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A test of the social cohesion hypothesis: interactive female marmots remain at home

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Individuals frequently leave home before reaching reproductive age, but the proximate causes of natal dispersal remain relatively unknown. The social cohesion hypothesis predicts that individuals who engage in more (affiliative) interactions are less likely to disperse. Despite the intuitive nature of this hypothesis, support is both limited and equivocal. We used formal social network analyses to quantify precisely both direct and indirect measures of social cohesion in yellow-bellied marmots. Because approximately 50 per cent of female yearlings disperse, we expected that social relationships and network measures of cohesion would predict dispersal. By contrast, because most male yearlings disperse, we expected that social relationships and cohesion would play a less important role. We found that female yearlings that interacted with more individuals, and those that were more socially embedded in their groups, were less likely to disperse. For males, social interactions were relatively unimportant determinants of dispersal. This is the first strong support for the social cohesion hypothesis and suggests that the specific nature of social relationships, not simply the number of affiliative relationships, may influence the propensity to disperse.

Keywords: dispersal; proximate causes; social cohesion hypothesis; yellow-bellied marmot

1. INTRODUCTION

Over 30 years ago, Marc Bekoff developed the social cohesion hypothesis to explain variation in dispersal patterns (Bekoff 1977). Bekoff focused on affiliative interactions, specifically pre-dispersal play behaviour, and predicted that individuals who socialized with others were less likely to disperse (i.e. ‘individuals who play together, stay together’; Poirier *et al.* 1978). The social cohesion hypothesis makes specific predictions about the nature of social interactions and dispersal; namely, that social interactions and relationships should be primary determinants of philopatry.

Despite over 30 years of subsequent research on dispersal, few studies have quantified the relationship between the nature of individual interactions and an individual’s subsequent likelihood of dispersal. Those that have done so provide equivocal findings. In support of the hypothesis, Harcourt & Stewart (1981) studied four young male gorillas (*Gorilla gorilla*) and found that individuals who had more affiliative social interactions with the dominant male were less likely to disperse. Harris & White (1992) used an indirect measure of interactiveness (the extent of chewing on plastic ear tags) and found that female red fox (*Vulpes vulpes*) cubs that had their tags chewed more by adult foxes were less likely to disperse. By contrast, in a much more quantitative behavioural analysis of individuals, Sharpe (2005) found no relationship between play behaviour in meerkats (*Suricata suricatta*) and the time of subsequent dispersal in either

females (who are evicted from the group) or males (who appear to leave on their own).

Recent advances in the application of social network analysis to studying animal behaviour (Krause *et al.* 2007; Croft *et al.* 2008; Wey *et al.* 2008; Whitehead 2008) provide a timely opportunity to re-evaluate the social cohesion hypothesis. Social network statistics allow us to quantify different attributes of social relationships in a consistent way. Individuals in a social group have direct relationships when they are observed to interact. However, other attributes of sociality that incorporate indirect interactions, such as how embedded individuals are in their social group, may also have consequences. For instance, the probability of getting a sexually transmitted disease not only depends on with whom one has sex, but also with whom one’s sex partner had sex and the entire network of sexual relationships (Liljeros *et al.* 2003). It may be beneficial for subordinates to interact with those who interact with dominant animals.

If social relations influence dispersal decisions, then the extent to which an individual is integrated into a social group should predict its likelihood of dispersal. Moody & White (2003) defined a measure of social embeddedness based on social integration. Briefly, in a network of nodes and ties, a path is an alternating sequence of contiguous nodes and ties beginning and ending with a node, in which no node occurs more than once. Paths are node-independent if they share no nodes (figure 1). A k -component is a maximal subset of nodes in which all nodes are mutually reachable by at least k node-independent paths using only nodes in the subset. Maximal means that no other node can be added to the set while ensuring that all members still be k connected (figure 1). A node’s social embeddedness is the largest k -component to which it belongs (for detailed

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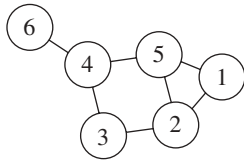


Figure 1. A simple network illustrating concepts used in determining embeddedness.

Node-independent paths. There is at least one path between every node. There are also at least two node-independent paths between each of nodes 1–5. For example, between nodes 1 and 3, there are four distinct paths (1 2 3; 1 2 5 4 3; 1 5 2 3; and 1 5 4 3) but only two node-independent paths because node 2 appears in all the first three and node 5 appears in all the last three. The two node-independent paths are 1 2 3 and 1 5 4 3. As another example, there are three node-independent paths between nodes 2 and 5 (directly between them, through 1 and through 3 and 4). ***k*-components.** All six nodes are mutually reachable through at least one node-independent path and hence are a one-component. Nodes 1–5 are mutually reachable by two node-independent paths and since all these paths use only nodes 1–5, they are a two-component. While nodes 2 and 5 are connected by three node-independent paths, if we consider only nodes 2 and 5, only one path exists between them. The other two paths use other nodes beyond the set of 2 and 5, hence they are not a three-component. Therefore, node 6 has embeddedness of 1, and all other nodes have embeddedness of 2. Note that embeddedness captures a distinctly different aspect of sociality than does degree (the number of ties a node has). Node 6 has degree 1, nodes 1 and 3 have degree 2, and nodes 2, 4 and 5 have degree 3.

explanation see the electronic supplementary material). We extend the concept of social embeddedness as a measure of an animal's integration into a social group, which should be relevant to many behavioural decisions. From the standpoint of an individual facing a dispersal decision, the more independent connections it has to others in a group, the stronger its membership or integration into that group and the less likely it should be to disperse. Conversely, an individual with no or few independent connections will be a peripheral group member and may be more likely to disperse. It remains an empirical question as to whether a measure of direct interactions only, a measure of connectedness that includes indirect relations, or a combination of both types of relationships influence dispersal; and, if they all do, which is the most important. By applying formal network analyses, it will be possible to test Bekoff's social cohesion hypothesis in a novel and, perhaps, more revealing way.

