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Is sharing really caring? Are spatial association networks associated with behavioral networks in a facultatively social mammal?

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Abstract

Spatial proximity and conspecific interactions can shape social organization and social structure within animal groups, but that may or may not mean that one's nearest neighbor and closest social partner are the same individual. Individual behaviors towards conspecifics can indicate social structure within an animal group; however, determining the extent to which spatial interaction networks reflect social organization and social structure will improve understanding of social systems. Multilayer networks offer a method to test this and can examine an individual's varying roles within their social environment. While spatial and behavioral interaction networks have been studied in other species, those studies examined social interactions with home range overlap, foraging, and mating behavior. Yellow-bellied marmot (*Marmota flaviventer*) behavioral and spatial networks have been extensively studied, but little is known about whether, and to what degree, these networks are similar. We studied the concordance between spatial and behavioral networks, focusing on marmot social interactions and their burrow-sharing networks. We found the largest correlation between the spatial network and the affiliative network with smaller correlations between affiliative and agonistic networks and the spatial and agonistic network. We found that centrality was highest in the multilayer network for degree and strength, and for individual networks, highest in the spatial network. Group size and predation pressure had negligible effects on spatial and affiliative network correlation. Across the overall system, yearlings were most central, and for the agonistic network, males and adults independently were most central. Through this study, there is a clearer understanding of the network and individual dynamics in yellow-bellied marmots, which will further advance comprehension of social dynamics of complex societies.

Introduction

Animals often share space with conspecifics and other species for many reasons, including because they are kin (Faulkes & Bennett, 2001), to avoid predation (Rubenstein, 1978), or to increase foraging success (Sridhar et al., 2009). Observations of spatial patterns and variation have been used to test whether proximity influences social interactions (Sailer & Gaulin, 1984), to indicate overall social organization (Kappeler, 2019), to analyze movement patterns and resource acquisition (Jacoby et al., 2012; Roshier et al., 2008), and to examine territoriality and

habitat use (Brown & Orians, 1970). Besides individual preferences, animals may also come together to secure resources (Harcourt & De Waal, 1992), because of environmental constraints (Olson & Blumstein, 2010), or because physical features may cluster them together (Chen et al., 2015). A way to identify spatial structure is by developing a spatial network.

Proximity can determine association (i.e., 'the Gambit of the Group') (Whitehead & Dufault, 1999). The Gambit of the Group hypothesis postulates that individuals found together are all associated (Franks et al., 2010) and, when frequently co-occurring, may form a social group (Chan et al., 2025; Franks et al., 2010). In a similar sense, a spatial network incorporates the co-occurrence of an individual with other individuals in the same space to describe a system (Haddadi et al., 2011). Social groups may emerge from animals sharing space (Farine et al., 2016). However, spatial analysis alone and the Gambit of the Group fail to account for non-proximity-based interactions, or may miss identifying cliques within the overall group (Pinter-Wollman et al., 2014; Wolf et al., 2007). Thus, a comprehensive analysis of social structure must combine spatial and behavioral interaction networks.

Behavioral networks are calculated from observed interactions, or associations between individuals (Makagon et al., 2012), but examining different types of interactions often produces different networks. Networks can be constructed from different types of interactions, like affiliative behaviors (Blumstein et al., 2009), such as grooming (Brent et al., 2013; Madden et al., 2009) and play (Coleing, 2009), as well as agonistic behaviors, such as physical aggression and displacement (Büttner et al., 2015a), and these networks can vary in structure and overall group dynamics (Foris et al., 2019). Affiliative and agonistic networks can be used to quantify social structure (Lea et al., 2010), which may be associated with future reproductive patterns (Krause et al., 2015; Oh & Badyaev, 2010), pathways of information transfer (Bates et al., 2025), and disease transmission (Albery et al., 2021; VanderWaal et al., 2020).

Logically, animals that share space may elect to interact (Webber et al., 2023), and multilayer networks (Silk et al., 2018), which can capture more dimensions of sociality, may have novel insights about social variation. A multilayer network incorporates individuals, behavioral-specific interactions, and spatial association. Analysis can identify how an individual

or group is connected in space and across different subgroups, such as foraging, grooming, and play groups (Finn et al., 2019).

Affiliative interactions may be closely associated with spatial proximity (Koene & Ipema, 2014; Van Dierendonck et al., 2004). Agonistic networks may differ from those based on spatial proximity and, reasonably, could fragment a social group and lead individuals to overlap less frequently (Evers et al., 2011). By comparing these networks to one another, potentially behaviorally correlated or disparate activity patterns can be analyzed (Finn et al., 2019).

Centrality is a measure of individual influence in a group (Lusseau & Newman, 2004), and as network composition can differ, individual centrality in one type of network may not be present in another. Multilayer centrality can address this by identifying those who are influential across all networks (Fisher & Pinter-Wollman, 2021). If spatial and behavioral networks are correlated, the individuals most central in one network could likewise be central in others, and identifying those individuals can indicate who might control social connections within the group (Büttner et al., 2015b) and individuals with a high risk of disease transmission (Makagon et al., 2012; Pierron et al., 2024). Thus, analyzing individual centrality complements overall network analysis by providing insights into both network structure and individual importance within those networks.

