

**Are social network measures associated with the propensity to alarm call in yellow-bellied
marmots (*Marmota flaviventris*)?**

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Abstract

Alarm calling is a behavior that typically benefits individuals through an increase in indirect fitness, an increase in social status, or in relation to reciprocity. Despite the risk of potentially higher detection by predators, callers emit these vocalizations in response to a threat. While previous studies have examined the costs and benefits of alarm calling, few have examined how individual factors such as social network position can influence the propensity to alarm call. Social network position may have a strong influence on how an individual behaves. Individuals can vary in how central, involved or influential, and connected to other individuals they are in a network. Thus, how interactive an individual is or the strength of relationships between individuals can influence the rate of alarm calling. We examined how various social network measures (degree centrality, closeness centrality, eigenvector centrality, strength, and embeddedness) were related to the likelihood of yellow-bellied marmots (*Marmota flaviventris*) to call by running a principle component analysis to produce two factors, ‘superficial popularity’ and ‘relationship strength’. Using generalized linear mixed effects models, we found that the wild or natural rate of alarm calling increased for marmots that were less superficially popular, while the in-trap rate of alarm calling increased for marmots involved in weaker relationships. Less popular marmots could be seeking a status gain, participating in reciprocal alarm calling, allocating more time to vigilance, or deterring predators without the aid of others. Similarly, marmots in traps are faced with an imminent and individualized threat, thus those in weaker relationships cannot rely on other marmots to alarm call, so they call in order to deter predators.

Introduction

Alarm calls are vocalizations emitted in response to potential danger (Caro, 2005). One function of alarm calling is to alert conspecifics that a predator is present (Sherman, 1977). By calling, individuals may suffer a direct fitness cost since it may direct a predator's attention to the caller (Maynard Smith, 1965). While this behavior may seem altruistic, it may actually be a more subtle way of increasing fitness through kin selection (Wheeler, 2008). If callers are related to the other individuals in their area, they would accrue direct and potentially indirect fitness benefits by warning conspecifics (e.g., Dunford, 1977; Sherman, 1977; Schwagmeyer, 1980). However, while many studies have focused on testing hypotheses about fitness acquired by calling, other factors can influence the probability of emitting an alarm vocalization.

Alarm calling has multiple functions, which can influence how animals react to the presence of a threat. Alarm calling can be used as an antipredator response to deter predators (Woodland, Jaafar, & Knight, 1980; Zuberbühler, Noë, & Seyfarth, 1997). For example, six species of monkeys in the Taï forest increased their rates of alarm calling to deter stealth predators (Zuberbühler, Jenny, & Bshary, 1999). Separately, individuals may be calling because they have a reciprocal relationship and take turns vocalizing (Trivers, 1971). Previous studies have shown that animals are capable of remembering individual callers (Wich & Vries, 2006), thus they would be able to reciprocate calling.

It is important to realize that not all individuals emit alarm calls when they encounter a predator. In Steller's jays (*Cyanocitta stelleri*), individuals that took more risks were more likely to call (Gabriel & Black, 2010). Additionally, bolder great tits (*Parus major*) called more often than their less aggressive counterparts (Hollander, Overvld, Tokka, & Matthysen, 2008). Adult female yellow-bellied marmots (*Marmota flaviventris*) with pups alarm called more than any

other age-sex group in response to threatening stimuli (Blumstein, Steinmetz, Armitage, & Daniel, 1997). Glucocorticoid and cortisol levels provide a proximate mechanism that may also explain variation in the propensity to emit alarm calls (e.g., Blumstein, Patton, & Saltzman, 2006; Bercovitch, Hauser, & Jones, 1995).

Individuals often vary in consistent, repeatable ways—that is they have personality (Gosling, Rentfrow, & Swann Jr., 2003). Differences in personalities between individuals could potentially influence the likelihood of emitting alarm calls. For instance, docile yellow-bellied marmots (*Marmota flaviventris*) are less likely to call when approached in a trap (Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013). Docility is a repeatable personality trait in a number of different species (wild eastern chipmunks *Tamias striatus*, Montiglio, Garant, Pelletier, & Réale, 2012; bighorn sheep *Ovis canadensis*, Réale, Gallant, Leblanc, & Festa-Bianchet, 2000; alpine marmots *Marmota marmot*, Ferrari et al., 2013). But, there are other aspects of how individuals interact with their environment that may be repeatable.

