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Original Article

Extending the social cohesion hypothesis: is group social structure associated with dispersal in yellow-bellied marmots (*Marmota flaviventer*)?

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Abstract

Dispersal is an important individual decision which may influence individual fitness as well as population viability. The social cohesion hypothesis posits more social individuals remain at home, which is supported by prior work across taxa. However, how the sociality and connectivity of the group an individual resides in—their group social structure—relates to dispersal decisions has not been explored. We extend the social cohesion hypothesis to predict individuals residing in more social groups would remain at home, and we quantified the affiliative and agonistic social network structure of female yellow-bellied marmots (*Marmota flaviventer*), a facultatively social ground-dwelling squirrel, where about half of all females disperse. Using mixed-effects models, we found no support for the hypothesis that affiliative group structure explained any variation in a marmot's decision to disperse. We did find marmots in groups with less agonistic centralization (around one or few individuals) were less likely to disperse. The former finding may result from limited ability to perceive group structure whereas the latter may reflect individuals in less agonistically centralized groups are less likely to be reproductively suppressed. These results suggest individual dispersal decisions are more impacted by individual sociality and not that of their social group. Thus, the social cohesion hypothesis may not scale to the level of the group. Further work is required to determine whether dispersal decisions in obligately social species are influenced by group social structure.

Key words: dispersal, social cohesion, social relationships, yellow-bellied marmot.

Dispersal is defined as an organism's permanent movement from their natal home range to where they breed (Lidicker 1975; Anderson 1989). Much has been written about how this is a mechanism of gene flow that maintains genetic diversity, reduces inbreeding, and controls population density (Wolff 1988; Clobert et al. 2004; Bowler and Benton 2005; Matthysen 2005; Biek et al. 2006; Armitage et al. 2011). Dispersal is often costly to dispersers because individuals experience novel environments and threats while dispersing and settling (Bonte et al. 2012; Maag et al. 2019). Dispersal is important in the Anthropocene because the products of dispersal—the ability to move to more suitable habitats, produce genetically diverse offspring, and reduce resource competition—facilitate species resilience in an increasingly stochastic and harsh environment (Gundersen and Andreassen 1998; Gibbs et al. 2010). But what mechanisms drive individuals to disperse?

The social cohesion hypothesis posits that the more an individual interacts affiliatively with others, the less likely they are to disperse (Bekoff 1977). Bekoff's hypothesis is based on the principle that early play behavior creates social bonds, which discourage dispersal and its associated costs. One test of this hypothesis with gorillas (*Gorilla gorilla*) found affiliative interactions with the dominant male were positively correlated with philopatry (Harcourt and Stewart 1981). Conversely, Sharpe's (2005) investigation of dispersal in meerkats (*Suricata suricatta*) saw no correlation between play behavior and time of dispersal in either males or females. Blumstein et al. (2009) extended the application of this hypothesis by examining the relationship between dispersal and an individual's embeddedness in their social network, which accounts not only for their direct interactions with others, but also their indirect relations with others in their group. They found that female yellow-bellied marmots (*Marmota flaviventer*) that were more embedded in their social group were less likely to disperse.

The social cohesion hypothesis has also been tested for aggressive behaviors, where an individual would be more likely to disperse as a result of more frequent aggressive interactions. In prairie voles (*Microtus ochrogaster*), increased aggression was non-significantly associated with dispersal (Gaines et al. 1990). Yearling male roe deer (*Capreolus capreolus*), conversely, were more likely to disperse as agonistic behavior from adult bucks increased (Wahlström 1994). An individual's position within their group's dominance hierarchy has also been identified as an important determinant of

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dispersal in many species, such as coyotes (*Canis latrans*; Gese et al. 1996) and male red-cockaded woodpeckers (*Picoides borealis*; Pasinelli and Walters 2002).

