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Original Article

Are social attributes associated with alarm calling propensity?

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Emitting alarm calls may directly benefit individuals if callers have an increased chance of surviving, if calling increases the caller's status, or if calling functions through reciprocity. Although previous studies have examined the costs and benefits of alarm calling, few have examined how an individual's social position can influence the propensity to emit calls. An individual's position in its social network may vary and individuals differ in the strength and degree to which they are connected to others. We hypothesized that this variation could influence the rate at which individuals emit calls. We examined how various social attributes (degree centrality, closeness centrality, eigenvector centrality, strength, and embeddedness) were related to the likelihood that yellow-bellied marmots (*Marmota flaviventris*) emitted calls. To do so, we first defined 2 principle components—"popularity" and "relationship strength"—and used generalized linear mixed effects models to explain both the natural rate of alarm calling and the rate of trap-induced calling. We found that the natural rate of alarm calling increased for marmots that were less popular (i.e., involved in fewer connections with other marmots) and that the rate of trap-induced calling increased for marmots involved in weaker relationships. These findings refute the reciprocity hypothesis. However, less popular marmots could be seeking to enhance their social status by calling, or they could be deterring predators without the aid of others. Similarly, marmots in traps are faced with an imminent personal threat. Thus, marmots in weaker relationships that cannot rely on other marmots may call to deter predators.

Key words: **alarm calling, centrality, predator-directed calls, reciprocity, social network, status signaling, yellow-bellied marmots.**

INTRODUCTION

Alarm calls are vocalizations emitted in response to potential danger and may be directed at predators or conspecifics (Caro 2005). By calling, individuals may suffer a direct fitness cost because calling may direct a predator's attention to the caller (Maynard Smith 1965). However, calling also provides direct and indirect benefits that may outweigh such costs. Callers may directly discourage pursuit by predators that require stealth (Woodland et al. 1980; Zuberbühler et al. 1997), or they may directly reduce the risks of calling by taking turns and engaging in reciprocal bouts of calling (Trivers 1971). Much has been written about the indirect benefits of calling gained by warning conspecifics (e.g., Dunford 1977; Sherman 1977; Schwagmeyer 1980). However, an individual may call for reasons other than these potential benefits.

At a proximate level, a variety of factors can influence an individual's probability of emitting an alarm vocalization. To understand why, it is important to realize that not all individuals emit alarm calls when they encounter a predator. For example, individual Steller's jays (*Cyanocitta stelleri*) that took more risks were more likely to call (Gabriel and Black 2010), and bolder great tits (*Parus major*) called more often than their less aggressive counterparts (Hollander et al. 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 et al. 1997). Glucocorticoid and cortisol levels provide another proximate mechanism that may explain an individual's variation in the propensity to emit alarm calls (e.g., Bercovitch et al. 1995; Blumstein et al. 2006). Thus, variation between individuals can influence an individual's probability to emit calls.

Social animals are involved in an intricate web of social relationships. A variety of social attributes can be quantified to capture both direct and indirect interactions with others (Wey et al. 2008; Blumstein 2013). Many of these have been demonstrated to be repeatable, and some may have significant heritability (Krause et al. 2010; Lea et al. 2010; Wilson et al. 2013; Maldonado-Chaparro et al. forthcoming). Because these social attributes might be individualistic (i.e., they may vary between individuals), and because individuals differ in their propensity to emit calls, it is conceivable that attributes that describe network centrality or positional

