

LAY SUMMARY

To better understand drivers of an individual's dispersal from their natal range, we asked if the structure of an individual's social groups influenced their decision to leave. We found that marmots seemingly do not consider their groups' 'friendly' social structure when deciding when to disperse. However, they are somewhat sensitive to the pattern of their aggressive relationships. This could be explained by cognitive limitations on marmots' ability to know the structure of their social group.

Extending the social cohesion hypothesis: Is group cohesion associated with dispersal?

Running head: Social influences on dispersal

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ABSTRACT

Dispersal is an important decision for an individual to make which may influence individual fitness as well as population viability. Prior work has shown that dispersal decisions can be influenced by an individual's position in their social network (the social cohesion hypothesis), but the dispersal consequences of group social structure have not been explored. 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, and using mixed-effects models, asked whether group structure was associated with dispersal. We found no support for the hypothesis that affiliative group structure explained any variation in a marmot's decision to disperse but marmots in groups with less agonistic centralization were less likely to disperse. The former finding may result from cognitive limitations on social knowledge while the later finding might reflect that individuals in less agonistically integrated groups are less likely to be reproductively suppressed. Regardless, these results raise important questions about the limits of social knowledge and suggest the social cohesion hypothesis – more social individuals remain at home – does not scale to the level of the group. Further work is required to determine whether dispersal decisions in obligately social species are influenced by knowledge of their group structure.

Keywords: dispersal, social cohesion, social relationships, yellow-bellied marmot

INTRODUCTION

Dispersal is defined as an organism's permanent movement from their natal home range to where they breed (Anderson 1989, Lidicker 1975). Much has been written about how this is a

mechanism of gene flow that maintains genetic diversity, reduces inbreeding, and controls population density (Armitage et al. 2011, Biek et al. 2006, Bowler & Benton 2005, Clobert et al. 2004, Matthysen 2005, Wolff 1988). Dispersal is often costly to dispersers because individuals experience novel environments and threats while dispersing and settling (Bonte et al. 2011, 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—facilitates species resilience in an increasingly stochastic and harsh environment (Gundersen & Andreassen 1997; Gibbs et al. 2010). But what mechanisms drive individuals to disperse?

The social cohesion hypothesis posits that the more an individual interacts with others, the less likely they are to disperse (Bekoff 1977). One test of this hypothesis with gorillas (*Gorilla gorilla*) found affiliative interactions with the dominant male were positively correlated with philopatry (Harcourt & 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.

Group-level social factors have also been identified as important determinants of dispersal in many species, such as white-faced capuchin (*Cebus capucinus*) monkeys where group instability and smaller group size increases rates of male natal dispersal (Jack et al. 2012). In coyotes (*Canis latrans*), lower-ranking individuals within the pack tend to disperse more (Gese et al.

1996). Similarly, smaller and weaker male red-cockaded woodpeckers (*Picoides borealis*) are more likely to disperse compared to larger individuals who may be socially dominant (Pasinelli & 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 (Kappeler 2019; Philson et al. 2022). Group social structure influences key evolutionary and ecological processes (Kurvers et al. 2014) such as group movement patterns, regulation, and formation (Dufour et al. 2011; 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. Group social structure can be quantified via social network measures that describe the connectivity, reciprocity, and social heterogeneity of a group (Philson et al. 2023b; Costello et al. 2023).

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, making the mechanisms underlying female dispersal a biologically relevant phenomenon to study (Blumstein et al. 2009). Additionally, an individual's social network position influences dispersal in females (Blumstein et al. 2009) and group social structure is

associated with some fitness correlates in this system (Philson et al. 2022; Philson & Blumstein 2023a; Philson & Blumstein 2023b). Therefore, group social structure may have relevant and important implications for dispersal decisions.

