respiratory disease, evaluating both clinical symptoms and lung consolidation, and gastrointestinal illness. Our observed prevalence of respiratory disease (~40%) aligns with studies in similar climates (~30%; ranging from 0–56%¹³), although reported rates in colder climates may be lower (~20%^{14,29}). Our results of group-level differences in disease prevalence align with survey work revealing variable herd-level prevalence of disease (1.8 to 38% for diarrhea; 4.5 to 49.6% for respiratory disease¹⁰ differences which may be attributed to both the social environment and management practices.

A major finding of our study is that calves in groups with a higher prevalence of illness had lower centrality, suggesting that behavior of healthy calves is affected by sick animals in the group. Social withdrawal or lethargy in sick calves may reduce social opportunities for healthy calves; for example, play behavior of a healthy calf shifted towards individual locomotor play and less frontal pushing (a component of social play) when a companion calf was less healthy²⁷. Further, evidence across species suggests that healthy individuals may actively avoid sick conspecifics (e.g., infection risk drives social avoidance in bullfrogs; *Rana catesbeiana*³⁰). Although no previous study of dairy calves has looked at the effect of group-level factors on centrality, group-level factors have been related to centrality in other species. For example, the presence of pups in small social groups of marmots (*Marmota flaviventris*) was associated with lower aggression²⁸. In dairy calves, social behavior may be affected by various group-level management factors (e.g., group size³¹, age range within the group³², sex composition²³, and space allowance³³). Previous findings suggest that calf age within the group can be a strong predictor of centrality in groups with a wider age range¹⁸ than the present study, and these group dynamics could mediate both group-level differences and effects of health status on individual centrality within a network. Sex was not related to social network centrality in the present experiment; however, it has previously been shown to influence the social interactions of group-housed calves (e.g., higher degree of interaction for male calves in mixed-sex groups²³). Therefore, the varied composition of each group in the present study may play a role in shaping individual social networks.

Predictor	Model	Fixed effects	Estimate ± SE	z/t Values	p Values
Eigenvector	M1	Intercept	0.92 ± 0.03	27.06	< 0.01
		Week	-0.01 ± 0.01	-0.14	0.88
		Sex	-0.01 ± 0.01	-0.98	0.34
		Resp	0.02 ± 0.04	0.65	0.51
		Lung	-0.03 ± 0.02	-1.58	0.11
Strength	M1	Intercept	2.03 ± 0.17	11.63	< 0.01
		Week	0.13 ± 0.03	4.25	< 0.01
		Sex	-0.03 ± 0.05	-0.57	0.57
		Resp-prev	-1.12 ± 0.21	-5.25	< 0.01
		Lung-prev	-0.45 ± 0.21	-2.11	0.03
	M2	Intercept	2.05 ± 0.17	11.68	< 0.01
		Week	0.12 ± 0.03	3.93	< 0.01
		Sex	-0.03 ± 0.05	-0.57	0.57
		Resp-prev	-0.95 ± 0.23	-4.10	< 0.01
		Lung-prev	-0.46 ± 0.21	-2.19	0.02
	M3	Intercept	2.05 ± 0.20	9.81	< 0.01
		Week	0.10 ± 0.03	3.39	< 0.01
		Sex	-0.03 ± 0.05	-0.65	0.51
		Resp-prev	-0.95 ± 0.23	-4.07	< 0.01
		Gast-prev	-0.25 ± 0.15	-1.69	0.09
M4	Intercept	2.05 ± 0.22	9.00	< 0.01	
	Week	0.10 ± 0.02	3.55	< 0.01	
	Sex	-0.02 ± 0.04	-0.58	0.56	
	Resp-prev	-1.02 ± 0.21	-4.64	< 0.01	
	Gast	-0.16 ± 0.08	-1.96	0.05	
Closeness	M1	Intercept	-0.66 ± 0.08	-7.89	< 0.01
		Week	-0.08 ± 0.01	-5.80	< 0.01
		Sex	0.02 ± 0.02	0.93	0.35
		Resp-prev	0.64 ± 0.09	6.79	< 0.01
		Lung-prev	0.35 ± 0.09	3.72	< 0.01

Table 2. Results from the pre-weaning stage of LMMs testing the relationship between individual centrality (eigenvector, strength, and closeness) and individual health measures [binary classification with clinical respiratory disease (Resp), lung consolidation (Lung), or gastrointestinal infection (Gast); reference level = healthy] and group-level health status [continuous variable describing group-level prevalence of clinical respiratory disease (Resp-prev), lung consolidation (Lung-prev), and gastrointestinal infection (Gast-prev)], while controlling for sex (reference level = bull) and week of age (week 2 and 4 post-grouping), for top sub-models (listed as M1, M2, etc.).

