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ORIGINAL PAPER

Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success

Tina W. Wey · Daniel T. Blumstein

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Abstract Studying the structure of social interactions is fundamental in behavioral ecology as social behavior often influences fitness and thus natural selection. However, social structure is often complex, and determining the most appropriate measures of variation in social behavior among individuals can be difficult. Social network analysis generates numerous, but often correlated, measures of individual connectedness derived from a network of interactions. We used measures of individual connectedness in networks of affiliative and agonistic interactions in yellow-bellied marmots, *Marmota flaviventris*, to first determine how variance was structured among network measures. Principal component analysis reduced our set of network measures to four “social attributes” (unweighted connectedness, affiliation strength, victimization, and bullying), which revealed differences between patterns of affiliative and agonistic interactions. We then used these extracted social attributes to examine the relationship between an individual’s social attributes and several performance measures: annual reproductive success, parasite infection, and basal stress. In male marmots, bullying was positively associated with annual reproductive success, while in females, affiliation strength was negatively associated with annual reproductive success. No other social attributes were significantly associated with any performance measures. Our study highlights the utility of considering multiple dimensions when measuring the structure and functional consequences of social behavior.

Keywords Affiliation · Agonism · Social behavior · Performance measures · Animal social networks

Introduction

Understanding the evolution of animal sociality is of longstanding interest in behavioral ecology, and group living has coevolved with associated patterns of mating opportunities, food acquisition, and predation and parasite risk (Alexander 1974; Krause and Ruxton 2002). Social behaviors are important components of animal societies, and quantifying the nature, structure, and consequences of social behaviors is thus an important way to study the evolution of sociality (Hinde 1976; Whitehead 2008). Individuals can engage in many types of social behaviors, which take place in different contexts, such as cooperation, competition, or mating. Variation in the number, strength, or pattern of interactions can be associated with individual performance measures. For example, stronger affiliative bonds may enhance female reproductive success (Silk et al. 2003, 2009; Cameron et al. 2009); increased social contact should increase parasite risk, but allogrooming could reduce parasitism (Altizer et al. 2003; Keeling and Eames 2005); and dominance rank can influence chronic stress levels (Creel 2001; Sapolsky 2004;

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T. W. Wey · D. T. Blumstein
Department of Ecology and Evolutionary Biology,
University of California, Los Angeles,
621 Charles E. Young Drive South,
Los Angeles, CA 90095-1606, USA

D. T. Blumstein
The Rocky Mountain Biological Laboratory,
P.O. Box 519, Crested Butte, CO 81224, USA

Present Address:
T. W. Wey (✉)
Department of Environmental Science and Policy,
University of California, Davis,
One Shields Avenue,
Davis, CA 95616, USA
e-mail: twwey@ucdavis.edu

Young et al. 2006). Individuals can have complex networks of different social interactions, which may be associated with different performance measures.

An individual's full social context can include the entirety of interactions among all group members—their extended social network. In the social network paradigm, both direct connections and indirect connections are potentially important. Thus, two individuals that do not interact directly can still exert social influence on each other if they are connected through intermediaries. Social network analysis offers a set of tools for analyzing interactions among group members, including various measures of individual connectedness (Wasserman and Faust 1994). For example, different "centrality" measures can reflect how many or how structurally important an individual's direct and indirect network connections are, while "clustering" and "embeddedness" measures reflect how well connected an individual's local neighborhood is. Both types of concepts have been used to quantify an individual's social context. Additionally, information about the strength and direction (who initiates and who receives the interaction) can also be incorporated into many measures. While different measures are calculated differently and may be of simultaneous interest, many measures (e.g., different centrality measures) can in practice be correlated, and the selection of measures that capture quantitatively different aspects of network connectedness is itself of importance.