We studied how social relationships influenced subsequent dispersal in yearling yellow-bellied marmots (*Marmota flaviventris*), a facultatively social rodent. Marmots are particularly well suited for this study because approximately 50 per cent of female yearlings and most male yearlings disperse (Armitage 1991; Van Vuren & Armitage 1994), and previous studies suggest that sociality and kinship influence dispersal (Armitage 1986a). Thus, if the social cohesion hypothesis explained patterns of dispersal in marmots, we expected that social relationships would be relatively more important for the facultatively dispersing females than for the more obligately dispersing males. Marmots engage in a variety of social interactions, including, but not limited to, play behaviour (Nowicki & Armitage 1979), and they are easily observed

early in the season, the time of year when most social interactions occur. Thus, by formally quantifying both direct measures of interactions and how well individuals were embedded in their group, we are able to test the social cohesion hypothesis of dispersal in marmots.

2. MATERIAL AND METHODS

Studies were conducted with free-living yellow-bellied marmots in the East River Valley in and around the Rocky Mountain Biological Laboratory in Gunnison County, CO, a location where marmots have been studied since 1962 (Blumstein *et al.* 2006). Marmots were live-trapped and permanently marked for identification with unique ear tags, weighed, and uniquely marked on their dorsal pelage with black Nyanzol dye for observation from afar. Marmots were observed from distances that did not interfere with their normal behaviour; distances depended on the social group and ranged from 20 to 150 m.

Marmots emerge from hibernation in April and May, and are active in the morning and late afternoon. Between mid-April and August from 2003 to 2007, during most mornings and some afternoons (07:00–10.00 and 16:00–19:00 h respectively, the periods of peak marmot activity; Armitage 1962), we used all occurrence sampling of social interactions during focal group watches to identify the initiator, the recipient and the individual who was displaced following all bouts of social behaviour (detailed ethogram in the electronic supplementary material). For analysis, we combined all affiliative behaviour (allogrooming, forage together within 1 m, greet, sit <1 m apart, play and sniff anogenital region), and all agonistic behaviour (aggression, displacement), into two categories—affiliative and agonistic. In those (few) cases where we could not distinguish between a bout of affiliative or agonistic behaviour, we removed the interaction from the dataset.

From the set of social interactions observed between emergence from hibernation and pup emergence (the time of year by which yearlings typically disperse), we calculated unweighted (i.e. binary) and weighted (i.e. based on the number of observed interactions) pair-wise interaction matrices separately for the set of all affiliative interactions, all agonistic interactions and then the subsets of yearling–yearling and yearling–adult affiliative and agonistic interactions. We broke down social interactions into these categories for the following reasons. First, the social cohesion hypothesis specifically focuses on affiliative interactions. However, we wished to examine also the set of agonistic interactions alone, to see if either was correlated with dispersal. Second, we wished to explore the importance of relationships between older and younger animals. While the social cohesion hypothesis (as Bekoff envisioned it) focused more on yearling–yearling interactions, adult–yearling interactions could also be associated with dispersal if adults actively evicted yearlings. We did not subdivide interactions by sex, but rather focused on age cohort because the social cohesion hypothesis makes no specific predictions about the nature of male–female relationships within or between age cohorts. We focused on four colony sites, and defined social networks within them annually; our data consist of 20 colony-years. At each colony site, marmots shared burrows and space with a subset of all possible individuals and we refer to these as social groups; our data consist of 73 social group-years. We justify treating groups differently

each year because group composition changed dramatically as a result of births, deaths and dispersal. We calculated degree from binary and symmetric networks (which measures how many interactants an individual has), as well as from weighted and symmetric networks (which measures interaction strength) to see if it explained more variation in dispersal. Embeddedness is the same whether it is calculated for a weighted or unweighted network. We did not calculate directional network measures both because the social cohesion hypothesis is agnostic with respect to initiator, and because we elected (as described above) to examine subsets of interaction types.

By design, we did not ‘filter data’ (i.e. eliminate relationships with fewer than x observations, where x might be one or a few observations; Croft *et al.* 2008). Filtering is commonly used when studying fission–fusion societies (e.g. Rubenstein *et al.* 2007; Sundaesan *et al.* 2007) to eliminate chance interactions. However, marmots live in seasonally stable social groupings, and we watched each of these groups regularly throughout the season. Thus, we believe rare events accurately reflect pairs of individuals who rarely interact. Eliminating them would make our network unnecessarily sparse and would underestimate weak, but potentially important, links. For studies focusing on stable social groups, determining the effort required to obtain stable estimates (see Wey *et al.* 2008) is essential. In such cases, filtering may provide misleading results.

We calculated the following social network statistics for each subset of data (definitions for degree follow Wey *et al.* 2008; see also Wasserman & Faust 1994; Moody & White 2003; Whitehead 2008) using UCINET v. 6 (Borgatti *et al.* 2006). *Degree* is the number of other individuals with whom a focal subject was observed to interact. It is a direct measure of social cohesion: individuals with a greater degree are better integrated into the group. *Normalized degree* is standardized for group size. By normalizing it, we controlled for the different opportunities available for interactions with different-sized groups. In both unweighted and weighted analyses, we calculated the normalized degree. As described above, *embeddedness* is the k of the largest k -component to which an individual belongs, and it is a measure of how well integrated an individual is in its group. It is a measure of sociality that also captures indirect interactions, where those in larger k -components are more socially integrated than those in smaller k -components. Degree captures direct interactions only, while embeddedness incorporates direct and indirect interactions. Embeddedness does not account for all of an individual’s indirect interactions in the network, but rather the indirect interactions of those in the individual’s k -component. Thus, it captures a subset of the network interactions that are still close to the focal individual and likely to factor into dispersal decisions. By contrast, network centrality measures calculated on the basis of all of an individual’s indirect interactions are more appropriate when trying to determine the individual’s potential influence on the rest of the network. Embeddedness is also appropriate for networks with disconnected subgroups (such as in our system), whereas other metrics such as eigenvector centrality or information centrality are not.

