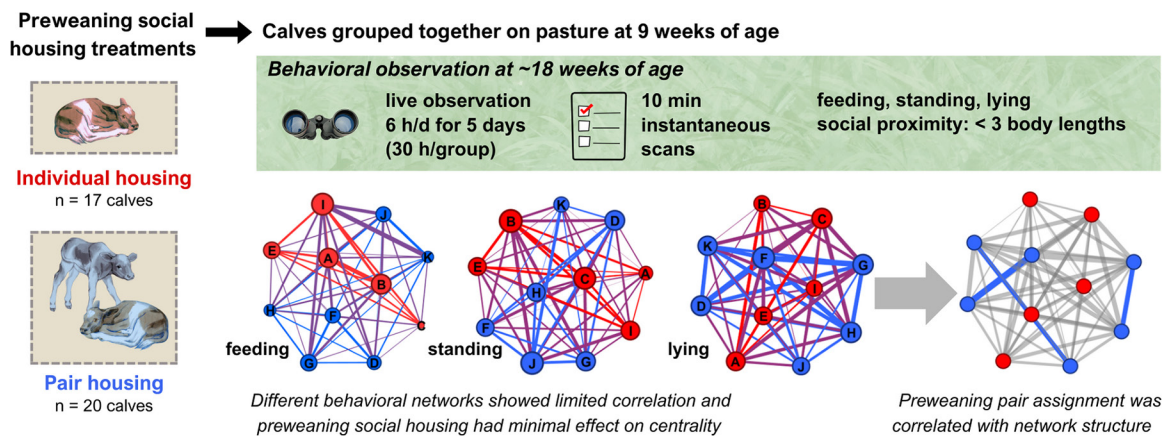


# Characterizing social networks and influence of early-life social housing in weaned heifers on pasture

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## Graphical Abstract

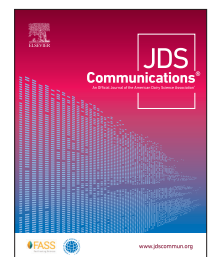


## Summary

We characterized social networks in weaned heifers housed in groups on pasture and assessed the effects of preweaning social housing on behavior. Proximity-based social networks surrounding feeding, standing, and lying showed limited correlation, suggesting that they captured different aspects of social behavior. Social housing during the preweaning period had minimal effect on centrality measures describing connectedness within the social network, but preweaning pair assignment was correlated with standing and lying network structure for certain groups. Previously pair-housed heifers stood for longer in the morning, but lying and feeding time did not differ between preweaning housing treatments. Our results suggest that previous social housing may have subtle effects on sociality that persist following weaning, but behavior may be more influenced by immediate social context.

## Highlights

- We characterized social networks of weaned dairy calves housed on pasture.
- Prewearing social housing had minimal effects on network centrality of weaned heifers.
- Proximity to a former penmate predicted aspects of social network structure.
- Prewearing social housing may subtly influence longer-term behavior, but immediate social context may be more influential.