Yellow-bellied marmots (*Marmota flaviventer*), hereafter referred to as ‘marmots’, are an ideal study system to examine the association between spatial and behavioral networks because they live in colonies (geographic locations) in which there can be one or more matrilines (Armitage, 1991; Blumstein, 2025; Ozgul et al., 2006), and one or more social groups that contain individuals who interact with one another. As previously mentioned, cliques can form within a larger spatial group (VanderWaal et al., 2014). Potential cliques have been evident in marmot colonies, in which specific individuals interact with one another at a higher rate than is typical (Wey et al., 2008). This may be advantageous, as being strongly embedded within one’s social group decreases the likelihood of dispersal (Blumstein et al., 2009). As individual marmots vary in their influence on their social groups (Wey & Blumstein, 2010), centrality within social networks may highlight the most influential individuals across different network types. Based on

the natural history of marmots, we have developed the following general hypothesis and subsequent predictions.

We hypothesized that the relationships between spatial and behavioral networks will vary by behavioral network type. We predicted that spatial and affiliative networks will be associated, because animals that interact affiliatively tend to share space. We also predicted a weaker association between spatial and agonistic networks, since agonistic interactions can lead to increased spacing and decreased conspecific interactions (Evers et al., 2011). We predicted that yearling female marmots, with strong behavioral affiliations, will have the strongest spatial association, because social embeddedness is associated with a lower probability of dispersal (Blumstein et al., 2009; Wey & Blumstein, 2010). Since female relationships define matrilines, we predicted that females would be the most central across affiliation, spatial, and the overall multilayer network. Since male marmots have been shown to have the greatest centrality in agonistic networks in previous research (Zenth et al., 2023), we predicted they will play a similar role in a multi-level perspective. We predicted that spatial and affiliative networks will be most correlated in areas of high predation pressure and in groups with more individuals, as grouping behavior can allow for shared vigilance and protection against predation (Beauchamp, 2003).

Methods

We studied a wild population of yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (RMBL; 38°77'N, 106°50'W, elevation ~ 2895 m). Details of the study site and species are elsewhere (Armitage 2014). We focused on observations made between mid-April and the end of June of each year from 2003 - 2025, the period when yellow-bellied marmots are most socially active and before most pups emerged. We live-trapped marmots using Tomahawk live traps between mid-May and early September annually. We marked marmots with unique symbols using Nyanzol fur dye to assist with identification from a distance during social observations, and we gave marmots unique four- to five-digit ear tags for permanent identification (Blumstein et al., 2013). We observed individuals during daily activity periods (approximately 7:00-11:00 and 16:00-18:00). Trained observers quantified affiliative and agonistic behaviors and interactions (Table 6) as well as who initiated

it, where it took place, the time it occurred, and which individual ‘won’ the interaction (described as an individual that remained in the same position while the other was displaced).

Statistical Analysis

We conducted all statistical analyses in R version 4.6.0 (R Core Team, 2025) using tidyverse (Wickham et al., 2019) to organize, clean, and facilitate data management, igraph (Antonov et al., 2023; Csárdi et al., 2026; Csárdi & Nepusz, 2006) to create matrices and assign groups, muxViz (Domenico, 2026) to analyze and compare networks, and plyr (Wickham, 2011) to fit models to spatial locations and time points.

Spatial Network Analysis

We combined recorded instances of marmots at burrow and colony locations to calculate the spatial network. We assigned social and trap data to their respective years, and we excluded pups (age 0) from the analysis, as we are focused on adult and yearling marmots. We removed individuals seen fewer than 5 times in a given year, because they were likely transients. We created pairwise association indices using a Simple Ratio Index (SRI), which calculated the sum of days on which two individuals were seen occupying the same burrow, divided by the sum of days each individual was seen. If there were more than two individuals, we made unique pairings for all individuals. We used these associations to determine the likelihood of space-use overlap across individuals, which we used to form social groups.

Determining Spatial Groups

To create discrete spatial groups, we converted spatial association matrices into a weighted network, where we weighted edges between individuals according to their simple ratio index. We used 100 runs of the Map Equation algorithm (Infomap) to conduct a random walk simulation to define groups. As males may overlap in multiple colonies, we assigned them to groups where they were most spatially associated. We then assigned individuals from one year to one group.

Behavioral Network Analysis

Using the individuals in the spatial network, we created two behavioral networks for each social group, affiliative and agonistic. The affiliative behavioral network used only positive interactions

(play, sitting or foraging within 1 m, sitting in body contact), while the agonistic network only included aggressive interactions (displacement behaviors or fighting). Within each group-year, we calculated the total number of directional interactions between individuals, creating a square matrix.

Layer Association Creation

We used mean node overlapping, mean edge overlapping, and Jensen-Shannon divergence (JSD) statistics to assess structural similarity among the 3 layers (spatial, affiliative, and agonistic). We calculated all analyses using the R package muxViz (De Domenico et al., 2015; De Domenico, 2026). For each pair of layers, mean node-overlapping measures the proportion of individuals present in both layers, out of all individuals recorded for each group-year. Edge-overlap measures the consistency of the overall strength of relationships between a pair of layers by taking the lower edge weight in one layer, multiplying it by 2, and dividing by the sum of the edge weights in both layers. This process is repeated for all pairs of individuals to get an overall score. Quantum Jensen-Shannon divergence measures how structurally different a pair of networks are by comparing the von Neumann entropy of the pair's combined network and subtracting the average of each layer's entropy. A higher value indicates a larger divergence between the layers.

How Associated Are the Respective Layers?

