



Social security: are socially connected individuals less vigilant?



Rachael P. Mady^{a, b}, Daniel T. Blumstein^{b, c, *}

^a Department of Biological Sciences, Towson University, Towson, MD, U.S.A.

^b The Rocky Mountain Biological Laboratory, Crested Butte, CO, U.S.A.

^c Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA, U.S.A.

ARTICLE INFO

Article history:

Received 7 October 2016

Initial acceptance 6 November 2016

Final acceptance 12 September 2017

MS. number: A16-00883R4

Keywords:

antipredator behaviour

security

social attribute

social network

vigilance

yellow-bellied marmot

Group size effects, whereby animals allocate less time to antipredator vigilance as a function of increasing numbers of animals foraging together, are reported in many taxa, but group size is but one of many social attributes that could increase an individual's perception of predation risk or what might be referred to as a 'sense of security'. Indeed, meta-analyses suggest that group size only explains a small amount of variation in vigilance, and studies have shown that other social attributes, such as dominance status, also influence perceived risk and time allocated to vigilance. Social network analysis is an emerging technique to quantify a variety of specific social attributes, some of which have been suggested to influence 'security'. Using the proportion of time looking as an indicator of vigilance and predation risk assessment, we tested the prediction that more socially connected yellow-bellied marmots, *Marmota flaviventer*, look less while foraging compared to their less socially connected counterparts. For females and males separately, we used observational data to create intrasexual, weighted social networks. We used principal component analysis to reduce correlated measures to unrelated and independent descriptions of connectedness. Using linear mixed effect models to account for potentially confounding variables, we found that no social network measure explained variation in vigilance. Social group size explained variation in female vigilance after accounting for variation due to vegetation height and date. Foraging group size and vegetation height explained variation in male vigilance. While social network measures themselves were not significant, our results mirror the fact that yellow-bellied marmots live in female-dominated societies and suggest that overall social group size is relatively more important for females than for males. Systematically studying whether and how social factors and intrasexual social relationships influence antipredator behaviour in other animals will create a better understanding of the benefits of sociality.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Three models, dilution (Hamilton, 1971; Vine, 1971), detection (Pulliam, 1973) and security (Dehn, 1990), predict that foraging animals will reduce their antipredator vigilance as group size increases. This relationship, known as the 'group size effect' (Lima, 1995), has been studied in a variety of taxa (Elgar, 1989; Roberts, 1996), but a recent meta-analysis showed that group size explained less than 20% of variation in vigilance in birds (Beauchamp, 2008). While it has been assumed that individuals are safer in larger groups (Roberts, 1996), there is evidence that this is not always true (Treves, 2000). A group-living individual's actual safety or even perceived risk, which we refer to as its 'sense of security', may instead be influenced by their social role in the group

(Blumstein & Armitage, 1997; Hinde, 1976), dominance rank (De Laet, 1985; Hegner, 1985), or the subset of individuals nearby (Cameron & Du Toit, 2005).

Classic studies (e.g. De Laet, 1985; Hegner, 1985) found that, following a predator visit, lower-ranking individuals resumed foraging before higher-ranking individuals. While this may be due to a difference in hunger levels, it may also suggest that subordinates take more risks when foraging after a predator visit since they can forage with less competition. More recent work also considered the effect of a foraging individual's relationships with neighbours in altering perceived predation risk. In chimpanzees, *Pan troglodytes*, affiliative relationships, not dominance relationships, affected vigilance (Kutsukake, 2006). In giraffes, *Giraffa camelopardalis*, the presence of adult males affected the time that females allocated to scanning (Cameron & Du Toit, 2005).

Because factors other than simply group size explain variation in vigilance (Beauchamp, 2015), there is a need to develop a more

* Correspondence: D. T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90025-1606, U.S.A.

E-mail address: marmots@ucla.edu (D. T. Blumstein).

nuanced view of the effect of sociality and social relationships on risk assessment. One promising approach focuses on specific social attributes that can be calculated from formal social network statistics (e.g. Wey, Blumstein, Shen, & Jordán, 2008). Kelley, Morrell, Inskip, Krause, and Croft (2011) used social network statistics to study how predation risk affected social connections in a fusion–fusion society and found that female guppies, *Poecilia reticulata*, have more connections with higher strength in areas with high predation risk. More recent work has shown that increased predation risk is associated with the stability and differentiation of social relationships (Heathcote, Darden, Franks, Ramnarine, & Croft, 2017), and that predatory attacks modify the structure of social relationships (Voelkl, Firth, & Sheldon, 2016). Thus, an individual's 'sense of security' may not only be found when in larger groups, but may be a result of how connected an individual is to its social network.

To test the hypothesis that an individual's social connectedness creates a 'sense of security', we focused on yellow-bellied marmots, *Marmota flaviventris*. Yellow-bellied marmots are well suited to address this because they are facultatively social, which creates substantial variation in the nature and strength of their social relationships. Prior work on this species has provided evidence that while dominance rank does not affect time allocated to vigilance (Chmura, Wey, & Blumstein, 2016), social relationships seem to affect alarm-calling behaviour. Less socially connected, and supposedly less 'secure', individuals utter alarm calls at a higher rate naturally and when humans approach them in traps (Fuong, Maldonado-Chaparro, & Blumstein, 2015). Moreover, Blumstein, Fuong, and Palmer (2017) recently found that socially well-connected yellow-bellied marmots foraged more than their counterparts after an alarm call playback, suggesting that these relationships conferred increased security. Here we examined another measure of perceived predation risk: time allocated to vigilance during foraging bouts. If social connectedness creates a 'sense of security', then we would expect more connected individuals to allocate less time to vigilance than less connected individuals.