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importance may explain some variation in the propensity to emit alarm calls. We therefore hypothesize (and justify below) that the following social attributes, each of which describes some aspects of an individual's positional importance in its social network, 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 predict that marmots with many affiliative connections 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" over other members of the group (Lusseau and Newman 2004) or influence over information flow (Vital and Martins 2009) than less central animals. Degree centrality is the number of direct connections an individual has (Wey et al. 2008). Individuals with a higher number of direct connections are more central and, thus, have potentially more influence over surrounding individuals. Strength is another directed social attribute that describes the frequency of interactions and quantifies the sum of all of an individual's relationships' weights in a weighted network (Granovetter 1973). Typically, stronger relationships are associated with greater reciprocity (Granovetter 1973). Closeness centrality quantifies the influence of an individual on other individuals and the ability for information to spread throughout a group (Wey et al. 2008). It is a measure of how close an individual is to other individuals, taking into account the length of the relationships between an individual and all other individuals of the same social network (i.e., the shortest number of relationships or paths needed to associate 2 individuals; Newman 2001; Wey et al. 2008). Eigenvector centrality is a measure that describes how well connected an individual is based on direct and indirect relationships (i.e., it takes into account the connections of the individuals the focal individual is connected to; Ruhnau 2000). Because eigenvector centrality is proportional to an individual's neighbors' centralities (Newman 2004), more influential individuals will be more connected with other influential individuals. Lastly, embeddedness quantifies how isolatable an individual is or how involved in the network structure an individual is (Moody and White 2003). If all of an individual's connections with other individuals are severed, the individual would be isolated. Thus, higher embeddedness values mean that it is more difficult to isolate an individual.

Each of these 5 social attributes can be viewed as specific measures of how individuals interact and may influence 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 such that it can be spread through alarm calls.

Yellow-bellied marmots at the Rocky Mountain Biological Laboratory 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 there is variation in the propensity to emit calls (Blumstein and Armitage 1997). Second, over the past decade, we have amassed detailed data on social connections 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 (Petelle et al. 2013). Fourth, previous studies have documented that social network position and social relationships may have fitness consequences (Lea et al. 2010), can influence reproductive success (Wey and Blumstein 2012), and can vary in response to changes in the social environment (Maldonado-Chaparro et al. forthcoming). Because these social attributes could influence how individuals interact with other individuals in their network, they could, potentially, explain variation in their propensity to emit alarm calls.

METHODS

Study area

Each year, starting in 2002, teams of observers livetrapped and observed the behavior of free-living yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (38°77′N, 106°59′W). Marmots were observed during their active season—mid-April to mid-September—during periods of peak activity—between 0700 and 1100 hours and between 1630 and 1900 hours 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 remarked) individuals' dorsal pelages 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), whereas those with a score of 4 were considered docile. From the trapping behaviors, we were also able to calculate the in-trap rate of alarm calling for each subject by dividing the number of times they called when trapped in a given year by the total number of times they were trapped in that same year.

To obtain an individual's docility score, we calculated best linear unbiased predictors (BLUPs) for each individual per year from trapping data (Petelle et al. 2013). We fitted a linear mixed effects model that 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 as fixed effects. The random effects included a concatenated year and marmot unique identifier variable to produce one random effect for each individual per year (i.e., year-uid). We assigned each individual in a given year a docility BLUP, calculated as the conditional means of the random effects. BLUPs were calculated using the lme4 package 1.1.7 (Bates et al. 2014) in R 3.1.1 (R Development Core Team 2014).

Behavioral observations

Trained observers recorded marmot behavior from distances that ranged from 20 to 150 m. Using ×15–45 spotting scopes and 10 × 40 binoculars, observers recorded all social interactions (ethogram in Blumstein et al. 2009). 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 (unconstrained) rates of calling were included to provide a complementary data set for subsequent analyses.