These past studies, while describing properties at the group level such as size, mating system, and rates of specific behaviors, have not quantified the group's emergent social structure, which is more complex than averages of individual-level values (Wey et al. 2015; Kappeler 2019; Philson et al. 2022). Group social structure rather quantifies the nature, quality, and patterns of social relationships among directly and indirectly connected individuals (Kappeler 2019). The structure of a group may influence key collective evolutionary processes, such as genetic drift, fixation probability of genetic mutations, the effects of frequency-dependent selection, and social learning (Kurvers et al. 2014). It also may affect ecological processes in social groups, such as population stability, movement patterns, regulation, and formation (Dufour et al. 2011; Kurvers et al. 2014; Balasubramaniam et al. 2017). Despite well-documented research into the individual sociality basis for dispersal, the aspect of group social structure and its relation to dispersal has not been studied (Wey et al. 2015). Group social structure can be quantified via social network measures that describe the connectivity, reciprocity, and social heterogeneity of a group (Costello et al. 2023; Philson and Blumstein 2023a).

Here we extend the social cohesion hypothesis to the group level, which we refer to as the "social structure cohesion hypothesis," by quantifying group social structure's relationship with natal dispersal in a long studied wild population of yellow-bellied marmots. These marmots are a good system to study group social structure determinants of dispersal for three reasons. First, yellow-bellied marmots are the subject of a 62-year study and extensive social interaction data has been collected since 2003 (Blumstein 2013; Armitage 2014). Thus, there is a large dataset for analysis. Second, they are facultatively social and approximately half of all female marmots disperse (Blumstein et al. 2009; Armitage et al. 2011). The decision to disperse in this system is a multimodal one, with dam presence, play behavior, affiliative interactions with the mother, and space use overlap with females all discouraging a dispersal decision (Blumstein et al. 2009; Armitage et al. 2011). Thus, the mechanisms underlying female dispersal are a biologically relevant phenomenon to study. Third, females with more central and connected social network positions are more likely to remain at home (Blumstein et al. 2009) and individuals residing in more connected group social structures experience mostly negative associations with many fitness correlates in this system, such as mass gain (Philson et al. 2022), summer survival (Philson and Blumstein 2023a), and the number of weaned offspring (Philson and Blumstein 2023b). However, some benefits to more connected group social structures exist based on age and sex for mass gain rates (Philson et al. 2022) and winter survival (Philson and Blumstein 2023a). All told group social structure may have relevant and important implications for dispersal decisions.

While the social cohesion hypothesis asks how social and connected an individual is and how it influences their dispersal decision, the social structure cohesion hypothesis asks how social and connected is the group an individual resides in and how this influences their dispersal decision. The social structure cohesion hypothesis is relevant for both affiliative and agonistic social interactions given that aggressive interactions with others may influence an individual's decision to leave more than affiliative interactions influence an individual's decision to stay.

We focused on seven group-level measures of sociality and developed a priori hypotheses for the social structure cohesion hypothesis in networks constructed from either affiliative or agonistic social interactions. Density, the proportion of social relationships out of all possible relationships, quantifies how connected a group is (Burt 1992; Wasserman and Faust 1994; Grund 2012). Transitivity similarly quantifies group connectedness as the proportion of connected triads in a group (Wasserman and Faust 1994; Milo et al. 2002; Faust 2010). Reciprocity quantifies the proportion of relationships where both individuals initiate at least one interaction with each other (Wasserman and Faust 1994; Kankanhalli et al. 2005; Squartini et al. 2013). Degree assortativity quantifies the social homogeneity of the group based on the distribution of how many social partners each individual in the group has (McPherson et al. 2001; Currarini et al. 2016). If we found that density, transitivity, reciprocity, and degree assortativity were positively associated with philopatry in affiliative networks, we could infer support for the social structure cohesion hypothesis. On the contrary, in agonistic networks, a negative relationship between these social network measures and philopatry would provide support for the social structure cohesion hypothesis.