METHODS

Study Site and Species

We studied yellow-bellied marmots in the upper East River Valley around the Rocky Mountain Biological Laboratory in Gothic, Colorado, U.S.A. (38°57'N, 106°59'W; 2900 m above sea level). Marmots at this site have been studied since 1962 (Armitage, 2014). The size and composition of social groups can vary considerably, consisting of one or more adult females, one or more adult males, yearlings of both sexes, and pups (Armitage, 2014). Colonies are spatially discrete areas that contain one or more marmot social groups. A variety of aerial and terrestrial predators prey on marmots (Armitage, 2004; Van Vuren, 1991, 2001), and previous work suggests that vigilance varies as a function of predation risk, with vigilance increasing with increased predation risk (Blumstein, Barrow, & Luterra, 2008; Blumstein, Cooley, Winternitz, & Daniel, 2008; Blumstein et al., 2004; Monclús, Anderson, & Blumstein, 2015).

Behavioural Observations

Behavioural observation data were collected from 2002 to 2015. Marmots were trapped, marked and observed between mid-April and mid-September (details in Blumstein, 2013). Each colony was observed most days, weather permitting, for 2–6 h with observers using binoculars and 15–45× spotting scopes during times of peak

marmot activity, 0700–1000 hours and 1600–1900 hours Mountain Daylight Time. Using all-occurrence sampling, trained observers recorded marmot presence and social interactions (ethogram in Blumstein, Wey, & Tang, 2009) from a distance of 20–150 m depending on habitat and colony habituation (Huang, Wey, & Blumstein, 2011). Each social interaction was classified as affiliative or agonistic, and the initiator, recipient and winner (scored as the individual that stays at initial location) were noted (Fuong et al., 2015).

Additionally, observers conducted 2 min focal observations on foraging individuals in which the onset of quadrupedal foraging, bipedal foraging, quadrupedal looking, bipedal looking, walking, running and out-of-sight were dictated into a recorder (Blumstein et al., 2004). As with previous studies of this species, we conducted 2 min focals because individuals do not forage for extended periods, and our observations were restricted to actively foraging individuals. Focusing on foraging individuals helped to limit the possibility that more social individuals were less vigilant due to an increased number of social interactions (Blumstein, 1996). For each focal observation, observers recorded the incline (0–10°, 11–30°, >30°), substrate (stones, talus, dirt, low vegetation, high vegetation) and number of individuals within 10 m (details in Blumstein et al., 2004) because these factors can affect the time marmots allocate to vigilance (Chmura et al., 2016). Observations were terminated before the 2 min mark if an individual moved out-of-sight, began to engage in a social interaction, or if an alarm call was heard. The mean \pm SE focal duration was 112.7 \pm 0.6 s for females, and 115.2 \pm 0.8 s for males. The focal recordings were then scored in JWatcher 1.0 (Blumstein & Daniel, 2007), and the proportion of time in sight allocated to vigilance was calculated using the total time spent looking. Following Chmura et al. (2016), we only included focal samples >60 s, and we restricted our analysis to individuals that foraged on the most common substrate, vegetation, which was either 'high' (taller than a marmot's shoulders) or 'low' vegetation (lower than a marmot's shoulders).

Social Network Measures

Since yellow-bellied marmots live in female-dominated social groups (matrilines; Armitage, 2014), male and female life histories vary. We studied this variation by examining the importance of social bonds separately within each sex. Following Fuong et al. (2015) and Blumstein et al. (2017), we constructed annual social networks for each social group in the four main colonies.

We independently assigned social groups based on space use overlap. To exclude transients, we only included male and female yearlings and adults seen and/or trapped more than five times within a year. For each interacting pair, we used the simple ratio index (SRI, Cairns & Schwager, 1987; implemented in SOCPROG, Whitehead, 2009) from the set of observations that included all locations where each individual was observed and trapped (Nanayakkara & Blumstein, 2003). This was thus a weighted measure. The SRI was then entered into a random walk algorithm in Map Equation (Rosvall & Bergstrom, 2008) to identify social groups. For each social group defined based on location data, we focused exclusively on the set of observed affiliative interactions to create a behavioural association matrix and social network (Maldonado-Chaparro, Hubbard, & Blumstein, 2015). In each social network, nodes represented individuals and these nodes were connected by edges, the observed affiliative interactions. For the female analyses, female–female interactions were used, and for the male analyses, male–male interactions were used (this necessarily reduced our sample size since multimale groups were far less common than multifemale groups).

To measure social connectedness, we calculated the following social attributes for each individual: degree (in and out), strength (in and out), betweenness centrality, closeness (in and out), eigenvector centrality, embeddedness and clustering coefficient. We used weighted networks for social attributes that could be weighted and unweighted networks for social attributes that did not rely on weights (degree and embeddedness).

