



Social isolation of unfamiliar cattle by groups of familiar cattle

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ABSTRACT

Domestic herbivores show a strong motivation to form associations with conspecifics and the social dynamics of any group is dependant on the individuals within the group. Thus, common farm management practices such mixing may cause social disruption. Social integration of new group members has previously been defined as a lack of aggressive interactions within the group. However, a lack of aggression among group members may not represent full integration into the social group. Here we observe the impact of disrupting groups of cattle via the introduction of an unfamiliar individual, on the social network patterns of six groups of cattle. Cattle contacts between all individuals in a group were recorded before and after the introduction of the unfamiliar individual. Pre-introduction, resident cattle showed preferential associations with specific individuals in the group. Post-introduction, resident cattle reduced the strength of their contacts (e.g., frequency) with each other relative to the pre-introduction phase. Unfamiliar individuals were socially isolated from the group throughout the trial. The observed social contact patterns suggest that new group members are socially isolated from established groups longer than previously thought, and common farm mixing practices may have negative welfare consequences on introduced individuals.

1. Introduction

Domestic herbivores are gregarious animals that form social groups (Arnold and Pahl, 1974; Lazo, 1994; Reinhardt and Reinhardt, 1981). From an evolutionary perspective forming groups provide a number of functions including increased protection from predators and enhanced foraging efficiency (Krause and Ruxton, 2002). Group-living animals also show a strong motivation to form social associations and will work for access to conspecifics (Holm et al., 2002). Furthermore, social isolation can elicit stress responses such as increased locomotion, heart rate and plasma cortisol levels (Adeyemo and Heath, 1982; Boissy and Le Neindre, 1997). Herbivores have been shown to be capable of social discrimination (Hagen and Broom, 2003; Kendrick et al., 1996) and individuals are known to associate in a non-random way i.e. they show preferential associations for specific individuals (Færevik et al., 2007, 2006; Reinhardt and Reinhardt, 1981). Recently, the field of animal welfare has shifted focus from the prevention of negative welfare to the promotion of positive welfare, and affiliative behaviour is considered to be a promising indicator of positive affective states in farm animals (Boissy et al., 2007). Thus, a greater understanding of factors that lead to

affiliative behaviour and the impact of farm management practices on farm animal social dynamics has the potential to contribute to better farm animal welfare assessment.

In natural systems, group formation is a highly dynamic process where group size and composition can change frequently (Couzin and Laidre, 2009). In contrast, group composition of livestock herbivores is determined by farm management practices, and regrouping can lead to frequent changes in the social environment. The social structure and dynamics of a group is also dependant on the behavioural composition within that group (Croft et al., 2008). Thus, changes to the composition of individuals within a group may generate a disruption to the social group. The effects of social disruption in cattle groups has been studied via mixing of unfamiliar cattle and investigating the effects on aggressive behaviour and production traits e.g. weight gain and milk yield (Kondo and Hurnik, 1990; Nakanishi et al., 1991; Phillips and Rind, 2001). Following an introduction event, new animals have been defined as socially integrated when agonistic interactions between group members are predominantly non-physical, and the ratio of physical to non-physical interactions remains stable (Kondo and Hurnik, 1990). Under this definition, the effects of regrouping or the introduction of

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new individuals into a herd of cattle are restricted to a short period of 1–2 weeks (Boe and Faerevik, 2003). However, in gregarious animals such as cattle that are highly socially motivated, social integration based on a lack of aggressive interactions alone may not represent full integration into the group. Changes in the patterns of association between previously unfamiliar individuals may provide greater insight into the process of familiarisation between individuals and, consequently group stability. Furthermore, knowledge of the process of social integration in group-living animals will play an important role in applied management and welfare of group living captive animals. Additionally, a better understanding of social integration of unfamiliar animals may provide more insight into the disease implications associated with mixing new animals on farm.

The familiarisation period between dyadic pairs of unfamiliar cattle has shown a gradual reduction in the inter-individual distance after introduction, although there was no change in the pattern of close association over a 5-day period post introduction (Paton et al., 2010). The patterns of associations and the process of familiarisation following the introduction of unfamiliar individuals to groups of cattle have not previously been studied. However, the patterns of association might be expected to be more complex than those patterns observed in dyadic pairs. Furthermore, the impact of social disruption, via the introduction of unfamiliar individuals, on the resident individuals within the group is unknown. Thus, here we characterise the behaviour of groups of cattle before and after the introduction of an unfamiliar individual. Specifically, we test the hypotheses: 1) Social disruption, via the introduction of an unfamiliar individual will alter the contact behaviour between resident cattle relative to their previous behaviour 2) The unfamiliar introduced individual will show an increased pattern of associations with the established group members over time.

