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Research Article

The role of relatedness, age, and origin in shaping social networks for two bison (*Bison bison*) herds in north-central Montana

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Abstract

Species with fission–fusion social organization, where groups break apart and merge over time, show variable subgroup stability. Plains bison (*Bison bison bison* (Linnaeus, 1758)), a keystone species in North American grasslands, exhibit fission–fusion dynamics. However, it is unclear whether subgroups are stable over time nor whether they are composed of related individuals. We used fine-scale behavioral observations and movement data from GPS ear tags to construct social networks for two plains bison herds over multiple years at American Prairie in north-central Montana. These herds are semi-free roaming and graze year-round in 32.4 and 111.6 km^2 fenced pastures. While the bison in our study did exhibit fission–fusion behavior, we did not observe stable subgroups in time-aggregated social networks constructed over single growing seasons (eigenvector modularity ranged from −0.008 to 0.027). We used Mantel tests to assess the relationships between association strength and relatedness, age, and place of origin. We found that only first-order relatives were more likely to associate, and shared age and place of origin had no significant impact. The observed lack of stable subgroups challenges prevailing assumptions and highlights the need for future research into the mechanisms of fission–fusion dynamics in plains bison and other managed social species.

Key words: *Bison bison bison* (Linnaeus, 1758), bison, social network analysis, collective movement, fission–fusion

Introduction

Social structure is one of the most plastic traits of group-living species (Hasenjager and Dugatkin 2015; Orozco et al. 2021). Living in groups confers many benefits to social species, including protection from predators (Creel et al. 2014), increased mate choice (Jennions and Petrie 1997), and information sharing (Lister 2014). However, there is a trade-off between these benefits and the increasing cost of competition for resources and the rate of disease transmission as group size increases (Ward and Webster 2016).

In many social species, group membership is highly stable at all time scales, but some species display a flexible social organization where individuals or subgroups merge and break apart repeatedly over time, referred to as fission–fusion (Kummer 1967). These frequent, short-term changes in group size and composition often occur in response to fluctuating social and environmental conditions (Chapman 1990; Sueur et al. 2011*a*). In species displaying fission–fusion, the composition of subgroups can be fixed, with the same individuals consistently associating or more flexible with individuals shifting between subgroups (Aureli et al. 2008; Ward and Webster 2016). The mechanisms behind associations may be more complex and difficult to ascertain for taxa with highly dynamic fission–fusion social groups than for those with more stable group structures and well-defined subgroups (Cross et al. 2005).

Many social ungulate species display fission–fusion behavior. Some taxa, such as plains zebra (*Equus quagga* Boddaert, 1785) (Rubenstein and Hack 2004), form multilevel societies with nested hierarchical tiers, wherein individuals belong to basic social units (nuclear family groups) that are part of larger, higher tiers within the overall structure (Grueter et al. 2020). Other species, such as reindeer (*Rangifer tarandus* (Linnaeus, 1758)) (Hirotani 1990), woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) (Lesmerises et al. 2018), and pronghorn (*Antilocapra americana* (Ord, 1815)) (White et al. 2012), have less stable subgroups and fewer long-term associations between individuals. Given that ungulates have some of the most diverse social systems among mammals, it is not surprising that the factors that influence associations between individuals vary widely (Szemán et al. 2021). Despite this variation, groups are often composed of close relatives regardless of the ecological mechanism that promotes group formation. Long-term associations based on relatedness have been observed in many ungulates including white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) (Magle et al. 2013), wild boar (*Sus scrofa* Linnaeus, 1758) (Podgórski et al. 2014), bushbuck (*Tragelaphus scriptus* (Pallas, 1766)) (Wronski and Apio 2006), giraffe (*Giraffa camelopardalis* (Linnaeus, 1758)) (Bercovitch and Berry 2013; Carter et al. 2013*b*), and domestic sheep (*Ovis aries* Linnaeus, 1758) (Nituch et al. 2008). Associations can also be impacted by shared age (Carter et al. 2013*a*; Brambilla et al. 2022), sex (Mejía-Salazar et al. 2017), and nutritional needs (Lesmerises et al. 2018).

Plains bison (*Bison bison bison* (Linnaeus, 1758)), a subspecies of the American bison (*Bison bison* (Linnaeus, 1758)), are known to exhibit fission–fusion dynamics (Daniel et al. 2009; Merkle et al. 2015; Sigaud et al. 2017). Despite the common assertion that plains bison exhibit stable subgroups based on relatedness, the empirical evidence has been mixed, inconclusive, or based on small herds (Soper 1941; Mchugh 1958; Fuller 1960; Meagher 1973; Lott and Minta 1983). Support for this idea largely comes from studies that found support for mother–offspring bonds continuing post-weaning (Green et al. 1989; Brookshier and Fairbanks 2011). On the other hand, Lott and Minta (1983) and Van Vuren (1983) found that plains bison associated randomly and did not form stable subgroups. However, the first study only involved 16 adult females and eight calves, while the latter included six known adult females. Lott and Galland later found that group stability increased with higher forage quality. Plains bison in Prince Albert National Park were more likely to follow a group with whom they were familiar (Merkle et al. 2015), providing evidence for non-random associations. King et al. (2019) found that a plains bison herd of 53 individuals displayed a linear dominance hierarchy that was stable over a 6-month period. Associations among European bison (*Bison bonasus* (Linnaeus, 1758)) females are largely based on matrilineal relatedness (Ramos et al. 2019). Despite existing literature on bison social dynamics, it remains unclear whether subgroups are stable over time, and if so, whether group membership is dependent on relatedness.