In addition to the social network statistics described earlier, we included several additional variables in our logistic regression models because of their potential effect on social interactions. In large social groups, individuals may avoid interactions with other individuals (Armitage 1986a);

hence, group size, acting through its effect on social interactions, might independently influence dispersal probability. Not all individuals in the colonies spend the same amount of time together, so colonies may be further subdivided into social groups. *Social group size* was defined based on burrow-use overlap (i.e. animals detected using the same burrows both through observations and trapping). We used SOCPROG v. 2.3 (Whitehead 2009) to calculate the simple ratio, and when values exceeded 0.5 we classified animals as in the same social group (details in Nanayakkara & Blumstein 2003). Two other measures addressed the opportunity or constraints on social interactions: the *number of other yearlings of the same sex in the colony* and the *number of adults of the same sex in the colony*.

Because our measures of binary degree and embeddedness were highly correlated (r -values often exceeded 0.8), building models with all three or subsets of two variables in them created a multicollinearity problem. We therefore elected to fit separate models with our potentially important covariates and included unweighted degree, weighted degree or embeddedness in each model.

Marmots typically disperse before the young of the year emerge from their natal burrows (Armitage 1991). Because this date varied by year and by colony site, we conservatively defined dispersed individuals as those that were seen (and therefore known to be alive) earlier in the year and were no longer seen later in the year up to 10 days after the date of a colony site’s first pup emergence. Animals known to be dead (from predation or early-season starvation) were not included in our analyses, but we acknowledge that some disappearances could result from undetected mortality.

To study factors that influenced the likelihood of dispersal, we fitted a set of logistic regression models in SPSS v. 16 (SPSS, Inc. 2007) to explain the likelihood of dispersal in yearling females ($n = 130$, of which 55 dispersed) and yearling males ($n = 149$, of which 103 dispersed). Data for these analyses resulted from 3746 h of direct observations. For each model, we reported the percentage correctly predicted and used these values to calculate the adjusted count pseudo- R^2 value (Long 1997) as a descriptive measure to identify which types of interactions (affiliative or agonistic), and between which sets of individuals (all, yearling–yearling or adult–yearling), better accounted for dispersal. The adjusted count pseudo- R^2 value is not based on a specific likelihood model; thus it is comparable across different datasets. For a block of analyses—a block consists of a type of social interaction (affiliative or agonistic) between a set of individuals (all, yearling–yearling, adult–yearling) for a given sex—we used the Akaike information criterion to help identify the model within each of these blocks that best explained dispersal, and identified which variables significantly explained variation in dispersal, along with the direction of their effect. We report all the analyses to illustrate the pattern of results.

3. RESULTS

We observed 15 149 social interactions that could be classified as affiliative or agonistic. From these observations we calculated interaction matrices. Overall, social factors, particularly those that described the number and embeddedness of individuals with whom they interacted, significantly explained up to 31 per cent of the variation in the likelihood of female dispersal: more integrated females were less likely to disperse (electronic supplementary material, tables 1 and 2; figure 2).

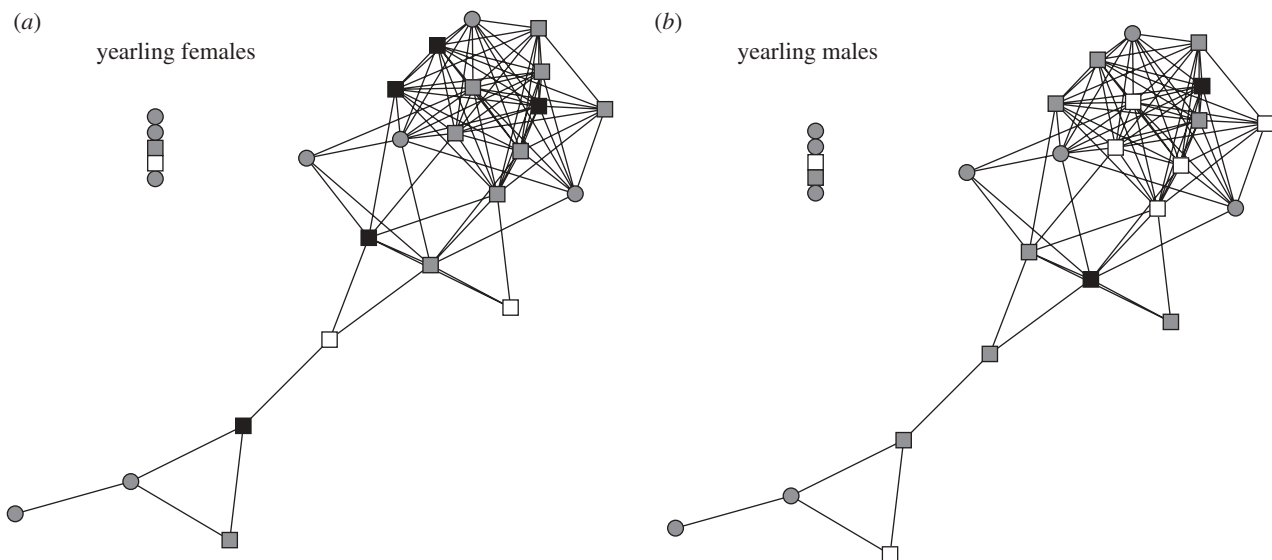


Figure 2. Illustrations of an affiliative social network based on all observed social interactions for the Marmot Meadow colony in 2007. Square, yearling; circle, adult; white, dispersed; black, not dispersed. (a) Female yearlings that dispersed are represented by white squares. Female yearlings that did not disperse are represented by black squares. All other individuals are grey. Note that female yearlings that dispersed tended to be more peripheral. (b) Male yearlings that dispersed are represented by white squares. Male yearlings that did not disperse are represented by black squares. All other individuals are grey. Note that male yearlings that dispersed were not always peripheral.

The best models were typically obtained when embeddedness was included, although embeddedness was not a significant predictor of dispersal in all cases. For females, analyses based on observations of affiliative interactions better explained the likelihood of dispersal than those based on agonistic interactions. Indeed, when we focused on the set of agonistic interactions, social group size, not network statistics, often predicted dispersal (i.e. animals in larger groups were less likely to disperse). This latter finding is not consistent with the hypothesis that competition may be important in female yearling dispersal.