Critically, we found that individual lung consolidation, a subclinical condition, was the primary predictor of centrality in calves during weaning, a health factor which has not previously been related to social behavior. Lung consolidation is associated with impaired performance (average daily weight gain³⁴), yet behavioral changes associated with lung consolidation have received minimal study. However, lung consolidation, as well as both clinical respiratory disease and gastrointestinal disease, has been associated with reduced calf willingness to approach a human or novel object³⁵, suggesting that other behavioral changes in the home pen may also be evident in calves with lung consolidation. Clinical respiratory disease has been more widely studied, with a demonstrated relationship with feeding behavior³⁶ and activity³⁷ and use of predictive models to detect changes in behavior days before diagnosis³⁸. In the present study, we found that lung consolidation during weaning was strongly predicted by pre-weaning co-occurrence of lung consolidation and clinical symptoms of respiratory disease, suggesting that reduced centrality in calves with lung consolidation during weaning may be a consequence of prolonged, chronic illness influencing the development of social behavior.

Further research is needed to assess how chronic health conditions in dairy calves may influence behavioral development and predict future behavior. There is limited research on the relationship between chronic disease during early life and behavioral ontogeny. Exposure to endotoxins results in permanent changes to hypothalamic-pituitary-adrenal axis activity in neonatal rats³⁹, suggesting lasting changes in stress responsiveness. In dairy cattle, most studies to date have examined individual characteristics other than health to predict short-term social contact (i.e., two weeks¹⁷), while none have considered the potential impact of social context. Longer-term work examining health and group dynamics could reveal how early experiences may shape social interactions later

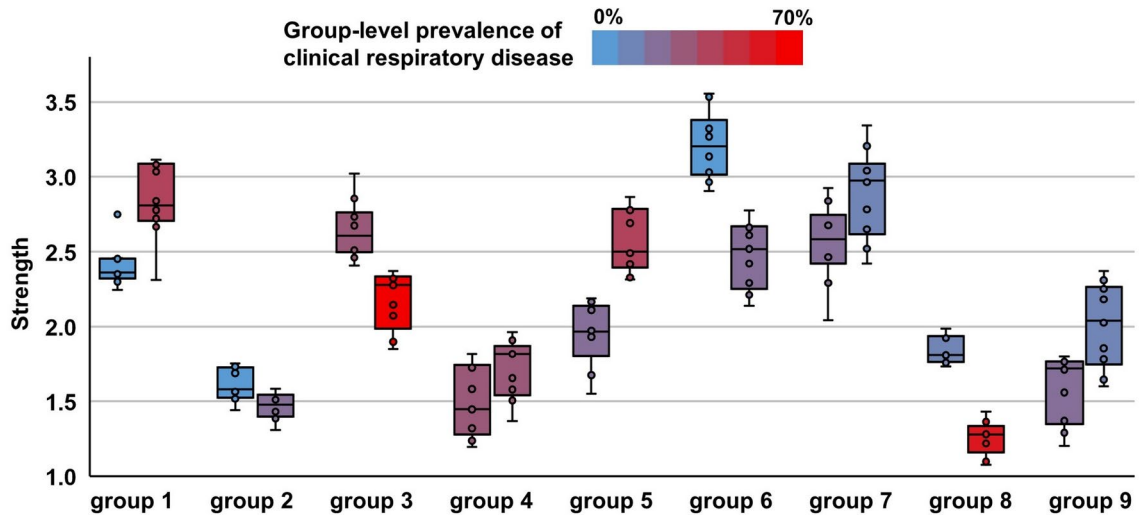


Fig. 2. Strength centrality shown by group (9 pens of 10 calves/group) for the two pre-weaning observation weeks (weeks 2 and 4 after grouping, shown in adjacent box plots for each group), with group-level prevalence of clinical respiratory disease shown with the color gradient (lowest prevalence in blue, highest prevalence in red).