2. Materials and methods

2.1. Animals and experimental design

The experiment was conducted at Belmont Research Station (150° 13'E, 23° 8'S) in central Queensland, Australia on six 2-ha experimental field plots consisting of mainly perennial Rhodes grass (*Chloris gayana*). Each plot was separated by a 10 m buffer zone. The experimental timetable (a total of 18 days) was divided into three phases: Phase 1 (days 1–6), a pre-introduction period with six groups of five cattle forming resident groups; Phase 2a (days 7–12), a 6-day period post-introduction of one unfamiliar individual into each resident group forming six groups of six cattle; Phase 2b (days 13–18), a further 6-day period post-introduction of the one unfamiliar individual into each resident group. Previous studies indicated that the effects of regrouping are restricted to a short period of 1–2 weeks (Boe and Faerevik, 2003), thus it was expected that the two post introduction phases would capture a change in contact patterns due to the process of familiarisation between the resident and the unfamiliar individuals. Contact data (duration of contacts and total duration of contacts) was analysed on both a phase and daily basis. Both analyses showed similar patterns of behaviour post-introduction (the results of the daily analysis are available in the [Supplementary material](#)); thus, the social network analysis (node strength and eigenvector analysis) was conducted on a phase basis only.

Thirty 1 yr old female Brahman cattle (*Bos indicus*) were selected from a commercial cattle herd that had been reared together since birth and divided into six groups of five animals ensuring the mean live weight of the animals within each group were the same (live mean weight 361.6 ± 4.34 kg [mean \pm SE]). These formed the 'resident group' individuals. Six 1 yr old female Brahman cattle (*B. indicus*) (live mean weight 376.0 ± 6.63 kg [mean \pm SE]) were sourced from a separate commercial herd. These formed the 'unfamiliar' individuals. Each unfamiliar individual was allocated to a resident group, ensuring that the mean live weight of the animals within each group were the

same.

2.2. Contact behaviour

Cattle contacts between all individuals in all groups were continuously recorded using proximity data loggers (Sirtrack Ltd., Havelock North, New Zealand). Inter-logger variation which may affect the resultant social contact networks has been associated with proximity loggers (Boylund et al., 2013; Drewe et al., 2012), however in order to minimize this inter-logger variability a replicated experimental design and manipulation of reciprocal contact data was employed. Each of the resident group individuals and the unfamiliar individuals were fitted with a proximity data logger on a neck collar to record close proximity with any other individuals in their group. The proximity loggers use an ultra high frequency (UHF) transceiver that transmits a unique code, while receiving code signals from other loggers. Individual cattle length can be up to 1.6 m. Cows will often camp together when resting, with some individuals in the camping group lying rear-to rear. Thus, the detection distance of the proximity logger was set to 4 m, allowing detection of close proximity and all body-to-body contact between individual cattle, including rear-to rear contacts. Once another data logger is detected, a contact continues until the receiving logger fails to detect the signal within the specified 'separation time', which was set to 30 s. Thus, two contact events less than 30 s apart, would be recorded as a single contact. Two contacts greater than 30 s apart would be recorded as two separate contacts. If two cattle came into contact with each other (i.e. two proximity loggers were within range of each other), the time, date and duration of the contact were recorded by the proximity logger.

In order to discard contact data that occurred while collars were being placed on the cattle, all data prior to animals being placed in their plots were deleted. Additionally, all contacts of 1 s or less were deleted as these may represent weak collar signals e.g. inter-logger variability (Drewe et al., 2012) or detection of collars at the edge of the detection range (Prange et al., 2006). Under field conditions, reciprocal contact data from two different collars are not completely symmetrical due to reflection, refraction and absorption of radio waves by environmental features (e.g. vegetation, terrain, etc.) (Paton et al., 2010; Swain and Bishop-Hurley, 2007). To account for this, contact duration was defined as starting when either logger recorded a contact and then ending when either logger failed to maintain contact (Hamede et al., 2009; Patison et al., 2010).