Social animals are involved in an intricate web of social relationships. Social network measures quantify a variety of specific social attributes that capture both direct and indirect interactions with others (Wey, Blumstein, Shen, & Jordán, 2008; Blumstein, 2013). Many of these have been demonstrated to be repeatable and indeed may be heritable (Krause, James, & Croft, 2010; Lea, Blumstein, Wey, & Martin, 2010; Wilson, Krause, Dingemanse, & Krause, 2013). It is conceivable that social network measures that describe attributes of network centrality or positional importance may explain some variation in the propensity to emit alarm calls.

We therefore hypothesize (and justify below) that the following social network measures, each of which describe some aspect of positional importance, may be related to the propensity to

emit alarm calls: degree centrality, closeness centrality, eigenvector centrality, strength, and embeddedness. Additionally, if these measures are related to alarm calling, we hypothesize that marmots with many affiliative interactions and strong relationships should call more to gain the potential adaptive benefits of enhanced social status and benefits of reciprocity.

Centrality can be calculated in different ways, but generally, central animals are more important in a group in that they may have more ‘control’ (Lusseau & Newman, 2004) or influence over information flow (Vital & Martins, 2009) than less central animals. Degree centrality is the number of direct connections an individual has. It suggests that a higher number of direct connections means an individual is more central, and thus has potentially more influence to surrounding individuals. Additionally, it may be relatively more important in the entire network because information could potentially reach more individuals (Wey et al., 2008). In a directed network, the direction of the interactions can influence the spread of information. Closeness centrality is a measure of how close an individual is to other individuals, or the length of the relationships between an individual and other individuals (Newman, 2001). It may influence propensity to call because it shows the influence of an individual on other individuals. It displays the power of these relationships and the ability for information to spread throughout a group (Wey et al., 2008). Eigenvector centrality suggests that individuals that have relationships with more central individuals are more central to the network (Ruhnau, 2000). Because centrality is proportional to an individual’s neighbors’ centralities (Newman, 2004), more influential individuals will be more connected with other influential individuals. Strength is another directed social network measure that examines the sum of all of an individual’s relationships weights in a weighted network. Embeddedness is how isolatable an individual is, or how involved in the network structure an individual is (Moody & White, 2003). If all of these connections were

severed, the individual would be isolated, thus higher embeddedness means it is more difficult to isolate the individual. Embeddedness can show how the flow of information, like that produced by alarm calls, can be stopped when individuals are removed or relationships are severed. All 5 of these social network measures can be viewed as specific attributes of how individuals interact with others. Importantly, all quantify specific ways that information could be spread throughout a network and how individuals can play a role in the transmission of this information.

Yellow-bellied marmots at the Rocky Mountain Biological Laboratory (RMBL) in Colorado are an ideal subject to study the association between attributes of sociality and the propensity to emit alarm calls for the following reasons. First, not all individuals call when they encounter a predator so that there is variation in the propensity to emit calls (Blumstein, 1997). Second, we have amassed over a decade of detailed data on social interactions that permit us to study the relationship between social attributes and the relative frequency of calling. Third, some of these social attributes are known to be repeatable—thus they can be compared between individuals and years. Added to this, we have data on how docile animals are when trapped—a repeatable personality trait that has been seen to influence calling. Fourth, previous studies have documented that social network position and social relationships may have fitness effects (Lea et al., 2010) and can influence reproductive success (Wey & Blumstein, 2012). These social network measures could also influence their interactions with other individuals, including, potentially, their propensity to alarm call.

Methods

Each year, starting in 2002, teams of observers live trapped and observed the behavior of free-living yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (38°77'

N, 106°59' W; Figure 1). Marmots were observed during their active season—mid-April to mid-September—during periods of peak activity—between 0700 h and 1100 h and between 1630 h and 1900 h MDT. Observations were conducted at 6 different colony sites. Each colony site was geographically distinct and separated from other colony sites.