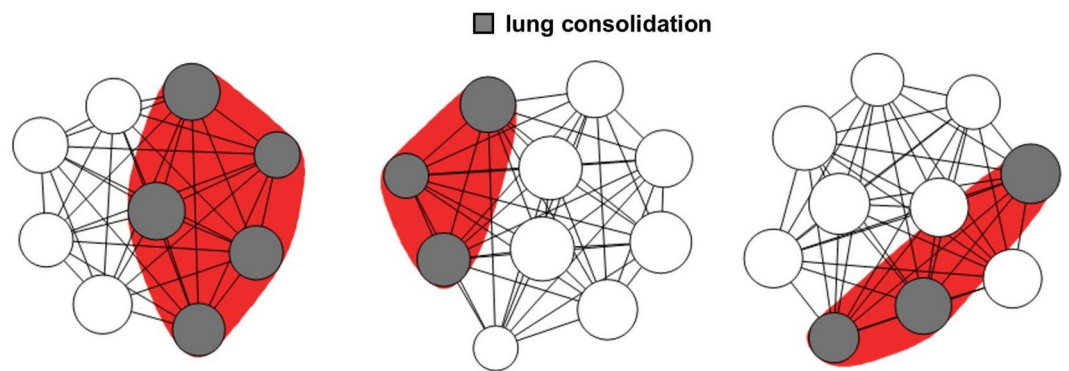


Fig. 3. Network representation of eigenvector centrality and lung consolidation shown for a subset of groups ($n = 3$) during the weaning period (week 5 after grouping). Individual calves (nodes) are represented by circles; size is based on eigenvector centrality; color is based on individual lung consolidation (grey circles marked in red outline); lines represent the weighted interactions among groupmates.

in life. It is possible that relationships between sickness behavior and social network centrality may vary as calves age; previously, we described decreased strength during weaning despite stable eigenvector centrality, suggesting that calves became more selective in social interactions with time¹⁹. Our findings additionally suggest a potential to evaluate early social networks as a potential predictor of future health or productivity, given that lung consolidation in calves is associated with impaired future reproductive outcomes and increased culling rate⁴⁰ and lower milk production⁴¹.

Automated approaches to continuous location tracking provide rich opportunity to characterize dyadic spatial associations and construct social networks on a scale not previously feasible, yet proximity-based networks are limited in that they fail to capture the direction (i.e., avoidance versus withdrawal) or nature of social contact while animals are in proximity. While changes in social behavior influence spatial associations, as captured in the present study, more detailed observation in other group-living animals suggests nuance in how illness may affect social interactions. For example, animals have been shown to both limit social contact⁴² and seek out affiliative interactions with familiar conspecifics⁴³ in response to an infection. Further, vampire bats (*Desmodus rotundus*) reduce allogrooming directed at disease-challenged conspecifics, but this decrease is mediated by pairwise level of familiarity⁴⁴. Dairy calves have also been shown to both reduce^{4,26} and increase²⁶ social interactions while sick, depending on the nature of direction of social behavior measured. Sick calves interacted with fewer conspecifics and spent less time in social contact yet initiated more contact than they received²⁶. Further, social networks based on social lying duration were not affected by a disease challenge²⁶, suggesting that active social interactions are more sensitive to health status, whereas passive social rest may not be, potentially because it is less energetically costly. Managed housing systems may also restrict isolation, which complicates

