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 pre-weaning 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 ± 0.4 weeks of age; mean ± SD). When heifers were 17.8 ± 1.0 (mean ± SD) weeks 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; SE = 0.03). Networks of different behaviors showed limited correlation, with some variability between groups. Centrality in social networks was minimally affected by pre-weaning 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. Pre-weaning 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 (63%; USDA-APHIS, 2014). It is well established that providing access between same age calves alleviates some 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 remain gaps in our knowledge of social behavior in older, weaned heifers. Further, despite evidence of short-term effects of social housing on social development, there is limited understanding of how early socialization may influence social behavior in older animals. Evidence suggests at least short-term benefits of pre-weaning social housing on behavior following post-weaning grouping, including reducing latency to begin feeding (de Paula Vieira, 2010) and increasing social behavior following grouping (Lindner et al., 2022; Duve and Jensen, 2012). Calves also establish preferences for familiar animals which may persist beyond the pre-weaning period (Rausi et al., 2010). These findings suggest that pre-weaning social housing may improve longer-term ability of heifers to integrate in social environments.

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 pre-weaning social housing on activity and social networks. We hypothesized that heifers that were housed individually during the pre-weaning 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, USA) 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 pre-weaning period is described in more depth by Lindner et al. (2022). In addition to methods described herein, these calves were exposed to novel object tests in the home pen and cognitive tests (at 9 weeks of age; unpublished data). Individually housed calves were reared in wire mesh pens (0.9 × 1.8 m; width x 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 × 2.2 m; width x depth). These housing treatments reflect 2 common approaches to rearing replacement dairy replacement heifers during the pre-weaning period (in Canada and the US; reviewed by Roche et al., 2023). 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 Nutri-
Post-weaning, at 8.8 ± 0.4 (mean ± SD) weeks of age, heifers were mingled between pre-weaning social housing treatments and moved in weekly cohorts of approximately 10 animals of the same age (born within 1 week) into an open pasture (15 × 45 m; ~67 m²/heifer). Pasture groups occasionally included non-study heifers born within the same week. Non-study calves had been individually housed for 2–3 weeks and then housed in small groups of 4 until weaning, according to standard farm operating procedure for heifer calves not enrolled in an experiment. 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) and the water trough was located halfway down the side fenceline. Heifers were provided ad libitum access to a pelleted starter ration (22% CP and 2% fat; Ampli-Calf Starter Warm Weather, Purina Animal Nutrition LLC, Shoreview, MN, USA), delivered at 0700 and 1700. Per farm management, heifers were moved to a new pasture pen of a similar layout (moving sequentially through adjacent pens as they aged) every 4–5 weeks, 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 ± 1.0 (mean ± SD) weeks 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. We did not perform a formal sample size calculation for this experiment, given a lack of previous data on expected effect sizes of longer-term effects of previous housing. While enrollment of specific numbers was somewhat constrained by farm management of animal movements, we aimed to double sample sizes from previous experiment revealing shorter-term effects of social housing on behavioral patterns, including feeding (i.e., 9–10 animals/housing treatment; Miller-Cushon and DeVries, 2016; De Paula Vieira et al., 2010). As animal movements before this observation period were subject to farm management, 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 balance of heifers from different former housing treatments in groups 1 and 2 specifically did not reflect original animal enrollment into different housing treatments (which was approximately alternating, as described above), and was likely due to some shuffling of animals by farm personnel during group movements. The observation week for each group was selected to coincide with heifers being present in a specific pasture pen, which had a vantage point which 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 one week 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 observation/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 with each group were observed (including the ‘non-study’ heifers in group 4). Individual heifers were identified based on unique coat patterns. The observer arrived to set up for observation 15 min before data collection began to allow animals to habituate to the observer’s presence, and remained outside the pen, using a chair located 4.5 m outside the observation pasture. This position provided a complete view of the pasture pen and binoculars were used as needed when animals were farthest away. Observations were completed over a period of 6 mo (April to October, 2022).