Plains bison are a keystone species in North America's grasslands and once occurred in the tens of millions across the continent until they were brought to the brink of extinction in the beginning of the 19th century (Knapp et al. 1999; McMillan et al. 2019). In recent decades, there have been increasing efforts to restore American bison to public, private, and tribal land across North America to improve ecosystem health, spur cultural revitalization, and restore foodways (Shamon et al. 2022*a*, 2022*b*). While reintroduction efforts aim to fully realize the ecological roles of plains bison, there are gaps in our understanding of how modern management may affect the social organization and collective behavior of these animals, potentially impacting conservation outcomes (Maldonado-Chaparro et al. 2021; Ramos et al. 2021). Research on the mechanism of plains bison social organization has often been limited to small groups in controlled settings, making it challenging to draw conclusions that can inform metapopulation management decisions. More broadly, our results are relevant for restoration efforts of social species that involve translocations or manipulation of group size and composition.

Here, we utilized direct observation, genetic information, and GPS tracking devices on plains bison in two semi-free roaming herds in north-central Montana to test the hypothesis that plains bison form stable subgroups composed of related individuals. We assessed the stability of subgroups and explored the impact of relatedness, age, and place of origin on association patterns by employing social network analysis and Mantel tests. We predicted that within single years, we would observe community structure within the social networks and that individuals who were more related and of shared age and place or origin would be more likely to associate than random. This study aims to clarify whether the observed fission–fusion dynamics in plains bison herds lead to stable social structures, providing insight into the social organization of this keystone species as it is restored to North American grasslands.

Materials and methods

Study site

This study was conducted on two plains bison herds managed by American Prairie, a private, non-governmental organization (www.americanprairie.org) during 2020, 2021, and 2022. The herds are located in north-central Montana (latitude: 47.761, longitude: −107.775). The vegetation is dominated by mixed grass prairie, upland prairie, and sagebrush steppe (Charboneau et al. 2013). Natural predators of plains bison such as gray wolves (*Canis lupus* Linnaeus, 1758) and grizzly bears (*Ursus arctos* Linnaeus, 1758) have been extirpated from this area and there have been no known predation events on the studied herds.

Since 2005, American Prairie has reintroduced plains bison to three large parcels of private land and a mixture of private land and leased grazing allotments managed by the Bureau of Land Management (BLM) of the US Department of the Interior. These pastures are not connected to each other and are surrounded by electric fences with minimal internal fencing, so the entirety of each pasture is accessible year-round. The pastures included in this study, Dry Fork (DF) and Sun Prairie, have areas of 32.4 and 111.6 km^2, respectively (Table 1). In DF, there were 152 bison in June of 2021. In Sun Prairie, there were 424 bison in June of 2020 and 408 bison in June of 2022. The numbers of each sex and age class for DF and Sun Prairie for the years they were studied are shown in Table 1. Aerial population surveys are conducted annually by American Prairie staff. The number of individuals maintained in each pasture corresponds to stocking rates based on normal-year precipitation estimates calculated by BLM staff for public grazing allotments and by a private contractor (EMPSi Inc., Boulder, CO) and conform to the United States Department of Agriculture Natural Resources Conservation Service recommendations for private parcels (Freese et al. 2018). Bison pop-

Table 1. Pasture sizes, density of plains bison (*Bison bison bison*), and demographic information for each pasture for each year that was included in the study.

	Dry Fork 2021	Sun Prairie 2020	Sun Prairie 2022
Pasture Size (km^2)	32.4	111.6	111.6
Bison per pasture	172	424	408
Density (bison per km^2)	4.7	3.8	3.7
# Adult females	67 (40.0%)	137 (32.3%)	143 (35.0%)
# Adult males	51 (29.7%)	201 (47.4%)	137 (33.6%)
# Yearling females	9 (5.2%)	20 (4.7%)	27 (6.6%)
# Yearling males	27 (15.7%)	5 (1.2%)	29 (6.9%)
# Calves	18 (10.5%)	61 (14.4%)	72 (17.6%)

ulations are controlled by public harvesting opportunities, transfers of animals to and from other conservation herds, and chemical contraception (Freese et al. 2018). The bison originally reintroduced on American Prairie originated from Wind Cave National Park in South Dakota, United States, and Elk Island National Park in Alberta, Canada.

Handling

Bison handling was conducted approximately every other year in each bison pasture by American Prairie staff as part of routine disease testing and management practices. American Prairie used a low stress handling facility, moving each bison through a series of corrals and chutes into a hydraulic squeeze, where GPS ear tags are attached, and hair follicle samples are taken from the tail for DNA analysis. Location devices, as described in more detail below, were deployed during bison handlings in DF in January in 2021 and in Sun Prairie in January of 2020 and February of 2022. When possible, all bison were also equipped with a numbered dangle ear tag for individual identification. Particularly in 2020 and 2021, few males were handled due to size limitations of the handling equipment. Due to the frequency of handling and individual identification, the age and place of origin are known for most individuals. Because year of birth is not always known for translocated individuals not born at American Prairie, we coarsened age into categories dependent on the availability of data for each dataset (Fig. 1). Handling, ear tag deployment, and DNA sampling procedures were conducted with prior institutional animal and use committee (IACUC) approval from the Smithsonian Institution (protocol #19-01) and Montana State University (protocol #2021-176) IACUC committees.