We used a Quadratic Assignment Procedure (QAP) correlation test to test individual-level associations across layers. For every group-year, the QAP tested the correlation of dyadic tie strength in each pair of layers, and compared the correlations against a null distribution generated from 1000 permutations. We then computed correlation coefficients (r), z-scores, and p-values for each layer pair, across every group-year. Finally, we summarized z-scores from every group-year using Stouffer's method to create a summarized z-score for each layer-pair, which we then used to create a p-value for each layer-pair. We performed Benjamini-Hochberg (BH) correction on these p-values.

Reducibility Analysis

We conducted a reducibility analysis (De Domenico, 2022) to understand what the effects of merging two distinct layers would be. We used reducibility analysis to take the Von Neumann entropy of the input layers and utilize a cost function to understand how much structural information is lost when layers are combined. As the paired differences were not normally distributed, we utilized a Wilcoxon test with Benjamini-Hochberg (BH) correction to assess if there was a significant difference in structural information with and without merges.

Centrality Across Layers and the Multilayer Network

We conducted degree, strength, and eigenvector centrality for all individual layers and the multilayer network. We calculated the centrality measurements for each group-year, and summarized the results.

How Do Predation and Group Size Influence Layer Association and Centrality?

We used a Generalized Linear Mixed Model to assess the impacts of predator pressure and valley position on mean node overlapping, mean edge overlapping, and Jensen-Shannon divergence (JSD), and centrality. We used an ordered beta distribution for the model as the scores fell between $0 \leq x \leq 1$. We included year as a random effect to control for repeated sampling of similar groups and individuals across multiple years. We calculated predator pressure from recorded events of a predator being seen or heard at a colony location at any point. We noted the species, time, and location of the predator sighting, and created the index from the proportion of predator sightings to the number of observation sessions at each colony per year (Adler & Blumstein, 2026). Valley position was determined from an elevational gradient, where “up” valley sites have increased elevation, and “down” sites have lower elevation.

How Do Yearling Females Affect Spatial Connectivity?

To test how yearling females might affect spatial connectivity, we analyzed their spatial degree, strength, and eigenvector centralities in a Generalized Linear Mixed Model, with sex and age class as an interaction, and group size, which we standardized to the mean and scaled to standard deviation units, and valley position as additional predictors. The age of marmots was converted into two levels, yearling and adult, based on the number of years old they were (1 for yearling, 2 and above for adult). The year was additionally treated as a random effect.

Yearling Males Effect on Agonistic Networks, and Sex Effect on Overall Networks

To understand how yearling males may affect agonistic networks, and how sex and age may affect overall network connectivity, we analyzed the degree, strength, and eigenvector centralities for male and female marmots, and yearling and adult marmots, across all individual networks and the multilayer network. We incorporated valley position and group size, because this may influence the ability of individuals to form connections, and year as a random effect.

Results

Layer Comparison

The spatial-affiliative pair had the highest mean node overlapping among all pairs, the second-highest mean edge overlapping, the highest QAP correlation coefficient, and was the least structurally dissimilar to each other, compared to the other pairs. The affiliative-agonistic network had the least mean node overlapping, the highest mean edge overlapping, the second-highest QAP correlation coefficient, and was the second least structurally dissimilar to each other, compared to the other pairs. The spatial-agonistic pair had the second highest mean node overlapping, the lowest mean edge overlapping, the lowest QAP correlation coefficient, and was the most structurally dissimilar to each other, compared to the other pairs (Table 2). Not all groups were significant under QAP testing, with ~ 34.5% of all spatial-affiliative group-years being significant, ~ 8.5% of all affiliative-agonistic group-years being significant, and ~10.3% of all spatial-agonistic group-years being significant. While not all group-years were significant, the Stouffer p-value for the QAP testing was significant for all overall pairs (Table 1).

Table 1: Combined Layer Association Scores

Pair	Mean Node Overlapping	Mean Edge Overlapping	Mean Jensen-Shannon divergence	Mean QAP r	% Groups QAP Significant	QAP Stouffer P-value
Spatial-Affiliative	0.755	0.322	0.067	0.479	36.30	**< 0.001**

Affiliative-Agonistic	0.514	0.337	0.156	0.252	6.306	**< 0.001**
Spatial-Agonistic	0.523	0.207	0.156	0.224	10.32	**< 0.001**

Reducibility Analysis

The reducibility analysis revealed that information is lost anytime two distinct layers are merged together. Among separate layers, however, the least information was lost when the spatial and affiliative layers were merged together, indicating their high association and similarity. Keeping all layers separate was preferred for 53.9% of group-years versus merging the spatial and affiliative layer, 76.3% of group-years versus merging the spatial and agonistic layer, and 81.1% of group-years versus merging the affiliative and agonistic layers. With the network pairs at large, Wilcoxon p-values were insignificant with BH correction for merging the spatial and affiliative layer, indicating that the loss of information is not significant enough to justify keeping the layers separate. With the spatial and agonistic layer, and the affiliative and agonistic layer, the Wilcoxon p-values were significant with BH correction, indicating that there is a significant amount of information lost when these layers are merged (Figure 3, Table 2).