The number of cut points quantifies how easily a group can fracture into two or more groups (Wasserman and Faust 1994; Borgatti 2006). Average path length calculates how far every individual is from all others (Watts and Strogatz 1998; Broder et al. 2000). Centralization quantifies if interactions flow through few (high centralization) or many (low centralization) individuals in the group (Freeman 1979; Wasserman and Faust 1994; Kang 2007). If we found that cut points, average path length, and centralization were positively associated with dispersal in affiliative networks (generally meaning less social connectivity associated with dispersal), we could reject the social structure cohesion hypothesis. For agonistic networks, if increased cut points, average path length, and centralization were negatively associated with dispersal, this pattern would be consistent with the social structure cohesion hypothesis. Considering an animal's dispersal through the lens of the group social structure from which they come provides novel insights into the mechanisms of dispersal across levels.

Materials and Methods

Data collection

We studied yellow-bellied marmots at seven colony sites in and around the Rocky Mountain Biological Laboratory in the East River Valley in Gunnison County, CO, USA (38°57′N, 106°59′W). Marmots were livetraped with Tomahawk traps after which they were given unique, numbered ear tags, and their dorsal pelage was given a unique fur mark using Nyanzol fur dye for identification from afar. Marmots were studied under the research protocol ARC 2001-191-01 (approved by the UCLA Animal Care Committee on 13 May 2002 and renewed annually), protocols approved by the Rocky Mountain Biological Laboratory, and trapped under permits issued annually by the Colorado Division of Wildlife (TR-917).

From mid-April, when marmots emerge from hibernation to mid-September when they begin to hibernate, we conducted near-daily behavioral observations in the morning (7:00 AM to 11:00 AM) and in late afternoon (4:00 PM to 6:00 PM) (weather permitting) when the marmots were most active. We observed individuals from distances that did not overtly modify marmot behavior (this ranged from 20 to >100 m, depending on the site; Blumstein et al. 2009). While observing marmots, we noted all affiliative and aggressive social interactions (full ethogram in Blumstein et al. 2009) and recorded the initiator, recipient, and the "winner" (which marmot remained in place) of each interaction. Some 79% of interactions were between identified individuals and 88% of these interactions were affiliative (Philson and Blumstein 2023a).

Pups emerge from their natal burrows between mid-June to late-July annually and remain in their natal colony until the following year when, as yearlings, many individuals generally disperse within 10 days of their colony's first pup emergence (Armitage 1991). Thus, we defined natal dispersal as those yearlings that were last observed or trapped within our study site before 1 August but were not seen the following spring (Edic et al. Unpublished data). We excluded animals confirmed to be dead (see Edic et al. Unpublished data). We included dispersal events from seven colonies studied between 2003 and 2020 that have been consistently observed and had social networks calculated.

Social networks

We used directed and weighted matrices constructed annually from affiliative and agonistic interactions between yearlings and adults for 2003–2020. We filtered out transients by excluding individuals who were seen and/or trapped fewer than five times in a given location. We excluded pups from networks because they almost exclusively interacted with other pups and their mother since they emerge from their natal burrows halfway through the active season. Only interactions in April, May, and June were used to calculate networks because this timeframe (from marmot emergence from hibernation to when pups emerge from natal burrows) is when most social interactions occur, when we have the highest resolution of observation data (vegetative growth begins to impair observations later in the season), and the three months leading up to dispersal begins (when pups emerge).

Social groups for affiliative and agonistic networks were determined based on space use overlap since yellow-bellied marmots share space with a subset of all possible individuals within their colony area. Using SOCPROG (Whitehead 2009), we calculated simple-ratio pairwise association indices (Cairns and Schwager 1987) based on individuals seen, trapped, or observed around/using the same burrow within the same day. To identify social group membership, these simple-ratio indices were then run through the random walk algorithm Map Equation (Csardi and Nepusz 2006; Rosvall and Bergstrom 2008; Rosvall et al. 2009).