# Characterizing social networks and influence of early-life social housing in weaned heifers on pasture

D. Clein,  K. C. Burke,  and E. K. Miller-Cushon\* 

**Abstract:** Dairy cattle are gregarious animals that are commonly managed in social groups, yet group-level social dynamics remain underexplored in weaned heifers. We characterized activity and social networks after weaned heifers had been raised in social groups on pasture for approximately 2 mo and examined effects of preweaning social housing. Holstein heifers raised in individual pens ( $n = 17$ ) or paired pens ( $n = 20$ ; 10 pens of 2) were mingled between treatments and grouped (10–11 heifers/group; total of 4 groups observed) on pasture following weaning ( $8.8 \pm 0.4$  wk of age; mean  $\pm$  standard deviation). When heifers were  $17.8 \pm 1.0$  (mean  $\pm$  standard deviation) wk of age, we conducted live observation over a period of 5 d (6 h/observation day; morning: 0800 to 1100 h and afternoon: 1200 to 1500 h) for a total of 30 h observation/group. Using instantaneous scans at 10 min intervals, we recorded behavior (feeding, lying, or standing) and social proximity ( $<3$  body lengths of another heifer, with neighbor identity noted) of all heifers. Duration of lying and feeding did not differ between previous housing treatments, but heifers reared in pairs stood for longer in the morning than previously individually housed heifers (30% vs. 24% of scans; standard error = 0.03). Networks of different behaviors showed limited correlation, with some variability between groups. Centrality in social networks was minimally affected by preweaning social housing, although previously pair-housed calves had greater strength (sum of an individual's edge weights) and eigenvector centrality (sum of the centralities of an individual's connections) in the lying social network for one group. Preweaning pair assignment was correlated with network structure for lying and standing networks for some groups. These results suggest that preweaning social housing may subtly affect activity and social behavior longer-term, but that behavior may be most subject to current social context.

Cattle are gregarious species capable of developing long-term bonds with kin and familiar animals under natural conditions (Reinhardt et al., 1978), yet it remains most common to raise dairy calves in individual pens before weaning in the United States (reviewed by Roche et al., 2023). It is well established that preweaning social housing alleviates negative consequences of early-life social isolation, allowing for motivated social contact between calves (Ede et al., 2022) and supporting the development of some normal social behavior (reviewed by Whalin et al., 2021).

While the social development of young calves has received attention in recent years, there is limited understanding of how early socialization may influence social behavior in older animals. Evidence suggests at least short-term benefits of preweaning social housing on behavior following postweaning grouping, including reducing latency to begin feeding (De Paula Vieira et al., 2010). Calves also establish preferences for familiar animals (Duve and Jensen, 2011; Lindner et al., 2022) that may persist into adulthood (Raussi et al., 2010).

The aim of this study was, first, to characterize activity and social networks of weaned heifers on pasture and, second, to assess the influence of preweaning social housing on activity and social networks. We hypothesized that heifers that were housed individually during the preweaning period would be less social, and correspondingly less central in proximity-based social networks, than heifers raised in pairs.

At birth, Holstein heifer calves were enrolled at the University of Florida Dairy Unit (Hague, FL) and assigned to 1 of 2 housing treatments: individual housing (IH) or pair housing (PH). Heifers were alternately assigned to different housing treatments, but for automatic assignment of calves to IH if a second calf was not born within 48 h. Calves were managed under standard operating procedures for the facility, and all procedures were reviewed and approved by the University of Florida Institutional Animal Care and Use Committee (protocol # 201910617). Calves used in this study were part of a larger long-term trial examining effects of early social housing on a range of outcomes, and management during the preweaning period is described in more depth by Lindner et al. (2022). Individually housed calves were reared in wire mesh pens ( $0.9 \times 1.8$  m; width  $\times$  depth) that allowed visual and auditory but not physical contact. Pair-housed calves were similarly housed in pens that were twice the area ( $1.8 \times 2.2$  m; width  $\times$  depth). Pens were bedded with sand that was replaced weekly. All calves received 8 L/d (in 2 meals/d at 0600 and 1500 h) of milk replacer (28% CP and 20% fat; Suwannee Valley Feeds; 150 g/L). Calves had ad libitum access to calf starter (22% CP and 2% fat; Ampli-Calf Starter Warm Weather, Purina Animal Nutrition LLC, Shoreview, MN) and water. Calves were weaned over 10 d and completely weaned at 8 wk of age.