Table 2: Reducibility Analysis, n = 228

Comparison	No merge, mean q	Merge, mean q	Mean Difference	Median Difference (95% CI Interval)	% Groups favoring no merge	*P (BH)*
Spatial and Affiliative	0.186	0.167	0.0182	0.004 (0, 0.010)	53.90%	0.087
Spatial and Agonistic	0.186	0.103	0.0824	0.040 (0.032, 0.052)	76.30%	**< 0.001**
Affiliative and Agonistic	0.186	0.088	0.0975	0.064 (0.055, 0.078)	81.10%	**< 0.001**

Centrality

Among individual networks, the spatial network had the highest degree, strength, and eigenvector centralities relative to all other individual layers. Additionally, the spatial network had higher eigenvector centrality compared to the multilayer network. The affiliative network

had the second highest degree, strength, and eigenvector centralities, and the agonistic network had the lowest centralities, compared to all individual networks. The multilayer network had higher degree and strength centrality compared to the individual layers, and had the second highest eigenvector centrality (Table 3).

Table 3: Centrality Measurements Across Layers and Multilayer Network

Network	**Variable**	**Mean**	**Median**	**Range**
Spatial	Degree	7.46 (± 5.65)	6	0 - 30
	Strength	1.40 (± 1.24)	1.03	0 - 7.31
	Eigenvector	0.65 (± 0.34)	0.778	0 - 1
Affiliative	Degree	3.61 (± 3.14)	3	0 - 19
	Strength	0.13 (± 0.14)	0.07	0 - 0.5
	Eigenvector	0.42 (± 0.40)	0.28	0 - 1
Agonistic	Degree	1.77 (± 2.20)	1	0 - 21
	Strength	0.11 (± 0.15)	0.03	0 - 0.5
	Eigenvector	0.33 (± 0.39)	0.13	0 - 1
Multilayer	Degree	7.51 (± 5.65)	6.00	0 - 30
	Strength	2.06 (± 1.48)	1.87	0 - 8.48
	Eigenvector	0.53 (± 0.37)	0.50	0 - 1.73

Do predation and group size create highly correlated spatial and affiliative networks?

For spatial and affiliative networks, mean node overlapping significantly increased with group size ($P < 0.001$), indicating that larger groups showed higher spatial and affiliative node overlapping. Otherwise, there was no influence of any other main effect or interaction on mean node overlapping (Table 4). Mean edge overlapping significantly decreased with group size ($P < 0.001$), and this decline was stronger under lower predation pressure ($P = 0.013$), meaning larger groups with lower predation pressure had weaker mean edge overlapping. Additionally, colonies up-valley had weaker mean edge overlapping ($P < 0.001$). The only significant main effect on Jensen-Shannon Divergence (JSD) was valley position, where colonies up-valley significantly increased the JSD, meaning the spatial and affiliative layers were significantly more dissimilar.

Finally, valley position was the only significant main effect that influenced the QAP r ($P < 0.001$), with up-valley colonies showing a significantly weaker correlation between dyadic pair strength for the spatial and affiliative layer.

Table 4: Predation and Group Size Effect on Spatial and Affiliative Networks

Analysis	Family	Variable	Estimate	P-value
Node Overlap (n = 238)	Ordbeta	Intercept (year)	1.119 (± .106)	**< 0.001**
		Predator (Low) * Group Size	0.340 (± 0.261)	0.193
		Predator (Low)	0.223 (± .146)	0.126
		Group Size	0.231 (± 0.064)	**< 0.001**
		Valley (Up Valley)	-0.192 (± 0.119)	0.107
Edge Overlap (n = 238)	Ordbeta	Intercept (year)	-0.166 (± 0.098)	0.09
		Predator (Low) * Group Size	-0.502 (± 0.202)	**0.013**
		Predator (Low)	-0.045 (± 0.135)	0.738
		Group Size	-0.563 (±0.083)	**< 0.001**
		Valley (Up Valley)	-0.425 (± 0.118)	**< 0.001**
JSD (n = 203)	Ordbeta	Intercept (year)	-2.418 (± 0.123)	**< 0.001**
		Predator (Low) * Group Size	0.269 (± 0.164)	0.101
		Predator (Low)	-0.172 (± 0.138)	0.214
		Group Size	0.075 (± 0.057)	0.188
		Valley (Up Valley)	0.526 (± 0.129)	**< 0.001**
QAP r (n = 176)	Gaussian	Intercept (year)	0.716 (± 0.040)	**< 0.001**
		Predator (Low) * Group Size	-0.041 (± -0.077)	0.593
		Predator (Low)	0.057 (± 0.051)	0.263
		Group Size	0.018 (± 0.023)	0.43
		Valley (Up Valley)	-0.172 (± 0.047)	**< 0.001**

Do Yearling Females Affect Spatial Connectivity?

Sex did not appear to affect spatial connectivity, but age and group size significantly affected spatial degree, strength, and eigenvector centrality. Valley position significantly affected spatial

degree and strength centrality. Yearling marmots, larger groups, and up-valley colonies all increased spatial centrality, except for group size and valley position with eigenvector centrality, where smaller groups led to a strengthened eigenvector centrality, and valley position had no influence (Table 5).

Do Yearling Males Affect Agonistic Networks?

Adults and males all had a significant effect on agonistic centrality measures, where males increased all agonistic centrality measurements, and adults increased strength and eigenvector centralities. The interaction between age and sex, however, was not significant. Group size was significant for all agonistic centralities and valley position for strength and eigenvector centrality, where smaller groups and down-valley colonies increased strength and eigenvector centralities, and larger groups increased degree centrality (Table 5).