Calculating individual social attributes

We calculated the social attributes of each yearling and adult individual (we excluded juveniles from the analysis) in each colony for each year from 2002 to 2013. We focused on affiliative connections recorded during the entire active season to construct the affiliative social matrix and the corresponding social network for each colony site. We then estimated the subsequent social attributes for each individual in the colony. Social networks consisted of nodes (female marmots ≥ 1-year old) connected by edges (i.e., observed affiliative connections between individuals). For each individual, we calculated the following social attributes: 1) degree (in and out), which represents the number of interactions received or initiated by an individual (Wasserman and Faust 1994); 2) strength (in and out), which was calculated by summing the weights of the adjacent edges of a focal individual; 3) closeness centrality, which corresponds to the reciprocal of the sum of the shortest path lengths between the focal and other individuals (Wasserman and Faust 1994; Wey et al. 2008); 4) eigenvector centrality, which was calculated as the eigenvector associated with the maximal eigenvalue of an adjacency matrix (Bonacich 2007); and 5) embeddedness, which was calculated by identifying the cohesive substructures of the network (Moody and White 2003). Degree (in and out) was based on directed, unweighted networks; strength (in and out) was calculated using directed, weighted networks; and closeness centrality, eigenvector centrality, and embeddedness were calculated using undirected, unweighted networks. Closeness was normalized by multiplying the raw closeness by $(n - 1)$, where n is the number of vertices in the graph. All our calculations were conducted in the iGraph package 0.7.0 (Csardi and Nepusz 2006) in R 3.1.1 (R Development Core Team 2014).

Dimension reduction

Because social attributes are often correlated (Wey and Blumstein 2012), we used principle components analysis to reduce our set of 7 potentially correlated variables (indegree, outdegree, instrength, outstrength, closeness centrality, eigenvector centrality, and embeddedness) to 2 uncorrelated variables (extractions based on eigenvalue > 1 with varimax rotation; SPSS 21.0; IBM Corp., Armonk, NY; IBM Corp 2012).

Statistical analysis

To determine whether the natural (unconstrained) rate of alarm calling was influenced by social relationships, we fitted a generalized linear mixed effects model with a gamma family log link function. We first log-10 transformed unconstrained rates of alarm calling. Our fixed effects included colony, colony size, individual's sex, age class (yearling or adult), docility, principle component 1 score (later determined to be "popularity" and referred to as PC 1), and principle component 2 score (later determined to be "relationship strength" and referred to as PC 2). Our random effects included the marmot's unique identity (UID) and year. We tested for goodness of fit by using a pseudo-R^2 estimated as the squared correlation between the predicted and the observed values (but see Nakagawa and Schielzeth 2013 for other methods).

To determine whether the proportion of times a subject called when trapped was influenced by social attributes, we fitted a 2-step mixed effects model because our response variable was zero inflated. First, we analyzed whether or not the individual called in the trap. We fitted a generalized mixed effect model with a binomial family logit link function error distribution. For the second step of the model (i.e., only individuals that called in trap), we square root transformed the response variable and fitted a linear mixed effect model with a Gaussian family identity link function error distribution. For both models, we included as fixed effects the colony, colony size, individual's sex, age class (yearling or adult), docility, PC 1 score (popularity), and PC 2 score (relationship strength). The random effects included marmot identity and year. We tested for goodness of fit by estimating the R^2 of the generalized linear mixed effects models (Nakagawa and Schielzeth 2013) using the function r.squaredGLMM implemented in the package MuMIn 1.10.5 (Bartoń 2013) in R 3.1.1 (R Development Core Team 2014). This function estimated the marginal R^2 (i.e., proportion of variance explained by the fixed factor(s) alone) and the conditional R^2 (i.e., proportion of variance explained by both the fixed and random factors).

All models were fitted using the R 3.1.1 (R Development Core Team 2014) package lme4 1.1.7 (Bates et al. 2014). We calculated P-values for all models using type III Wald chi-square tests with the Anova function in the car package 2.0.20 (Fox and Weisberg 2011).

RESULTS

Our final data set contained 209 observations of rates of alarm calling from 141 individuals (yearlings and adults) that were collected 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 over 157 observation years (an individual studied over a year) and 55 unique males observed over 57 observation years. Fifty-five of these individuals were adults and were observed over 106 observation years, whereas 108 individuals were yearlings (which, by definition, can only be observed in a single year).

We extracted 2 principle components (Table 1). PC 1 accounted for 63.5% of variance, and PC 2 accounted for 16.8% of variance. We interpreted PC 1 as "popularity" because it was composed of social attributes based on the number of affiliative connections with and how close an individual was to other individuals (incloseness, outcloseness, indegree, outdegree, and eigenvector centrality). We interpreted PC 2 as "relationship strength" because it consisted of both measures of strength and how tightly connected (or embedded) an individual was (instrength, outstrength, and embeddedness).