Postweaning, at  $8.8 \pm 0.4$  (mean  $\pm$  SD) wk of age, heifers were mingled between preweaning social housing treatments and moved

in weekly cohorts of approximately 10 animals of the same age (born within 1 wk) into an open pasture (15 × 45 m). Pasture groups occasionally included non-study heifers (individually housed for 2 to 3 wk and then housed in small groups of 4 until weaning, according to standard farm operating procedure). The pasture pen consisted of a shade structure, water trough, shaded feed bunk, and approximately 50% dirt coverage and 50% grass coverage. A feed bunk was located at the front of the pasture (containing 14 head gates; allowing all heifers to feed simultaneously). Heifers were provided ad libitum access to the same starter ration as preweaning, delivered at 0700 and 1700 h. Per farm management, heifers were moved to a new pasture pen of a similar layout (moving sequentially through adjacent pens as they aged) every 4 to 5 wk, with animal movements subject to farm management decisions such that some regrouping and mingling of adjacent pens occurred and sequentially enrolled calves were not consistently kept together.

At  $17.8 \pm 1.0$  (mean  $\pm$  SD) wk of age, we conducted live observations to characterize behavior of heifers in their pasture pen. Observations were performed on a total of 4 groups, which included a total of  $n = 17$  previously IH heifers and  $n = 20$  previously PH heifers. While enrollment was constrained by farm management of animal movements, we aimed to double sample sizes from previous experiments revealing shorter-term effects of social housing on behavioral patterns, including feeding (i.e., 9–10 animals/housing treatment; De Paula Vieira et al., 2010; Miller-Cushon and DeVries, 2016). Due to farm management prior to this observation period, the composition of the groups varied in terms of animals raised on previous housing treatments, although all groups contained animals from each previous housing treatment (group 1: 2 PH, 9 IH; group 2: 8 PH, 2 IH; group 3: 6 PH, 5 IH; group 4: 5 PH, 1 IH; and 4 non-study heifers). The observation week for each group was selected to coincide with heifers being present in a specific pasture pen, which had a vantage point that provided an unobstructed view of the complete pen and was not in the way of laneways or other farm activities, such that the observer could remain stationary. We allowed all groups of heifers 1 wk to habituate following the most recent pasture movement before observing them in this pen. Animals could see the group on either side of the observation pasture with fenceline contact, thus the focal pen was not isolated from the influence of surrounding groups. Heifers on pasture received weekly veterinary checks and all animals were considered healthy at the time of the study.

Observations were conducted over a period of 5 d (6 h/observation day; morning: 0800 to 1100 h and afternoon: 1200 to 1500 h) for a total of 30 h observations/group. These observation times were selected to avoid periods of time where farm personnel were working in this area, to avoid external disturbances. Observations were conducted by a single observer who was blind to previous housing treatments. All heifers were observed (including the non-study heifers in group 4). Individual heifers were identified based on unique coat patterns. The observer arrived 15 min before data collection began to allow animals to habituate to their presence, and remained in a chair located 4.5 m outside the pasture. Observations were completed over a period of 6 mo (April to October, 2022).

Using instantaneous scans at 10-min intervals (per previously validated methods; Kitts et al., 2011) we characterized the following behaviors: feeding, defined as the heifer standing at the feed-bunk with her head through a head gate; standing, defined when

the heifer was upright (including walking, grazing, and any other locomotor activity, but excluding time at the feedbunk); and lying. Social proximity was defined when the focal heifer was  $\leq 3$  body lengths from another heifer (with other heifer's identity noted), and "alone" defined when  $>3$  body lengths from any other heifer. This proximity threshold was applied consistently regardless of behavior, and it encompassed the whole feeding area (such that if the focal heifer was feeding, any other heifer within the feeding area was considered to be within social proximity). This proximity threshold was based on previous work where we characterized both "close proximity" ( $<1$  body length) and "moderate proximity" (between 1 and 3 body lengths) of heifers observed in the same pasture pens (Horvath and Miller-Cushon, 2018) and found that durations of close proximity and total proximity ( $<3$  body lengths) were highly correlated ( $R^2 = 0.8$ ). Intraobserver reliability was assessed before data collection using still images of pasture observations (100% agreement for behavioral categories and proximity thresholds, achieved for 10 animals in one group over a series of 5 photographs; further ad hoc reliability assessments were made during data collection by taking photographs that were referenced by external reviewers to confirm correct behavioral categorization). To control for effects of external environment on behavior, temperature data were collected on observation days at 0800, 1100, and 1500 h via the Gainesville Regional Airport Weather Station (Gainesville, FL; 23 km from study site) and were summarized by observation day ( $25.2 \pm 2.7^\circ\text{C}$ ; mean  $\pm$  SD).