Live-trapping and quantifying docility

We set Tomahawk single door live traps, baited with horse feed (Omalene 100, Ralston Purinia, St. Louis, MO) at known burrow locations. When trapped, subjects were transferred into canvas handling bags during which time in-trap behaviors were recorded. These behaviors included whether the marmot tooth chattered, alarm called, struggled in trap, tried to bite through the cage, or failed to immediately walk into the bag. Once in the handling bag, we checked or inserted ear tags (#3 monel fingerling fish tags—National Band and Tag, Newport, KY), and uniquely marked (or re-marked) individuals' dorsal pelage with Nyanzol fur dye (Albinal Dyestuff Inc., Jersey City, NJ) for identification from a distance.

We calculated the docility index by subtracting the maximum potential score of 4 by the sum of numbers given from each trap behavior—tooth chattered (0 = no; 1 = yes in trap); struggled in trap (0 = no; 1 = yes); tried to bite through cage (0 = no; 1 = yes); and immediately walked into the bag (0 = yes without coercion; 1 = no) (Petelle et al., 2013). Because we were interested in studying how docility influenced the propensity to emit alarm calls, we did not calculate docility with alarm calling as a potential behavior. Individuals with a docility index score of 0 were considered non-docile (Réale et al., 2000), while those with scores of 4 were considered docile. From the trapping behaviors, we were also able to calculate the in-trap rate of alarm calling, by dividing the number of times an individual called in trap in a given year by the

total number of times an individual was trapped in a given year. In addition, for each subject, we calculated the proportion of times they emitted alarm calls when trapped.

Behavioral observations

Trained observers quantified marmot behavior from distances selected to not obviously influence marmot behavior. These distances varied by site and ranged from 20 m to 150 m. Using 15-45x spotting scopes and 10 x 40 binoculars, observers quantified all social interactions (Table 1).

Each time seen, we noted the initiator, recipient, and the winner of these interactions (defined as the marmot that maintained its location). Additionally, we quantified all bouts of alarm calls and attempted to record the identity of all marmots emitting calls (this was often not possible for bouts containing a single call). From this, we calculated annual rates of alarm calling by dividing the number of times an individual was observed to call by the number of hours a colony site was observed on days when that individual was seen. By restricting hours to those days in which the individual was seen, we accounted for individuals that dispersed or died during the season. Only individuals with both trapping rates of calling and wild rates of calling were included to provide a complementary data set for subsequent analyses.

Calculating social network measures

Using our set of observed affiliative social interactions, we calculated social network measures for yearlings and adults (we excluded juveniles). Because alarm calls could be heard throughout the colony, we calculated social attributes at the colony level.

Statistical analyses

To quantify docility, and following Petelle et al. (2013), we calculated best linear unbiased predictors (BLUPs) for each individual per year from trapping data. BLUPs were calculated using a linear mixed effects model in R 3.1.1 (R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) and the lmer function in the lme4 package (Bates, Maechler, Bolker, & Walker, 2014). Fixed effects included trapping date, time of day (morning or afternoon), days between trapping events, number of times an individual was trapped in a given year, and the sex of the individual. Random effects included a combined year and marmot unique identifier variable to produce one random effect for each individual per year. The conditional means of the random effects were calculated with the lme4 package function ranef to assign each individual in a given year a docility BLUP.

Because social network measures are often correlated (Wey & Blumstein, 2012), we used principle components analysis to reduce our set of 8 potentially correlated variables to 2 uncorrelated variables or factors (extractions based on eigenvalue > 1 with varimax rotation; SPSS 21.0 (IBM, Armonk, NY, U.S.A.)).

We fitted a generalized linear mixed effects model to determine whether the natural rate of alarm calling was influenced by social relationships. Models were fitted using the R package lme4. We first log-10 transformed natural rates of alarm calling, and then specified a Gamma family log link function when we fitted the model using the glmer function in lme4. Our fixed effects included colony, colony size, sex of individual, age class of individual (yearling or adult), an individual's docility BLUP, factor 1 score, and factor 2 score. Our random effects included the marmot's identity and year. Because the initial model failed to converge, we set control parameters using BOBYQA to specify the maximum number of function evaluations used. To

calculate p-values using type III Wald Chi-square tests, we used the Anova function in the car package (Fox & Weisberg, 2011).