Predictor	Model	Fixed effects	Estimate ± SE	z/t Values	p Values
Eigenvector	M1	Intercept	0.08 ± 0.09	9.60	< 0.01
		Week	0.02 ± 0.01	0.20	0.83
		Sex	0.09 ± 0.01	0.06	0.95
		Resp-prev	-0.02 ± 0.03	-0.61	0.55
		Lung	-0.03 ± 0.01	-1.98	0.05
	M2	Intercept	0.88 ± 0.09	9.36	< 0.01
		Week	0.01 ± 0.01	0.19	0.84
		Sex	0.01 ± 0.01	0.37	0.71
		Resp-prev	-0.01 ± 0.03	-0.34	0.73
		Lung-prev	-0.03 ± 0.03	-1.03	0.31
	M2	Intercept	0.08 ± 0.09	9.62	< 0.01
		Week	0.02 ± 0.01	0.14	0.88
		Sex	0.03 ± 0.01	0.02	0.98
		Resp	-0.01 ± 0.01	-0.15	0.90
		Lung	-0.03 ± 0.01	-1.95	0.05
Strength	M1	Intercept	0.03 ± 0.03	11.85	< 0.01
		Week	-0.02 ± 0.04	-5.55	< 0.01
		Sex	-0.09 ± 0.04	-0.01	0.99
		Resp	-0.01 ± 0.05	-0.22	0.81
		Lung	-0.08 ± 0.05	-1.57	0.11
Closeness	M1	Intercept	-1.48 ± 0.15	-9.63	< 0.01
		Week	0.10 ± 0.02	4.48	< 0.01
		Sex	-0.01 ± 0.02	-0.28	0.77
		Resp-prev	-0.02 ± 0.09	-0.24	0.80
		Lung-prev	0.18 ± 0.15	1.20	0.23

Table 3. Results from the weaning stage of LMMs testing the relationship between individual centrality (eigenvector, strength, and closeness) and individual health measures [binary classification with clinical respiratory disease (Resp), lung consolidation (Lung), or gastrointestinal infection (Gast); reference level = healthy] and group-level health status [continuous variable describing group-level prevalence of clinical respiratory disease (Resp-prev), lung consolidation (Lung-prev), and gastrointestinal infection (Gast-prev)], while controlling for sex (reference level = bull) and week of age (week 5 and 6 post-grouping), for top sub-models (listed as M1, M2, etc.).

the expression and detection of sickness behavior²². Future work describing direction and context of social interactions may provide further insight into how sickness behavior and group-level disease prevalence affect social behavior.

In summary, our results suggest that disease coincides with reduced social proximity in group-housed dairy calves. In younger, pre-weaned calves, our findings revealed reduced strength and higher closeness in calves in groups with a higher prevalence of clinical respiratory disease or lung consolidation, whereas individual health status was not a significant predictor. During the weaning stage, eigenvector centrality was lower in calves with lung consolidation. Our results provide novel insight into a nuanced relationship between individual sickness behavior and social network position, which depends on the nature of the health condition and appears to depend strongly on social context, which is affected in turn by group-level disease prevalence. These findings additionally reveal promising avenues for future work, examining influences of group-level factors in social networks and factors that influence the development and long-term predictive value of social networks in young dairy calves.

Materials and methods

This study was approved by the University of Florida Animal Care and Use Committee (protocol no. 201910860) with all animal management conducted in accordance with institutional guidelines.

Animal management

We enrolled a total of 9 pens of Holstein dairy calves, reared in groups of 10 calves [(90 calves total; including both heifers (n = 57) and bulls (n = 33)] at the University of Florida Dairy Unit (Hague, FL, USA) from January 2021 to September 2022. Calves were pair housed within the first 24 h of life. At approximately 2 weeks of age (15.1 ± 2.9 d of age; mean ± SD; range 6 – 21 d), groups were formed of 10 calves born within the same week (within-group age range 4.6 ± 1.4 d; mean ± SD; range 3 – 7 d). All groups contained both heifer and bull calves (groups were 60 ± 10% female; mean ± SD; range 50 – 90%). Group pens (7.4 × 8.0 m; 5.9 m²/calf) were located under an open-sided barn with overhead fans for air circulation and deep-bedded with sand (4 identical pens

available at a time). Each pen provided a water trough, a feed tray supplying ad libitum access to pelleted calf starter (22% CP and 2% fat; Ampli-Calf Starter Warm Weather, Purina Animal Nutrition LLC, Shoreview, MN, USA) and an automated milk feeder (DeLaval CF1000X, DeLaval, Kansas City, MO) supplying calves with 8 L/d of milk replacer (28% CP and 15% fat; Southeast Milk, Inc., Mayo, FL, USA). Calves were weaned gradually over 10 d, beginning at 43 ± 2 d of age.