Degree is the number of connections to others (outdegree) or from others (indegree) (Wasserman & Faust, 1994) and was calculated from directed networks (following Fuong et al., 2015). Strength is the sum of the weights of an individual's adjacent ties initiated (outstrength) or received (instrength) and was calculated from a directed network. Betweenness centrality was calculated based on the number of shortest paths between each pair of members in a focal individual's social network and refers to an individual's importance as a point of connection, information transfer and group stability (Wey et al., 2008). Betweenness was calculated from undirected networks (following Maldonado-Chaparro et al., 2015). Closeness (in and out) is a measure that reflects how connected an individual is via both direct and indirect relationships, reflecting an individual's potential influence on its group (Wey et al., 2008); it was calculated as the reciprocal of the sum of the shortest tie lengths between a focal individual and other individuals in its social network (Wasserman & Faust, 1994; Wey et al., 2008). Following Fuong et al. (2015), we calculated both incloseness and outcloseness using directed networks. Eigenvector centrality refers to an individual's connectedness in the network by factoring in connections of the individuals connected to the focal individual (Ruhnau, 2000) and was calculated as the eigenvector of the maximal eigenvalue of an adjacency matrix (Bonacich, 2007). Embeddedness was calculated based on the cohesive substructures of the network (Moody & White, 2003). Eigenvector centrality and embeddedness were calculated using undirected networks (following Fuong et al., 2015). The clustering coefficient indicates how densely a network is clustered around a focal individual and was calculated by dividing the number of actual edges by the total possible edges between an individual's neighbours (Wey et al., 2008). All social attributes were calculated with the igraph package 0.7.0 (Csardi & Nepusz, 2006) in R 3.1.1 (R Core Team, 2016).

Because these social attributes are somewhat correlated (Wey & Blumstein, 2012; Table 1), we used SPSS (IBM Corp., 2012) to perform a principal component analysis (PCA) to reduce the set of social network attributes to three uncorrelated, independent components (extractions based on eigenvalue >1 with varimax rotation). Then, we looked at which attribute loaded the highest on each independent component. The highest-loading attributes were different for females and males. For females (Table 2), the highest-loading attributes were outdegree, incloseness and embeddedness. For males (Table 3), the highest-loading attributes were outdegree, outcloseness and clustering coefficient.

Table 1

Pearson correlation coefficients of the set of social network measures calculated for each individual annually

	Indegree	Outdegree	Betweenness	Outcloseness	Clustering coefficient	Incloseness	Eigenvector centrality	Outstrength	Instrength	Embeddedness
Indegree		0.60	0.28	-0.14	-0.20	0.23	0.54	0.24	0.30	0.08
Outdegree	0.54		0.17	0.13	-0.18	-0.09	0.56	0.43	0.40	0.21
Betweenness	-0.10	-0.13		0.15	-0.14	0.18	-0.06	-0.12	-0.12	-0.17
Outcloseness	-0.05	0.13	0.02		0.21	0.32	-0.01	-0.40	-0.40	-0.08
Clustering coefficient	0.01	0.06	-0.41	0.16		0.09	-0.21	-0.15	-0.15	0.21
Incloseness	0.23	0.16	0.13	0.63	-0.06		0.08	-0.37	-0.41	-0.09
Eigenvector centrality	0.30	0.42	-0.10	-0.11	-0.42	-0.07		0.38	0.37	0.08
Outstrength	0.30	0.26	-0.21	-0.59	-0.01	-0.39	0.26		0.86	0.47
Instrength	0.31	0.11	-0.20	-0.50	0.08	-0.49	0.20	0.86		0.46
Embeddedness	0.26	0.18	-0.22	0.48	0.46	0.48	-0.15	-0.02	-0.02	

Correlation coefficients are shown in bold for the female data set and in regular font for the male data set.

Table 2

Rotated component scores from the principal component analysis of the social network measures for females

Social attribute	PC 1	PC 2	PC 3
Indegree	0.802	0.191	-0.047
Outdegree	0.838	0.063	0.005
Betweenness centrality	0.289	0.447	-0.311
Outcloseness	0.084	0.694	0.165
Clustering coefficient	-0.405	0.153	0.606
Incloseness	0.124	0.781	0.104
Eigenvector centrality	0.768	-0.019	-0.086
Outstrength	0.577	-0.665	0.272
Instrength	0.577	-0.670	0.277
Embeddedness	0.173	-0.027	0.871

Values in bold are the social attributes used in analysis because their absolute value loaded the highest on the respective PC factor.

Table 3

Rotated component scores from the principal component analysis of the social network measures for males

Social attribute	PC 1	PC 2	PC 3
Indegree	0.784	0.038	0.151
Outdegree	0.843	0.111	-0.025
Betweenness centrality	0.139	0.187	-0.678
Outcloseness	0.174	0.820	0.135
Clustering coefficient	-0.064	0.058	0.789
Incloseness	0.209	0.791	0.171
Eigenvector centrality	0.745	-0.062	-0.297
Outstrength	0.515	-0.711	0.233
Instrength	0.503	-0.714	0.273
Embeddedness	0.274	0.294	0.753

Values in bold are the social attributes used in analysis because their absolute value loaded the highest on the respective PC factor.