Overall Sex and Age Effects on Centrality

Overall, the only significant effect of sex was for the agonistic network, where males significantly influenced agonistic centrality. Otherwise, sex had no effect across the spatial and affiliative networks and the overall multilayer network. Age significantly affected all but one centrality analysis - agonistic degree. The interaction between age and sex was never significant. Group size was significant in all centrality analyses, and valley position was significant for all but four - spatial eigenvector, agonistic degree, and multilayer strength and eigenvector centralities. Yearlings significantly increased all centrality analyses, except for the agonistic layer, where adults and males independently significantly increased strength and eigenvector centralities (Table 5). Notably, many analyses did not fully satisfy residual tests.

Table 5: Sex Effects on Network Centrality

Layer	Analysis	Estimate (Female vs Male)	Sex significance (BH)	Estimate (Yearling vs	Age significance (BH)	Estimate (Sex * Age)	Sex * Age Significance	Estimate (Group Size)	Group Size Significance	Estimate (Up Valley vs	Valley Position Significance	Residuals

				Adult)					(BH)	Down Valley)	(BH)	
Spatial	Degree	0.007 (± 0.044)	0.868	0.192 ± 0.043	**< 0.001**	-0.010 ± 0.051	0.847	0.537 (± 0.014)	**< 0.001**	0.307 (± 0.033)	**< 0.001**	**Dispersion Significant**
	Strength	-0.033 (± 0.078)	0.806	0.565 ± 0.073	**< 0.001**	0.078 ± 0.086	0.580	0.346 (± 0.023)	**< 0.001**	0.149 (± 0.052)	**0.007**	**Dispersion Significant**
	Eigenvector	0.080 (± 0.101)	0.732	0.736 ± 0.109	**< 0.001**	-0.027 ± 0.133	0.847	-0.494 (± 0.032)	**< 0.001**	0.063 (± 0.070)	0.495	Dispersion Insignificant
Affiliative	Degree	-0.130 (± 0.077)	0.250	0.433 ± 0.075	**< 0.001**	0.126 ± 0.089	0.384	0.411 (± 0.025)	**< 0.001**	0.117 (± 0.052)	**0.037**	Dispersion Insignificant
	Strength	-0.053 (± 0.092)	0.806	0.555 ± 0.096	**< 0.001**	-0.100 ± 0.116	0.580	-0.689 (± 0.033)	**< 0.001**	-0.265 (± 0.058)	**< 0.001**	**Dispersion Significant**
	Eigenvector	-0.127 (± 0.110)	0.500	0.881 ± 0.118	**< 0.001**	-0.067 ± 0.143	0.847	-0.390 (± 0.036)	**< 0.001**	-0.306 (± 0.072)	**< 0.001**	Dispersion Insignificant
Agonistic	Degree	-0.313 (± 0.120)	**0.035**	-0.100 ± 0.120	0.406	0.220 ± 0.147	0.384	0.269 (± 0.040)	**< 0.001**	-0.047 (± 0.086)	0.619	Dispersion Insignificant
	Strength	-0.467 (± 0.110)	**< 0.001**	-0.476 ± 0.122	**< 0.001**	0.429 ± 0.155	0.069	-0.488 (± 0.046)	**< 0.001**	-0.415 (± 0.079)	**< 0.001**	Dispersion Insignificant
	Eigenvector	-0.380 (± 0.130)	**0.021**	-0.329 ± 0.134	**0.016**	0.323 ± 0.159	0.256	-0.217 (± 0.037)	**< 0.001**	-0.387 (± 0.079)	**< 0.001**	**Dispersion Significant**
Multilayer	Degree	0.008 (± 0.044)	0.868	0.192 ± 0.043	**< 0.001**	-0.012 ± 0.051	0.847	0.537 (± 0.014)	**< 0.001**	0.307 (± 0.033)	**< 0.001**	**Dispersion Significant**
	Strength	-0.109 (± 0.067)	0.250	0.426 ± 0.066	**< 0.001**	0.122 ± 0.079	0.384	0.172 (± 0.021)	**< 0.001**	-0.023 (±	0.619	Dispersion

									0.045)		Insignificant
Eigenvector	-0.032 (± 0.074)	0.806	0.299 ± 0.080	**< 0.001**	0.107 ± 0.098	0.550	-0.599 (± 0.028)	**< 0.001**	0.025 (± 0.050)	0.619	**Dispersion Significant**

Discussion

Layer Association

Spatial and affiliative layers had the strongest association; the layer-pair had the highest values of the Quadratic Assignment Procedure (QAP) test, mean node overlapping, and the lowest value from the Jensen-Shannon Divergence (JSD) test. The affiliative and agonistic layers followed, with the second-highest values on the QAP test and mean node overlapping, the highest mean edge overlapping, and the second-lowest Jensen-Shannon Divergence. Finally, the spatial and agonistic layers were still significantly associated with one another, but least so compared to all other layer-pairs. The spatial and agonistic layers had the lowest values of the QAP test, mean node overlapping, mean edge overlapping, and the highest JSD test. All layers were significantly correlated with one another yet still distinct, indicating that information in one layer may be present in another, but still, there is great value for individual layer analysis. Valley position and predator index appeared not to affect mean node and edge overlapping, and Jensen-Shannon Divergence (Tables 2-4).