Linear mixed effects models showed that social network position (as described by the 2 principle components) explained significant variation in calling behavior (Table 2). After controlling for significant variation explained by colony size and colony ($P < 0.01$), marmots that were less popular (PC 1) emitted calls at higher rates in the wild (Figure 1; pseudo-$R^2 = 0.511$). Similarly, when looking at individuals that called in trap, and after accounting for variation explained by colony ($P < 0.01$), marmots that were less docile and marmots involved in weaker relationships (PC 2) called more in traps (Figure 2; step 1: marginal $R^2 = 0.339$, conditional $R^2 = 0.847$; step 2: marginal $R^2 = 0.399$, conditional $R^2 = 0.650$).

DISCUSSION

Overall, we found that yellow-bellied marmots were more likely to alarm call if they were less popular. When unconstrained, less popular marmots (PC 1) called more, whereas, when in traps, docile marmots involved in weaker relationships (PC 2) called more. These patterns were contrary to our original expectations because we expected that more central and connected individuals would call more to benefit from enhanced social status or enhanced reciprocity. Below we discuss possible explanations for natural calling rates in unconstrained marmots and trap-induced calling behavior.

How social relationships are associated with unconstrained natural-rates calling

Yellow-bellied marmots live in female-biased social groups consisting mostly of relatives (Armitage 1991), and individuals in social networks are more genetically related than would be expected by chance (Wey and Blumstein 2010). While calling may not be that risky because marmots 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 popularity was likely not driven by the benefits of increasing indirect components of fitness.

Table 1

Rotated (varimax rotation) principle component scores from the principle component analysis

Social attribute	PC 1 (popularity)	PC 2 (relationship strength)
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**

Bold values indicate those social attributes used to define the principle component.

Additionally, if animals emitted alarm calls to obtain reciprocal benefits, we might expect animals that were more connected with others to call more. We did not find this. It is possible that unconnected individuals were calling more in an attempt to develop reciprocal relationships, but experimental support for this nonparsimonious hypothesis is lacking. For now, we conclude that calling was not driven by reciprocal benefits; rather, following Blumstein et al. (1997), it seems calling that is driven by potentially increasing direct components of fitness.

Marmots that are less popular could be calling more in an attempt to increase their social status or reputation. Social status or prestige is when an individual participates in a seemingly altruistic behavior so as to appear to other group members as a cooperative, high-quality member (Zahavi 1995). For example, subordinate adult male capybaras (*Hydrochaeris hydrochaeri*) alarm call more than dominant males. By actively participating in group defense, capybaras slowly move up the social hierarchy and gain status and reproductive success (Herrera and Macdonald 1993). Thus, increasing social status can be a means to enhance future direct fitness, and individuals who participate in riskier "altruistic" behaviors could increase future direct fitness. Our existing marmot data, however, prevent us from refuting this status hypothesis.

Alternatively, less popular marmots could call at higher rates because they cannot rely on other marmots to warn them or repel predators with their calls. In a situation where less popular individuals do not typically interact with others, they may be more obligated to call directly at predators in order to deter them (Krams et al. 2006). This hypothesis suggests that calling is directed to the predator, likely to deter pursuit, and is consistent with our findings that less popular marmots called more.