In recent years, there has been growing interest in using the network framework to study animal social structure and function (Croft et al. 2008; Wey et al. 2008; Sih et al. 2009). Notably, network analysis provides existing terminology and measures to quantify concepts about social cohesion and conflict that are intuitively important in animal societies. In humans, individual connectedness in a social network has been linked to various health indices (House et al. 1988; Uchino et al. 1996; Friedman and Aral 2001; Sapolsky 2004). Recent studies also indicate that an individual's network connectedness can be associated with various performance measures in a growing number of species, including parasite infection in brushtail possums, *Trichosurus vulpecula* (Corner et al. 2003), gidgee skinks, *Egernia stokesii* (Godfrey et al. 2009), and tuataras, *Sphenodon punctatus* (Godfrey et al. 2010); reproductive success in long-tailed manakins, *Chiroxiphia linearis* (McDonald 2007) and wire-tailed manakins, *Pipra filicauda* (Ryder et al. 2008); and fitness in forked fungus beetles, *Bolitotherus cornutus* (Formica et al. 2012).

Additional studies in non-human systems are needed to help determine the generality of these patterns. Furthermore, most existing studies have focused on one type of social interaction network at a time and hence have not accounted for the multidimensional aspect of social behavior. Studies looking at multiple types of interaction networks are generally lacking (but see Flack et al. 2006; Madden et al. 2009; Lusseau et al. 2011). Network measures could add to our understanding of the structure and function of social behaviors by highlighting aspects of connectedness that are prominent in different types of networks or that are associated with performance measures in animal societies.

We illustrate this with a study of facultatively social yellow-bellied marmots (*Marmota flaviventris*). We used 6 years of data from free-living yellow-bellied marmots to study variation in individual patterns of network connectedness in affiliative and agonistic behavior and the functional correlates of this variation. We first extracted important social factors (hereafter referred to as "social attributes") from a suite of network measures of individual connectedness and then used these social attributes to test hypotheses about relationships between individual social attributes and several performance measures: annual weaning success, parasite infection, and stress hormone metabolite levels. Below, we develop the specific hypotheses tested.

Hypotheses

Annual reproductive success

Social factors differentially influence reproductive success in female and male marmots (Armitage 1991b). Males move into sites and attempt to defend multiple females, while females recruit female offspring into natal colonies (Armitage 1991b; Olson and Blumstein 2010). Given the social structure and higher incidence of female relatedness in social groups, we hypothesize that females, but not males, should gain reproductive benefits from increased social affiliation in this system. We thus predict that measures of the strength, extensiveness, or embeddedness of affiliative interactions would be related to higher annual reproductive success in female marmots. Additionally, given that dominance status is positively associated with male, but not female, annual reproductive success (Huang et al. 2011), we hypothesize that male, but not female, reproductive success should be related to agonistic interaction networks. We predict that measures of a male's importance in initiating or being more central in agonistic networks would be positively related to his reproductive success.

Parasite infection

Parasites often constitute a cost of sociality (Alexander 1974; Krause and Ruxton 2002; Altizer et al. 2003; Nunn and Altizer 2006). An underlying assumption is that increased social contact contributes to increased risk of infection (Anderson and May 1991), and infection by contagious parasites does generally increase with group size (Côté and Poulin 1995; Nunn and Altizer 2006). However, both increased social contact and host density could contribute to this effect (Altizer et al. 2003). A previous study in yellow-bellied marmots found that ectoparasites are not a cost of sociality (Van Vuren 1996), but this study did not focus on social behavior. We hypothesize that individual differences in patterns of social interactions will lead to differences in parasite exposures and loads. Thus, we predict that increased number, strength, or extensiveness of network connections of any interaction type would be positively correlated with parasite infection.

Stress hormones

Social factors can both increase and alleviate stress (De Vries et al. 2003). Allogrooming can lower stress in primates (Cohen et al. 1992; Das et al. 1998), and dominance interactions are related to different patterns of chronic stress in a variety of species (Creel 2001). Fecal glucocorticoid metabolites (FGMs) can provide an integrated measure of stress hormone production over time and have been used as a non-invasive measure of baseline or chronic stress in wildlife populations (Millspaugh and Washburn 2004; Keay et al. 2006). FGM levels vary by season, age, sex, and individual in yellow-bellied marmots (J. E. Smith et al., in review). We hypothesize that social affiliation includes lower stress interactions and that aggression includes relatively stressful interactions. Specifically, we predicted that individuals with stronger or more extensive affiliative interactions or those who receive more affiliation would have lower levels of FGMs and also that individuals with stronger agonistic interactions or receiving more aggression would have higher levels of FGMs.