Considerably less variation in male dispersal (<9%) was explained by measured variables (electronic supplementary material, table 1). In no case was a model based on observations of yearling males significant. In those cases where variables significantly explained the likelihood of male dispersal, weighted degree explained more variation than unweighted degree or embeddedness. In models based on the set of observed agonistic interactions, yearling–yearling interactions seem important, but, again, as with females, males in larger groups are less likely to disperse. In many cases, no social variables significantly predicted yearling male dispersal.

4. DISCUSSION

As predicted by Bekoff's social cohesion hypothesis, the nature of social relationships influenced the pattern of yearling female dispersal: well-embedded females were less likely to disperse. Models with unweighted degree explained slightly more variation than those with weighted degree. However, models with embeddedness systematically explained more variation in the likelihood of dispersal than either measure calculated from only direct interactions, suggesting that indirect interactions are important. Moreover, affiliative relationships explained more variation in the likelihood of dispersal

than agonistic relationships. This suggests that agonistic relationships may be relatively less important for predicting dispersal in this system. Hence, female marmots appear to disperse not because they are evicted following agonistic interactions with others, but rather because they have not developed strong affiliative ties with others (see also Bekoff 1977). By contrast, we found that social factors are relatively less important in explaining variation in the likelihood of yearling male dispersal, and variation in yearling male dispersal remains mostly unexplained. We believe this is because most yearling males ultimately disperse in this system, regardless of social factors. For females, however, we believe that our findings provide the strongest quantitative support yet for Bekoff's (1977) social cohesion hypothesis.

This study is novel for dispersal studies because direct and indirect attributes of social relationships were identified by calculating formal social network statistics from interaction matrices. By using network statistics, we were able to identify specific aspects of sociality that were most important in determining female dispersal. For female marmots, we found that being part of a more cohesive subgroup was more important than simply interacting with more individuals or interacting more frequently. Formal social network analyses have begun to shed novel insights into key players in social groups (Flack *et al.* 2006), the development of social skills (Ryder *et al.* 2008), the differences in social organization among species (Sundaresan *et al.* 2007) and applied welfare management (McCowan *et al.* 2008). Our findings join these, and other, recent discoveries that illustrate the utility of applying formal social network analyses to study animal behaviour (Croft *et al.* 2008; Wey *et al.* 2008).

Our main finding about dispersal tendencies of female marmots differs from Armitage's (1986*b*) report that in large colony sites, adult females can avoid interacting

with their young and thus may be more likely to recruit daughters. We found that yearling females who had more interactions with adults (who were likely to be mostly relatives) were more likely to remain in the group. However, Armitage (1991) also summarized a series of studies that demonstrated that sociable adult females (as measured in a mirror-image-stimulation test) were more likely to recruit young to their group. Perhaps some of the difference in these studies is the target of study: our study focused on the potential disperser and demonstrates that females who have both direct and indirect affiliative interactions with others are more likely to remain in their natal social group, while Armitage focused on attributes of females who recruited daughters.

Overall, for female (but not male) marmots, we found convincing support of Bekoff's (1977) social cohesion hypothesis, and in the few cases where interactions explained male dispersal, results were consistent with the social cohesion hypothesis. Criticisms of the social cohesion hypothesis (e.g. Smith 1982) highlight Bekoff's initial focus (Bekoff 1977; but see Bekoff 1984) on the importance of play behaviour as a route to social cohesion. Indeed, Sharpe (2005) questioned whether play was even a type of affiliative behaviour because rates of play behaviour were not correlated with rates of affiliative allogrooming behaviour in meerkats. Our support for the social cohesion hypothesis in female yearlings is strong because we did not focus exclusively on play, but rather on all types of interactions. Our statistical models that included all affiliative interactions explained more variation in yearling dispersal than those that focused on agonistic interactions. Our results thus parallel previous work showing that aggression was not always the proximate cause of dispersal in a variety of species (reviewed in Bekoff 1977).

Clearly, social cohesion does not explain all the variation in the likelihood of female dispersal, and it explains extremely limited variation in the likelihood of male dispersal. Thus, these results are a call for more comprehensive future research on the proximate determinants of dispersal. Our conclusions can be rigorously tested in other social systems. We expect that social relationships will predict variation in dispersal when there is equal opportunity to stay or leave (as with yearling females in our system), but not when there is little variation in the number of individuals who disperse (as with yearling males in our system). We did not investigate the predictive value of different types of interactions within 'affiliative' and 'agonistic' groupings; future studies could focus on the roles that particular behaviours may play in determining dispersal.

The proximate causes underlying dispersal have important implications for conservation behaviour (Blumstein & Fernández-Juricic 2004) because time allocated to social behaviour may be reduced when animals are disturbed by anthropogenic disturbances (Pollard & Blumstein 2008). Thus, it is important to understand better the role that social relationships play in dispersal. For species where social cohesion influences dispersal, anthropogenic disturbances that may reduce the number and kind of social interactions could lead to increased rates of dispersal. Increased dispersal might reduce local adaptation (Postma & van Noordwijk 2005), as well as having deleterious effects on complex, yet adaptive, social behaviours (e.g. Chapais *et al.* 2001; Holmes 2001).

Our results are also necessarily correlative. While it might be possible to manipulate the nature and number of social relationships, such social deprivation experiments create a variety of problems in their interpretation (Bekoff 1976; Pellis 2002). Nevertheless, employing formal social network analyses on a variety of other species will probably help us develop novel insights into the proximate correlates of dispersal and better evaluate the importance of social cohesion on dispersal.