Using R (version 4.2.0; R Development Core Team 2023) and the package "igraph" (version 1.4.2; Csardi and Nepusz 2006), for affiliative and agonistic groups separately, we calculated seven group-level measures to quantify social structures for each social group: density, transitivity, cut points, and average path length, which quantify connectedness, as well as reciprocity, degree assortativity, and centralization, which quantify social homophily. We selected these measures because, in this system, they have an impact on individual health and reproductive success (Philson et al. 2022; Philson and Blumstein 2023a, 2023b) as well as the structural balance of groups (Wey et al. 2019).

Data analysis

Our final affiliative data set consisted of 18 years and 239 observations of dispersal (79 dispersing and 160 remaining in their natal colony) and group social structure collected across 84 distinct social groups, and our final agonistic data set consisted of 18 years and 188 observations of dispersal (50 dispersing and 138 remaining in their natal colony) and group social structure collected across 66 groups. Using "lme4" (version 1.1-33; Bates et al. 2015), we fitted a generalized linear mixed effect model with a binomial distribution (1 = dispersed; 0 = did not disperse) and used a bobyqa optimizer with 10,000 function evaluations. The initial model had density, transitivity, cut points, average path length, reciprocity, degree assortativity, centralization, dam presence, group size, and embeddedness as fixed effects, (the latter three have been known to affect dispersal in this (Blumstein et al. 2009; Armitage et al. 2011) and other systems (Jack et al. 2012). Embeddedness is an individual social network measure, providing an interesting comparison across social scales. Year, colony, and litter were fitted as random effects to account for any similarities among yearling marmots that dispersed at the same time, from the same place, or came from the same litter. To meet model assumptions, before fitting the affiliative model, embeddedness was log-transformed. Before fitting the agonistic model, density, average path length, centralization, and embeddedness were log-transformed. In both models, all continuous variables were standardized (mean-centered and divided by 1 standard deviation).

Both initial models had multicollinearity issues, namely density had a variance inflation factor (VIF) of 9.55 in the affiliative model and 7.99 in the agonistic model. Thus, we removed density and re-fitted both models; the refined models met all required statistical assumptions and are reported here. To ensure multicollinearity was not confounding our results, we additionally fitted a suite of models with each social network measure in a model without the other social network measures. Dam presence, group size, and embeddedness were again fit as fixed effects and year, colony, and litter as random effects.

To estimate effect sizes, we used "partR2" (version 0.9.1; Nakagawa and Schielzeth 2013; Stoffel et al. 2021, 2022) to calculate the marginal and conditional R^2 values and the semi-partial marginal R^2 that estimate variance explained by each fixed effect using. We estimated 95% confidence intervals (100 parametric bootstrap iterations) for the R^2 values).

Results

We found no statistically significant relationship between affiliative social structure and female yearling dispersal in yellow-bellied marmots (Table 1): transitivity ($B = -0.120$, $P = 0.688$), reciprocity ($B = -0.053$, $P = 0.842$), degree assortativity ($B = 0.012$, $P = 0.967$), cut points ($B = -0.294$, $P = 0.269$), average path length ($B = 0.309$, $P = 0.409$), centralization ($B = 0.134$, $P = 0.562$), embeddedness ($B = -0.319$, $P = 0.238$), and dam presence ($B = 0.06$, $P = 0.918$). Additionally, there was no significant relationship between group size and dispersal in the affiliative model ($B = -0.502$, $P = 0.234$). This model explained 5.74% of the marginal variance and 28.02% of the conditional variance. Semi-partial marginal R^2 for each fixed effect is reported in Table 1.

Table 1. Estimates, standard errors, P-values, and marginal part R^2 values from the generalized linear mixed model of affiliative networks.