From observed social proximities, adjacency matrices were constructed from proximity data of heifers across the entire observation period, with matrices defined separately for each of the 3 behaviors performed by the focal heifer (standing, lying, feeding), regardless of behavioral state of the neighbors. This resulted in asymmetric adjacency matrices due to proximity interactions when behavior was not synchronized. Reciprocity (proportion of dyads with reciprocated edges relative to the number of dyads that have any edge) was calculated in the *igraph* R package for the standing, lying, and feeding networks of each group. We found high reciprocity for the feeding (0.75, 0.97, 0.93, 0.91), lying (0.93, 0.93, 0.94, 0.92), and standing (0.88, 0.80, 0.80, 0.88) networks for groups 1 to 4, respectively. Given this evidence of a high degree of behavioral synchrony and our focus on proximity versus actively initiated behaviors, we analyzed the data as undirected, weighted networks. We examined direct and indirect connections by calculating strength (weighted degree centrality) and eigenvector centrality. These measures were calculated using the *igraph* package (Csárdi et al., 2024) in R (version 4.1.1, R Core Team, 2013). Strength centrality measures the sum of weights assigned to the node's direct connections, and eigenvector centrality measures the sum of the centralities of an individual's neighbors and the centrality of that individual's direct and indirect connections (Farine and Whitehead, 2015).

We first evaluated the structural similarity of the proximity-based social networks for standing, lying, and feeding. Using the Mantel test in the "vegan" R package (Dixon, 2003), matrix correlations were run separately for each group with 1,000 permutations to generate *P*-values. Second, to assess effects of previous housing treatment, data were analyzed using general linear mixed models (proc GLIMMIX, SAS v. 9.4; SAS Institute Inc.). We summarized the percentage of scans where the heifer was performing the behavior by time of day (morning or afternoon) across the

observation period. These data were analyzed in a model including fixed effects of previous housing treatment (IH or PH), time of day (morning or afternoon), and their interaction, mean temperature during the observation period, and heifer and group as random effects. We had no specific predictions related to the influence of time of day on our results, but given assumptions of diurnal patterns of behavior (Kilgour, 2012) and external influences on behavior (e.g., feed delivery time; Greter et al., 2014), we summarized data separately by time period and included time of day in the model. One observation session for one group was excluded due to an external disturbance (broken farm machinery). We then generated separate mixed-effect models with our social network centrality measures (eigenvector and strength) as response variables, given a well-specified parametric model can replace node permutations when centrality metrics are regressed against nodal covariates (Hart et al., 2022). In addition to our models meeting this criterion, heifers were sampled equally over the study period and were restricted to their respective pasture pens. We included previous housing treatment as a fixed effect, in addition to group and the interaction between group and previous housing treatment, considering that size and composition varied somewhat between groups. The 4 non-study heifers in group 4 were excluded from this analysis. In the case of interactions ( $P < 0.10$ ) between treatment and group, effects of housing treatment were tested by group using the SLICE statement to conduct partitioned analyses. Model residual plots were screened to assess for normality. All values reported are least squares means.

Two groups containing the most pair-housed calves that were former penmates (group 2: PH = 8 [4 former pairs], IH = 2; and group 3: PH = 6 [3 former pairs]; IH = 5) were used for further investigation of the influence of preweaning pair assignment on network structure. We ran a multiple regression quadratic assignment (MRQAP-DSP) that performs regressions with matrices to test whether an entered predictor variable significantly contributes to the explanation of the dependent matrix. This method controls for autocorrelations using Monte Carlo network-level permutations to generate coefficients (Krackhardt, 1988; Dekker et al., 2007). To test whether patterns of social proximity could be predicted by preweaning pair assignment, dyads were labeled 1 if they were previous pair-housed penmates and all other dyads were labeled 0. We generated separate tests for both groups with the feeding, standing, and lying social networks entered as the dependent variable. Tests were run with 10,000 permutations in the *asnipe* R package (Farine, 2013).