We focused on seven group-level measures of social complexity and developed *a priori* hypotheses for the social structure cohesion hypothesis in networks constructed from affiliative interactions. Density, the proportion of social relationships out of all possible relationships, quantifies how connected a group is (Burt 1992, Wasserman & Faust 1994, Grund 2012). Transitivity similarly quantifies group connectedness as the proportion of connected triads in a group (Wasserman & Faust 1994, Milo et al. 2002, Faust 2010). Reciprocity quantifies the proportion relationships where both individuals initiate at least one interaction with each other (Wasserman & 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.

The number of cut points quantifies how easily a group can fracture into two or more groups (Wasserman & Faust 1994, Borgatti 2006). Average path length calculates how far every individual is from all others (Watts & Strogatz 1998, Broder et al. 2000). Centralization quantifies if interactions flow through few or many individuals in the group (Freeman 1979, Wasserman & Faust 1994, Kang 2007). If we found that increased cut points, average path length, and centralization were positively associated with dispersal in affiliative networks, we could reject 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.

After analyzing our a priori hypotheses using affiliative networks, we then also analyzed networks calculated from agonistic interactions to further investigate the social structure cohesion hypothesis 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.

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 livetrapped 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 to 11:00 h) and in late afternoon (16:00 to 18:00 h) (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 meters, 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 2023b).

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. in revision). We used this definition because virtually all pups had emerged by this date, and yearlings generally disperse within 10 days of their colony’s first pup emergence (Armitage 1991). We excluded animals confirmed to be dead (see Edic et al. in revision). 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 as 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 & 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 & Nepusz 2006; Rosvall & 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 & 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 & Blumstein 2023a, Philson & Blumstein 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 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 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 (Armitage et al. 2011, Blumstein et al. 2009) 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 estimate effect sizes, we used “partR2” (version 0.9.1; Nakagawa & Schielzeth 2013; Stoffel et al. 2021; Stoffel et al. 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 ($B = -0.319$, $P = 0.238$), 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 are reported in Table 1.

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 ($B = -0.043$, $P = 0.888$), 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 are reported in Table 2.

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 & Blumstein 2023a, Philson & Blumstein 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 & Keller 2019, Snyder-Mackler et al. 2020).

Most previous associations between social network measures and fitness correlates in yellow-bellied marmots are negative (Philson et al. 2022, Philson & Blumstein 2023a, Philson & Blumstein 2023b). Individual closeness and increased network degree are both associated with decreased survival in this system, as opposed to what has been reported in primates, ungulates, whales, and hyraxes, for whom closer and stronger affiliative networks are associated with increased survival (Snyder-Mackler et al. 2020). As marmot groups became more connected, individuals gained less mass (Philson et al. 2022) and experienced decreased winter survival (Philson & Blumstein 2023b). Increased group fragmentability is modestly associated with a greater number of offspring weaned (Philson & Blumstein 2023a), suggesting a potential fitness benefit of living in less connected groups. Each of these findings reflect the relative lack of, if not negative, influence that social connectivity has on fitness in yellow-bellied marmots. However, they do not explain the complete lack of influence that social network structure has on dispersal decisions seen here.

For group structure to impact marmot dispersal decisions, individuals may have to be aware of their groups' social structure. Given their facultatively social nature and the lack of benefits they gain from individual and group connectivity, they may not possess the cognitive adaptations to assess their group's structure.

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 & Woodruff 1978). Povinelli et al. (1990) found that obligately social chimpanzees (*Pan troglodytes*) were able infer covert mental states from overt behavior when they distinguished

between a human who knew the location of food under a cup and one who did not. 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, for whom sociality increases with absolute brain size (Matějů et al. 2016).

Yellow-bellied marmots have a below-average relative brain size compared to other mammals, perhaps explaining their limited ability to evaluate the covert behaviors of their peers (Figure 1). 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.

Despite their apparent lack of awareness of their affiliative group structure, yellow-bellied marmots in this system 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 advanced cognitive abilities (such as social awareness of others or the group) 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 towards you. Thus, individuals residing in groups with low centralization may decide that they are not experiencing enough aggression to disperse, thus deciding to remain in their natal group.