Using instantaneous scans at 10 min intervals (per previously validated observation methods; Mitloehner et al., 2001; Kitts et al., 2011) we characterized the following behaviors: feeding, defined as the heifer standing at the feedbunk 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. Proximity from other heifers (with identity of those heifers noted) was also characterized with every scan, with ‘social proximity’ defined when a heifer was ≤3 body lengths from another heifer, and ‘alone’ defined when the heifer was >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 duration of close proximity and total proximity (<3 body lengths) were highly correlated (R² = 0.8). Previously under naturalistic conditions, within 10 m has been considered voluntary social proximity (Wood-Gush et al., 1984) and while this may not reflect social choices in conventional confined housing, in the present experiment with observations conducted in a large pasture pen, heifers could easily choose greater social proximities than our selected threshold. 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 which were referenced by external reviewers to confirm correct behavioral categorization). Data were recorded directly on a hand-held tablet using a spreadsheet in Excel (Microsoft, Inc.). To control for effects of external environment on behavior, temperature data were collected on observations 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.

From observed social proximities, adjacency matrices were constructed from proximity data of heifers across the entire ob-
servation 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 to consider the effect of directing/undirecting the networks during analysis. We found behavioral synchrony with 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 1–4, respectively. Given this evidence of high reciprocity (vs. e.g., reciprocity 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 to consider the effect of directing/undirecting the networks during analysis. We found behavioral synchrony with 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 1–4, respectively. Given this evidence of high reciprocity (vs. e.g., reciprocity of grooming interactions in macaques with a maximum reciprocity of 0.35; McCowan et al., 2008) 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 (Csardi 2013) in R (R Development Core Team, Version 4.1.1). Strength centrality, or weighted degree centrality, measures the sum of weights assigned to the node’s direct connections and represents the node’s strength (e.g., strength centrality in the lying network refers to the total number of observations where the focal heifer is lying in proximity to any other heifer, weighted by the number of scans in proximity). 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, 2015; e.g., eigenvector centrality in the standing network reflects both the degree of proximity interactions where the focal heifer was standing in proximity to any other heifer, and the degree of their partner’s proximity interactions).

We first evaluated the structural similarity of the proximity based social networks for standing, lying, and feeding to explore whether the 3 networks show meaningful differences. Using the mantel test in the ‘vegan’ R package (Dixon, 2003), matrix correlations were run separately for each group with 1000 permutations to generate P-values. Second, to assess effects of previous housing treatment, data were analyzed using general linear mixed models (proc GLIMMIX in SAS). 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, calculated across the entire observation period) 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 significant interactions 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. For this analysis, we ran a multiple regression quadratic assignment (MRQAP-DSP) which 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 with a ‘1’ if they were previous pair housed penmates and all other dyads were labeled with a ‘0’. We generated separate tests for both groups with the feeding, standing, and lying social networks entered as the dependent variable and prior housing as the predictor variable. Tests were run with 10,000 permutations in the aspine R package (Farine, 2013).

Social networks are visualized for descriptive purposes 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 significant correlation between the feeding, lying, or standing proximity networks for group 2 (feeding/standing: \( r = 0.10, p(\text{perm}) = 0.21 \); feeding/lying: \( r = 0.14, p(\text{perm}) = 0.17 \); lying/standing: \( r = 0.08, p(\text{perm}) = 0.34 \)) or group 3 (feeding/standing: \( r = 0.06, p(\text{perm}) = 0.35 \); feeding/lying: \( r = -0.21, p(\text{perm}) = 0.85 \); lying/standing: \( r = -0.19, p(\text{perm}) = 0.76 \)). The results for the feeding and standing proximity networks in group one suggests a positive relationship (\( r = 0.30, p(\text{perm}) = 0.06 \)), however the other networks were not correlated (feeding/lying: \( r = -0.30, p(\text{perm}) = 0.92 \); lying/standing: \( r = -0.24, p(\text{perm}) = 0.85 \)). The feeding and lying proximity networks in group 4 were correlated (\( r = 0.37, p(\text{perm}) = 0.01 \)), while the other networks were not related (feeding/standing: \( r = 0.06, p(\text{perm}) = 0.32 \); lying/standing: \( r = 0.03, p(\text{perm}) = 0.39 \)).