Relatedness

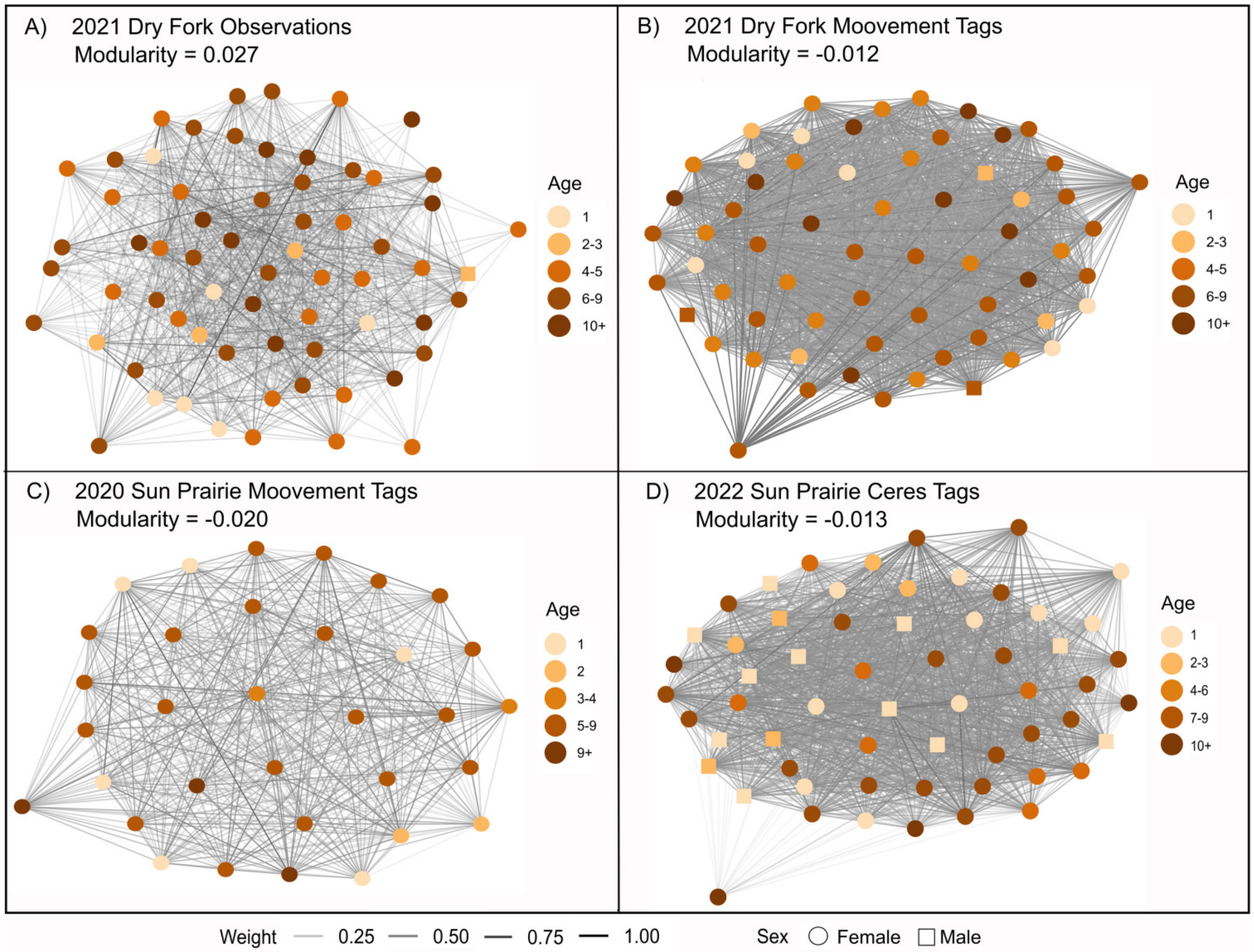
For estimation of genetic relatedness among sampled individuals, collected hair samples were shipped to the GeneSeek Operations of Neogen Corporation (Lincoln, NE, USA) to be sequenced with the Illumina BovineHD BeadChip, a comprehensive genome-wide bovine single nucleotide polymorphism (SNP) chip developed for cattle. This chip features 777 962 SNPs evenly spanning the bovine genome with an average gap size of 3.43 kb (Illumina Inc., CA, USA). Samples were processed (DNA extraction and genotyping) at NeoGen in two batches based on sample collection events. Genotypes were mapped to the Bos_taurus_UMD_3.1.1 reference genome assembly (NCBI GenBank accession GCA_000003055.5) by NeoGen staff, and pedigree (PED) and MAP files were generated for use in PLINK v1.9 (www.cog-genomics.org/plink/1.9/) (Chang et al. 2015). The data files from the two batches were merged using the merge-ped command in PLINK.

Plains bison genotypes were filtered in PLINK for (1) missing data (variants with >10% missing data, individuals with >10% missing data removed) with the –geno and –mind commands (default settings of 0.1), (2) minor allele frequency (—maf 0.03), and (3) linkage disequilibrium (–indep-pairwise command with a window size of 50 kb, a step size of 10, and an r^2 threshold of 0.5), leaving 32 442 SNPs for 185 samples. Pairwise relatedness estimates were generated in PLINK, using a method-of-moments approach to calculate the probability of sharing 0, 1, or 2 alleles (averaged across the genome) due to identity-by-descent (shared ancestry) (Purcell et al. 2007). Pairwise relatedness estimates were generated for each herd-year, except for Sun Prairie 2022, when DNA samples were not available for analysis. We categorized relatedness values into first order (≥0.4), second order (≥0.2 and <0.4), third order (≥0.1 and <0.2), and unrelated (<0.1) (Manichaikul et al. 2010) (Supplemental Fig. 1).