Social networks are visualized in Figure 1A, where we show examples of feeding, standing, and lying social networks for 1 group (group 3), with identity of each individual heifer noted. The feeding, lying, and standing networks based on proximity between heifers showed minimal correlation, although this varied depending on the group and behavior. Results from the Mantel test showed no correlation between the feeding, lying, or standing proximity networks for group 2 ( $P > 0.17$ ) or group 3 ( $P > 0.35$ ). The results for the feeding and standing proximity networks in group 1 suggested a weak, positive relationship ( $r = 0.30$ ,  $P = 0.06$ ); however, the other networks were not correlated ( $P > 0.85$ ). The feeding and lying proximity networks in group 4 were correlated ( $r = 0.37$ ,  $P = 0.01$ ), whereas the other networks were not correlated ( $P > 0.32$ ).

Effect of preweaning social housing had minimal effects on social network centrality (Table 1). For the standing social network,

previous social housing did not affect eigenvector or strength centrality, and there was no interaction between group and previous housing treatment (visualized in Figure 1B). For the feeding social network, there was no effect of previous housing treatment on eigenvector centrality, and no interaction between group and previous housing treatment. However, in the lying social network, there was a significant interaction between previous housing treatment and group for both eigenvector centrality and strength centrality. In group 3, previously individually housed heifers had lower eigenvector centrality ( $P = 0.030$ ; see lying in Figure 1A) and strength centrality ( $P = 0.012$ ), with no significant differences between other housing treatments within other groups ( $P > 0.27$ ). Strength centrality, but not eigenvector centrality, varied between groups for all networks (Table 1).

Prewaning pair assignment was a significant predictor for the standing network in group 2 ( $R^2 = 0.12$ ,  $P < 0.001$ ), the lying network in group 3 ( $R^2 = 0.11$ ,  $P = 0.01$ ), and there was some evidence for a relationship with the lying network in group 2 ( $R^2 = 0.07$ ,  $P = 0.06$ ), as visualized in Figure 1C. We did not find relationships between preweaning pair assignment and the standing network for group 3 ( $R^2 = 0.01$ ,  $P = 0.44$ ), or with the feeding networks for either group (group 2:  $R^2 = 0.03$ ,  $P = 0.21$ ; group 3:  $R^2 = 0.01$ ,  $P = 0.55$ ).

Time spent standing (Figure 2) varied between previous housing treatment depending on time of day (weak interaction between housing treatment and time of day:  $P = 0.064$ ), where previously pair-housed heifers stood more in the morning than previously individually housed heifers ( $P = 0.042$ ). Percentage of lying time (Figure 2) did not differ between previous housing treatments ( $P = 0.43$ ) but was slightly greater in the morning ( $P = 0.07$ ). Feeding time (Figure 2) did not differ between previous housing treatments ( $P = 0.90$ ) but was greater in the afternoon ( $P = 0.04$ ). We found a weak positive association between temperature during the observation period and lying time ( $P = 0.079$ ), but not feeding time ( $P > 0.83$ ).

Given limited study of social dynamics in weaned dairy heifers, our aims were first to characterize social networks specific to different behaviors of heifers on pasture, and second to assess effects of preweaning social housing on the later expression of social behavior. We found that social networks specific to standing, lying, and feeding were largely uncorrelated, with some exceptions in certain groups. In general, our findings suggest that social proximity during different activities may be motivated by different factors. Lying and feeding networks showed the strongest correlation in one group, suggesting that social partners when feeding were related to social partners when resting.