Fixed effects	Estimate	Standard error	P-value	Marginal part R^2 (%)
(Intercept)	−1.061	0.577	0.066	5.74 (3.71–19.84)
Transitivity	−0.110	0.277	0.688	0.07 (0.0–14.19)
Reciprocity	−0.053	0.266	0.842	0.09 (0.0–14.21)
Degree assortativity	0.012	0.283	0.967	0.0 (0.0–14.12)
Cut points	−0.294	0.266	0.269	0.94 (0.0–15.1)
Average path length	0.309	0.374	0.409	0.67 (0.0–14.83)
Centralization	0.134	0.231	0.562	0.09 (0.0–14.21)
Embeddedness	−0.319	0.270	0.238	0.78 (0.0–14.94)
Group size	−0.502	0.422	0.234	1.34 (0.0–15.53)
Dam presence	0.060	0.581	0.918	0.02 (0.0–14.14)
Random effects		Variance		
Litter effect	(Intercept)	1.037		
Year	(Intercept)	0.361		
Colony	(Intercept)	0		

Table 2. Estimates, standard errors, and P-values from the generalized linear mixed model of agonistic networks.

Fixed effects	Estimate	Standard error	P-value	Marginal part R^2 (%)
(Intercept)	−1.653	0.728	0.0232	8.49 (5.85–33.58)
Transitivity	−0.211	0.368	0.567	0.23 (0.0–26.78)
Reciprocity	0.306	0.304	0.313	0.9 (0.0–27.32)
Degree assortativity	0.101	0.236	0.668	0.24 (0.0–26.79)
Cut points	0.092	0.305	0.764	0.0 (0.0–26.55)
Average path length	0.051	0.272	0.851	0.08 (0.0–26.66)
Centralization	−0.729	0.345	0.034*	4.84 (1.94–30.43)
Embeddedness	−0.043	0.306	0.888	0.02 (0.0–26.61)
Group size	−0.068	0.283	0.811	0.05 (0.0–26.64)
Dam presence	0.290	0.720	0.687	0.07 (00.0–26.66)
Random effects		Variance		
Litter effect	(Intercept)	1.169		
Year	(Intercept)	0		
Colony	(Intercept)	0		

We found a statistically significant negative relationship between centralization and female yearling dispersal in the agonistic networks (Table 2): ($B = -0.729$, $P = 0.034$). The other agonistic social structure measures were insignificant (Table 2): transitivity ($B = -0.211$, $P = 0.567$), reciprocity ($B = 0.306$, $P = 0.313$), degree assortativity ($B = 0.101$, $P = 0.668$), cut points ($B = 0.092$, $P = 0.764$), average path length ($B = 0.051$, $P = 0.851$), embeddedness ($B = -0.043$, $P = 0.888$), and dam presence ($B = 0.290$, $P = 0.687$). Additionally, there was no significant relationship between group size and dispersal in the agonistic model ($B = -0.068$, $P = 0.811$). This model explained 8.49% of the marginal variance and 25.49% of the conditional variance. Semi-partial marginal R^2 for each fixed effect is reported in Table 2.

Our additional models with each social network measure fitted independently of the other social network measures found the same results: no relationship between affiliative social structure and dispersal (Supplementary Table S1) and a statistically significant negative relationship between centralization and dispersal (Supplementary Table S2).

Discussion

We found no statistically significant relationship between affiliative group social structure and dispersal in female yearling yellow-bellied marmots. This result was initially surprising because affiliative social relationships at the individual level have been shown to impact dispersal in this system (Blumstein et al. 2009) and group social structure has an impact, albeit a modest one, on fitness in this system (Philson et al. 2022; Philson and Blumstein 2023a, 2023b). However, yellow-bellied marmots are facultatively, not obligately social, and this distinction has been shown to attenuate the social benefits of group living across species (Lucas and Keller 2019; Snyder-Mackler et al. 2020). Thus, yellow-bellied marmots may not possess certain adaptations for group living, such as the capability to assess their groups' social structure, which may be needed for social structure to inform life-history decisions.