Movement locations

To follow the movement of individuals, we deployed two types of GPS ear tags throughout the study (image in Supplemental Fig. 2). In 2020 and 2021, we used long-range (LoRa) Internet of Things sensors with solar-powered GPS ear tags developed by mOOvement (South Brisbane, Queensland, Australia), a company focused on livestock applications for ranchers (https://www.mOOvement.com.au/). These ear tags were placed on 97 individuals in DF in January 2021 and 89 individuals in Sun Prairie in January 2020. LoRa Internet of Things operates in the unlicensed industrial, scientific, and medical sub-gigahertz frequency bands (United States 915 MHz) provided by low-power wide area networks (LPWANs) (Centenaro et al. 2016). LPWAN is a cellular-like coverage network suitable for short-range devices. Three base stations with Lorix One 915 MHz LoRa gateways (https://www.thethingsshop.com/products/lorix-one) were installed 32 feet above the ground at each bison pasture. Their locations were determined using a line-of-sight model that considers factors

Fig. 1. Visualized networks for the duration of each dataset show no evidence of stable subgroups. The modularity for each network is well below the commonly used threshold of 0.3, indicating significant network structure. Each node represents an individual plains bison (*Bison bison bison*) colored according to age category and with the shape representing sex. The weight of the lines connecting each pair of nodes represents the association strength between each pair of bison.



such as the gateway's range (specified as 5 km), the height above ground, and elevation data. Before deployment, tag radio transmissions were tested at various locations across the field site to validate the tag-gateway connections. Radio models indicated that the gateways provided a minimum of approximately 30% coverage overlap between them. The GPS ear tags recorded hourly positions and sent the location to the nearest LoRa base station. The base station connects to the internet via 4G and uploads data to cloud storage for data access. The ear tags are attached like a standard cattle dangle tag. Data collected in 2022 used a different solar-powered GPS ear tag developed by Ceres (https://www.cerestag.com/). The Ceres tags worked on the GlobalStar Satellite Network and were programmed to send one fix every 6 h. They are attached with two prongs onto the back of the ear, with the solar panel facing out. Neither GPS tags sent locations on a fixed time schedule, so locations are asynchronous between bison. The Ceres tags were placed on 93 individuals in Sun Prairie in February 2022. The mOOvement brand ear tags were all no longer working and were removed during the 2022 handling, so the two brands were not working concurrently during this study.

Behavioral observations

We conducted behavioral observations of the DF herd from May to October 2021 to describe a social network using fine-scale associations. A 2-week observation period was conducted at the beginning of the study to minimize response to observer presence. All observations occurred between 7 am and 4 pm. We observed the herd from vehicles and maintained a minimum distance of 50 m to minimize disturbance of natural behaviors and avoid provoking movement. Because social behaviors are rare and challenging to observe between bison, proximity is often used as a proxy for affiliative relationships (Lott and Minta 1983; Ramos et al. 2019). Due to the difficulty of following moving herds, observations were limited to times when the herd was not making directed movements. We conducted threshold focal observations as described by Davis et al. (2018). We randomly selected a focal individual with a random number generator and recorded the ear tag ID of the focal individual and all individuals, excluding calves, within five body lengths (~13.5 m) of the focal individual. We chose this distance threshold to include individuals within ~20% of the average group spread, as recommended by Davis et al. (2018). We excluded calves due to their strong associations with their mothers and lack of numbered ear tags for individual identification (Green et al. 1989). We did not exclude males from the observations, but few males had consistently observable numbered ear tags. The process was repeated every 10 min with a new focal individual.

Social network analysis

Social network analysis is commonly used to visualize and interpret complex social and ecological interactions (Farine and Whitehead 2015). Networks consist of nodes, representing individuals, connected by edges, representing the strength of observed associations between individuals (Farine and Whitehead 2015). In our networks, each node is one individual bison, and the edges are measures of association strength between each pair of bison, controlling for the number of times they could have been seen together. We constructed four separate social networks: one based on direct observation in DF in 2021, two based on GPS locations from mOOvement ear tags in DF in 2021 and Sun Prairie in 2020, and one based on GPS locations from Ceres ear tags in Sun Prairie in 2022. For the thresholded focal observations from DF in 2021, we defined association strength as the number of times individual A was focal and within five body lengths of B ($A_F B$) and the number of times B was focal and within five body lengths of A ($B_F A$) divided by the total number of times that either A or B were focal ($A_F + B_F$) (eq. 1). This metric is similar to the commonly used simple index ratio (Cairns and Schwager 1987), but only considers pairwise associations where one of the individuals in the pair was the focal individual to ensure that only pairs of bison within five body lengths of each other were considered associated.

$$\frac{A_F B + B_F A}{A_F + B_F} \tag{1}$$

For the location data obtained from the ear tags, we defined association strength as the number of 6 h time windows in which each pair of individuals were within 800 m of each other, divided by the number of time windows in which they both sent locations. We used 800 m as the distance threshold to minimize incorrectly classifying pairs with asynchronous fix schedules as non-associated because the group is likely to move over the 6 h time window (see below for sensitivity analysis for these threshold values). We used fixed 6 h time windows to correspond with the fix rate of the Ceres tags. This time window length ensured that all locations from all functioning tags were included in each time window despite asynchronous relocations. This association strength metric controls for variable tag failure rates between individuals by only including periods when both individuals were detected.

We constructed and visualized separate networks for each year sampled within each pasture using the igraph and ggraph packages in R version 4.3.1 (Csardi 2005; Pedersen 2022). Due to the GPS ear tags' relatively high failure rate, we removed individuals with poorly performing tags from the analysis. For each dataset, we chose a minimum threshold of locations, to remove individuals whose tags fell off or stopped working shortly after deployment. For the datasets using the movement ear tags with hourly fix rates, we filtered out individuals with fewer than 400 locations, or about half a month of data. We used a threshold of 200 locations for the Sun Prairie 2022 dataset, which covered about 1 month of locations, due to the coarser 6 h fix rate for the Ceres tags and longer sampling duration. For the DF observational dataset, we filtered out individuals that we observed as focal animals fewer than 10 times.