Table 2

Fixed effects that explain variation in the rate of alarm calling

	Wild/natural rate		Step 1: in-trap rate		Step 2: in-trap rate	
	Estimate (SE)	*P*	Estimate (SE)	*P*	Estimate (SE)	*P*
Intercept	**−2.584 (0.497)**	**<0.001**	−0.986 (2.560)	0.700	**0.747 (0.156)**	**<0.001**
Colony size	**−0.453 (0.112)**	**<0.001**	−1.892 (1.126)	0.093	−0.046 (0.028)	0.095
PC 1 (popularity)	**−0.350 (0.108)**	**0.001**	−1.117 (0.919)	0.224	0.004 (0.030)	0.885
PC 2 (relationship strength)	−0.128 (0.086)	0.134	−0.960 (0.709)	0.175	**−0.063 (0.025)**	**0.010**
Colony (gothic town)	−0.838 (0.473)	0.077	−2.343 (3.036)	0.440	−0.232 (0.159)	N/A
Colony (horse mound)	0.904 (0.556)	0.104	−3.470 (3.944)	0.379	−0.228 (0.178)	N/A
Colony (marmot meadow)	**−1.139 (0.473)**	**0.016**	−3.183 (3.271)	0.331	−0.383 (0.155)	N/A
Colony (picnic)	−0.614 (0.512)	0.231	−1.113 (2.875)	0.699	−0.327 (0.155)	N/A
Colony (river-bench)	−0.837 (0.553)	0.130	1.587 (2.883)	0.582	−0.164 (0.160)	N/A
Sex (male)	−0.220 (0.155)	0.156	−1.008 (1.171)	0.390	0.072 (0.046)	0.121
Age class (yearling)	0.123 (0.147)	0.402	2.515 (1.488)	0.091	−0.024 (0.048)	0.610
Docility BLUP	−0.043 (0.220)	0.843	−6.273 (3.396)	0.065	**0.004 (0.030)**	**0.018**

Wild rates are calculated from the number of bouts of calls heard divided by the time animals were observed (see text for details). The in-trap rate was divided into 2 separate analyses. Step 1 focused on whether individuals emitted any calls or not when approached in a trap. Step 2 focused on the subset of individuals that called and calculated rates based on the proportion of trapping events in which they emitted calls. Estimates with standard errors (SEs) are given with *P* values. Bold values indicate significant effect; N/A: not applicable.

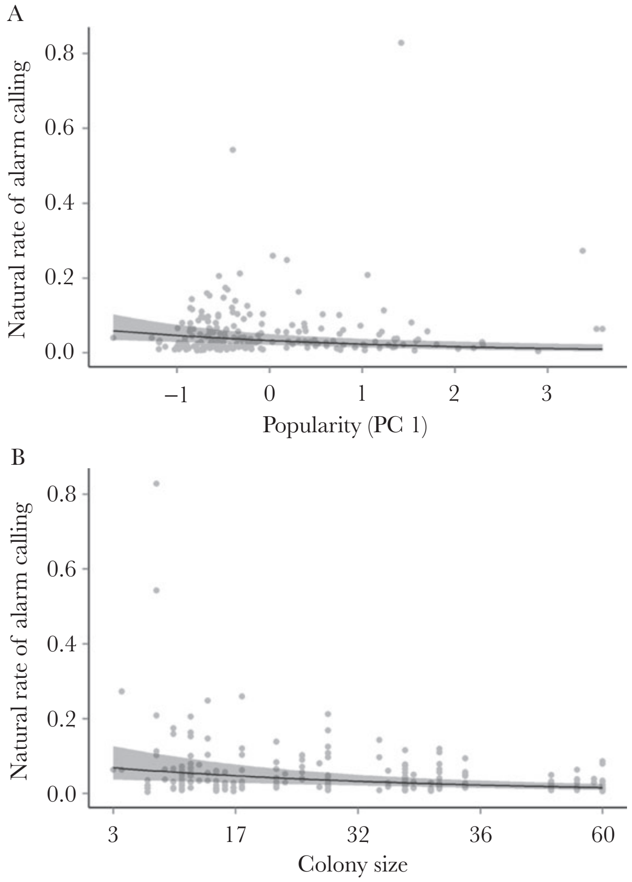

Figure 1

(a) Marmots that were less popular (PC 1) emitted alarm calls at higher rates in the wild, which is seen after controlling for (b) significant variation explained by colony size. Grey indicates 95% CI on the mean estimate.