With correlation between the spatial and affiliative layers and supplemented through a correlation between spatial and agonistic layers, there is support for the Gambit of the Group hypothesis, which implies that those who share space are associated, which can indicate social groups (Franks et al., 2010; Whitehead & Dufault, 1999). However, many of the group-years were non-significant, indicating that layer correlation and support for the Gambit of the Group hypothesis may highly vary from group to group. As affiliative behavior and agonistic behavior alike can indicate distinct elements of a social group (Foris et al., 2019), and they were significantly correlated to the spatial layer, these correlations together provide additional support for the hypothesis. While not all group-years were significant in their associations between networks, this may be because marmots are facultatively social, meaning they can choose

whether to be social. However, with a significant combined z-score across all network pairs, these associations can reliably indicate a spatial network's influence on social behaviors.

Since the affiliative network and agonistic layers were correlated, there is evidence that biological "frenemies" exist, in which animals that are most affiliated or friendly with each other also predictably can be the most hostile to one another. However, this was not true in numerous group-years, and this contrasts with research on dairy cattle, where the affiliative and agonistic networks were not correlated (Foris et al., 2019), indicating that this phenomenon may apply to select species. Supporting the coexistence of affiliation and aggression, previous research examining post-conflict affiliation has revealed that socio-positive interactions and support can increase the chance of post-conflict affiliation, but do not remove the chances of renewed aggression. In fact, the chances of renewed aggression were more likely with post-conflict affiliation than without it (Patzelt et al., 2009). The ability to shift between affiliation and aggression provides a telling story of frenemies. At one instance, animals may interact affiliatively, and the next, aggressively.

Reducibility

We found from our reducibility analysis that at any level, combining networks loses information about the overall system. However, merging the spatial and affiliative network lost the least amount of information, and we found that a merge could occur without a significant amount of information being lost. As we have seen high layer associations between the affiliative and spatial layers, we have additional support for the merging of these two layers. As we have already seen support for the Gambit of the Group hypothesis with layer association analyses, our reducibility analysis provides additional evidence that animals in proximity can very much indicate aspects of the social group.

Centrality

Our centrality results indicated that the spatial layer allowed for the highest centralities among any other individual layers. The centralities were only trumped by the multilayer network for

degree and strength centrality, as the multilayer network took the aggregation of all the individual layers. Notably, eigenvector centrality can be lower than an individual network because it is a relative measure rather than an additive one, where an individual with a strong spatial eigenvector centrality but a low agonistic eigenvector centrality can cause the multilayer eigenvector centrality to be less so than the spatial. With these results in mind, we have evidence that the spatial layer is the most indicative of an individual's overall centrality and importance in a social group.

Predation and Group Size

We had weak evidence of predation pressure and larger group size leading to more associated spatial and affiliative layers. As animals can utilize group vigilance behavior for antipredator response, we had predicted that with higher predator pressure and larger groups, marmots may cluster together to protect themselves from predation, which can in turn lead to a highly associated and spatial layer, as animals in proximity would be more likely to interact. However, we only observed mean node overlapping to increase between the layers as a result of higher group size, and the only effect of predation pressure was in an interaction with group size, where mean edge overlapping decreased as group size increased, and this effect was stronger with lower predation pressure. From this, we cannot assume that predation pressure and group size strongly influence the correlation between the affiliative and agonistic network.

Age and Sex Effects on Connectivity

While females largely dictate the structure of matrilines in marmot societies, we found that females did not have significantly stronger centrality across any networks, and interestingly, we found that males were more central in agonistic networks compared to females. We did find support for yearlings influencing centrality across the spatial, affiliative, and multilayer networks, but not the agonistic network. As yearlings have been influential for group membership and colony composition (Blumstein et al., 2009) in previous literature, our findings provide support. We also predicted that yearling males would be most central in agonistic networks, as they would compete with one another for territory and must decide whether or not to disperse, and while we did find evidence of males being most influential in the agonistic network, we found that adults, rather than yearlings, were also most influential, with no

interaction between age and sex. As adult male marmots compete for mates in a colony, our results in the agonistic network may indicate that there is significantly more aggression between males at this age because of competition for mates.

Limitations

As many of our group-years contained no agonistic interactions between any individuals, the Jensen-Shannon Divergence (JSD) did not consider these group-years in analysis, which may have influenced the effect that the remaining groups had on the entire system. Additionally, some interactions for specific years contained no burrow location data, causing us to drop the data from this analysis. We collected our data purely from observer interactions; there most likely were interactions between individuals that were missed or not recorded, but as our study took place over the course of 20+ years, these effects should be negligible.

Future Directions

As this is the first marmot study to create and analyze a multilayer network, we encourage future studies to look at additional variables, demographics, or environmental constraints that may influence network associations, reducibility, and centrality. As foraging networks have been included in previous multilayer network studies, we encourage analysis of a foraging network for marmots, along with affiliation, agonistic, and spatial networks. While our data on foraging is based on 2-minute audio recordings or their behavior, this would prove difficult in our system, but in other marmot systems, or in future years, this could be implemented. In our study, we found that each layer provides unique information that contributes to the overall group, and additional layers, behaviors, and variables will contribute to the knowledge base of networks in complex social organisms.