We found some effects of preweaning social housing on behavior of group-housed calves after about 9 wk in mixed groups on pasture. However, this depended on time of day, where previously pair-housed heifers stood longer in the morning compared with previously individually housed heifers, but with difference in the afternoon. This interaction between previous housing treatment and time of day could be related to external cues related to farm management or varying motivation for other activities, such as rest. We found that lying varied slightly with temperature during the observation window. Although some previous findings suggest that higher temperatures led to increased standing for evaporative cooling (Strong et al., 2015), we found that heifers spent numerically more time lying during hotter observation periods, which,

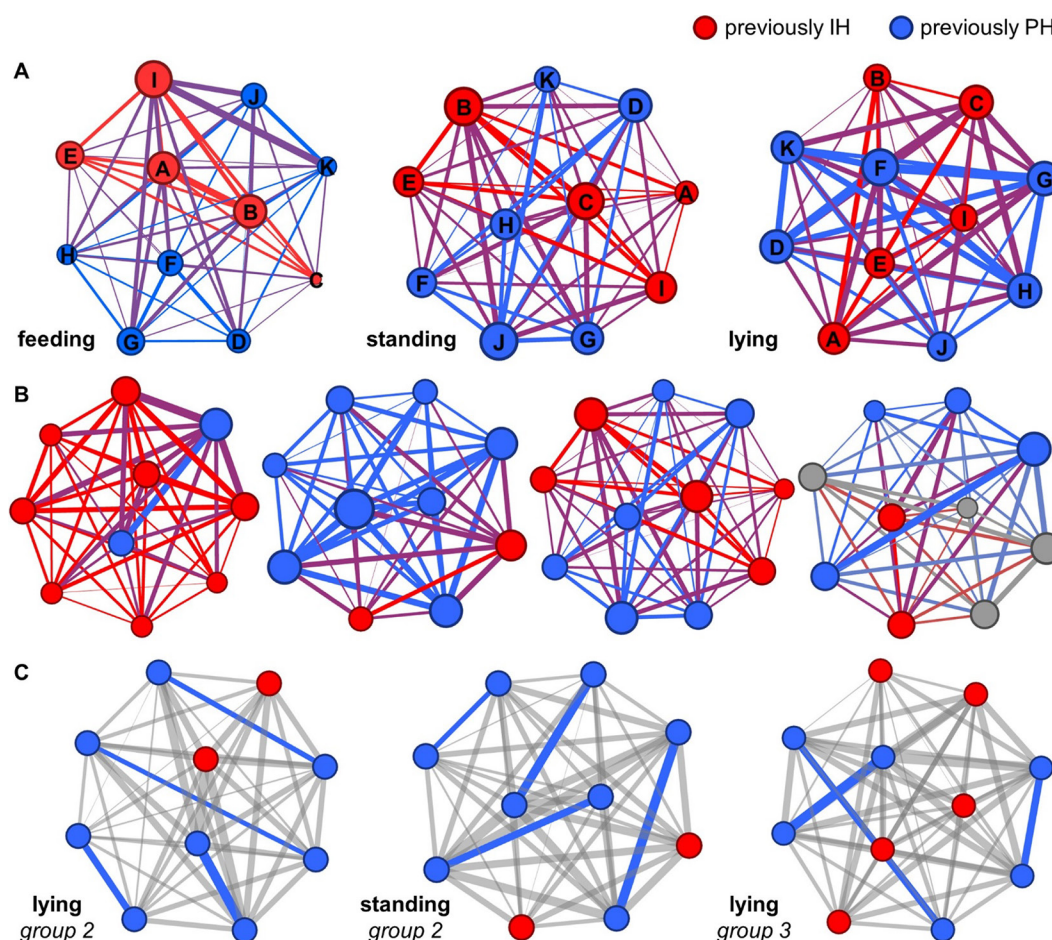


**Table 1.** Social network centrality measures for feeding, standing, and lying for heifers  $17.8 \pm 1.0$  (mean  $\pm$  SD) wk of age group-housed on pasture<sup>1</sup>