Effect of pre-weaning social housing had minimal effects on social network centrality (Table 1). For the standing social network, previous social housing did not significantly affect eigenvector centrality 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, heifers previously raised in...
individual housing 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).

Effects of pre-weaning pair assignment were explored in groups 2 and 3, which each included 3–4 pairs of previous PH penmates. The results from MRQAP-DSP regression indicated that pre-weaning 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 ($R^2 = 0.07, P = 0.06$). These networks where pre-weaning pair assignment played a role in network structure are visualized in Figure 1C. We did not

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**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 (L to R: groups 1 to 4), and C) networks where pre-weaning pair assignment was a significant predictor of network structure (standing and lying for group 2, lying for group 3). Nodes (circles representing individual heifers) are colored to indicate previous pre-weaning housing treatment (red for IH, blue for 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.
find any significant relationships between pre-weaning pair assignment and the standing network for group 3 \( (R^2 = 0.01, P = 0.44) \), or with the feeding networks for either group \( (R^2 = 0.03, P = 0.21) \; \text{group 2}; \; R^2 = 0.01, P = 0.55) \; \text{group 3}.

We found some evidence to suggest that the percentage of time spent standing (Figure 2) varied between previous housing treatment depending on time of day (interaction between housing treatment and time of day; \( P = 0.064 \)), where previously pair-housed heifers were standing for a greater percentage of observations in the morning than previously individually housed heifers \( (P = 0.042) \). Percentage of lying time (Figure 2) did not differ significantly between previous housing treatments \( (P = 0.43) \) but was numerically greater in the morning \( (P = 0.07) \). The percentage of observations where animals were feeding (Figure 2) did not differ between previous housing treatments \( (P = 0.90) \) but was greater in the afternoon \( (P = 0.04) \). Our results suggested a weak association between temperature during the observation period (AM: 25.2 ± 2.7°C; PM: 29.6 ± 2.1°C; mean ± SD) and the number of observations where heifers were lying down \( (P = 0.079) \) but temperature was not related to 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 pre-weaning 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 pre-weaning social housing on behavior of group-housed calves after about 9 weeks in mixed groups on pasture. However, this depended on time of day, where previously pair-housed heifers were standing during a greater percentage of observations in the morning compared with previously individually housed heifers, but there was no difference between previous housing treatments in the afternoon. This interaction between previous housing treatment and time of day could be related to external cues related to farm management or due to greater temperatures in the afternoon which may have influenced motivation for shade use or rest. We found that lying, but not feeding, varied slightly with temperature during the observation window. While some previous findings suggest that higher temperatures lead to increased standing for evaporative cooling (Strong et al., 2015), we found that heifers spent numerically more time lying during hotter observation periods which, 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 affiliative behavior, such as sniffing and licking, is increased following regrouping in socially housed calves in the shorter-term (Duve and Jensen, 2012), as well as in calves raised with their dam (Wagner, 2012). 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, Lecors 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 pre-weaning social housing on feeding behavior after weaning, including increased feeding time (De Paula Vieira et al., 2010). Our results suggest that pre-weaning social housing did not have persistent effects on feeding time in the post-weaning 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 behavior at the feedbunk are evident only in more competitive feeding scenarios. Pre-weaning social housing has at least short-term benefits for competitive success (Duve et al., 2012) and our previous findings also suggest that competitive

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**Table 1.** Social network centrality measures for feeding, standing, and lying for 17.8 ± 1.0 (mean ± SD) week old heifers group housed on pasture. Heifers were previously raised individually \( (IH; n = 17) \) or in pairs \( (PH; n = 20) \) until \( (8.8 ± 0.4 \text{ weeks of age}; \text{mean ± SD}) \), at which point they were mixed between previous housing treatments and raised in groups \( (n = 4) \) on pasture.