Social network analysis was carried out on the contacts using UCINET software (Borgatti et al., 2002). As all individuals within the groups contacted each other, weighted network metrics were calculated. A weighted network is one which not only gives the binary presence or absence of a contact between individuals, but also assigns a value to the contacts between individuals. The frequency of contacts between individuals were used to produce weighted symmetrical adjacency matrices (e.g., using valued reciprocal data) to calculate node strength and eigenvector centrality. The node strength is a function of the number of connections an individual has and the sum of their weights. This metric was chosen to give an indication of gregariousness or prominence within the network e.g., an individual with a high strength is more gregarious than an individual with a low strength. Eigenvector centrality was chosen to give a measure of influence or importance of individuals within the group. Eigenvector centrality considers who each individual is connected to e.g. an individual with high eigenvector centrality is connected to individuals that are themselves well connected (Borgatti et al., 2013). Both the node strength and eigenvector centrality were calculated for each individual animal using the frequency of contacts between resident individuals only in all phases of the experiment (1, 2a and 2b), and using the frequency of contacts between all individuals after the introduction of the unfamiliar individual (Phase 2a and 2b). Contact duration is also an important variable in measuring the overall social behaviour, as individuals may have the same frequency of contacts but different durations of those contacts. Thus, contact duration

was also considered to provide a fuller picture of the contact behaviour. In order to determine the impact of the introduction of the unfamiliar individual on the contact duration between individual animals over the whole study, weighted symmetrical adjacency matrices were produced and social network diagrams were visualised using NetDraw (Borgatti et al., 2002).

2.3. Statistical analysis

Associations between phase effects (Phase 1, 2a and 2b) and animal type effects (resident or unfamiliar) on cattle contact behaviour (mean duration of contacts per cow per day; total duration of contacts per cow per day; node strength; eigenvector centrality) were analysed in a general linear mixed model using two different sets of REML models analysing 4 variables. REML set 1 assessed the effect of social perturbation via the introduction of an unfamiliar individual on the residents, and thus used the contact data between resident individuals only in all three phases of the trial. Phase was included as a fixed effect. Group, an interaction between group and phase and animal nested within group were included as random effects. A Tukey's honest significant difference test was applied post-hoc for significant models in order to determine where the differences lie. REML set 2 assessed the effect of animal type on contact behaviour and used data from both resident and unfamiliar individuals from Phase 2a and 2b only (e.g. after the introduction of the unfamiliar individual). Animal type, phase (2a or 2b only) and their interactions were included as fixed effects. Group, an interaction between group and phase and animal nested within group were included as random effects. The Wald test from the REML model was used to determine significant differences, with the Wald statistic (W) presented with the relevant degrees of freedom and probability value for the fixed effects of the REML model. Models for mean duration of contact and total duration of contact are not independent of one another. Similarly, models for node strength and eigenvector centrality (which are both calculated from the frequency of contacts) are not independent of one another. To account for this, we adjust the p -values to account for the false discovery rate so that the overall rate of rejection of the null hypothesis, where it to be true, is correctly set at 5% (Benjamini and Hochberg, 1995).

To assess the consistency of the contact behaviour of resident individuals in each group across the three phases (1, 2a and 2b) a repeatability estimate (R) for node strength and eigenvector centrality was calculated. Repeatability gives an indication of the proportion of variation among individuals that is due to differences between individuals (Boake, 1989). The variance components (i.e. between individual variance and the within individual variance) obtained from a REML analysis, using phase nested in animal ID as random effects was used to estimate repeatability ($R = \text{variance between individuals} / (\text{variance between individuals} + \text{variance within individuals})$) (Lessells and Boag, 1987). Repeatability estimates range from 0 to 1, with estimates close to 0 indicating, in our data, that the contact behaviour of individuals changes during each phase. Repeatability estimated close to 1 would indicate that contact behaviour was highly repeatable, with most of the variation occurring between cows rather than within cows.

Mean duration of contacts, total duration of contacts and node strength were normalised using logarithmic transformation before analysis. The data for eigenvector centrality (proportional data) were arcsine transformed before being analysed (Zar, 1984). Back-transformed means are presented with upper and lower 95% confidence limits. All statistical analysis was performed in GenStat (fifteenth edition, VSN International Ltd, Hertfordshire, UK) and differences were considered statistically significant if the p -value was less than 0.05 (5%).

3. Results

3.1. Contact behaviour between resident individuals

The observed cattle contact networks for all phases indicate that all resident individuals were directly connected to all other resident individuals in the group (Fig. 1). The proximity contact behaviour of the resident groups differed between the 3 phases of the experiment (Table 1). There was a reduction in node strength for contacts between resident individuals in the post-introduction phases relative to phase 1 (i.e., 1 vs 2a and 2b) ($W = 15.72$, $df = 2$, $P = 0.02$). However, the eigenvector centrality ($W = 3.34$, $df = 2$, $P = 0.24$), the mean duration of contacts per cow per day ($W = 9.18$, $df = 2$, $P = 0.08$), and the total duration of contacts per cow per day ($W = 2.17$, $df = 2$, $P = 0.38$), between resident individuals remained the same throughout the experiment (Table 1). The within cow repeatability estimate for node strength and eigenvector centrality was 0.73 (high repeatability) and 0.48 (moderate repeatability), respectively.