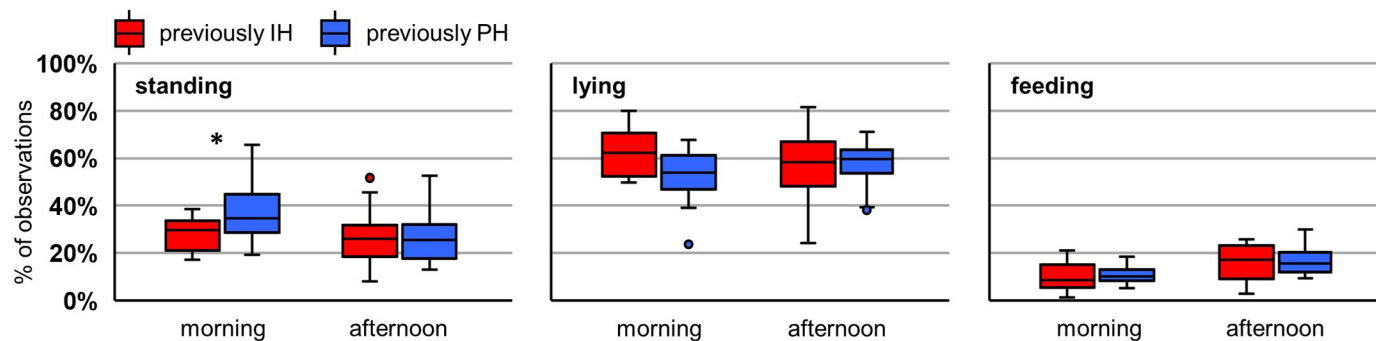
Centrality measure <sup>2</sup>	Treatment			Treatment		Group		Treatment $\times$ group	
	IH	PH	SE	$F_{1,29}$	$P$	$F_{3,29}$	$P$	$F_{3,29}$	$P$
Feeding									
Eigenvector	0.82	0.82	0.054	0.01	0.93	1.78	0.17	0.44	0.73
Strength	178.1	177.3	10.1	0.01	0.95	43.3	<0.001	0.44	0.72
Standing									
Eigenvector	0.83	0.89	0.032	2.14	0.15	0.021	0.9	0.63	0.60
Strength	478.7	515.2	20.1	2.14	0.15	5.04	0.006	0.62	0.61
Lying									
Eigenvector	0.93	0.91	0.019	1.01	0.32	2.18	0.11	3.13	0.041
Strength	1,197.3	1,179.0	27.9	0.28	0.60	83.4	<0.001	3.23	0.037

<sup>1</sup>Heifers were previously raised individually (IH;  $n = 17$ ) or in pairs (PH;  $n = 20$ ) until  $8.8 \pm 0.4$  wk of age (mean  $\pm$  SD), at which point they were mixed between previous housing treatments and raised in groups ( $n = 4$ ) on pasture.

<sup>2</sup>Centrality measures: eigenvector and strength, calculated from social networks constructed based on pairwise proximity (<3 body lengths) between heifers.



**Figure 1.** Visualization of the undirected social network graphs depicting (A) an example of networks for feeding, standing, and lying for one group (group 3, with individual heifers identified with letters), (B) standing networks for all groups (left to right: groups 1 to 4), and (C) networks where preweaning pair assignment was a predictor of network structure (standing and lying for group 2, lying for group 3). Nodes (circles representing individual heifers) are colored red for individual housing (IH) or blue for pair housing (PH). Non-study calves were included for group 4; these calves were not included in analyses of node-level centrality metrics but are shown here in gray. Node size is scaled to indicate eigenvector centrality in panels A and B. Edge (line) thickness is scaled to indicate weight (i.e., percentage of scans that each pair was within proximity of one another) in all panels. Edge color matches the color of nodes involved in each pairwise interaction (only edges between former penmates are colored in panel C). Networks were visualized using Gephi software (v. 0.9.2, Bastian et al., 2009), shown using a Fruchterman-Reingold layout.