We calculated Newman eigenvector modularity for each network, hereafter referred to as "modularity", a commonly used metric for detecting community structure. Modularity measures whether a high proportion of edge weight is within or between groups as a measure of social clustering and subgroups (Newman 2006; Farine and Whitehead 2015). This metric ranges from −1 to 1, where a score of 1 indicates a perfect division of the network into stable subgroups, and a score of −1 indicates no community structure with relatively few edges within groups and many edges between groups. Modularity scores reflect the stability of associations between individuals over time, with higher values indicating more consistent and well-defined subgroup composition. In contrast, low or negative modularity suggests fluidity in subgroup membership, where individuals interact more frequently across the network rather than forming stable, long-term subgroups. We also calculated the network density of each network, which is the number of observed associations between individuals divided by the number of possible associations within the herd (Sueur et al. 2011*b*). High network density suggests that most individuals are connected to each other, indicating a highly cohesive group, while low density indicates that fewer individuals are associating with each other, potentially reflecting more distinct subgroups.

To examine the time scales at which subgroups are present, we constructed separate networks and calculated Newman eigenvector modularity for every day, week, and month in the study period for each dataset (excluding the DF observations) using the same method and metrics to define association strength as described above. We also constructed networks and measured eigenvector modularity using only days with modularity above 0.3 to filter out days when the entire herd was likely to be congregated to test whether the inclusion of low-modularity days might make consistent subgroup composition during periods of fission more difficult to detect. The threshold of 0.3 Newman eigenvector modularity is commonly used as an indicator of community structure (Newman 2006).

We tested whether mean pairwise association strength and Newman eigenvector modularity for the networks constructed from ear tag location data were sensitive to our choice of filtering low-performing tags, distance, and time window thresholds. To assess the impact of the minimum number of locations received from an individual, we constructed networks filtering out individuals one by one based on the number of locations they sent within the study period (from 1 to 5000). We constructed networks where we defined

Table 2. The range of dates and number of individual plains bison (*Bison bison bison*) of each age/sex class included in the social network analysis for each dataset.

Network	2021 Dry Fork observations	2021 Dry Fork mOOvement tags	2020 Sun Prairie mOOvement tags	2022 Sun Prairie Ceres tags
Time frame	13 May 2021–21 September 2021	1 March 2021–30 September 2020	1 March 2020–31 August 2020	1 March 2022–30 November 2022
# Individuals in the network	65	64	33	61
# Adult females	58	55	27	35
# Adult males	1	3	0	11
# Yearling females	6	6	6	3
# Yearling males	0	0	0	10

association strength using different distance thresholds in increments of 100 m from 100 to 3000 m. We also examined the impact of time window length by constructing networks with time windows between 1 and 24 h. These sensitivity analyses are plotted in Supplemental Fig. 3.

We used Mantel tests to test the hypotheses that association strength between pairs is correlated to relatedness, shared age, and shared place of origin. Mantel tests measure the correlation between two pairwise distance matrices through node-based permutation (Mantel 1967). We ran a separate Mantel test for each pasture in each year studied. All Mantel tests were run with 999 replicates using the “ade4” package in R (Dray and Dufour 2007). For the Mantel tests measuring the correlation between association strength and shared age or shared place of origin, we created dummy matrices with 1s when both bison shared the category in a pair and 0 when they were not. We used Tukey multiple comparisons of means tests to assess whether there was a difference between the average pairwise association strengths for different orders of relatedness.

Results

Network metrics

We found little evidence for stable subgroup structure in any of the herds using our association metrics. After filtering out individuals with few observations, the resulting networks from the DF 2021 observations (DF21 observation), DF 2021 mOOvement tags (DF21 mOOvement), Sun Prairie 2020 mOOvement tags (SP20), and Sun Prairie 2022 Ceres tags (SP22) had 65, 64, 33, and 61 nodes, respectively (Table 2). These sample sizes corresponded to 42.2% and 41.6% of the DF herd and 9.1% and 18.2% of the Sun Prairie herd, respectively, excluding calves. Each network had eigenvector modularity scores close to zero or negative values, showing a lack of community structure (DF21 observation = 0.027, DF21 mOOvement = −0.012, SP20 = −0.008, SP22 = −0.008) (Fig. 1). Each network also had remarkably high network density, indicating that a high proportion of possible connections between individuals are realized (DF observation = 0.532, DF mOOvement = 0.982, SP 2020 = 0.953, SP 2022 = 0.919).

The average modularity over each day (DF21 mOOvement = 0.114, SP20 = 0.270, SP22 = 0.273) was higher than the average weekly modularity (DF21 mOOvement = 0.004, SP20 = 0.084, SP22 = 0.068), which was higher than the monthly modularity (DF21 mOOvement = 0.006, SP20 = 0.001, SP22 = −0.011) (Figs. 2 and 3). We found that 22.4% of days in DF 2021, 43.4% of days in Sun Prairie 2020, and 44.0% of days in Sun Prairie 2022 were above the 0.3 modularity threshold, indicating that the bison were likely split into subgroups rather than aggregated into one group (Supplemental Fig. 4).

Effects of relatedness, age, and place of origin on associations

In Mantel tests for the three networks with information on relatedness, we only found a positive correlation between pairwise relatedness and association strength for the DF observation network, which measured association at a fine spatially and temporal scale with a Mantel statistic of 0.106 and a *p*-value of 0.001 (Table 3). The DF network constructed from the ear tag locations did not show a significant positive or negative correlation with a Mantel statistic of −0.008 and a *p*-value of 0.753. There was also no evidence that more related individuals were more or less likely to associate than expected by chance in 2020 in Sun Prairie with a Mantel statistic of 0.004 and a *p*-value of 0.321. The full results from the Tukey multiple comparisons of means, comparing the average pairwise association strength between different orders of relatedness, are reported in Supplemental Table 1. Notably, for the fine-scale direct DF observations, only the difference between first-order relatives and all lower orders of relatedness had a *p*-value below 0.05. No comparisons were significant for DF 2021 or Sun Prairie 2020 movement data (Supplemental Table 1).