Methods

Field data collection

From 2003 to 2008, we observed yellow-bellied marmots at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA, where marmots have been studied since 1962 (Schwartz et al. 1998; Armitage 2010; Ozgul et al. 2010). We regularly collected behavioral and physiological data to measure social behavior and performance measures. Marmots were individually marked for identification, allowing us to record the initiator, recipient, social interaction type (affiliative/agonistic), location, and time of each behavioral interaction (method details in Blumstein et al. 2009 and Wey and Blumstein 2010). Additionally, we noted each individual's presence at pre-defined burrow locations within colonies, independent of interactions with other individuals, in order to determine overlap in burrow usage. Observations and trapping took place during mornings and afternoons when marmots were most active (Armitage 1991b), throughout the majority of the active season (mid-April to mid-September).

We divided observed interactions into affiliative and agonistic datasets. Affiliative interactions included cohesive behaviors, such as greeting, allogrooming, sitting in close proximity, and foraging together, while agonistic interactions included competitive behaviors such as aggression (biting, chasing, fighting) and displacements. We constructed separate social networks for affiliation and agonism based on observations of four marmot colonies (Bench River, Marmot Meadow, Picnic, Town) per year. Colonies were geographically distinct, with almost no exchange of individuals or interactions among them. A sizeable portion of colony membership changes each year through birth, death, and dispersal (Schwartz et al. 1998). Therefore, we defined a network as the set of colony members and the interactions among those members in a year. Only individuals observed on more than five occasions in a year were included in networks. This restriction was intended to eliminate transient animals from analysis. All interactions with a clear initiator and recipient were retained (as in Lea et al. 2010 and Wey and Blumstein 2010).

Determination of social attributes and neighbor overlap

Network measures were calculated in UCINET (Borgatti et al. 2006) and the iGraph package (Csárdi and Nepusz 2009) in R (R Development Core Team 2009). For both affiliative and agonistic networks, we separately calculated the following network measures: degree, out-degree, in-degree, strength, out-strength, in-strength, closeness centrality, betweenness centrality, and embeddedness. We selected these indices because they measure different concepts of potential biological importance and used the definitions below.

Degree and strength

"Degree" is the number of social partners a marmot has, regardless of directionality. "Out-degree" is the number of social partners to which a marmot directs behavior, while "in-degree" is the number of social partners from which a marmot receives behavior. We use "strength" to describe the total number of interactions in which a marmot is involved, including multiple interactions with the same social partner, similar to concepts used in other weighted measures of connectedness (Barthélemy et al. 2005). These measures all reflect the amount of direct interaction at a local level and do not account for overall network dynamics. Degree is the most basic measure of connectedness. Out-degree reflects the potential to affect others through direct interactions, whereas in-degree reflects the potential to be affected by others through direct interactions. Strength is conceptually similar to degree but is weighted by multiple repeated interactions between two individuals and allows for more variation than degree. We also calculated out-strength and in-strength, as weighted versions of out-degree and in-degree.

Closeness centrality

In many social networks, there will be network members that are not directly connected to each other. However, individuals may also be connected to, and therefore influence or be influenced by, others in the network through indirect connections. Measures that incorporate indirect interactions reflect an individual's connectedness in the overall network rather than only on a local level. "Closeness centrality" is generally defined as the reciprocal of the sum of the shortest path lengths between the focal node and all other nodes in the network (where the shortest path length between A and B is 1 if they directly interact, shortest path length is 2 if A and B are most closely connected through one other individual, and so on). We used a modified calculation (sum of reciprocal distances—Borgatti et al. 2006), which takes the reciprocals of the shortest path lengths before summing, so that unconnected nodes have a 0 value rather than undefined value for closeness centrality. We also standardized closeness centrality for network size.