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Figures and Tables

Table 6: Ethogram of yellow-bellied marmot behavior. *Adapted from the Book of Marmot (REF)*

Type	**Description**
Aggression - agr	After an aggressive interaction, the marmots will probably quickly separate rather than sit calmly near each other as they would for play. Aggressive interactions tend to be quicker than play interactions, and you hear vocalizations (squeaks, yelps, growls, etc.) more often with aggression.
Bite - agr_bite	Initiator marmot bites receiver marmot in an aggressive manner
Box - agr_box	Stands on hind legs, using paws to strike opponent in an aggressive manner
Chase - agr_chase	Initiator marmot chases receiver marmot in an aggressive manner
Grab/slap/push - agr_grab/slap/push	Initiator marmot grabs, boxes, slaps, or pushes receiver marmot in an aggressive manner
mouth spar agr_mouthspar	When both initiator marmot and receiver marmot lunge at each other with open mouths in an aggressive manner; they may lock teeth
Pounce - agr_pounce	Initiator marmot pounces on receiver marmot in an aggressive manner
Snap/snarl/ hiss - agr_snap/snarl/ hiss	Initiator marmot vocalizes aggressively towards a receiver marmot
Wrestle - agr_wrestle	Initiator marmot and receiver marmot wrestle with each other in an aggressive manner
Play - play	The participants don't look as intense as in aggressive interactions. They sometimes get interrupted, look around, pause, or do other things that make them seem less invested. Unlike aggressive

	interactions, after play bouts, marmots are likely to sit next to each other. Play is generally 'bouncier' than aggression and is often characterized by individuals changing roles repeatedly and shifting from one type of behavior to another regularly. Behaviors appear to be done in a playful/non-aggressive (P/N-A) manner.
Bite - play_bite	Initiator marmot bites receiver marmot in a P/N-A manner
Box- play_box	Stands on hind legs, using paws to strike opponent in a P/N-A manner
Chase - play_chase	Initiator marmot chases receiver marmot in a P/N-A manner
Grab/slap/push play_grab/slap/push	Initiator marmot grabs, slaps, or pushes receiver marmot in a P/N-A manner
mouth spar - play_mouthspar	When both initiator marmot and receiver marmot lunge at each other with open mouths in a P/N-A manner; they may lock teeth
Pounce - play_pounce	Initiator marmot pounces on receiver marmot in a P/N-A manner
Mount - play_mount	A mount in the context of play where one marmot places its forepaws on the other's back, and/or mounts it.
Wrestle - play_wrestle	Initiator marmot and receiver marmot wrestle with each other in a P/N-A manner
Sniff AG -sniff_ag	Initiator marmot sniffs butt-end of receiver marmot
Greet - greet	Initiator marmot touches nose of receiver marmot with its nose
Allogroom- allogroom	One marmot grooming another or multiple marmots grooming each other. Often concentrated in places a subject cannot reach (back of neck).
Cheek rub -	When a marmot rubs its cheek on an object or

cheek_rub	sometimes on another marmot
Displacement - disp	When one marmot displaces another. There are two types of displacement
Simple - disp_simple	There is contact between two marmots and one ends up changing locations
Proximity - disp_proximity	By just approaching rather than physical means. Distance for displacement proximity is 1 meter. If it is farther than 1 meter and you are sure it was a displacement, score it and make a note in the comments.
Sit - sit	Two or more marmots sitting:
< 1m - sit_<1m	Within 1 meter of each other but not in body contact
body contact - sit_bc	In physical contact with each other
Follow - follow	When one marmot approaches another, and the approached animal moves, and this whole interaction occurs three or more successive times
Forage together - fg_tog	Marmots are together out feeding in an area with food within 1 meter of each other or obviously moving together (not greater than 5 meters apart)
Mount - mount	One marmot mounts another. This may be part of a complex bout of play, or it may simply be a mount. Score it as a mount unless it's an obvious play mount or sexual mount.

Figure 1:

Mean node overlapping, edge overlapping, and Jensen-Shannon Divergence across all network pairs. Numbers above network pairs indicate (r) correlation. Higher values of structural divergence indicate pair dissimilarity.

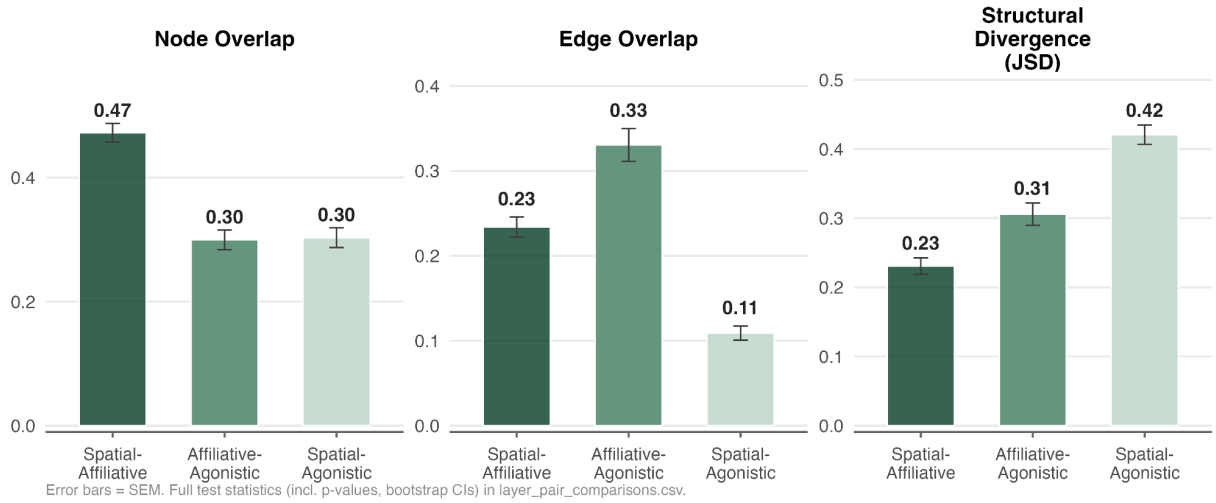

Figure 2:
Quadratic Assignment Procedure test for each network pair.