Additional Potentially Important Covariates

In addition to measuring individual social network measures, we examined other factors known to influence time allocated to vigilance in other species and marmots, including apparent predation pressure (see below), age (i.e. yearling or adult; Armitage & Corona, 1994; Carey & Moore, 1986; Lea & Blumstein, 2011), foraging group size (i.e. number of individuals within 10 m during focal observation; Carey & Moore, 1986), incline (see above; Chmura et al., 2016), vegetation height (see above; Chmura et al., 2016), the bisexual social group size (i.e. total number of individuals assigned by the random walk algorithm to the focal individual's social group; Blumstein, 1996), faecal glucocorticoid metabolites (FGM) (see below), breeding status (i.e. whether or not a female had pups that year; Elgar, 1989) as well as marmot identity and year (which we included as random effects). We also included day of the year as a covariate because vegetation presence and

abundance vary seasonally, and the annual number of social observations of each individual was included as a covariate because some marmots are seen interacting more than others.

Since vigilance can be used as an antipredator strategy (Beauchamp, 2014, 2015), the presence or absence of predators could influence variation in time allocated to vigilance. To quantify potential predation pressure, we calculated an annual predator index for each colony. The index was calculated as the proportion of observation sessions during which we detected a predator between mid-April, when the marmots first emerged from hibernation, to the end of June, after which the growing vegetation made it difficult to detect terrestrial predators (see Monclús, Tiulim, & Blumstein, 2011; Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013). Observed predators included red foxes, *Vulpes vulpes*, coyotes, *Canis latrans*, American badgers, *Taxidea taxus*, American black bears, *Ursus americanus*, domestic dogs, *Canis lupus familiaris*, pine martens, *Martes martes*, and weasels (*Mustela* spp.), along with golden eagles, *Aquila chrysaetos*, and red-tailed hawks, *Buteo jamaicensis* (Armitage, 2004, 2014; Van Vuren, 1991, 2001). Each colony site was assigned low or high predator pressure based on a median cut calculated across all of the years (2002–2015).

Since glucocorticoids have been linked to increased foraging (Landys, Ramenofsky, & Wingfield, 2006) and other antipredator behaviours like alarm calling (Blumstein, Patton, & Saltzman, 2006), we used FGM, a measure of basal stress hormone levels, in our analysis. Adult female yellow-bellied marmots are more likely to alarm-call when their FGM levels are high (Blumstein et al., 2006). FGMs were extracted from faecal samples collected opportunistically from identified individuals during routine, biweekly trapping sessions, immediately placed on ice, and frozen at -20°C within 2 h of collection. We used a radioimmunoassay to quantify FGM levels (details in Blumstein et al., 2006; Smith, Monclús, Wantuck, Florant, & Blumstein, 2012). If an individual was trapped twice during a trapping session or within 24 h of a previous trapping session, we only used the FGM from the first collected sample in analysis. Trapping can be a stressful event and there is evidence that those animals that struggle in traps have higher FGM levels within the next 24 h (Smith et al., 2012). The number of days between faecal sample collection and focal observation was also included as a covariate.

Statistical Analyses

The final data set included 638 focal observations on 109 unique adult and yearling females observed and/or trapped a mean \pm SE of 89 ± 4.4 times, and 180 focal observations on 54 unique adult and yearling males observed and/or trapped 74 ± 9.9 times. We square root-transformed the proportion of total time spent looking to normalize its distribution. All continuous predictor variables were mean centred and divided by their standard deviation to create standardized coefficients before fitting models for easier interpretation of results.

To determine whether social connectedness influenced the proportion of total time looking, our estimate of vigilance, we fitted linear mixed effect models using the package lme4 1.1.7 (Bates, Maechler, Bolker, & Walker, 2015) in R 3.3.1 (R Core Team, 2016). We used lmerTest 2.0–32 to calculate the standard error and P values for the coefficients using the Satterthwaite approximation (Kuznetsova, Brockhoff, & Christensen, 2016). We then used a null model method involving network permutation procedure (described below) to determine whether observed estimates of the social network variables fell outside the 95% confidence intervals.

The model fitted for females included all possible fixed effects and covariates: outdegree, incloseness, embeddedness, FGM, age, breeding status, focal Julian date, number of days between the FGM

sample and focal observation, predator index, slope, incline, foraging group size, social group size and an individual's annual number of social observations. The model fitted for males included all the same possible fixed effects and covariates except for breeding status, and the social network measures differed (outdegree, outcloseness, clustering coefficient). To prevent pseudoreplication, individual identity (ID) was included as a random effect. To account for annual variation, year was included as random effect.

We evaluated assumptions of the mixed effects models by examining residuals and Q–Q plots; residuals were roughly normal and Q–Q plots were straight with no substantial outliers. We used a null model approach and performed node permutation tests to properly evaluate the effects of the social network variables (Farine, 2017; Whitehead, 2008). We randomized the nodes within each social network 1000 times, maintaining the social network structure, and calculated social network measures for each randomly permuted social network. For both male and female models, we then refitted the full model 1000 times. We compared the observed coefficient of each social network statistic to the 95% range of coefficients generated from the 1000 permutations. We interpreted values that fell outside the 95% range as significantly different from that expected by chance.

Ethical Note

All procedures were approved under research protocol ARC 2001–191–01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually, as well as annual permits issued by the Colorado Division of Wildlife (TR-917). After trapping, individuals were released immediately at the trap location. Marmots were in traps no longer than 2–3 h, and typically for much less time. Traps were shaded with vegetation on warm days. Marmot handling was brief (typically 5–15 min depending upon the data to be collected), and marmots were not injured during handling. All marmots were handled while inside of a conical cloth-handling bag to reduce stress. We swabbed ears with alcohol before tagging individuals to reduce the chance of infection. Observations were conducted at distances chosen to not overtly affect marmot behaviour.