3.2. Contact behaviour between the unfamiliar and resident animals

Fig. 1 illustrates that all resident individuals in all groups contacted the unfamiliar individual in both Phase 2a and 2b. However, the observed contact behaviour of the two animal types differed (Table 2). Unfamiliar individuals had shorter mean duration of contacts per cow per day ($W = 62.10$, $df = 1$, $P < 0.001$), shorter total duration of contacts per cow per day ($W = 74.05$, $df = 1$, $P < 0.001$), lower values for node strength ($W = 56.78$, $df = 1$, $P < 0.001$), and lower values for eigenvector centrality ($W = 17.26$, $df = 1$, $P < 0.001$) relative to resident individuals.

Within the overall network (familiar and unfamiliar animals together over phase 2a and 2b) the mean duration of contacts per cow per day ($W = 2.84$, $df = 1$, $P = 0.15$), the total duration of contacts per cow per day ($W = 5.27$, $df = 1$, $P = 0.14$), the node strength ($W = 0.49$, $df = 1$, $P = 0.98$), or the eigenvector centrality ($W = 0.00$, $df = 1$, $P = 0.98$) did not change throughout period 2 of the experiment. No animal type by phase interactions were evident for the mean duration of contacts per cow per day ($W = 0.02$, $df = 1$, $P = 0.88$), the total duration of contacts per cow per day ($W = 1.12$, $df = 1$, $P = 0.88$), the node strength ($W = 0.45$, $df = 1$, $P = 0.51$), or the eigenvector centrality ($W = 1.17$, $df = 1$, $P = 0.51$) (Table 2).

4. Discussion

The experimental design of this study is representative of standard farm practices. For example, Phase 1 in which resident animals are placed into new groups represents regular re-grouping of the herd, whilst Phase 2 represents the introduction of new unfamiliar individuals brought onto the farm. The introduction of an unfamiliar individual into a group of individuals that were reared together and were socially familiar, was associated with changes in the contact network structure of the resident cattle. After the introduction of the unfamiliar individual, resident individuals maintained the total duration of time spent together each day. However, the introduction of the unfamiliar animal was associated with a reduction in node strength (e.g., the frequency of the interactions). This is a subtle but consistent change in behaviour of the resident individuals following the introduction of the unfamiliar individual and demonstrates a disruption in social behaviour between familiar individuals. This was also accompanied by a tendency for an increase in the average duration of the mean contact duration in Phase 2a suggesting individuals may be spending increased time with familiar individuals when the unfamiliar animal is first introduced to the group, although this is not statistically significant. The eigenvector centrality measure remained constant throughout the experiment. As a measure of how well connected individuals are within a group (Borgatti et al., 2013), the lack of change in the eigenvector centrality suggests that