We did not find strong correlations between association strength and shared age or place of origin (Table 3). Mantel tests for shared place of origin and association strength resulted in *p*-values of 0.758 for DF Observations, 0.772 for DF movement data, 0.527 for Sun Prairie 2020 movement data, and 0.889 for Sun Prairie 2022 movement data (place of origin networks are visualized in Supplemental Fig. 5). Mantel tests for shared age and association strength resulted in *p*-values of 0.289 for DF Observations, 0.808 for DF movement data, 0.134 for Sun Prairie 2020 movement data, and 0.157 for Sun Prairie 2022 movement data.

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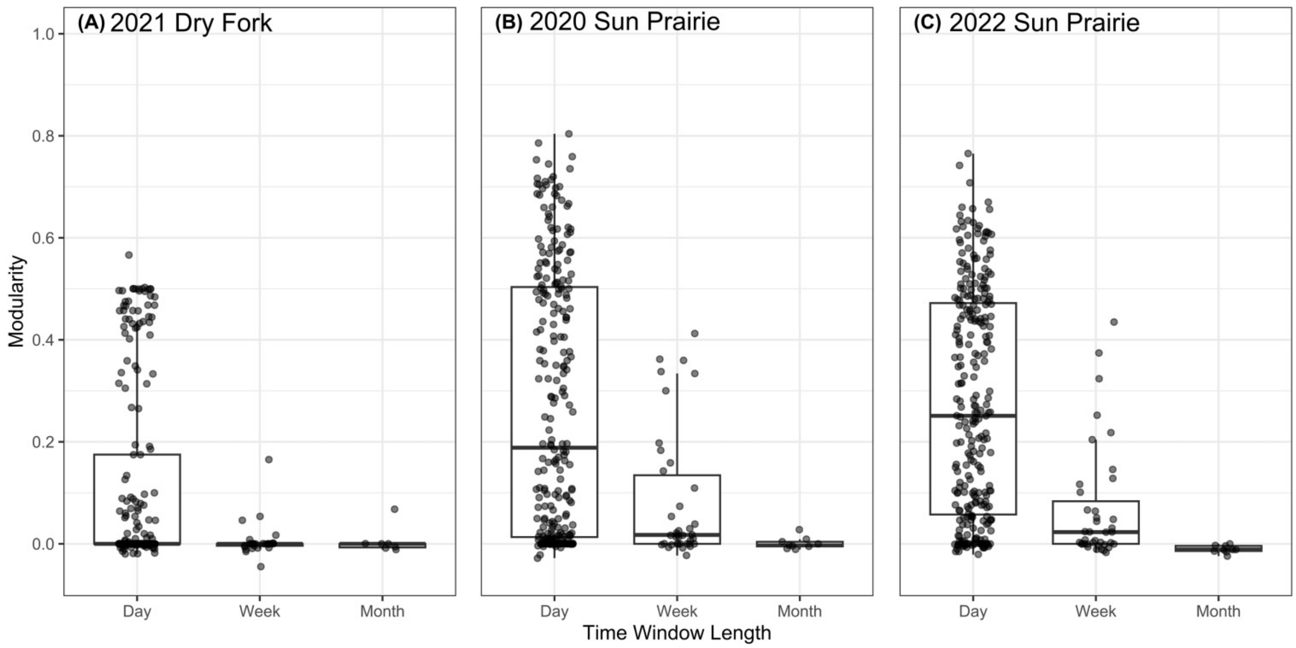
Fig. 2. Boxplots of modularity for the networks constructed from each day, week, and month in the (A) 2021 Dry Fork Observation network, (B) 2020 Sun Prairie Movement Tag Network, and (C) 2022 Sun Prairie Ceres Tag network. Each point represents the Newman eigenvector modularity of a single network.



Discussion

Despite their fission–fusion social structure, we did not observe significant network structure to suggest that stable subgroups existed at the scales we observed in either of the two plains bison herds we studied at American Prairie. Both the fine-scale social network constructed from behavioral observations and the coarser-scale network constructed from GPS ear tag data collected in the DF herd in 2021 had near-zero modularity and high network density. This was also consistent across two different years in the larger Sun Prairie herd with GPS ear tags with different fix rates each year. The consistently low modularity scores were not sensitive to our choice of distance threshold, time window, or sample size to measure association strength from the GPS ear tag data. Further, our results showed consistent patterns across herds despite variations in the proportion of each herd included in each network analysis.

The low modularity scores we observed did not result from an absence of fission–fusion dynamics or consistent aggregations of all individuals in the herd. There is considerable variation in modularity at the daily and weekly scales, showing that there are frequent periods in which the herd breaks into smaller groups. Moreover, modularity did not increase when we created networks using data only from days with modularity scores over 0.3; this indicates that periods with greater network structure were not masked by periods in which the entire herd was aggregated. This lack of modularity occurred because the composition of subgroups resulting from fission events was not consistent over time. This finding contradicts a common narrative that plains bison form stable subgroups that persist across fission–fusion events. However, our results are consistent with the findings of Lott and Minta (1983) and Van Vuren (1983) using observations from smaller herds.