RESULTS

Overall, after controlling for variation in vigilance explained by other factors, females in larger social groups looked less and males in larger foraging groups looked less (Tables 4, 5). For both sexes, the observed coefficients of the social network measures did not fall outside the 95% range of coefficients generated from the 1000 permutations (Figs 1 and 2); therefore, modelled social network measures did not predict the proportion of time spent looking. Across sexes, vegetation height significantly explained the proportion of time looking; both males and females looked more in low vegetation, and importantly, the effect size for vegetation was larger than that for social factors for both males and females (Tables 4, 5).

Using likelihood ratio tests, we found that including individual ID ($\chi^2_1 = 5.7673$, $P = 0.002$) and year ($\chi^2_1 = 4.5194$, $P = 0.002$) significantly improved the fit of the model for females. For males, including individual ID ($\chi^2_1 = 0$, $P = 0.132$) did not significantly improve the fit of the model, but including year ($\chi^2_1 = 0$, $P = 0.010$) did. Additionally, when the model included both individual ID and year together, the fit was significantly improved compared to the model with just individual ID ($\chi^2_1 = 4.8952$, $P = 0.027$) or just year ($\chi^2_1 = 6.1254$, $P = 0.013$) for females only. For the full model, including both random effects, the amount of variation explained by ID was similar for both females and males (females: 7.40%;

Table 4

Results from the linear mixed effects model for proportion of time looking (square-root transformed) for females only

	Variable	Estimate (SE)	df	t	P	
Fixed effects	Intercept	0.5115 (0.0206)	43	24.788	<0.001	
	Outdegree	0.0016 (0.0089)	320	0.178	0.859	
	Incloseness	-0.0075 (0.0071)	239	-1.063	0.289	
	Embeddedness	0.0009 (0.0099)	229	0.096	0.924	
	FGM	-0.0137 (0.0078)	134	-1.756	0.081	
	Breeding status (NB)	0.0262 (0.0169)	298	1.549	0.122	
	Foraging group size	-0.0063 (0.0056)	622	-1.108	0.268	
	Social group size	-0.0201 (0.0100)	276	-2.017	0.045	
	Days between	-0.0070 (0.0062)	427	-1.128	0.260	
	Age (Yearling)	-0.0124 (0.0187)	319	-0.663	0.508	
	Predator Index (Low)	0.0275 (0.0149)	146	1.855	0.066	
	Incline (11–30°)	-0.0045 (0.0130)	556	-0.343	0.732	
	Incline (>30°)	-0.0420 (0.0222)	465	-1.893	0.059	
	Vegetation (Low)	0.0329 (0.0153)	620	2.146	0.032	
	Date	-0.0176 (0.0075)	331	-2.343	0.020	
	Number of observations	-0.0082 (0.0103)	195	-0.800	0.425	
	Random effects	Variable	Variance	SD		
		Individual ID	0.0015	0.0388		
		Year	0.0013	0.0361		

Note that these results do not describe the results from the permutation tests on social network measures. All continuous independent variables were scaled and zeroed to create standardized coefficient estimates for comparison. For each fixed effect, estimates, standard error, degrees of freedom, *t* values and *P* values are included. The factor labels in parentheses indicate the factor level for which the estimates refer to. NB refers to nonbreeding individuals. For random effects, the variance and standard deviation are included. Terms and values in bold are those found to be significant ($P < 0.05$).

Table 5

Results from the linear mixed effects model for proportion of time looking (square-root transformed) for males only

	Variable	Estimate (SE)	df	t	P	
Fixed effects	Intercept	0.4434 (0.0502)	47	8.832	<0.001	
	Outdegree	0.0001 (0.0168)	42	0.005	0.996	
	Outcloseness	-0.0070 (0.0182)	42	-0.383	0.703	
	Clustering coefficient	0.0062 (0.0149)	30	0.417	0.680	
	FGM	-0.0037 (0.0135)	111	-0.271	0.787	
	Foraging group size	-0.0305 (0.0124)	180	-2.465	0.015	
	Social group size	-0.0130 (0.0176)	81	-0.743	0.460	
	Days between	-0.0124 (0.0125)	104	-0.991	0.324	
	Age (Yearling)	0.0641 (0.0447)	30	1.435	0.162	
	Predator index (Low)	-0.0362 (0.0325)	43	-1.114	0.271	
	Incline (11–30°)	-0.0285 (0.0271)	168	-1.053	0.294	
	Incline (>30°)	0.0055 (0.0560)	178	0.099	0.922	
	Vegetation (Low)	0.0808 (0.0374)	167	2.159	0.032	
	Date	0.0068 (0.0158)	135	0.427	0.670	
	Number of observations	0.0210 (0.0202)	28	1.039	0.308	
	Random effects	Variable	Variance	SD		
		Individual ID	0.0017	0.0417		
	Year	0.0000	0.0000			

Note that these results do not describe the results from the permutation tests on social network measures. All continuous independent variables were scaled and zeroed to create standardized coefficient estimates for comparison. For each fixed effect, estimates, standard error, degrees of freedom, *t* values, and *P* values are included. The factor labels in parentheses indicate the factor level for which the estimates refer to. For random effects, the variance and standard deviation are included. Terms and values in bold are those found to be significant ($P < 0.05$).

males: 7.49%), and the amount of variation explained by year varied by sex (females: 6.40%; males: 0%).