<table>
<thead>
<tr>
<th>Centrality measures</th>
<th>Treatment IH</th>
<th>PH</th>
<th>SE</th>
<th>Treatment F1,29</th>
<th>P</th>
<th>Group F3,29</th>
<th>P</th>
<th>Treatment × Group F3,29</th>
<th>P</th>
</tr>
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<tbody>
<tr>
<td>Feeding Eigenvector</td>
<td>0.82</td>
<td>0.82</td>
<td>0.054</td>
<td>0.01</td>
<td>0.93</td>
<td>1.78</td>
<td>0.17</td>
<td>0.44</td>
<td>0.73</td>
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<tr>
<td>Feeding Strength</td>
<td>178.1</td>
<td>177.3</td>
<td>10.1</td>
<td>0.01</td>
<td>0.95</td>
<td>43.3</td>
<td>&lt;0.001</td>
<td>0.44</td>
<td>0.72</td>
</tr>
<tr>
<td>Standing Eigenvector</td>
<td>0.83</td>
<td>0.89</td>
<td>0.032</td>
<td>2.14</td>
<td>0.15</td>
<td>0.021</td>
<td>0.9</td>
<td>0.63</td>
<td>0.60</td>
</tr>
<tr>
<td>Standing Strength</td>
<td>478.7</td>
<td>515.2</td>
<td>20.1</td>
<td>2.14</td>
<td>0.15</td>
<td>5.04</td>
<td>0.006</td>
<td>0.62</td>
<td>0.61</td>
</tr>
<tr>
<td>Lying Eigenvector</td>
<td>0.93</td>
<td>0.91</td>
<td>0.019</td>
<td>1.01</td>
<td>0.32</td>
<td>2.18</td>
<td>0.11</td>
<td>3.13</td>
<td>0.041</td>
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<tr>
<td>Lying Strength</td>
<td>1197.3</td>
<td>1179.0</td>
<td>27.9</td>
<td>0.28</td>
<td>0.60</td>
<td>83.4</td>
<td>&lt;0.001</td>
<td>3.23</td>
<td>0.037</td>
</tr>
</tbody>
</table>

1Centrality measures: eigenvector (measure of influence from an individual calf on a group) and strength (weighted degree centrality; degree to which one calf is connected to other calves in a group), calculated from social networks constructed based on pairwise proximity (<3 body lengths) between heifers.
behavior acquired during the pre-weaning period may persist for months after weaning (Miller-Cushon et al., 2014).

We found that pre-weaning 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 pre-weaning social housing on proximity-based social networks of dairy calves for one month 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 post-weaning groups were mingled between previous housing treatment, such that findings of long-term effects of preweaning social housing may be conservative due to social influences from animals on the opposite housing treatment and a high degree of behavioral synchrony. In a practical setting-on-farm, consistent housing protocols would be applied across all preweaned calves and post-weaning groups would thus be formed of heifers all reared individually, potentially fostering different longer-term social dynamics. However, in a research setting, this experimental design is typically avoided as it limits the number of experimental replicates. It is also a limitation of the present study that the composition of each observation group varied in numbers of animals reared in different housing treatments, as we were subject to farm management decisions regarding heifer movements. To address this, we considered effects of group and interaction between previous housing treatment and group in our analysis. It is interesting to note that 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 our observed effects of pre-weaning social housing may be modulated by post-weaning experience. In the present study, heifers were exposed to dynamic social groups which and pasture movements, which can induce agonistic behavior and alter activity patterns (Raussi et al., 2005). In future work, it may be meaningful to measure effects of pre-weaning social housing in stable social groups, and at multiple time points to better characterize development of social behavior over time.

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 and focal behavior. We also found that social housing before weaning slightly increased standing time, dependent on time of day but had no effect on duration of lying or feeding. Overall, our results suggest that preweaning housing may have subtle effects on increasing social behavior that are somewhat resilient to social facilitation, but that present social context may have a greater influence on the behavioral expression of group-housed, weaned heifers.

References


**Notes**

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