Betweenness centrality

Rather than having a large absolute amount or extensiveness of connections, an individual could be important in a network because it connects others that would otherwise be unconnected or less well connected. "Betweenness centrality" is the proportion of shortest path lengths in the network between all other pairs of individuals on which an animal lies (Freeman 1979). This centrality measures incorporate indirect interactions also but focus on the potential importance of short path lengths in transmission processes (e.g., for disease or information). We also standardized betweenness centrality for network size.

Embeddedness

Social integration into a cohesive subgroup may also be an important component of attachment or unity in human networks (Moody and White 2003) and life history decisions in animals (Blumstein et al. 2009). Generally speaking, an individual may have many connections, but if these are connections to disparate subgroups within the network, that individual will be less integrated into a community than another individual whose connections fall within a social subgroup whose members are well connected among themselves. We define "embeddedness" as the maximal *k*-core component to which an animal belongs, where a *k*-core 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 are still *k* connected (for example, an individual with embeddedness of 4 belongs to a 4-core, which is a group of individuals that are all mutually connected to each other by at least four independent paths that exist among group members). See Moody and White (2003) and Blumstein et al. (2009) for details on the embeddedness measure used.

Simplifying social attributes

The above network measures were highly correlated ("Appendix 1"), so we performed a principal component analysis (PCA) on the sets of affiliative and agonistic measures separately to extract a smaller number of less correlated social attributes (see "Appendix 2"). PCA was performed in SPSS 16.0 Grad Pack (SPSS Inc. 2007) with Varimax rotation with Kaiser normalization and minimum eigenvalue of 1.

In addition to physical interactions, we were interested in the effect of proximity or overlap with other colony members as another measure of sociality. We thus calculated "neighbor overlap" as the number of other individuals with which a given marmot overlapped in burrow usage during that season.

Performance measures

From 2003 to 2008, we counted the number of pups that emerged from burrows (i.e., the number of pups that survived to weaning) that were assigned to each adult per year, using a comprehensive pedigree (see Blumstein et al. 2010 and Olson and Blumstein 2010 for pedigree details). While behavioral observations provided similar results when there was only a single candidate mother or father, parentage assignment from the pedigree was necessary for cases where pups associated with more than one adult female and when more than one male was present in a colony.

In 2007 and 2008, we aimed to comb marmots once every 2 weeks during trapping and counted fleas (*Thrassis stanfordi*—Van Vuren 1996) that were displaced onto a white flannel cloth. Larger hosts may tend to have more parasites (Shine 1989); thus, we converted the absolute number of fleas into fleas per kilogram and averaged these values for each individual each year. From 2003 to 2008, we collected feces from marmots that defecated in traps and performed fecal floats using Ova Float™ Zn 118 (zinc sulfate heptahydrate) on up to one sample per individual per month. We then scored wet slides for presence of three fecal-orally transmitted intestinal parasites: *Eimeria* spp., *Entamoeba* sp., and *Ascaris* sp. Our measure of parasite diversity therefore reflected the number of parasite species detected for each individual in a given year.

From 2003 to 2008, we extracted and measured FGM from frozen fecal samples, up to one sample per individual per month (as described in Blumstein et al. 2006). FGM levels were used as indicators of baseline stress levels, not as measures of acute stress response (Sheriff et al. 2011). We only included fecal samples collected in the morning in this study due to daily fluctuations in glucocorticoid levels (Blumstein et al. 2006). Glucocorticoid levels did not differ between reproductive and non-reproductive adults in previous studies in this system (Armitage 1991a; Blumstein et al. 2006), so we did not include reproductive status as a variable in our analysis. We averaged FGM for each individual to obtain a yearly index.

Analysis

We fitted generalized linear mixed models (GLMMs) with the "lme4" package (Bates and Maechler 2009) in the statistical environment R (R Development Core Team 2009), with extracted social attributes and neighbor overlap as independent variables and performance measures as dependent variables. We included individual as a random effect and year and colony as fixed factors in all models described below.