DISCUSSION

Our results suggest that the social factor, social group size, may influence the time female, but not male, yellow-bellied marmots

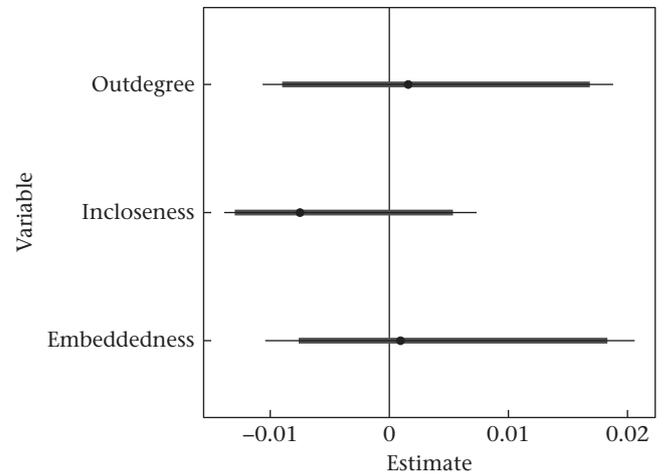


Figure 1. Results of the permutation tests for females. Thin black lines illustrate the 95% confidence intervals and the thick grey lines illustrate the 90% confidence intervals of the estimates. Observed estimates from the empirical data set are plotted as a circle on these distributions.

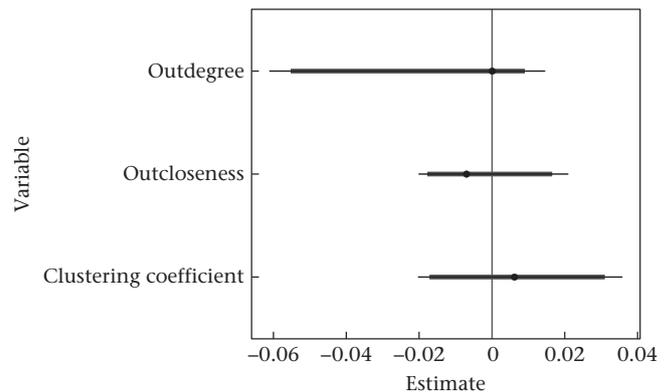


Figure 2. Results of the permutation tests for males. Thin black lines illustrate the 95% confidence intervals and the thick grey lines illustrate the 90% confidence intervals of the estimates. Observed estimates from the empirical data set are plotted as a circle on these distributions.

allocate to looking while foraging, our measure of vigilance. Rather, and more simply, males in larger foraging aggregations looked less, providing support for the ‘group size effect’ (Lima, 1995). We interpret our results to suggest that foraging group size is a metric that is likely to be independent of social relationships. Thus, only female marmots’ perceived risk, or what we refer to as a ‘sense of security’, was influenced by any of our measured social factors, specifically social group size. Females, not males, seem to perceive greater security (i.e. do not look as much while foraging) when they live in larger (bisexual) groups that permit the potential for more intrasexual and perhaps intersexual relationships.

Unlike previous studies in our system that showed that intrasexual social network position influences perceptions of security (Blumstein et al., 2017; Fuong et al., 2015), in this study no social network measures stood out as significantly affecting vigilance. Nevertheless, our findings demonstrate the power of social network statistics to identify specific attributes of social relationships that may affect perceived risk, actual risk, and hence, potentially, survivorship. Using social network statistics to study perceptions of security could be useful in identifying the importance of social relationships on perceptions of risk in other systems in which individuals live in stable groups or colonies in which social relationships may be important.

Our findings also suggest that sociality and the resulting social interactions may affect the sexes differently, a finding consistent with what we understand about yellow-bellied marmot life history (Armitage, 2014). These marmots live in female-dominated social groups containing one or few males. Perhaps male vigilance is affected only by immediate foraging group size, and not by intra-sexual social relationships, because males typically live in unimale groups and do not have the opportunity to form or generally benefit from social relationships. By contrast, female vigilance is influenced by other conspecifics because they form matrilineal and hence live in groups with more than one female.

We acknowledge that the effect sizes of the significant predictors are relatively small. Interestingly, in our large and highly variable set of vigilance observations, factors that explained time allocated to vigilance or time allocated to foraging in previous analyses conducted in this population (e.g. incline: Chmura et al., 2016; Blumstein et al., 2004; log-transformed FGM: Chmura et al., 2016) either were not significant, or their effect was relatively small. It is important to realize that while animals do largely trade off vigilance and foraging, and there is a strong correlation between the two in our population (Chmura et al., 2016), different factors seem to explain variation in these behaviours.

Because our analyses were correlative, we were unable to tease apart causality. Although our results suggest that the factors influencing vigilance vary by sex, we were unable to identify the immediate stimulus triggering vigilance (sensu Gaynor & Cords, 2012), or the target of looking, and thus could not better understand the social dynamics underlying vigilance. Additionally, we could only quantify visual, not olfactory or auditory, vigilance (Blumstein, 1996), two modalities marmots use to assess predation risk (Blumstein, Barrow, & 2008).