Data collection

Individual and group-level health classification

During each week, calves were individually classified with clinical respiratory disease, gastrointestinal infection, and/or lung consolidation, as defined below, and weekly group-level prevalence of these three health categories was additionally calculated. Classification with clinical respiratory disease and/or gastrointestinal infection was based on clinical health exams performed twice weekly (by a single trained researcher with veterinary oversight), with all calves within the group scored on the same day. Clinical health scores were based on an established scoring system which assigns points from 0 (normal) to 3 (severely abnormal) for the following categories: rectal temperature, cough, nasal discharge, eye discharge, ear position, and fecal score⁴⁵. These scores were used to individually classify calves during each observation week with respiratory disease and/or a gastrointestinal infection, the two most prevalent diseases affecting dairy calves, which are associated with behavioral changes in group-housed calves³⁵.

Calves were categorized with clinical respiratory disease for an observation week if either clinical health exam yielded a score ≥ 2 in at least 2 categories describing respiratory disease symptoms (nasal, eye, ear, cough, or rectal temperature), aligning with current recommendations for interpreting this clinical scoring chart to best detect bovine respiratory disease^{13,46}. Calves were categorized with clinical gastrointestinal infection if presenting with diarrhea (fecal score = 3; describing watery feces) and at least moderately abnormal rectal temperature (rectal temperature ≥ 38.9 °C), a more conservative benchmark than is sometimes used to characterize neonatal calf diarrhea alone¹², which was intended to capture calves experiencing diarrhea with signs of systemic infection⁴⁷. Per standard facility procedures, calves were provided electrolytes if experiencing diarrhea for ≥ 2 d with reduced appetite, and antibiotic treatment of respiratory disease was administered as needed per independent veterinary exams conducted weekly (based on clinical health scores only).

Given evidence that dairy calves commonly experience lung consolidation in the absence of clinical respiratory symptoms^{14,48}, thoracic ultrasounds were performed weekly by a single trained researcher to characterize lung consolidation, according to the protocol designed by Ollivett and Buczinski (2016). Briefly, each intercostal space (ICS) on both the right and left thorax was scanned with a linear rectal ultrasound probe starting at the level of the scapula from the 6th to the 1st ICS. The probe was moved ventrally toward the sternum until appropriate landmarks were visualized. 70% isopropyl alcohol was used as a transducing agent. Areas of consolidated lung tissue were counted and measured. We initially characterized calves with lung consolidation if a lesion ≥ 1 cm in depth was present, according to a simplified scoring system for describing lung consolidation⁴⁶. Based on observations in our specific study population and previous evidence of negative long-term effects associated with any lung consolidation (lung lesions of any size⁴⁰), we subsequently included an additional small subset of calves which had substantial small areas of consolidation (≥ 2 lesions ≥ 0.5 cm) with severe diffuse comet-tailing artifacts (pleural roughening) in our classification of lung consolidation.

Characterization of social networks

Upon entry to group housing, calves were fitted with collar-based tags (54 × 40 × 14 mm, 26 g) using a real-time location tracking platform (TrackLab, Noldus Information Technology, Wageningen, the Netherlands), which utilizes SEWIO ultra-wideband (UWB) technology⁴⁹ and has been validated for calves and cows in similar environments^{18,50}. During each week, we selected consecutive 4-day periods of data where $> 80\%$ of calves in the group had no missing data to maintain the reliability of the social network metrics without significantly affecting their accuracy⁵¹. Calves ($n = 10$) in 6 (out of 9 groups) had missing data for one or more 4-day periods. Positional data cleaning protocol and generation of the social networks has been previously described¹⁹. Briefly, positional data were converted using spatial (1 m threshold) and temporal (3 min threshold) grouping of individual calves using the *spatsoc*⁵² package in R (version 4.3.2)⁵³. Calves within this spatial and temporal threshold were assigned to the same group and assumed to be in association. We then generated non-directed weighted proximity based social networks from these group by individual matrices and calculated nodal metrics using the *asnipe* and *igraph* packages^{52,54,55}. Individual calves' networks were characterized with three centrality measures: closeness (number of steps to nearest neighbors), strength (sum of an individual's edge weights), and eigenvector (sum of the centralities of an individual's direct and indirect connections)⁵⁵. We applied these three measures because they have proved relevant in describing other dairy calves' social networks⁶, while strength has been shown to be a reliable measure for small networks⁵⁶.