We analyzed annual reproductive success for females and males separately because there was a different degree of reproductive skew between the sexes. For females, the dependent variable was number of offspring weaned in a year (Poisson distribution, log link function), while for males, the dependent variable was the $\log_{10}$-transformed number of offspring weaned in a year. Adult relative mass was associated with annual reproductive success in a previous study (Huang et al. 2011), so we included relative mass as a covariate.

There were no significant age × sex interactions in models of parasite infection, so we analyzed all age–sex groups together. The dependent variables were the $\log_{10}$-transformed fleas per kilogram in models of flea infection and parasite diversity (0–3) for models of intestinal parasite infection.

There were no significant age × sex interactions in models of stress hormone metabolite levels, so we analyzed all age–sex groups together. The dependent variable was the $\log_{10}$-transformed FGM level (nanograms per gram).

Results

We used a total of 9,652 affiliative interactions and 2,013 agonistic interactions in respective networks, from 4,845 h of observation. Our final dataset included 357 individuals and 676 total cases: 272 on adult females, 105 on adult males, 138 on yearling females, and 161 on yearling males. GLMM results are shown in Tables 2, 3, 4, and 5. We report year and colony effects, but do not specifically try to interpret them as they were intended to account for uncontrollable environmental variation.

PCA and social attributes

PCA of affiliative and agonistic social network measures generated two affiliative and two agonistic factors (Table 1). In both cases, the first two components explained >80 % of variance. Based on high factor loadings (>0.7), we designated these four factors as social attributes, which we referred to as unweighted connectedness, affiliation strength, victimization, and bullying. Affiliative PC1 (unweighted connectedness) reflected multiple aspects of overall affiliative connectedness; high factor loadings included degree, out-degree, in-degree, closeness centrality, and embeddedness. Affiliative PC2 (affiliation strength) reflected weighted connections specifically; high factor loadings included strength, out-strength, and in-strength. Agonistic PC1 (victimization) reflected received agonism and being in a well-connected subgroup; high factor loadings included in-degree, in-strength, and embeddedness. Agonistic PC2 (bullying) mainly reflected initiated agonism and serving as a connection point; high factor loadings included degree, out-degree, out-strength, and betweenness centrality.

Annual reproductive success

Females that had higher annual reproductive success had lower affiliation strength (estimate=−0.640, $P<0.001$) and experienced lower neighbor overlap (estimate=−0.024, $P=0.007$) (Table 2). The covariance of random effect for individual in this model was 0.322 (SD=0.568). Males that had higher annual reproductive success had higher values for bullying (estimate=0.064, $P=0.044$) and had greater relative body mass (estimate=0.186, $P<0.001$) (Table 3). The covariance of random effect for individual in this model was 0.026 (SD=0.162). There were some year and colony effects common to both males and females. Average reproductive success was higher in years 2004 and 2006 (relative to 2003) and colony Picnic (relative to Bench River).

Parasite infection

There was male-biased flea load (estimate for "sex=male"= 0.105, $P=0.018$), and animals with higher affiliation strength had fewer, though not significantly fewer, fleas (estimate=−0.033, $P=0.073$) (Table 4). There was no significant difference in average flea infections in 2007 and 2008, but average number of fleas was higher in the colonies

Table 1 Factor loading scores from PCA of network measures

Network measure	Affiliative PC1 (unweighted connectedness)	Affiliative PC2 (affiliation strength)	Agonistic PC1 (victimization)	Agonistic PC2 (bullying)
Degree	0.921	0.311	0.627	0.735
Out-degree	0.842	0.388	0.315	0.900
In-degree	0.839	0.381	0.939	0.164
Strength	0.245	0.961	0.637	0.682
Out-strength	0.189	0.919	0.327	0.856
In-strength	0.205	0.913	0.871	0.148
Closeness centrality	0.866	0.179	0.696	0.445
Betweenness centrality	0.458	−0.039	0.061	0.776
Embeddedness	0.879	0.310	0.847	0.376
Variance explained, %	45.9	34.7	42.8	39.3

PCA was performed separately for affiliative and agonistic measures. High loadings (>0.7) are in bold. The total variance explained by affiliative factors is 80.6 %. The total variance explained by agonistic factors is 82.1 %

Picnic and Town. The covariance of random effect for individual in this model was <0.001 (SD<0.001). No social variables were significantly associated with gut parasite diversity (Table 5). However, average parasite diversity appeared to be higher in later years. The covariance of random effect for individual in this model was <0.001 (SD<0.001).