Despite these limitations, the approach we adopted here should not be viewed as a marmot-specific approach. Indeed, some recent experimental studies have found that predators influence social responses. Voelkl et al. (2016) found that birds attacked by model raptors modified group structure for several hours after the attack. In guppies, predation risk seemed to influence coordinated movement (Ioannou, Ramnarine, & Torney, 2017), and, in another study, how guppies perceived predation risk modified the stability and structure of their social relationships (Heathcote et al., 2017). These recent discoveries showing how changes in actual predation risk influence social interactions, combined with our results, highlight the importance and utility of using a social network/social attribute-based approach to understand variation in how animals perceive safety, and they have created new insights into our understanding of vigilance.

While variation in neither female nor male marmot vigilance was explained by the social network measures as we quantified them here, the approach we have adopted is, nevertheless, promising. Using a single social attribute, and not accounting for potentially confounding variables, overlooks significant variation because it assumes all individuals experience and perceive risk equally (Beauchamp, 2003; Treves, 2000). Future work on 'social security' and other aspects of sociality should consider this network-based approach to better understand the inner workings of social groups.

Acknowledgments

We thank the marmoteers who helped collect these data as well as Xochitl Ortiz Ross, Tiffany Armenta, Gabriela Pinho, Holly Fuong and Adriana Maldonado-Chaparro for considerable help with R code. Adriana also provided invaluable help with our randomization. We thank Adriana, Scott Johnson and two astute and persistent anonymous referees for very constructive comments on the

manuscript, and Adriana, Holly, Noa Pinter-Wollman and Mason Porter for extensive discussions about the analysis of social networks. R.P.M. was a National Science Foundation Research Experience for Undergraduates fellow. D.T.B. was supported by the National Geographic Society, the University of California Los Angeles (Faculty Senate and the Division of Life Sciences), a Rocky Mountain Biological Laboratory research fellowship, the National Science Foundation (IDBR-0754247, DEB-1119660 and 1557130), and by grants DBI 0242960, 0731346 and 1226713 to the Rocky Mountain Biological Laboratory.

References

- Armitage, K. B. (2004). Badger predation on yellow-bellied marmots. *American Midland Naturalist*, 151, 378–387.
- Armitage, K. B. (2014). *Marmot biology: Sociality, individual fitness, and population dynamics*. Cambridge, U.K.: Cambridge University Press.
- Armitage, K. B., & Corona, M. C. (1994). Time and wariness in yellow-bellied marmots. *Ibex Journal of Mountain Ecology*, 2, 1–8.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Beauchamp, G. (2003). Group size effects on vigilance: A search for mechanisms. *Behavioral Processes*, 63, 141–145.
- Beauchamp, G. (2008). What is the magnitude of the group-size effect on vigilance? *Behavioral Ecology*, 19, 1361–1368.
- Beauchamp, G. (2014). *Social predation: How group living benefits predator and prey*. London, U.K.: Academic Press.
- Beauchamp, G. (2015). *Animal vigilance: Monitoring predators and competitors*. London, U.K.: Academic Press.
- Blumstein, D. T. (1996). How much does social group size influence golden marmot vigilance? *Behaviour*, 133, 1133–1151.
- Blumstein, D. T. (2013). Yellow-bellied marmots: Insights from an emergent view of sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20120349.
- Blumstein, D. T., & Armitage, K. B. (1997). Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist*, 150, 179–200.
- Blumstein, D. T., Barrow, L., & Luterra, M. (2008). Olfactory predator discrimination in yellow-bellied marmots. *Ethology*, 114, 1135–1143.
- Blumstein, D. T., Cooley, L., Winternitz, J., & Daniel, J. C. (2008). Do yellow-bellied marmots respond to predator vocalizations? *Behavioral Ecology and Sociobiology*, 62, 457–468.
- Blumstein, D. T., & Daniel, J. C. (2007). *Quantifying behavior the JWatcher way*. Sunderland, MA: Sinauer.
- Blumstein, D. T., Fuong, H., & Palmer, E. (2017). Social security: Social relationship strength and connectedness influence how marmots respond to alarm calls. *Behavioral Ecology and Sociobiology*, 71, 145. <https://doi.org/10.1007/s00265-017-2374-5>.
- Blumstein, D. T., Patton, M. L., & Saltzman, W. (2006). Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biology Letters*, 2, 29–32.
- Blumstein, D. T., Runyan, A., Seymour, M., Nicodemus, A., Ozgul, A., Ransler, F., et al. (2004). Locomotor ability and wariness in yellow-bellied marmots. *Ethology*, 110, 615–634.
- Blumstein, D. T., Wey, T. W., & Tang, K. (2009). A test of the social cohesion hypothesis: Interactive female marmots remain at home. *Proceedings of the Royal Society B: Biological Sciences*, 276, 3007–3012.
- Bonacich, P. (2007). Some unique properties of eigenvector centrality. *Social Networks*, 29, 555–564.
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, 35, 1454–1469.
- Cameron, E. Z., & Du Toit, J. T. (2005). Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. *Animal Behaviour*, 69, 1337–1344.
- Carey, H. V., & Moore, P. (1986). Foraging and predation risk in yellow-bellied marmots. *American Midland Naturalist*, 116, 267–275.
- Chmura, H. E., Wey, T. W., & Blumstein, D. T. (2016). Assessing the sensitivity of foraging and vigilance to internal state and environmental variables in yellow-bellied marmots (*Marmota flaviventris*). *Behavioral Ecology and Sociobiology*, 11, 1901–1910.
- Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *International Journal of Complex Systems*, 1695. <http://igraph.org>.
- De Laet, J. F. (1985). Dominance and anti-predator behaviour of great tits *Parus major*: A field study. *Ibis*, 127, 372–377.
- Dehn, M. M. (1990). Vigilance for predators: Detection and dilution effects. *Behavioral Ecology and Sociobiology*, 26, 337–342.
- Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews*, 64, 13–33.
- Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*. <https://doi.org/10.1111/2041-210X.12772>. Advance online publication.