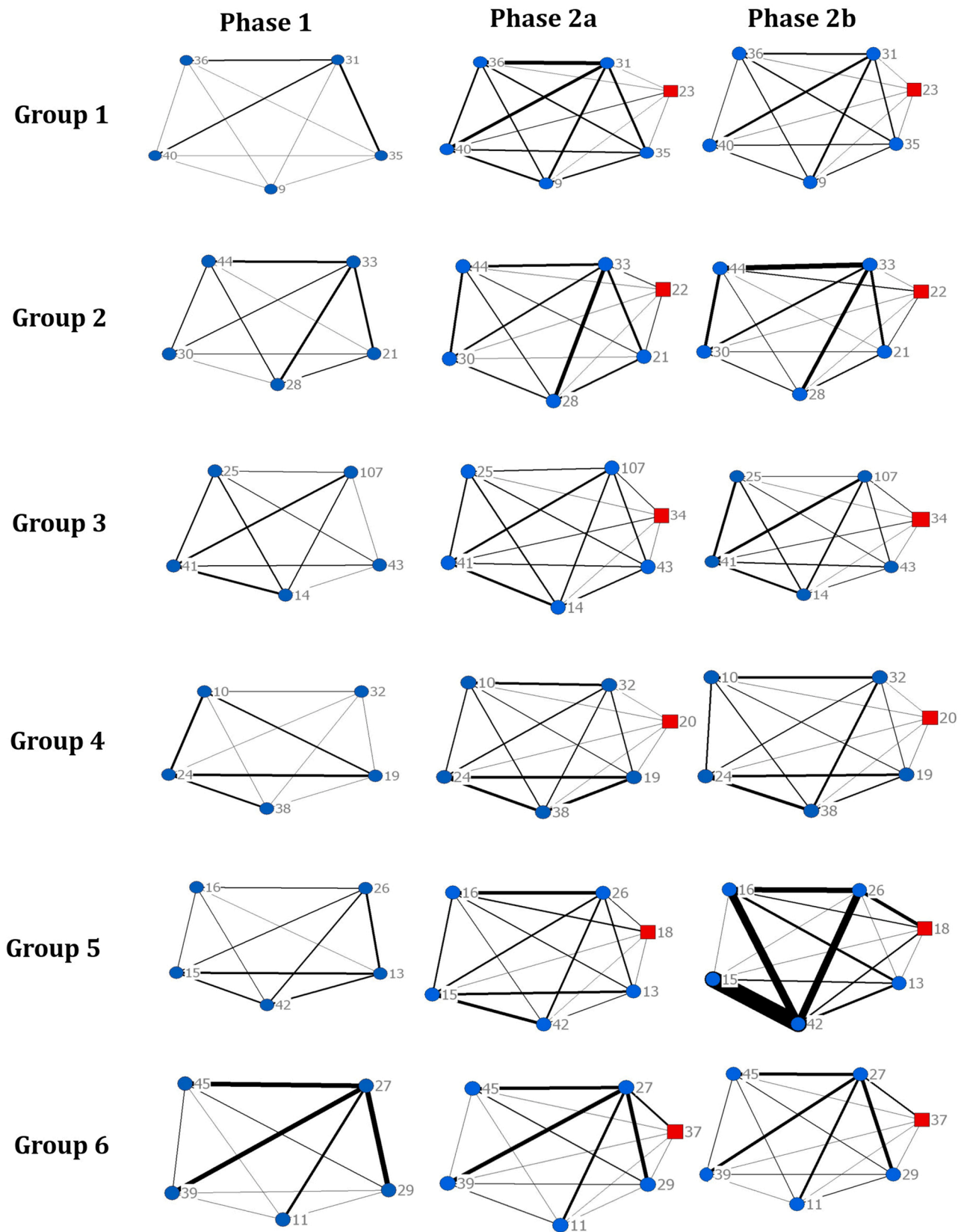


Fig. 1. : Social network graphs of each group of cattle (groups 1–6) for each phase of the study. Phase 1 = Days 1–6 of the study, a period of social stability (pre introduction of unfamiliar individual); Phase 2a = Days 7–12 of the study (a 6-day period post-introduction of unfamiliar individual); Phase 2b = days 13–18 of the study (a further 6-day period post-introduction of an unfamiliar individual). Circles represent individual ‘resident’ cattle, squares represent individual ‘unfamiliar’ cattle. Line thickness represents the strength of association between two individuals based on total duration spent in contact per phase.

Table 1

Contact behaviour between resident individuals. Phase 1 = Days 1–6 of the study, a period of social stability (pre introduction of unfamiliar individual); Phase 2a = Days 7–12 of the study (a 6-day period post-introduction of unfamiliar individual); Phase 2b = days 13–18 of the study (a further 6-day period post-introduction of an unfamiliar individual). Values given are backtransformed predicted means from the fitted model (with their associated upper and lower 95% confidence limits). NS = $P > 0.05$, * $P < 0.05$, ** $P < 0.01$. The results of the Tukey honest significant difference test are denoted by superscript letters where identical letters indicate groups which are not statistically significantly different at the 5% level.

| Phase | 1 | 2a | 2b | Mean | Phase Effect |
|--|--|--|---|---------|--------------|
| duration of contacts per cow per day (sec) | 53.5 (40.5–70.5) | 73.1 (55.5–96.3) | 68.2 (51.7–89.8) | 64.9 | NS |
| total duration of contacts per cow per day (sec) | 19229.9 (11371.5–32518.5) | 18534.3 (10960.1–31342.2) | 15558.7 (9200.4–26310.4) | 17774.3 | NS |
| node strength per cow per phase | 2460.4 ^a (1588.1–3811.7) | 1766.0 ^b (1139.9–2736.0) | 1671.1 ^b (1078.65–2588.9) | 1965.8 | ** |
| eigenvector centrality per cow per phase | 0.4 (0.4–0.5) | 0.4 (0.4–0.5) | 0.4 (0.4–0.5) | 0.4 | NS |

Table 2

Contact behaviour between cattle after the introduction of an unfamiliar individual. Phase 2a = Days 7–12 of the study (a 6-day period post-introduction of unfamiliar individual); Phase 2b = days 13–18 of the study (a further 6-day period post-introduction of an unfamiliar individual). Values given are backtransformed predicted means from the fitted model (with their associated upper and lower 95% confidence limits). NS = $P > 0.05$, ** $P < 0.01$, *** $P < 0.001$.