Because our GPS ear tags operated for under a year, we were not able to assess the stability of social bonds across the years. It is possible that more stable network structures and social bonds may arise from data collected over multiple years. However, it is unlikely that structure would emerge at a longer time scale that was not apparent at shorter scales. Because our GPS ear tags were only operational in the growing season, we also did not directly test for differences in herd structure between seasons. None of the month-scale networks constructed throughout our data collection periods, which included calving, post-calving, and rut, showed high enough modularity to suggest stable subgroups were present during any of these biologically defined phases.

We did find moderate but inconsistent support for the hypothesis that more related individuals are more likely to associate. This was most significant for the fine-scaled observations of the DF herd, indicating that relatedness may impact the position of individuals within a group more than the composition of groups. First-order relatives were most likely to associate despite not including calves in the dataset, showing that bonds between relatives persist beyond those between calves and mothers. However, we did not determine the exact relationship between most pairs of bison. We did not find evidence to support the hypothesis that individuals of the same age or the same origin herd were more likely to associate.

While we studied herds larger than those in earlier studies of plains bison sociality, the DF and Sun Prairie herds had fewer individuals and a more restricted range than historical free-ranging plains bison, particularly prior to their widespread extirpation in the late 1800s. The pastures for

Fig. 3. Examples of social network visualizations at different time scales and modularities from the plains bison (*Bison bison bison*) in the Sun Prairie pasture with Ceres GPS ear tags in 2022. Left to right, each column shows low, medium, and high modularity relative to the range of the modularity in networks aggregated over a day, week, or month within this dataset. The range of modularity was greater at shorter time scales, reflecting fission–fusion dynamics.

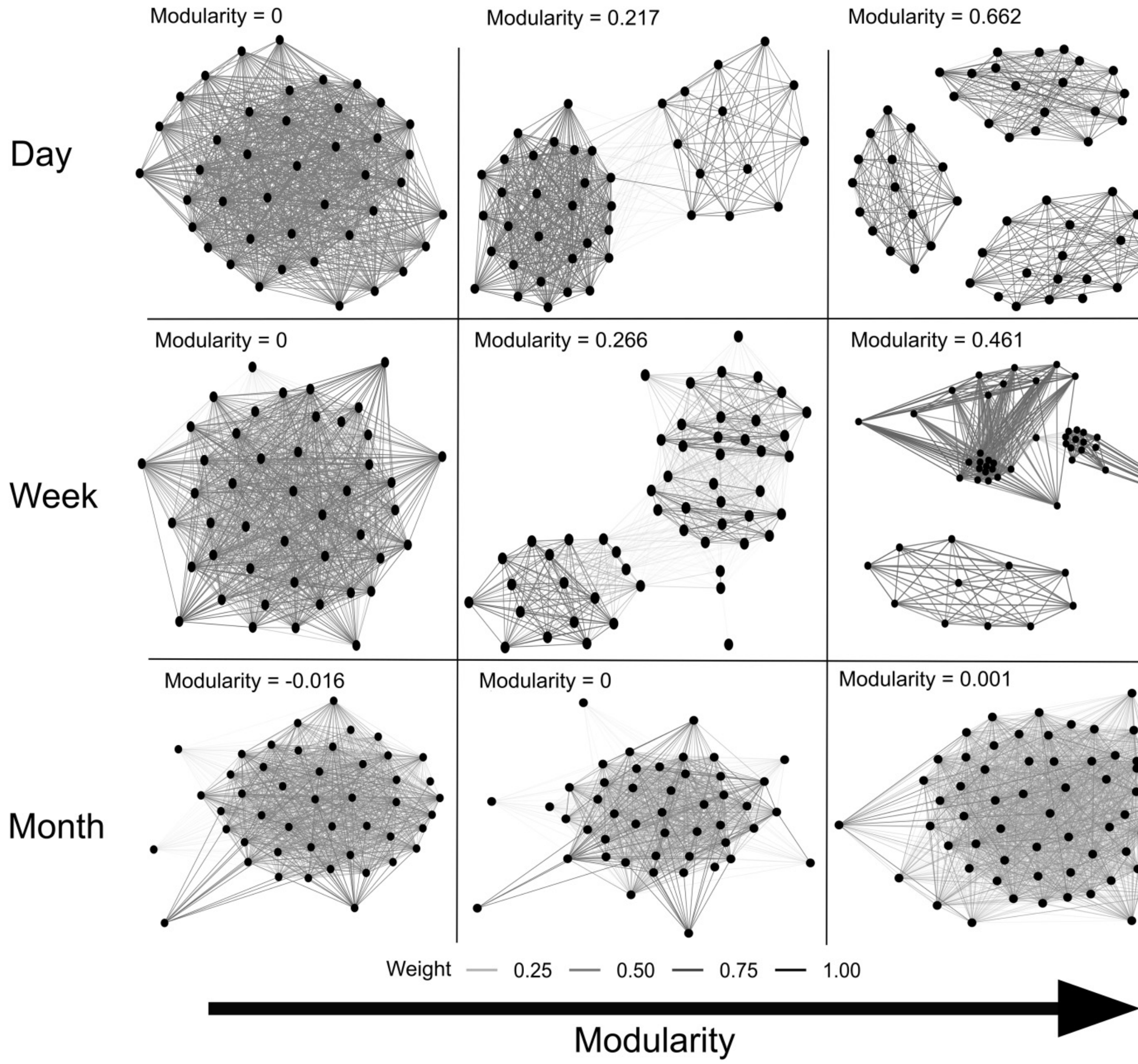


Table 3. Results from mantel tests of pairwise association strength and pairwise relatedness, sharing place of origin, and sharing age categories for each dataset.