Marmots were studied under research protocol ARC no. 2001-191-01, approved by the UCLA Animal Care Committee on 13 May 2002 and renewed annually, and trapped under permits issued by the Colorado Division of Wildlife. We thank Janice Daniel and Lucretia Olson for help managing the marmot database, and Rick Grannis for introducing us to the embeddedness statistic, supplying detailed explanations found in Appendix A and providing a great sounding board for all things 'network'. We are particularly grateful to Lucretia, who also helped manage our volunteers who kept marmots identified and social interactions quantified. Partial support for this research came from the National Geographic Society, the Unisense foundation, UCLA Faculty Senate Faculty Research Grants and the UCLA Division of Life Sciences Dean's recruitment and retention funds (to D.T.B.), NSF-DBI-0242960 (to the Rocky Mountain Biological Laboratory), a US Department of Education GAANN Fellowship administered through UCLA, a UCLA George Bartholomew Research Fellowship and RMBL Snyder Graduate Research Fellowship (to T.W.W.). Finally, we thank Philip Ender and Xiao Chen for statistical advice, and Ken Armitage, Marc Bekoff, Rick Grannis, Brandt Ryder, Dirk Van Vuren, Hal Whitehead and an anonymous reviewer for astute comments on previous versions of this manuscript.

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ESM Table 1. Results (B-value (- values mean less likely to disperse), p-value, and the percent of dispersals correctly predicted) from logistic regression analysis predicting the likelihood of yearling dispersal that included Unweighted Degree, Weighted Degree, or Embeddedness as the social network independent variable. Variables in bold explain significant ($p < 0.05$), and variables italicized explain moderately significant ($0.1 > p > 0.05$) variation in the probability of dispersing. Adjusted count pseudo-R² values along with the model p-value and the AIC value are provided. Table A focuses on affiliative interactions and table B focuses on agonistic interactions. Interactions are further subdivided according to interactants (all, yearling-yearling and adult-yearling).

A	Females							Males							
	Set of social interactions	Variable	B	p-value	% correctly predicted	N	Pseudo R ²	AIC	Variable	B	p-value	% correctly predicted	N	Pseudo R ²	AIC
All affiliative	Model			0.001	68.5	130	0.255	155.012	Model		0.221	69.8	149	0.221	155.012
	Constant	0.709	0.337						Constant	1.455	0.043				
	Social Group Size	-0.026	0.382						Social Group Size	-0.042	0.163				
	Un-weighted Degree	-0.058	0.003						Un-weighted Degree	-0.016	0.304				
	N Same Sex Yearlings	0.003	0.960						N Same Sex Yearlings	0.05	0.285				
	N Same Sex Adults	0.012	0.723						N Same Sex Adults	-0.034	0.715				
All affiliative	Model		<0.001	66.9	130	0.218	155.142	Model		0.106	69.8	149	0.106	155.142	
	Constant	0.609	0.397					Constant	1.757	0.018					
	<i>Social Group Size</i>	-0.047	<i>0.094</i>					<i>Social Group Size</i>	-0.046	0.096					
	Weighted Degree	-0.196	0.004					<i>Weighted Degree</i>	-0.079	<i>0.088</i>					
	N Same Sex Yearlings	0.029	0.622					N Same Sex Yearlings	0.028	0.572					
	N Same Sex Adults	0.008	0.801					N Same Sex Adults	-0.027	0.769					
All affiliative	Model		<0.001	70.8	130	0.309	145.894	Model		0.246	70.5	149	0.246	145.894	
	Constant	-0.168	0.784					Constant	1.195	0.053					
	Social Group Size	0	0.997					Social Group Size	-0.037	0.258					

Embeddedness	-0.325	<0.001
N Same Sex Yearlings	0.046	0.422
N Same Sex Adults	0.044	0.170

Embeddedness	-0.074	0.384
N Same Sex Yearlings	0.059	0.189
N Same Sex Adults	-0.009	0.916

YY
affiliative

Model		0.001	66.4	128	0.189	149.184
Constant	0.364	0.622				
Social Group Size	-0.02	0.525				
Un-weighted Degree	-0.036	0.004				
N Same Sex Yearlings	0.002	0.970				
N Same Sex Adults	0.024	0.465				

Model		0.291	71.4	147	
Constant	1.245	0.084			
Social Group Size	-0.051	0.092			
Un-weighted Degree	-0.004	0.702			
N Same Sex Yearlings	0.052	0.317			
N Same Sex Adults	0.002	0.964			

YY
affiliative

Model		<0.001	65.6	128	0.17	151.619
Constant	0.578	0.438				
Social Group Size	-0.042	0.141				
Weighted Degree	-0.117	0.003				
N Same Sex Yearlings	0.004	0.956				
N Same Sex Adults	0.025	0.448				

Model		0.105	69.4	147	
Constant	1.764	0.019			
Social Group Size	-0.046	0.104			
Weighted Degree	-0.042	0.098			
N Same Sex Yearlings	0.008	0.883			
N Same Sex Adults	0.017	0.850			

YY
affiliative

Model		0.001	65.1	129	0.167	147.782
Constant	-0.398	0.503				
Social Group Size	-0.005	0.893				
Embeddedness	-0.292	0.003				
N Same Sex Yearlings	0.056	0.319				
N Same Sex Adults	0.036	0.258				

Model		0.308	70.5	149	
Constant	1.13	0.069			
Social Group Size	-0.048	0.135			
Embeddedness	-0.032	0.708			
N Same Sex Yearlings	0.064	0.155			
N Same Sex Adults	-0.01	0.910			

AY
affiliative

Model		<0.001	66.9	130	0.218	140.242
Constant	0.802	0.278				
Social Group Size	-0.063	0.024				
Un-weighted Degree	-0.169	0.002				
N Same Sex Yearlings	-0.015	0.806				
N Same Sex Adults	0.041	0.192				

Model		0.074	71.8	149	
Constant	1.606	0.018			
Social Group Size	-0.043	0.124			
<i>Un-weighted Degree</i>	-0.086	<i>0.051</i>			
N Same Sex Yearlings	0.039	0.411			
N Same Sex Adults	-0.018	0.843			