We fitted a two-step model to determine whether the proportion of times a subject called when trapped was influenced by social network measures: a generalized linear mixed effects model of 1/0 called or did not call in trap binomial data using glmer in lme4, and a linear mixed effects model of those individuals that called in trap using lmer in lme4. We fitted two models because the continuous data was zero-inflated. For the binomial data in the generalized mixed effects model, we specified a binomial family logit link function error distribution. Because the initial model failed to converge, we set control parameters using BOBYQA to specify the maximum number of function evaluations used. For the data with only individuals that called in trap, we square root transformed the data. We specified a Gaussian family error distribution by using the lmer function because a Gaussian distributed generalized linear mixed effects model using glmer is the same as a linear mixed effects model using the lmer function. For both models, the fixed effects included were colony, colony size, sex of individual, age class of individual (yearling or adult), an individual's docility BLUP, factor 1 score, and factor 2 score. The random effects included marmot identity and year. We calculated p-values for both models using type III Wald Chi-square tests with the Anova function in car.

Results

Our final data set contained 209 observations of rates of alarm calling from 141 individuals over 12 years. Mean observation time per individual per year was 86.9 ± 66.8 h. Individuals were typically trapped 5.9 ± 4.3 times per year. There were 91 unique females observed 157 times and

55 unique males observed 57 times. 55 individuals were classified as adults and observed 106 times, while 108 individuals were classified as yearlings.

We extracted two factors (Table 2). Factor 1 accounted for 63.5% of variance and factor 2 accounted for 16.8% of variance. We interpreted the first factor as ‘superficial popularity’ because it was comprised of social network measures based on the number of affiliative interactions with and how close an individual was to other individuals. We interpreted the second factor as ‘relationship strength’ because it consisted of both measures of strength and how tightly connected (or embedded) an individual was.

Social network position explained significant variation in wild calling behavior. After controlling for significant variation explained by colony size (estimate = -0.45, $p < 0.01$) and colony ($p < 0.01$), marmots that were less superficially popular (factor 1 estimate = -0.35, $p < 0.01$) were observed to emit calls at higher rates.

Similarly, social network position explained significant variation in the rate of in-trap calling. When looking at individuals that called in trap and after accounting for variation explained by colony ($p < 0.01$), marmots that were less docile (estimate = -0.13, $p = 0.02$) and marmots in weaker relationships (factor 2 estimate = -0.06; $p = 0.01$) called more.

Discussion

We found that yellow-bellied marmots were more likely to call in the wild if they were less superficially popular. This pattern was contrary to our hypothesis and could emerge for at least five different reasons: (1) to increase indirect fitness; (2) to increase status or reputation; (3) to ensure there are future benefits acquired from reciprocity; (4) to allocate time normally spent socially interacting towards vigilance; and (5) to deter predators.

Yellow-bellied marmots live in female-biased social groups consisting mostly of relatives (Armitage, 1991), and individuals in social networks are more related than would be expected by chance (Wey & Blumstein, 2010). While calling may not be that risky since individuals typically emit calls from safe locations (Collier et al., 2010), previous studies in this population showed that marmots selectively emitted alarm calls to maximize their direct, not indirect, components of fitness (Blumstein et al., 1997). Thus, the relationship between calling and superficial popularity was likely not driven by the benefits of increasing indirect components of fitness.

Marmots that are less superficially popular could be calling more in an attempt to increase their status or reputation. Social status or prestige is when an individual participates in a seemingly altruistic behavior in order to appear as a cooperative and quality member of the group (Zahavi, 1995). For example, subordinate adult male capybaras (*Hydrochaeris hydrochaeri*) alarm called more than dominant males. By actively participating in the group, they slowly moved up the social hierarchy and gained status, in turn increasing their individual matings as a dominant male (Herrera & Macdonald, 1993). Thus, social status can benefit future fitness, therefore participating in riskier ‘altruistic’ behaviors could increase fitness.

Additionally, marmots may be reciprocally emitting alarm calls at higher rates when they are less superficially popular. By calling, they may be trying to increase the number of marmots that can reciprocally call for them later. Reciprocal altruism in calling can be seen as maintaining an optimal group size, which can help reduce the amount of time being vigilant and increase the amount of time dedicated to foraging or other behaviors (Ekman, 1987). Reciprocity in alarm calling can be seen as higher rates of calling when surrounded by non-kin (great tits *P. major*, Krams, Krama, & Igaune, 2006). Because these marmots are not necessarily calling for their kin (Blumstein et al., 1997), increased calling can be attributed to reciprocal altruism.