Stress hormones

Higher FGM levels were observed in adults (estimate for "age=yearling"=−0.110, $P<0.001$) and males (estimate for "sex=male"=0.051, $P=0.038$) (Table 6). Social variables were not significantly associated with FGM levels. There was significant variation in average FGM levels among

Table 2 GLMM results for female annual reproductive success

Parameter	*df*	Estimate	*P* value
Intercept		1.024	<0.001
Year	5		
2003		–	–
2004		0.430	0.025
2005		−0.109	0.629
2006		0.524	0.008
2007		0.220	0.302
2008		0.279	0.195
Colony	3		
Bench River		–	–
Marmot Meadow		−0.145	0.570
Picnic		−0.598	0.003
Town		−0.190	0.467
Relative body mass	1	0.036	0.619
Unweighted connectedness	1	0.127	0.171
Affiliation strength	1	−0.640	< 0.001
Victimization	1	−0.078	0.403
Bullying	1	0.095	0.153
Neighbor overlap	1	−0.024	0.007

N=228, IDs=85, dependent variable=annual reproductive success

Estimate standardized coefficient for fixed effects

Table 3 GLMM results for male annual reproductive success

Parameter	*df*	Estimate	*P* value
Intercept		0.823	0.001
Year	5		
2003		–	–
2004		0.414	0.009
2005		0.211	0.249
2006		0.346	0.024
2007		0.069	0.634
2008		0.023	0.866
Colony	3		
Bench River		–	–
Marmot Meadow		−0.221	0.127
Picnic		−0.337	0.012
Town		0.028	0.872
Relative body mass	1	0.186	<0.001
Unweighted connectedness	1	−0.097	0.139
Affiliation strength	1	−0.121	0.173
Victimization	1	0.016	0.945
Bullying	1	0.064	0.044
Neighbor overlap	1	<0.001	0.785

N=44, IDs 23, dependent variable=$\log_{10}$(annual reproductive success)

Estimate standardized coefficient for fixed effects

Table 4 GLMM results for ectoparasites

Parameter	*df*	Estimate	*P* value
Intercept		−0.110	0.137
Year	1		
2007		–	–
2008		−0.021	0.650
Colony	3		
Bench River		–	–
Marmot Meadow		0.044	0.528
Picnic		0.114	0.065
Town		0.206	0.011
Age=yearling	1	−0.025	0.662
Sex=male	1	0.105	0.018
Unweighted connectedness	1	−0.044	0.175
Affiliation strength	1	−0.033	0.073
Victimization	1	−0.006	0.873
Bullying	1	−0.017	0.489
Neighbor overlap	1	−0.001	0.875

N=185, IDs=136, dependent variable=$\log_{10}$(mean N fleas/kg)

BR Bench River, *MM* Marmot Meadow, *P* Picnic, *T* Town, *Estimate* standardized coefficient for fixed effects

years, but not colonies. The covariance of random effect for individual in this model was <0.001 (SD<0.001).