| Animal Type | Resident | | Unfamiliar | | Effects | | | |
|--|------------------------------|-----------------------------|---------------------------|---------------------------|---------|-------------|-------|----------------|
| Phase | 2a | 2b | 2a | 2b | Mean | Animal type | Phase | Animal x Phase |
| duration of contacts per cow per day (sec) | 71.6 (56.2–91.1) | 67.1 (52.7–85.3) | 43.4 (34.0–55.3) | 40.2 (31.5–51.3) | 55.6 | *** | NS | NS |
| total duration of contacts per cow per day (sec) | 19452.6 (10803.7–35024.8) | 16671.5 (9259.0–30017.4) | 2916.4 (1619.4–5251.8) | 2850.0 (1582.5–5132.2) | 10472.6 | *** | NS | NS |
| node strength per cow per phase | 1766.0 (1067.7–2921.1) | 1671.1 (1010.3–2764.0) | 511.7 (309.4–846.3) | 522.4 (315.8–864.1) | 1117.8 | *** | NS | NS |
| eigenvector centrality per cow per phase | 0.4 (0.4–0.5) | 0.4 (0.4–0.5) | 0.2 (0.2–0.2) | 0.2 (0.2–0.3) | 0.3 | *** | NS | NS |

although the overall frequency of interactions in the group change, the pattern of connectiveness between resident individuals remains stable over time.

The repeatability estimate for the network measures of resident individuals indicate that there is a high repeatability for node strength and a moderate repeatability for eigenvector centrality over the three phases. Thus, although there is disruption in the group due to the introduction of an unfamiliar individual, the variation within individuals was less than that between individuals i.e., those individuals who had fewer contacts in Phase 1, also had fewer contacts after the introduction of the unfamiliar individual. The lower repeatability of the centrality measure could suggest that individual patterns of connectiveness are more random (individuals change their centrality) than the patterns of node strength over all three phases.

It was expected that the post-introduction period would capture a process of familiarisation between the resident and the unfamiliar individuals. However, the unfamiliar animals had a lower frequency of contacts, mean duration of contacts and total duration of contacts than the resident individuals in both phase 2a and 2b. The social network metrics are also consistent with shunning, with unfamiliar individuals having lower mean values for node strength and eigenvector centrality for both Phase 2a and 2b indicating that the unfamiliar individual is on the periphery of the group and is still not incorporated into the group at the end of the trial. Furthermore, there was no change in any of the contact metrics with the unfamiliar animal between the two post-introduction phases. This suggests that unfamiliar animals introduced to groups of familiar animals are socially isolated and for longer than previously thought. Thus, there are welfare implications associated with the potentially increased social stress experienced by the shunned individual. However, this study does not give an indication of likely timeframes for social inclusion and therefore the full period of social isolation experienced by the unfamiliar individual. Further work investigating longer post-introduction periods is required to gain a greater understanding on the familiarisation period for unfamiliar

individuals entering pre-existing groups.

The network graphs illustrate that before the introduction of the unfamiliar individual, all resident individuals contact each other. However, resident individuals also display thicker lines between certain individuals indicating that they spent longer durations of time with those individuals and that they may be showing preferential associations. This is consistent with previous studies which found that cattle associate preferentially with specific individuals (Færevik et al., 2007, 2006; Reinhardt and Reinhardt, 1981). The network graphs also illustrate that all resident individuals contact the unfamiliar individual in both post-introduction phases. However, the line thickness between resident individuals is up to 6.5 times greater than the line thickness between the unfamiliar individual and the resident individuals. Previously, preferential associations within groups of animals have been linked to phenotypic characteristics such as species, breed and sex (Alves et al., 2013; Guilhem et al., 2000; Krause et al., 2000). However, in this study phenotypic characteristics have been controlled for, emphasizing the importance of familiarity between individuals when forming preferential associations. In this study the resident individuals were regrouped into smaller groups at the beginning of Phase 1 and any preferential relationships between individuals prior to Phase 1 were unknown. Thus, there is the potential for previous relationships between individuals in the groups to increase the variability in social behaviour between groups. However, all resident individuals displayed immediate and strong connections with other residents in their group, which is in complete contrast to the connections with the unfamiliar individual which was introduced in Phase 2. The use of six social group replicates showed the consistency of the strong shunning behaviour but also the more subtle changes in the behaviour of the resident animals following the introduction of the unfamiliar.