AY affiliative	Model		0.001	63.1	130	0.127	148.415	Model		0.149	70.5	149
	Constant	0.43	0.534					Constant	1.401	0.031		
	Social Group Size	-0.06	0.030					<i>Social Group Size</i>	-0.048	<i>0.083</i>		
	Weighted Degree	-0.344	0.010					Weighted Degree	-0.124	0.149		
	N Same Sex Yearlings	0.009	0.872					N Same Sex Yearlings	0.05	0.285		
	N Same Sex Adults	0.036	0.247					N Same Sex Adults	-0.019	0.829		
AY affiliative	Model		<0.001	67.7	130	0.236	139.539	Model		0.210	69.1	149
	Constant	0	0.999					Constant	1.139	0.059		
	<i>Social Group Size</i>	-0.052	<i>0.065</i>					<i>Social Group Size</i>	-0.044	0.129		
	Embeddedness	-0.8	0.001					Embeddedness	-0.214	0.276		
	N Same Sex Yearlings	0.038	0.511					N Same Sex Yearlings	0.061	0.171		
	N Same Sex Adults	0.066	0.038					N Same Sex Adults	0.005	0.959		

Set of social interactions	B Females							Males						
	Variable	B	p-value	% correctly predicted	N	Pseudo R ²	AIC	Variable	B	p-value	% correctly predicted	N	Pseudo R ²	
All agonistic	Model		0.036	59.2	130	0.036	158.337	Model		0.309	69.1	149		
	Constant	-0.201	0.787					Constant	1.196	0.087				
	Social Group Size	-0.064	0.019					<i>Social Group Size</i>	-0.055	0.046				
	Un-weighted Degree	-0.019	0.416					Un-weighted Degree	-0.006	0.718				
	N Same Sex Yearlings	0.042	0.459					N Same Sex Yearlings	0.064	0.153				
	N Same Sex Adults	0.043	0.200					N Same Sex Adults	-0.011	0.904				
All agonistic	Model		0.041	60.8	130	0.073	160.869	Model		0.321	69.1	149		
	Constant	-0.305	0.683					Constant	1.018	0.126				
	Social Group Size	-0.066	0.015					<i>Social Group Size</i>	-0.053	0.049				

All agonistic	Weighted Degree	-0.034	0.554				
	N Same Sex Yearlings	0.043	0.471				
	N Same Sex Adults	0.048	0.145				
	Model		0.010	66.2	130	0.2	149.665
	Constant	-0.161	0.798				
	Social Group Size	-0.057	0.040				
	<i>Embeddedness</i>	-0.234	<i>0.066</i>				
	N Same Sex Yearlings	0.056	0.313				
N Same Sex Adults	0.042	0.182					

Weighted Degree	0.007	0.870				
N Same Sex Yearlings	0.068	0.134				
N Same Sex Adults	0.003	0.976				
Model		0.175	69.1	149		
Constant	1.441	0.033				
<i>Social Group Size</i>	-0.054	<i>0.050</i>				
Embeddedness	-0.127	0.192				
N Same Sex Yearlings	0.061	0.169				
N Same Sex Adults	-0.016	0.864				

YY agonistic	Model		0.011	60.9	128	0.057	136.374
	Constant	0.211	0.806				
	Social Group Size	-0.071	0.010				
	Un-weighted Degree	-0.03	0.118				
	N Same Sex Yearlings	0.027	0.667				
	N Same Sex Adults	0.036	0.292				

Model		0.239	69.4	147		
Constant	1.403	0.050				
Social Group Size	-0.059	0.033				
Un-weighted Degree	-0.01	0.402				
N Same Sex Yearlings	0.055	0.237				
N Same Sex Adults	-0.008	0.934				

YY agonistic	Model		0.010	58.6	128	0	137.503
	Constant	0.17	0.836				
	Social Group Size	-0.068	0.012				
	Weighted Degree	-0.048	0.123				
	N Same Sex Yearlings	0.01	0.880				
	N Same Sex Adults	0.043	0.180				

Model		0.264	70.1	147		
Constant	1.308	0.059				
Social Group Size	-0.057	0.038				
Weighted Degree	-0.014	0.515				
N Same Sex Yearlings	0.053	0.276				
N Same Sex Adults	0.001	0.988				

YY agonistic	Model		0.043	62	129	0.093	135.462
	Constant	-0.383	0.568				
	Social Group Size	-0.067	0.013				
	Embeddedness	-0.107	0.522				
	N Same Sex Yearlings	0.049	0.369				
	N Same Sex Adults	0.051	0.114				

Model		0.280	69.1	149		
Constant	1.257	0.061				
Social Group Size	-0.057	0.041				
Embeddedness	-0.074	0.518				
N Same Sex Yearlings	0.069	0.124				
N Same Sex Adults	-0.018	0.842				

AY agonistic	Model		0.014	59.4	128	0.055	148.226	Model		0.210	68.2	148
	Constant	0.343	0.638					Constant	1.353	0.053		
	Social Group Size	-0.056	0.042					<i>Social Group Size</i>	-0.051	<i>0.065</i>		
	<i>Un-weighted Degree</i>	-0.091	<i>0.084</i>					Un-weighted Degree	-0.042	0.286		
	N Same Sex Yearlings	0.005	0.940					N Same Sex Yearlings	0.049	0.310		
	N Same Sex Adults	0.033	0.297					N Same Sex Adults	-0.006	0.947		
AY agonistic	Model		0.029	56.3	128	-0.018	155.531	Model		0.272	68.9	148
	Constant	0.137	0.851					Constant	1.193	0.076		
	Social Group Size	-0.062	0.023					<i>Social Group Size</i>	-0.053	<i>0.054</i>		
	Weighted Degree	-0.113	0.224					Weighted Degree	-0.052	0.481		
	N Same Sex Yearlings	0.015	0.797					N Same Sex Yearlings	0.057	0.238		
	N Same Sex Adults	0.037	0.245					N Same Sex Adults	0	0.999		
AY agonistic	Model		0.002	64.4	130	0.164	144.184	Model		0.109	70.5	149
	Constant	-0.176	0.775					Constant	1.342	0.033		
	Social Group Size	-0.038	0.193					Social Group Size	-0.042	0.144		
	Embeddedness	-0.708	0.007					<i>Embeddedness</i>	-0.377	<i>0.091</i>		
	N Same Sex Yearlings	0.036	0.520					N Same Sex Yearlings	0.05	0.271		
	N Same Sex Adults	0.047	0.124					N Same Sex Adults	0.008	0.931		

ESM Table 2. Descriptive statistics contrasting dispersers and non-dispersers.