Less superficially popular marmots may be allocating the time typically spent interacting with others towards vigilant behavior, thus increasing their rate of alarm calling. In yellow-bellied marmots, individuals that call will continue to allocate time towards vigilance, which reduces time spent participating in other activities (Blumstein, 2007). With more time spent being vigilant, these marmots would be more likely to detect potential danger.

Lastly, individuals involved in fewer social interactions could be calling at higher rates because they cannot rely on other marmots to call for them. Because one of the functions of alarm calls is to deter predators (Woodland et al., 1980, Zuberbühler et al., 1997), in a situation where these individuals do not typically interact with others, they may be more obligated to call directly at predators in order to deter the predators (Krams et al., 2006).

Once in traps, marmots were more likely to call if they were involved in weaker relationships. This finding directly contradicts our initial hypothesis. We suggest three alternative hypotheses for this.

First, similar to less superficially popular marmots, relatively isolated individuals could call at higher rates because these individuals must deter predators by themselves. Without strong affiliations, other marmots may not be as obligated to call for them. Because these individuals are weakly connected with others, they may, in a potentially high-risk situation, realize that others will not call, as they are able to adjust their calling to situational circumstances (Blumstein & Armitage, 1997). If so, then they may have to call themselves to deter predators (Krams et al., 2006).

Another plausible explanation is marmots that are not as embedded or involved in the network are calling in an effort to gain status (Zahavi, 1995). Other marmots in the area know that there is a predator around, and yet the threatened marmot is calling in order to show that it is

capable of calling and aiding in predator detection (or deterrence). These individuals are reacting differently to predator presence, and thus alarm calling differently, because the threat is directed towards the individual caller.

Finally, animals may emit alarm calls in the traps because of their personality, which is drawn out through individualized and focused threats. Docility could be a context-specific measure, in that it is a strong measure of how individuals will respond in trap (Réale et al., 2000). Thus, less docile individuals will call when they are trapped.

Our results suggest that social network measures are related to the propensity to alarm call, and that superficially popular marmots and marmots with strong relationships will call more. While it cannot be determined whether these calls are because of a desire for status or based on reciprocal altruism, there is a significant relationship between network position and calling.

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Table 1. List of social behaviors.

behavior	description
Aggression	Following the interaction, individuals will separate. These are quicker and tend to be associated with vocalizations. Include bite, box, chase, grab/slap/push, mouth spar, pounce, snap/snarl/hiss, and wrestle.
Play	Individuals seem less invested than aggressive interactions. They will typically sit next to each other afterwards, and shift to other behaviors regularly. In a playful/non-aggressive manner, these include bite, box, chase, grab/slap/push, pounce, mount, and wrestle.
Sniff	Initiator sniffs butt-end of receiver.
Greet	Initiator touches nose of receiver with its nose.
Allogroom	One individual grooms another or multiple marmot grooming each other. Typically in areas that marmots cannot reach themselves (back of neck).
Cheek rub	Individual rubs its cheek on another marmot.
Displacement	When one individual displaces another with contact (simple) or by just approaching without physical contact (proximity).
Sit	Two or marmots sit within 1 m but not body contact (< 1 m) or with physical contact (body contact).
Follow	One approaches another and the approached moves. This occurs 3 or more successive times.
Forage together	Individuals feeding within 1 m or obviously moving together.
Mount	One mounts another. May be obvious play or sexual mount.
Nurse	Pup suckling from a mother.
Sex	Extended play followed by obvious lordosis, seen as mounting with thrusting, ejaculation, and more play.

Table 2. Components of factors from principle component analysis. These factors are comprised of 8 social network measures, produced through varimax rotation. Bolded values indicate social attributes in the factor.

social attribute	rotated (varimax) score factor 1	rotated (varimax) score factor 2
Incloseness	0.931	0.118
Outcloseness	0.909	0.186
Indegree	0.908	0.310
Outdegree	0.887	0.365
Eigenvector centrality	0.641	0.444
Outstrength	0.226	0.877
Instrength	0.300	0.869
Embeddedness	0.155	0.736

Figure 1. Map of study sites at the Rocky Mountain Biological Laboratory.