Given the increased stress responses associated with social isolation in cattle (Adeyemo and Heath, 1982; Boissy and Le Neindre, 1997), this study suggests that common farm mixing practices may have negative welfare consequences on introduced individuals. Furthermore, animal

contact patterns, rather than overall levels of aggression may provide a better measure of social integration in farm animals. In conclusion, the observed contact patterns suggest that new group members are socially isolated from established groups for extended periods of time.

CRedit authorship contribution statement

Lesley Smith: Conceptualization, Methodology, Investigation, Formal analysis, Visualisation, Writing – original draft, Writing – review & editing. **Dave Swain:** Conceptualization, Methodology, Writing – review & editing. **Giles Innocent:** Formal analysis, Writing – review & editing. **Michael Hutchings:** Conceptualization, Methodology, Writing – review & editing.

Conflicts of interest

None.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.beproc.2023.104847](https://doi.org/10.1016/j.beproc.2023.104847).

References

- Adeyemo, O., Heath, E., 1982. Social behaviour and adrenal cortical activity in heifers. *Appl. Anim. Ethol.* 8, 99–108. [https://doi.org/10.1016/0304-3762\(82\)90135-3](https://doi.org/10.1016/0304-3762(82)90135-3).
- Alves, J., Alves da Silva, A., Soares, A.M.V.M., Fonseca, C., 2013. Sexual segregation in red deer: is social behaviour more important than habitat preferences? *Anim. Behav.* 85, 501–509. <https://doi.org/10.1016/j.anbehav.2012.12.018>.
- Arnold, G., Pahl, P.J., 1974. Some Aspects of social behaviour in domestic sheep. *Anim. Behav.* 22, 592–600. [https://doi.org/10.1016/S0003-3472\(74\)80004-7](https://doi.org/10.1016/S0003-3472(74)80004-7).
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stats. Soc. Ser. B Methodol.* 57, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>.
- Boake, C., 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evol. Ecol.* 3, 173–182. <https://doi.org/10.1007/BF02270919>.
- Boe, K., Faerevik, G., 2003. Grouping and social preferences in calves, heifers and cows. *Appl. Anim. Behav. Sci.* 80, 175–190. [https://doi.org/10.1016/S0168-1591\(02\)00217-4](https://doi.org/10.1016/S0168-1591(02)00217-4).
- Boissy, A., Le Neindre, P., 1997. Behavioral, cardiac and cortisol responses to brief peer separation and reunion in cattle. *Physiol. Behav.* 61, 693–699. [https://doi.org/10.1016/S0031-9384\(96\)00521-5](https://doi.org/10.1016/S0031-9384(96)00521-5).
- Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., Aubert, A., 2007. Assessment of positive emotions in animals to improve their welfare. *Physiol. Behav.* 92, 375–397. <https://doi.org/10.1016/j.physbeh.2007.02.003>.
- Borgatti, S., Everett, M., Freeman, L., 2002. UCINET for Windows: Software for Social Network Analysis. Analytical Technologies, Harvard, MA.
- Borgatti, S., Everett, M., Johnson, J., 2013. *Analyzing Social Networks*. SAGE, London, UK.
- Boylard, N.K., James, R., Mlynski, D.T., Madden, J.R., Croft, D.P., 2013. Spatial proximity loggers for recording animal social networks: consequences of inter-logger variation in performance. *Behav. Ecol. Sociobiol.* 67, 1877–1890. <https://doi.org/10.1007/s00265-013-1622-6>.
- Couzin, I.D., Laidre, M.E., 2009. Fission – fusion populations. *Curr. Biol.* 19, R633–R635. <https://doi.org/10.1016/j.cub.2009.05.034>.
- Croft, D., James, R., Krause, J., 2008. *Exploring Animal Social Networks*. Princeton University Press, Woodstock, UK.
- Drewe, J.A., Weber, N., Carter, S.P., Bearhop, S., Harrison, X.A., Dall, S.R.X., McDonald, R.A., Delahay, R.J., 2012. Performance of proximity loggers in recording intra- and inter-species interactions: a laboratory and field-based validation study. *PLoS One* 7, e39068. <https://doi.org/10.1371/journal.pone.0039068>.
- Faerevik, G., Jensen, M.B., Bøe, K.E., 2006. Dairy calves social preferences and the significance of a companion animal during separation from the group. *Appl. Anim. Behav. Sci.* 99, 205–221. <https://doi.org/10.1016/j.applanim.2005.10.012>.