	Mean	StDev	Mean	StDev	Mean	StDev	Mean	StDev
All-Affiliative	Females-did not disperse		Females-dispersed		Males-did not disperse		Males-dispersed	
Degree	18.77	13.26	9.71	12.41	19.15	13.27	14.85	13.27
Weighted Degree	4.48	4.28	1.95	3.24	4.96	4.89	3.26	4.11
Embeddedness	4.49	2.80	2.36	2.21	4.52	2.59	3.68	2.62
N other yearlings	8.12	3.69	8.75	3.44	9.59	4.86	10.22	4.67
N adult females	12.40	6.70	14.22	6.47	14.65	7.04	13.11	7.26
N adult males	4.98	1.94	5.64	2.07	5.35	2.00	5.37	2.24
All-Agonistic	Females-did not disperse		Females-dispersed		Males-did not disperse		Males-dispersed	
Degree	8.53	7.94	5.91	10.31	9.83	10.10	8.00	11.26
Weighted Degree	2.54	3.39	1.52	3.82	2.38	3.13	2.38	4.65
Embeddedness	2.00	1.48	1.24	1.75	2.24	1.72	1.78	1.91
N other yearlings	8.12	3.69	8.75	3.44	9.59	4.86	10.22	4.67
N adult females	12.40	6.70	14.22	6.47	14.65	7.04	13.11	7.26
N adult males	4.98	1.94	5.64	2.07	5.35	2.00	5.37	2.24
AY-Affiliative	Females-did not disperse		Females-dispersed		Males-did not disperse		Males-dispersed	
Degree	5.85	5.81	2.44	3.59	5.18	4.70	3.33	3.82
Weighted Degree	2.26	3.17	0.80	1.18	1.88	2.54	1.17	1.84
Embeddedness	1.28	0.92	0.67	0.77	1.24	1.02	0.95	0.93
N other yearlings	8.12	3.69	8.75	3.44	9.59	4.86	10.22	4.67
N adult females	12.40	6.70	14.22	6.47	14.65	7.04	13.11	7.26
N adult males	4.98	1.94	5.64	2.07	5.35	2.00	5.37	2.24
AY-Agonistic	Females-did not disperse		Females-dispersed		Males-did not disperse		Males-dispersed	
Degree	4.72	4.69	2.39	5.32	4.79	4.88	3.41	5.13
Weighted Degree	2.05	2.86	1.01	2.78	1.82	2.42	1.34	2.63

Embededness	1.04	0.86	0.51	0.72	1.17	0.88	0.83	0.82
N other yearlings	8.12	3.69	8.75	3.44	9.59	4.86	10.22	4.67
N adult females	12.40	6.70	14.22	6.47	14.65	7.04	13.11	7.26
N adult males	4.98	1.94	5.64	2.07	5.35	2.00	5.37	2.24

YY-Affiliative	Females-did not disperse		Females-dispersed		Males-did not disperse		Males-dispersed	
Degree	30.18	21.35	14.48	17.39	29.40	19.58	24.01	21.51
Weighted Degree	10.22	11.22	3.47	5.06	10.17	10.18	6.79	7.82
Embededness	3.72	2.73	1.94	2.04	3.67	2.49	3.10	2.44
N other yearlings	8.12	3.69	8.69	3.44	9.59	4.86	10.22	4.67
N adult females	12.40	6.70	14.31	6.49	14.65	7.04	13.11	7.26
N adult males	4.98	1.94	5.64	2.09	5.35	2.00	5.37	2.24

YY-Agonistic	Females-did not disperse		Females-dispersed		Males-did not disperse		Males-dispersed	
Degree	11.88	15.34	6.17	13.11	11.19	14.71	9.11	15.72
Weighted Degree	6.78	11.78	2.78	7.32	5.56	8.99	4.32	8.28
Embededness	1.04	1.19	0.78	1.40	1.15	1.58	1.06	1.69
N other yearlings	8.12	3.69	8.69	3.44	9.59	4.86	10.22	4.67
N adult females	12.40	6.70	14.31	6.49	14.65	7.04	13.11	7.26
N adult males	4.98	1.94	5.64	2.09	5.35	2.00	5.37	2.24

ESM. Marmot ethogram.

Our ethogram of social behaviour was modified from Johns & Armitage (1979) and Nowicki & Armitage (1979), to include: aggression (bite, box, chase, mount, mouth spar, pounce, push, snarl/hiss, wrestle), allogrooming (typically around the back of the neck), simple displacement (scored when one animal approached another and one moved away), forage together within 1 m, greet (noses touch), sit <1 m apart, play (bite, box, chase, mount, mouth spar, pounce, wrestle), and sniff anogenital region. Play was distinguished from similar motor patterns seen in aggression by the following criteria. Play was less 'intense' than aggressive interactions (playing marmots sometimes got interrupted, looked around, paused, or did other things that made them seem less invested in the activity), and aggressive interactions were generally quicker and often accompanied by sounds of aggression or fear. Unlike aggressive interactions, after play bouts, marmots were likely to sit next to each other. Play was generally 'bouncier' than aggression and was often characterized by individuals changing roles repeatedly and shifting from one type of behaviour to another regularly during prolonged bouts.

Johns, D. W. & Armitage, K. B. 1979 Behavioral ecology of alpine yellow-bellied marmots. *Behav. Ecol. Sociobiol.* **5**, 133-157.

Nowicki, S. & Armitage, K. B. 1979 Behavior of juvenile yellow-bellied marmots: play and social integration. *Z. Tierpsychol.* **51**, 85-105.

ESM. Detailed description of embeddedness.

The terms network and graph, node and vertex, and tie and edge are equivalent. In the text we use network, node, and tie to be closer to common terminology in social network research. Here we use graph, vertex, and edge to be closer to the original graph theoretic literature on which these concepts are based.