**Figure 2.** Percentage of observations spent standing, lying, and feeding, in the morning (0800 to 1100 h) and afternoon (1200 to 1500 h) by heifers  $17.8 \pm 1.0$  (mean  $\pm$  SD) wk of age housed in groups ( $10 \pm 2$  heifers/group) on pasture. Heifers were previously reared individually (IH;  $n = 17$ ) or in pairs (PH;  $n = 20$ ) until  $8.8 \pm 0.4$  (mean  $\pm$  SD) wk of age. \* $P < 0.05$ . The box extends from the 25th to the 75th percentile with a line at the median. Whiskers extend from the box a distance of 1.5 times the interquartile range with values outside this range shown as circles.

anecdotally, usually occurred in the provided shade structure. This is consistent with how heat-stressed animals are more likely to seek shade than animals who are not (Schütz et al., 2008).

We found that social network centrality was minimally affected by previous housing treatment, although previously pair-housed calves had increased eigenvector and strength centrality in the lying social network in one group. This effect was in the direction of our prediction and agrees with previous findings that early social experience may influence longer-term social behavior (e.g., through establishment of social preferences; Raussi et al., 2010). We found no differences in centrality in standing social networks, suggesting that social networks are dependent on the behavior the heifer is performing. Expression of social preferences during different behavioral states may depend on the nature of the environment. For example, dairy cows have been shown to be more synchronous in behavior at pasture compared with indoors (Raussi et al., 2010). Furthermore, Lecorps et al. (2019) found that calves had individual consistency in social proximity patterns when standing, but not lying, which they attributed to constraints on choosing preferred lying social partners upon movement to a freestall barn.

We found no effect of previous housing treatment on time spent feeding or in centrality of the social network while feeding. Previous studies have found short-term effects of preweaning social housing on feeding behavior after weaning, including increased feeding time (De Paula Vieira et al., 2010). Our results suggest that preweaning social housing did not have persistent effects on feeding time in the postweaning group, possibly due to social facilitation, which strongly influences meal patterns in cattle (Albright, 1993). Alternatively, it is possible that effects of early-life social housing on feeding are evident only in more competitive feeding scenarios, given that preweaning social housing has at least short-term benefits for competitive success (Duve et al., 2012).

We found that preweaning pair assignment was a significant predictor of network structure for standing and lying, but not feeding, suggesting that former penmates had a greater likelihood of proximity interactions. Bolt et al. (2017) described effects of preweaning social housing on proximity-based social networks of dairy calves for 1 mo following weaning, and found that calves assorted based on familiarity but previously pair-housed calves decreased time with their former penmate between the first and last

observation week. More generally, previous familiarity and shared early-life experience has been found to increase proximity in adult cows (Raussi et al., 2010; Marina et al., 2023).

It is important to note that postweaning groups were mingled between previous housing treatment, such that findings of longer-term effects of preweaning social housing may be conservative in this study due to social influences from animals on the opposite housing treatment. It is a limitation of the present study that the composition of each observation group varied in numbers of animals reared in different housing treatments. Differences in centrality were evident only in group 3, which had the most balanced numbers of calves from both previous housing treatments. It may be more rigorous in future experiments to either enroll balanced groups of heifers from different housing treatments or to form groups consistently from different previous housing treatments. It is also possible that effects of preweaning social housing may be modulated by postweaning experience. In the present study, heifers experienced ample space and minimal competition for resources, although exposure to regrouping can induce agonistic behavior and alter activity patterns (Raussi et al., 2005).

In summary, we found that social networks of weaned heifers on pasture varied between feeding, standing, and lying. We found some evidence to suggest that social housing before weaning and preference for a former penmate may explain some aspects of social network structure, dependent on group composition. Overall, our results suggest that preweaning housing may have subtle effects on longer-term social behavior, but that present social context may have a greater influence on the behavior of group-housed, weaned heifers.

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## Notes

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**Nonstandard abbreviations used:** IH = individual housing; MRQAP = multiple regression quadratic assignment; PH = pair housing.