- Faerevik, G., Andersen, I.L., Jensen, M.B., Bøe, K.E., 2007. Increased group size reduces conflicts and strengthens the preference for familiar group mates after regrouping of weaned dairy calves (*Bos taurus*). *Appl. Anim. Behav. Sci.* 108, 215–228. <https://doi.org/10.1016/j.applanim.2007.01.010>.
- Guilhem, C., Bideau, E., Gerard, J., Maublanc, M., 2000. Agonistic and proximity patterns in enclosed mouflon (*Ovis gmelini*) ewes in relation to age, reproductive status and kinship. *Behav. Process.* 50, 101–112. [https://doi.org/10.1016/S0376-6357\(00\)00094-2](https://doi.org/10.1016/S0376-6357(00)00094-2).
- Hagen, K., Broom, D.M., 2003. Cattle discriminate between individual familiar herd members in a learning experiment. *Appl. Anim. Behav. Sci.* 82, 13–28. [https://doi.org/10.1016/S0168-1591\(03\)00053-4](https://doi.org/10.1016/S0168-1591(03)00053-4).
- Hamede, R.K., Bashford, J., McCallum, H., Jones, M., 2009. Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecol. Lett.* 12, 1147–1157. <https://doi.org/10.1111/j.1461-0248.2009.01370.x>.
- Holm, L., Jensen, M.B., Jeppesen, L.L., 2002. Calves' motivation for access to two different types of social contact measured by operant conditioning. *Appl. Anim. Behav. Sci.* 79, 175–194. [https://doi.org/10.1016/S0168-1591\(02\)00137-5](https://doi.org/10.1016/S0168-1591(02)00137-5).
- Kendrick, K.M., Atkins, K., Hinton, M.R., Heavens, P., Keverne, B., 1996. Are faces special for sheep? Evidence from facial and object discrimination learning tests showing effects of inversion and social familiarity. *Behav. Process.* 38, 19–35. [https://doi.org/10.1016/0376-6357\(96\)00006-X](https://doi.org/10.1016/0376-6357(96)00006-X).
- Kondo, S., Hurnik, J.F., 1990. Stabilization of social hierarchy in dairy cows. *Appl. Anim. Behav. Sci.* 27, 287–297. [https://doi.org/10.1016/0168-1591\(90\)90125-W](https://doi.org/10.1016/0168-1591(90)90125-W).
- Krause, J., Ruxton, D., 2002. *Living in Groups*. Oxford University Press, New York.
- Krause, J., Butlin, R.K., Peuhkuri, N., Pritchard, V.L., 2000. The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. *Biol. Rev. Camb. Philos. Soc.* 75, 477–501. <https://doi.org/10.1111/j.1469-185X.2000.tb00052.x>.
- Lazo, A., 1994. Social segregation and the maintenance of social stability in a feral cattle population. *Anim. Behav.* 48, 1133–1141. <https://doi.org/10.1006/anbe.1994.1346>.
- Lessells, C.M., Boag, P.T., 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104, 116–121. <https://doi.org/10.2307/4087240>.
- Nakanishi, Y., Mutoh, Y., Raizaburo, U., Masuda, Y., Goto, I., 1991. Changes in social and spacing behaviour of Japanese black cattle after introducing a strange cow into a stable herd. *J. Fac. Agric. Kyushu Univ.* 36, 1–11.
- Patison, K.P., Swain, D.L., Bishop-Hurley, G.J., Robins, G., Pattison, P., Reid, D.J., 2010. Changes in temporal and spatial associations between pairs of cattle during the process of familiarisation. *Appl. Anim. Behav. Sci.* 128, 10–17. <https://doi.org/10.1016/j.applanim.2010.10.001>.
- Phillips, C.J., Rind, M.I., 2001. The effects on production and behavior of mixing uniparous and multiparous cows. *J. Dairy Sci.* 84, 2424–2429. [https://doi.org/10.3168/jds.S0022-0302\(01\)74692-9](https://doi.org/10.3168/jds.S0022-0302(01)74692-9).
- Prange, S., Jordan, T., Hunter, C., Gehrt, S.D., 2006. New Radiocollars for the detection of proximity among individuals. *Wildl. Soc. Bull.* 34, 1333–1344. [https://doi.org/10.2193/0091-7648\(2006\)34\[1333:NRFTDO\]2.0.CO](https://doi.org/10.2193/0091-7648(2006)34[1333:NRFTDO]2.0.CO).
- Reinhardt, V., Reinhardt, A., 1981. Cohesive relationships in a cattle herd (*Bos indicus*). *Behaviour* 77, 121–150. <https://doi.org/10.1163/156853981x00194>.
- Swain, D.L., Bishop-Hurley, G.J., 2007. Using contact logging devices to explore animal affiliations: quantifying cow–calf interactions. *Appl. Anim. Behav. Sci.* 102, 1–11. <https://doi.org/10.1016/j.applanim.2006.03.008>.
- Zar, J., 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.