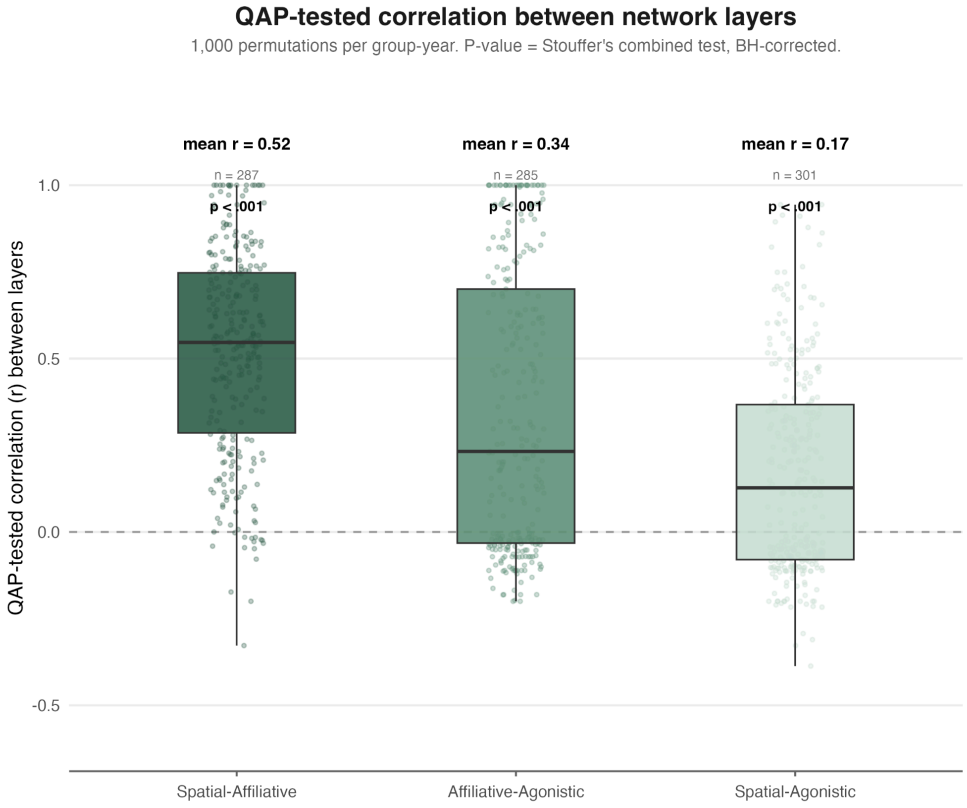

Figure 3: Scores of network pair merging.

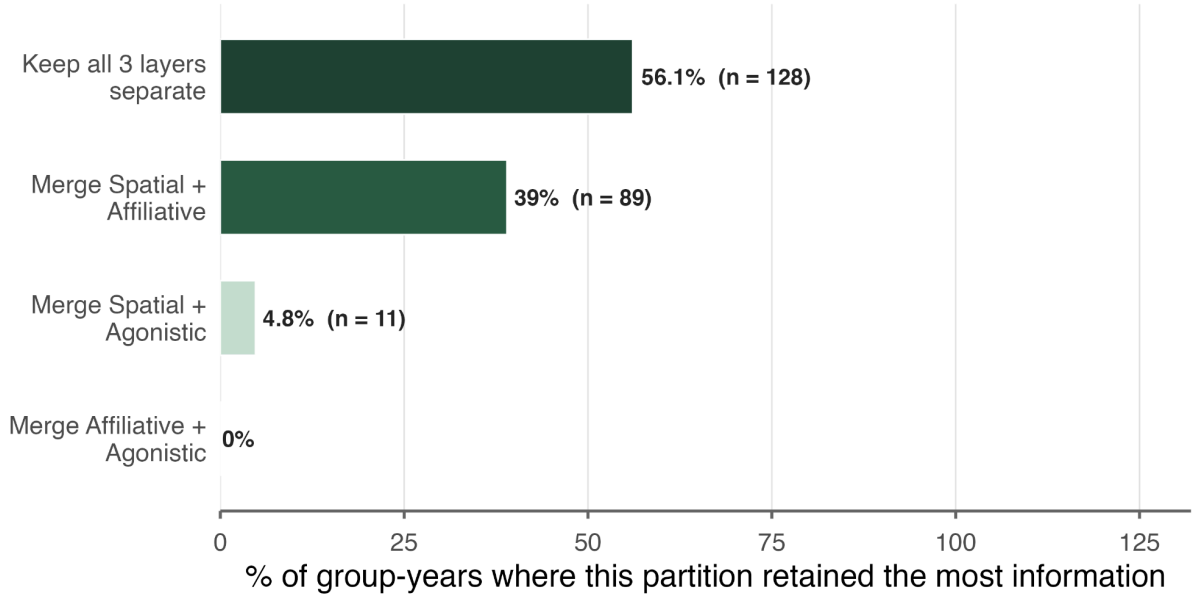

Figure 4: Information retention for network pair merges.