Table 5 GLMM results for intestinal parasites

Parameter	*df*	Estimate	*P* value
Intercept		0.328	0.112
Year	5		
2003		–	–
2004		0.357	0.077
2005		0.376	0.076
2006		0.445	0.031
2007		0.457	0.024
2008		0.412	0.047
Colony	3		
Bench River		–	–
Marmot Meadow		−0.004	0.970
Picnic		0.030	0.746
Town		−0.038	0.769
Age = yearling	1	0.033	0.728
Sex = male	1	−0.025	0.754
Unweighted connectedness	1	0.001	0.982
Affiliation strength	1	−0.005	0.892
Victimization	1	0.030	0.511
Bullying	1	0.015	0.704
Neighbor overlap	1	−0.001	0.923

N=428, IDs=230, dependent variable=annual gut parasite diversity

Estimate standardized coefficient for fixed effects

Discussion

Simplifying social attributes

Although we calculated the same set of network measures from affiliative and agonistic networks, the extracted components differed. For affiliative measures, PCA differentiated between unweighted interactions and weighted interactions (i.e., resulted in unweighted connectedness and affiliation strength), suggesting an important distinction between the presence and strength of cohesive interactions. This is consistent with research suggesting that the strength of cohesive connections can have an influence distinct from the simple presence of connections on performance measures in humans and other systems (House et al. 1988; Barrat et al. 2004; Newman 2004; Lusseau et al. 2008; Silk et al. 2009).

For agonistic measures, the PCA largely distinguished between received and initiated agonism, suggesting that directionality is a more important component than strength of aggressive interactions. The first agonistic component (victimization) also included embeddedness, a measure of local structural cohesion, while the second component (bullying) also included betweenness centrality, a measure of an individual's role as an overall connection point. Therefore, individuals that

Table 6 GLMM results for FGM

Parameter	*df*	Estimate	*P* value
Intercept		2.286	<0.001
Year	5		
2003		–	–
2004		−0.117	0.021
2005		−0.210	<0.001
2006		−0.193	<0.001
2007		−0.249	<0.001
2008		0.167	0.001
Colony	3		
Bench River		–	–
Marmot Meadow		−0.002	0.9462
Picnic		0.005	0.874
Town		−0.014	0.717
Age = yearling	1	−0.110	<0.001
Sex = male	1	0.051	0.038
Unweighted connectedness	1	0.006	0.681
Affiliation strength	1	0.016	0.120
Victimization	1	−0.019	0.207
Bullying	1	−0.013	0.287
Neighbor overlap	1	0.001	0.444

N=333, IDs=188, dependent variable=$\log_{10}$(annual mean ng/g fecal glucocorticoid metabolites)

Estimate standardized coefficient for fixed effects received more agonism were also embedded within more densely interconnected clusters of agonistic social partners, while individuals that initiated more agonism distributed their interactions more evenly among clusters and served as more important connection points in the overall network.

Given the diversity of animal societies, different social factors are likely to emerge from a similar analysis in other taxa, and these differences could be informative in testing hypotheses about different social systems. For example, more socially or cognitively complex species might be better able to monitor third party interactions or infer indirect consequences of their actions (Cheney et al. 1986; Engh et al. 2005). Thus in these species, network measures that capture indirect interactions might be more likely to represent important social factors than in less socially complex species. Studies in other systems are required to test this prediction and establish broader patterns. An interesting possibility is that different suites of correlated social network measures would emerge in different systems, but this could be strongly influenced by the original measures of interest selected.

Hypotheses

We found that patterns of female and male reproduction differed, which is consistent with previous work (Armitage 1991b). Contrary to expectations, measures of social affiliation strength and neighbor overlap were associated with lower annual female reproductive success. This does not support the idea that social cohesion can improve female reproductive success in this system and instead suggests possible costs to maintaining stronger social connections and negative effects of density. The pattern could emerge because females with higher reproductive success had reduced affiliation or because females with lower reproductive success increased their affiliation. While affiliation is more likely among related females in this system (Armitage 1998), females do not gain indirect benefits from relatives, and older females can suppress reproduction by daughters (Armitage 1991b, 1998). As expected, social cohesion did not influence male reproductive success. The positive effect of bullying on male annual reproductive success and the lack of association between agonistic social factors and female annual reproductive success supported the idea that male marmots use aggression for social competition and access to mates, but females did not. This adds to evidence that aggression influences different aspects of reproductive success in this species (Lea et al. 2010; Huang et al. 2011), but unlike indications from previous work (Armitage 1998), we did not detect associated negative effects of received aggression.