- Fuong, H., Maldonado-Chaparro, A., & Blumstein, D. T. (2015). Are social attributes associated with alarm calling propensity? *Behavioral Ecology*, *26*, 587–592.
- Gaynor, K. M., & Cords, M. (2012). Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. *Animal Behaviour*, *84*, 531–537.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*, 295–311.
- Heathcote, R. J., Darden, S. K., Franks, D. W., Ramnarine, I. W., & Croft, D. P. (2017). Fear of predation drives stable and differentiated social relationships in guppies. *Scientific Reports*, *7*, 41679.
- Hegner, R. E. (1985). Dominance and anti-predator behaviour in blue tits (*Parus caeruleus*). *Animal Behaviour*, *33*, 762–768.
- Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, *11*, 1–17.
- Huang, B., Wey, T. W., & Blumstein, D. T. (2011). Correlates and consequences of dominance in a social rodent. *Ethology*, *117*, 1–13.
- IBM Corp. (2012). *IBM SPSS statistics for Windows (version 21.0)*. Armonk, NY: IBM Corp.
- Ioannou, C. C., Ramnarine, I. W., & Torney, C. J. (2017). High-predation habitats affect the social dynamics of collective exploration in a shoaling fish. *Science Advances*, *3*, e1602682.
- Kelley, J. L., Morrell, L. J., Inskip, C., Krause, J., & Croft, D. P. (2011). Predation risk shapes social networks in fission–fusion populations. *PLoS One*, *6*(8), e24280.
- Kutsukake, N. (2006). The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology*, *112*, 581–591.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2016). *lmerTest: Tests in linear mixed effects models (R package version 2.0-32)*. <https://CRAN.R-project.org/package=lmerTest>.
- Landys, M. M., Ramenofsky, M., & Wingfield, J. C. (2006). Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *General and Comparative Endocrinology*, *148*, 132–149.
- Lea, A. J., & Blumstein, D. T. (2011). Age and sex influence marmot antipredator behavior during periods of heightened risk. *Behavioral Ecology and Sociobiology*, *65*, 1525–1533.
- Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: The group-size effect. *Animal Behaviour*, *49*, 11–20.
- Maldonado-Chaparro, A. A., Hubbard, L., & Blumstein, D. T. (2015). Group size affects social relationships in yellow-bellied marmots (*Marmota flaviventris*). *Behavioral Ecology*, *26*, 909–915.
- Monclús, R., Anderson, A. M., & Blumstein, D. T. (2015). Do yellow-bellied marmots perceive enhanced predation risk when they are farther from safety? An experimental study. *Ethology*, *121*, 831–839.
- Monclús, R., Tiulim, J., & Blumstein, D. T. (2011). Older mothers follow conservative strategies under predator pressure: The adaptive role of maternal glucocorticoids in yellow-bellied marmots. *Hormones and Behavior*, *60*, 660–665.
- Moody, J., & White, D. R. (2003). Structural cohesion and embeddedness: A hierarchical concept of social groups. *American Sociological Review*, *68*, 103–127.
- Nanayakkara, D. D., & Blumstein, D. T. (2003). Defining yellow-bellied marmot social groups using association indices. *Oecologia Montana*, *12*, 7–11.
- Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour*, *86*, 1147–1154.
- Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, *38*, 419–422.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour*, *51*, 1077–1086.
- Rosvall, M., & Bergstrom, C. T. (2008). Maps of random walks on complex networks reveal community structure. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 1118–1123.
- Ruhnau, B. (2000). Eigenvector-centrality: A node-centrality? *Social Networks*, *22*, 357–365.
- Smith, J. E., Monclús, R., Wantuck, D., Florant, G. L., & Blumstein, D. T. (2012). Fecal glucocorticoid metabolites in wild yellow-bellied marmots: Experimental validation, individual differences and ecological correlates. *General and Comparative Endocrinology*, *178*, 417–426.
- Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, *60*, 711–722.
- Van Vuren, D. (1991). Yellow-bellied marmots as prey of coyotes. *American Midland Naturalist*, *125*, 135–139.
- Van Vuren, D. (2001). Predation on yellow-bellied marmots (*Marmota flaviventris*). *American Midland Naturalist*, *145*, 94–100.
- Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology*, *30*, 405–422.
- Voelkl, B., Firth, J. A., & Sheldon, B. C. (2016). Nonlethal predator effects on the turnover of wild bird flocks. *Scientific Reports*, *6*, 33476.
- Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and application*. New York, NY: Cambridge University Press.
- Wey, T. W., & Blumstein, D. T. (2012). Social attributes and associated performance measures in marmots: Bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behavioral Ecology and Sociobiology*, *66*, 1075–1085.
- Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: A promising tool for the study of sociality. *Animal Behaviour*, *75*, 333–334.
- Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. Chicago, IL: University of Chicago Press.
- Whitehead, H. (2009). SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology*, *63*, 765–778.