Estimating transitivity, reciprocity, degree assortativity, cut points, and average path length, whether in an agonistic or affiliative network, would all require some knowledge of the indirect

interactions to evaluate. Thus, awareness of the agonistic centralization of one's group, more than any other emergent social structure measure, may be less cognitively demanding, and thus, within the ability of the relatively small-brained yellow-bellied marmot. To further test the social structure cohesion hypothesis, similar analyses on obligately social animals and those with larger brains are required.

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DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Schneidman SA, Philson CS, Blumstein DT. 2023. Data for: Extending the social cohesion hypothesis: Is group cohesion associated with dispersal?. doi: 10.17605/OSF.IO/MY8Z2

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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Figure 1. Body size-brain size regression plotted from data in Burger et al. (2019) with yellow-bellied marmot data point highlighted as a red star.

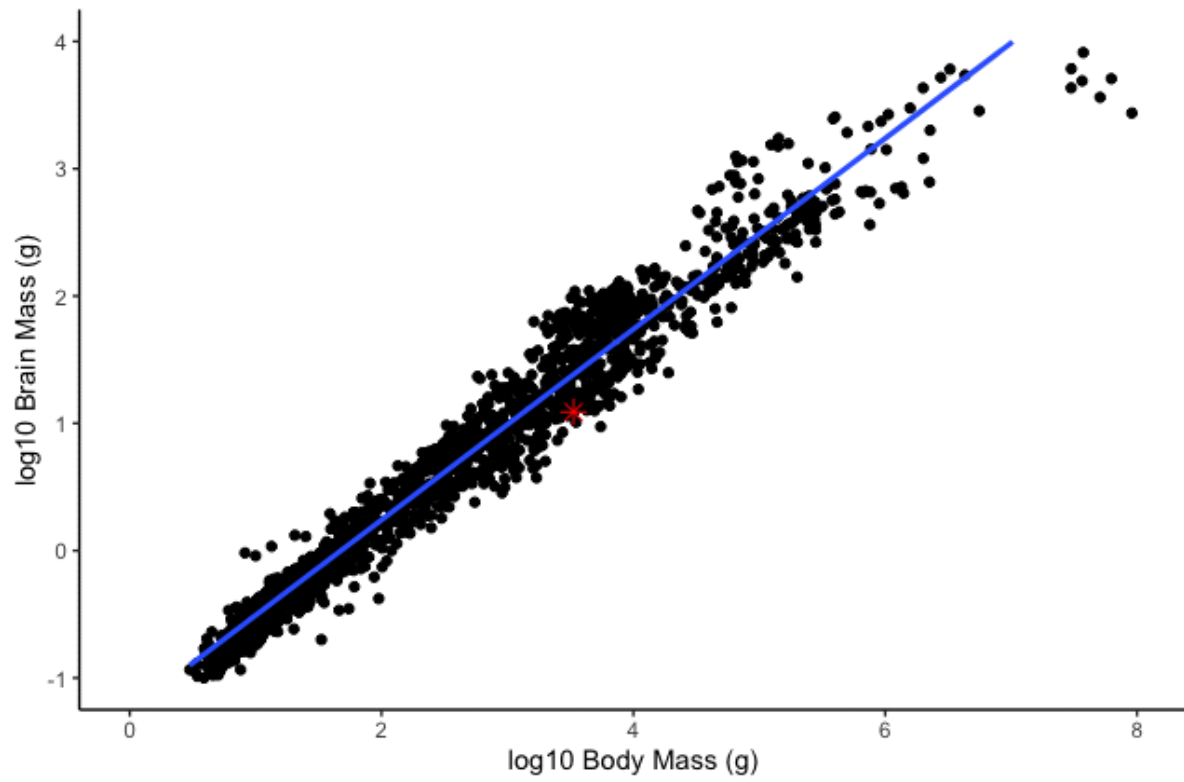


Table 1. Estimates, standard errors, p-values, and marginal part R^2 values from the generalized linear mixed model of affiliative networks

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
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Litter effect	(Intercept)	1.169
Year	(Intercept)	0
Colony	(Intercept)	0