There were no significant associations between individual social attributes and parasites or stress hormones. Though not significant, the result that individuals with higher affiliation strength had fewer fleas might be consistent with allogrooming effects or other forms of social compensation for ectoparasites (Moore 2002; Altizer et al. 2003; Bordes et al. 2007), but additional research is needed to support this suggested mechanism. There was male-biased parasitism, as seen in many mammalian systems (e.g., Harrison et al. 2010), but no significant effect of age on average flea infection. Individual variation in social attributes as measured is therefore a poor predictor of parasite infection in this system, a result consistent with previous research that looked at effect of social living on ectoparasites (Van Vuren 1996). Consistent with other findings (J. E. Smith et al., in review), adult and male marmots had significantly higher levels of FGMs, but social factors did not explain variation in FGM levels. In combination with a previous study on plasma glucocorticoid levels (Armitage 1991a), our results suggest that social interactions per se may not strongly affect baseline stress hormone levels in yellow-bellied marmots, unlike other social species (e.g., in meerkats, *Suricata suricatta*—Young et al. 2006). Nevertheless, FGM levels may provide limited information on the stress response, and other measures may be more appropriate for particular ecological questions (Sheriff et al. 2011). More detailed data on the timing of social behaviors and subsequent parasite infection and stress hormone level changes would be required to comprehensively rule out impacts of social behaviors on parasites and basal stress levels.

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Ethical standards The research was conducted in compliance with US regulations, under research protocol ARC no. 2001-191-01, approved by the University of California at Los Angeles Animal Research Committee on 13 May 2002 and renewed annually. Live animals were trapped under permits issued by the Colorado Division of Wildlife.

Conflict of interest The authors declare that they have no conflict of interest.

Appendix 1

Table 7 Correlations among network measures

	aff degree	aff strength	aff out-degree	aff in-degree	aff closeness centrality	aff betweenness centrality	aff embeddedness	ag degree	ag strength	ag out-degree	ag in-degree	ag closeness centrality	ag betweenness centrality
aff strength	0.513												
aff out-degree	0.938	0.570											
aff in-degree	0.912	0.549	0.802										
aff closeness centrality	0.780	0.404	0.716	0.730									
aff betweenness centrality	0.314	0.150	0.323	0.235	0.431								
aff embeddedness	0.921	0.489	0.848	0.885	0.785	0.164							
ag degree	0.610	0.384	0.637	0.524	0.529	0.289	0.540						
ag strength	0.490	0.414	0.534	0.441	0.399	0.235	0.418	0.853					
ag out-degree	0.454	0.228	0.509	0.325	0.377	0.277	0.366	0.903	0.798				
ag in-degree	0.558	0.495	0.541	0.605	0.495	0.175	0.540	0.725	0.680	0.417			
ag closeness centrality	0.597	0.432	0.584	0.575	0.683	0.273	0.590	0.778	0.614	0.592	0.698		
ag betweenness centrality	0.260	0.204	0.290	0.168	0.281	0.344	0.162	0.563	0.488	0.589	0.266	0.475	
ag embeddedness	0.593	0.429	0.595	0.604	0.572	0.195	0.600	0.836	0.728	0.642	0.822	0.823	0.287

Pearson correlation coefficients among network measures. All $N=676$, all $P<0.001$

aff affiliative, *ag* agonistic

Appendix 2

Table 8 Correlations among social factors

		Affiliation Strength	Victimization	Bullying	Neighbor Overlap
Connectivity	*r*	<0.001	0.465	0.307	0.520
	P value	1.000	<0.001	<0.001	<0.001
Affiliation Strength	*r*		0.399	0.025	0.008
	P value		<0.001	0.511	0.836
Victimization	*r*			<0.001	0.245
	P value			1.000	<0.001
Bullying	*r*				0.145
	P value				<0.001

Pearson correlation coefficients among factors from PCA and neighbor overlap. All $N=676$

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