One adaptation that might be required to assess group structure is a theory of mind which reflects an individual's awareness of others' intentions, knowledge, and experiences (Premack and Woodruff 1978). The cognitive scaffolding hypothesis posits that theory of mind is determined by cognitive capacity. Devaine et al. (2017) challenged seven non-human primate species to anticipate their opponents' actions in a hide-and-seek-type game and found that differences in brain volume were associated with the presence or lack of theory of mind as they studied it. The cognitive scaffolding hypothesis seems to be present in ground-dwelling sciurid rodents (like marmots), for whom sociality increases with absolute brain size (Matějů et al. 2016). Yellow-bellied marmots have a below-average relative brain size compared with other mammals, perhaps explaining their limited ability to evaluate the covert behaviors of their peers (Burger et al. 2019). Thus, there may be cognitive limitations that prevent marmots from assessing their overall group structure and thus we might not expect them to use this information to inform dispersal decisions.

Importantly, however, many factors influence brain size. Hooper et al. (2022) found that comparative studies of brain size as well as correlations between body size and cognition are not always accurate and they are often difficult to interpret. Therefore, comparative brain size studies may not provide a sound justification for a lack of specific cognitive abilities. Specific studies that focus on quantifying the theory of mind and social awareness in yellow-bellied marmots are needed to further understand whether marmots have cognitive limitations on social knoweldge.

Despite no relationships found when we examined the affiliative group structure, we found that yellow-bellied marmots were less likely to disperse when their agonistic networks were more centralized. Increased centralization in an agonistic network implies that these aggressive interactions often involve few individuals rather than many. Assessing this might not require assessment of the overall group structure because, in the context of agonistic interactions, it may simply require the knowledge that one or a few, rather than many individuals are acting aggressively toward you. Thus, individuals residing in groups with high centralization may decide that they are not experiencing enough aggression to disperse, thus deciding to remain in their natal group.

Compared with complex social awareness of group social structure, a more parsimonious explanation for higher agonistic centralization relating to philopatry is the feedback between individual social positions and group social structure (Cantor et al. 2021). Complex social network traits often arise from simple individual-level behaviors (Firth et al. 2017). Thus it is likely that individuals would be able to make decisions related to group-level social measures based on more simple social cues, such as the number of aggressive individuals with which an individual interacts. Further, given individuals structure groups and in turn, groups can influence individual social position (Cantor et al. 2021), social group structure may be influencing individual position in the network, which is then influencing dispersal decisions (as we see in this system in Blumstein et al. 2009). Importantly, if future research in another system does find that group social structure predicts dispersal, this alone does not provide sufficient evidence for complex social awareness of group social structure as it could be achieved through simple social behaviors (Firth et al. 2017). Specific exploration of the theory of mind and social awareness is needed across taxa in experimental and observational settings.

Dispersal is a multivariate decision. In this particular system, dam presence, play behavior, affiliative interactions with the mother, and space use overlap with females in the group are all proximate causes of dispersal (Armitage et al. 2011). Other aggressive individuals in a group, then, have shown to be another aspect of an individual marmot's decision to disperse. Estimating transitivity, reciprocity, degree assortativity, cut points, and average path length, whether in an agonistic or affiliative network, may all require some knowledge of the indirect interactions to evaluate. However, awareness of the agonistic centralization of one's group, more than any other emergent social structure measure, may be less cognitively demanding given it can be accessed via more simple individual-level behaviors that underline group social structures (Firth et al. 2017; Cantor et al. 2021).To further test the social structure cohesion hypothesis, similar examinations in a broad range of animals are required.

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Conflict of Interest Statement

The authors declare no conflicts of interest.

Data Availability

Analyses reported in this article can be reproduced using the data and code available on OSF: doi: 10.17605/OSF.IO/MY8Z2.

Ethics Statement

Data were collected under the UCLA Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and with permission from Colorado Parks and Wildlife (TR-917, renewed annually).

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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