	Relatedness		Place of origin		Shared age	
	r	*p*-value	*r*	*p*-value	*r*	*p*-value
2021 Dry Fork observations	0.106	0.001	−0.005	0.758	0.008	0.289
2021 Dry Fork mOOvement tags	0.004	0.321	−0.005	0.772	−0.012	0.808
2020 Sun Prairie mOOvement tags	−0.015	0.824	−0.001	0.527	0.008	0.134
2022 Sun Prairie Ceres tags	NA	NA	0.013	0.889	0.009	0.157

the DF and Sun Prairie herds (32.4 and 111.6 km^2, respectively) may be restricted enough to result in a single group, but there may be some herd or range size threshold where stable subgroups emerge. The relatively small, fenced pasture size may also lead to subgroups merging and reassorting more frequently due to their increased chance of encountering each other at higher densities. Nonetheless, our results showed little evidence for stable subgroup membership in herds of several hundred individuals, which are large enough to provide considerable scope for fission–fusion dynamics in other large herbivores. Further, significant modularity and non-random networks have been found in similarly or more intensely managed livestock, including domestic sheep (Ozella et al. 2020) and cows (De Freslon et al. 2020), demonstrating that network structure can emerge in groups of highly managed and range-restricted animals. Today, most American bison are managed in small, isolated herds, more like those in this study than historic free-ranging American bison populations (United States Department of the Interior Bison Working Group 2020).

The frequent removal and addition of individuals from the herds to control the population and promote genetic diversity may disrupt the social structure enough to prevent the formation of stable subgroups. American Prairie removes about a quarter of the herd every 2 years, potentially disrupting otherwise stable bonds. Social networks can be resilient to network perturbation, such as in African elephant (*Loxodonta africana* (Blumenbach, 1797)) groups disturbed by poaching (Goldenberg et al. 2016). However, altered social structure and reduced relatedness in social groups have been attributed to high population turnover from human-caused mortality in wild boars (Iacolina et al. 2009) The semi-regular introduction of new individuals without preexisting stable bonds may also reduce subgroup stability. In bighorn sheep (*Ovis canadensis* Shaw, 1804), it took translocated sheep a year to socially integrate into the local population (Poirier and Festa-Bianchet 2018). It is common for bison in North America to be translocated to maintain genetic diversity, control population size, and establish new herds (Ranglack et al. 2023). The Department of the Interior's 2020 Bison Conservation Initiative includes metapopulation management to restore gene flow across bison conservation herds as one of its primary goals (Department of the Interior 2020). Regular culling to maintain desired herd sizes and reduce the risk of disease transmission are also common management strategies in conservation herds (Millspaugh et al. 2008; White et al. 2011). However, little attention has been paid to the impact of management decisions on plains bison social networks.

Despite the limitations of our study system, our findings reveal meaningful patterns in the aggregation behavior of bison within two large, managed pastures (32.4 and 111.6 km^2). These bison were not forced to aggregate into one large group by the pasture size but rather display fission–fusion dynamics, as demonstrated by the variation in modularity values from daily networks. We believe the association patterns we observed are biologically significant because these proximity-based metrics reflect the groups they chose to aggregate and move with within the large pastures. If living within groups serves to share information like forage availability, predation threats, and mating opportunities, then the flexibility of individual associations we observed suggests that these communications do not depend on lineages (genetic or herd origin) or previous interactions. The lack of stable subgrouping over time indicates that rather than forming stable, socially motivated groups, bison exhibit flexible associations that respond dynamically to their environment. Further work is necessary to elucidate the fine-scale environmental and social drivers of fission–fusion events.

Our research leveraged new tracking technologies to contribute to our understanding of social organization in fission–fusion species. We found no evidence of the subgroup stability in many other wildlife species known to have fission–fusion dynamics (Rubenstein et al. 2015; Ramos et al. 2019; Brambilla et al. 2022). Many species with fission–fusion dynamics exhibit stable subgroups due to the fitness benefits of long-term social relationships, often based on kin-selection (Archie et al. 2006; Bercovitch and Berry 2013). In fission–fusion societies, there is a trade-off between the benefits of affiliative relationships and divergent movement patterns arising from differences in internal state and landscape knowledge (Sueur et al. 2011*a*). Even when animals are incapable of recognizing most individuals within their social groups, stable subgroups can emerge due to the attraction of individuals to conspecifics of shared size, age, or nutritional needs (Sueur et al. 2011*a*). However, non-stable subgroup composition may be more likely when a species does not have the cognitive capacity to keep track of many relationships in highly complex and dynamic social settings (Ramos-Fernandez et al. 2018). Evidence for random, non-stable associations has also been found in several species, including shorebirds (Conklin and Colwell 2008) and African forest elephants (*Loxodonta cyclotis* (Matschie, 1900)) (Schuttler et al. 2014). Semi-captive animal populations such as the bison herds at American Prairie may offer an opportunity to design experiments to elucidate the conditions under which non-stable groups persist in species displaying fission–fusion dynamics.

Considering the growing frequency of species reintroductions, it is crucial for decision-makers to understand how different management actions may affect social structure, collective movement, and ecological impact (Goldenberg et al. 2019). It Is largely unknown how social structure impacts the ecological function of large herbivores. While the grazing, nutrient cycling, trampling, wallowing, and seed dispersal by bison herds moving across the landscape have historically played an outsized role in shaping North American grasslands (Knapp et al. 1999), the influence of their social dynamics on these processes remains unclear. The observed lack of stable subgroups challenges prevailing assumptions and highlights the need to identify the environmental drivers of fission–fusion dynamics in bison. Further work is needed to investigate the impact of herd size, range size, and removal and addition of individuals on the social structure and ecological function of bison. The effects of management and translocation on the genetic structure of bison herds and other reintroduced species have been evaluated carefully (e.g., Cherry et al. 2019), but their effects on social structure and potential to alter patterns of movement and aggregation should also be considered.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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The authors declare there are no competing interests.

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Supplementary material

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