Statistical analysis

To characterize the relationship between individual health and group-level health factors and social networks, data were analyzed separately during the milk-feeding and weaning, given differences during these rearing periods with respect to feeding management and disease prevalence, and previous evidence of changes in social network centrality between rearing stages¹⁹. During the pre-weaning period, we selected weeks 2 and 4 following grouping for observation, excluding the initial week following grouping (during which calves are trained to use the automated milk feeder, and consequently study personnel may disturb normal behavior throughout the day) and week 3 following grouping (during which calves were subject to hot iron disbudding per routine farm management practice, which is painful and may have short-term effects on social behavior⁵⁷, despite adherence to pain mitigation best practices). Both weeks during weaning (weeks 5 and 6 following grouping) were included

in the analysis. Two calves which were euthanized due to chronic illness or injury (from different groups) were fully excluded from analysis and positional data was missing completely for one heifer.

Descriptive analysis of prevalence of health conditions

For descriptive analysis (conducted using SAS vs. 0.4; SAS Institute, Cary, NC, USA), associations between group-level prevalence of different health categories (between health categories and stages) were explored using Spearman rank-order correlation. At the individual level, we tested associations between concurrent health status classifications (e.g., whether respiratory disease status predicted lung consolidation) separately for the pre-weaning and weaning period, using generalized linear mixed models (GLIMMIX procedure, fit with a binary distribution) with observation week as a repeated measure (calf as subject) and group as a random effect. Using a similar model, we additionally tested whether any occurrence of a health classification during the pre-weaning period predicted health classification during the weaning period.

Analysis of relationship between health status and network centrality

We used an information theoretic approach to compare a sequence of models⁵⁸ to determine which best explained the patterns of variation in individual centrality (the response variable). Data were analyzed separately by pre-weaning and weaning periods, considering differences in management (milk feeding) and common disease risks during these different developmental periods. For the pre-weaning period, predictor variables describing health included individual disease status (for the three categories of clinical respiratory disease, gastrointestinal infection, or lung consolidation) and group-level measures of disease prevalence for the same three conditions for the pre-weaning period. For the weaning period, predictor variables excluded gastrointestinal infections (individual status and group-level measures) due to low occurrence of this health event. Our control variables included sex and age, with group and calf as nested random effects. We calculated Akaike Information criterion (AIC), delta AIC and AIC weights with the *MuMIn* package⁵⁹. Of all the models, we considered the best-approximating ones as those with an $\Delta AIC < 2$ (see Table S1 in Supplementary Material).

We fit a series of generalized linear mixed models using the package *lme4*⁶⁰ to help interpret the results of our best-approximating models. Social network data is inherently relational, violating the assumption of independence required for most statistical tests⁶¹. To control for non-independence in the data, we used parametric regression in lieu of permutation-based tests, given our centrality metrics were regressed against nodal covariates, calves were sampled equally through automated observational methods, and were restricted to their respective group pens⁶². Assumptions (i.e., residual normality distribution plots) were visually checked using the *performance* package⁶³. Response variables were log transformed when normality assumptions were not met (i.e., closeness centrality). We tested for multicollinearity of the independent factors by calculating the variance inflation factor “vif” in package *car*⁶⁴. There was no evidence of multicollinearity between factors (maximum variance inflation factor = 2.09).

Data availability

The data used in this study is available upon request (please contact the Corresponding Author: emillerc@ufl.edu).

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Author contributions

K.G. collected data and assisted with data analysis and manuscript writing. F.M. provided veterinary oversight and training and contributed to study design. K.C.B. and E.K.M.C. performed data analysis and manuscript writing. All authors approved of the final version of this manuscript and agree to be held accountable for the content therein.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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