Moody & White (2003) provide a measure of social embeddedness based on the k -connectivity of a graph (Harary 1969). In a graph composed of vertices connected by edges, a *path* is an alternating sequence of contiguous vertices and edges beginning and ending with a vertex, within which no vertex occurs more than once. Two (or more) paths are *vertex-independent* if they do not share any vertices. A k -component is a maximal subset of vertices in which the vertices are all mutually reachable by at least k vertex-independent paths composed exclusively of vertices within the subset. Maximal means that there is no other vertex that can be added to the set and for all its members to still be connected. Another equivalent way to think about this is that a k -component cannot be fragmented by fewer than k vertices. Vertices embedded in higher k -components are more integrated into the graph. If this idea of embeddedness is extended to social cohesion, then an individual's social embeddedness is the deepest level k , derived from its maximal k -component, in which it resides (see Moody & White 2003 for detailed elaboration and examples of structural cohesion and embeddedness).

A mathematical explanation is as follows:

A graph $G = (X, E)$ consists of a set $X = \{x_1, x_2, \dots, x_N\}$ of vertices and a set $E = \{e_1, e_2, \dots, e_M\}$ of edges.

Each edge $e_q = (x_k, x_u)$ is an unordered pair of vertices.

A path, e_1, e_2, \dots, e_q , joining the vertices x_k and x_u is a sequence of edges such that any two successive edges are adjacent, x_k is adjacent to the first edge only, x_u is adjacent to the last edge only, and all other vertices of the path are adjacent to precisely two of its edges.

Two paths connecting x_k and x_u are independent if they have only x_k and x_u in common.

Definition 1: A graph is a k -component if and only if every pair x_k, x_u of vertices of X are joined by k independent paths using only vertices in G .

The subgraph $G_A = (A, E_A)$ of G generated by $A \subset X$ is a graph having the set of vertices A and as edges those of G whose end-vertices are both in A : $E_A = \{e_q = (x_k, x_u) \mid e_q \in E, x_k \in A, x_u \in A\}$.

If G is connected and G_A is disconnected, then the set of vertices, $X - A$, separates G .

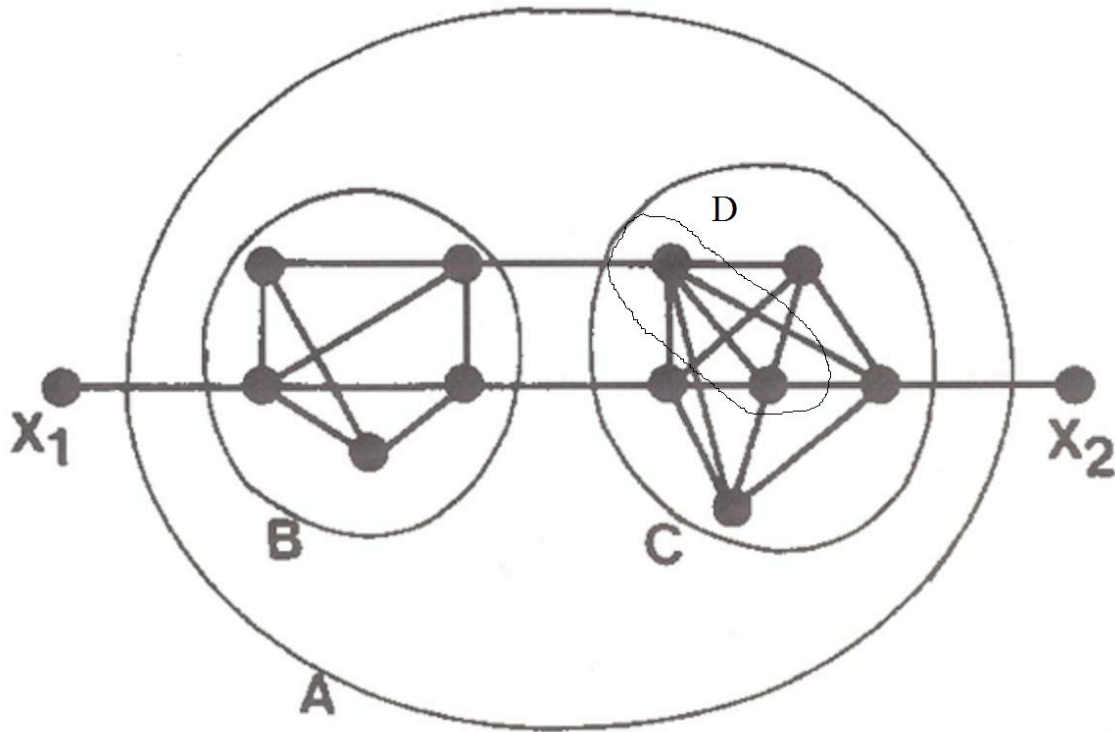
Definition 2: A graph G is a k -component ($k \geq 2$) if G has at least $(k + 2)$ vertices if and only if a set of k of its vertices separates it but no set of less than k of its vertices does so.

Menger (1927) proved that Definitions 1 and 2 of k -connectivity are identical.

In the graph G below, four potential subgraphs are identified: A , B , C , and D .

G is a 1-component, A is a 2-component, B is a 3-component, and C is a 4-component.

While the two vertices identified as D are connected by 5 independent paths, they are not a 5-component because only one of the 5 paths, the direct connection between them, is in D .



Moody & White (2003) provide a general algorithm for obtaining k -components in Appendix A of their paper. k -components can also be obtained in the program UCINET 6 (Borgatti et al. 2006), with the following steps:

1. Calculate the maximum flow of the network (Network>Cohesion>Maximum Flow).
2. Dichotomize at k of interest (Transform>Dichotomize). Cut-Off Operator GE (greater than or equal to) can be set to k .
3. Extract components (Networks>Regions>Components>Simple graphs).
4. Repeat steps 1-3 with extracted component(s). (So for each k of interest, steps 1-3 will be done twice.) Nodes left in the extracted component after the second round belong to that k -component.
5. Repeat the entire process at higher cutoff points to determine higher k -components.

Note that all isolates have maximal $k = 0$, and pendants have maximal $k = 1$. A node with maximal $k = 3$ may also belong to a 2-component and 1-component, but because its maximal k -component is a 3-component, then its embeddedness would be 3.

We thank Rick Grannis for providing a clear description of embeddedness.

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