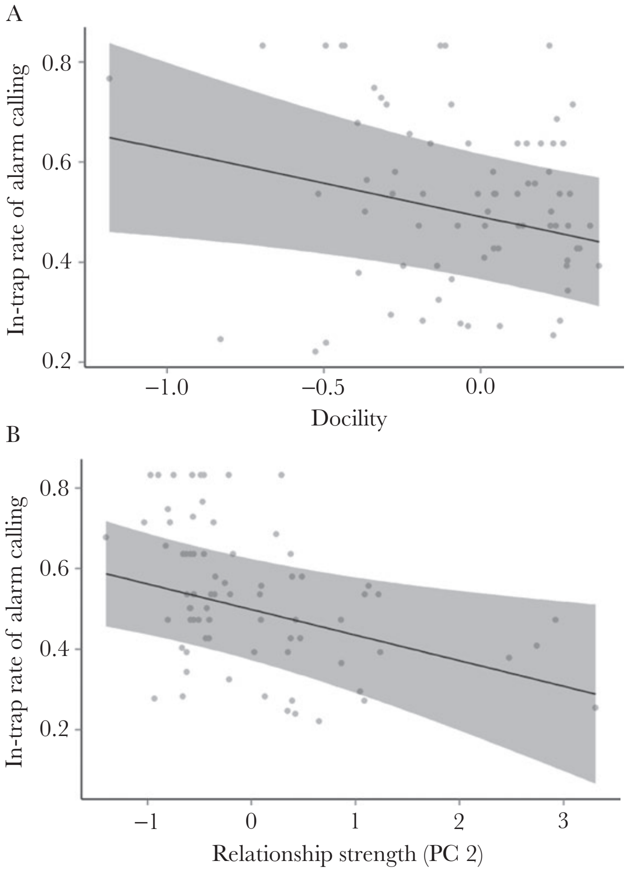

Figure 2

(a) Marmots that were less docile had higher in-trap rates of alarm calling. Additionally, (b) marmots that were in weaker relationships (PC 2) called more in traps. Grey indicates 95% CI on the mean estimate.

How social relationships are associated with trap-elicited calling

Once in traps, marmots were more likely to call if they were involved in weaker relationships (PC 2). This finding was also contrary to what we expected and might also be profitably explained by calls being directed to the predators.

Relatively isolated individuals could call at higher rates because these individuals must deter predators by themselves. These individuals are weakly connected with others, so they may call in a potentially high-risk situation such as when they are in traps. Well-connected individuals may have others who call in a potentially dangerous situations. Thus, because weakly connected individuals may not be able to rely on others to call and deter predators, these individuals must emit calls themselves to deter predators (Krams et al. 2006).

How marmot personality is associated with calling

We also found that less docile animals (those that were more likely to struggle in the trap) were also more likely to emit alarm calls when trapped. Individuals often vary in consistent, repeatable ways—that is, they have personality (Gosling 2001). Differences in personalities between individuals could potentially influence the likelihood of emitting alarm calls when encountering a predator. Some personality traits, such as docility, are context specific, meaning that they vary in different environmental conditions or population densities (Wilson et al. 1994). Because we found docility explained variation in trap-elicited calling but not natural calling, we suggest that docility is a context-specific personality trait.

CONCLUSIONS

Taken together, our results suggest that social attributes affect the propensity to emit alarm calls; less popular marmots and marmots with weaker social relationships call more. Our results are consistent with the hypothesis that calls are directed to predators because marmots with weaker relationships cannot expect to be warned by conspecifics or have others call to deter predators. We cannot refute the hypothesis that peripheral marmots call more to gain social status.

Although the original function of alarm calling in rodents was likely to deter predators (Shelley and Blumstein 2005), most of the explanations of alarm calling in extant species are in some way related to kin selection (Blumstein 2007). Previous studies of yellow-bellied marmots have shown that adult females call more when vulnerable offspring are around (Blumstein et al. 1997), but calling in other age–sex individuals was somewhat enigmatic. These results strongly suggest that calling has a predator-directed benefit. However, future studies are required to determine if predators are indeed deterred by these calls and if less connected individuals gain their direct fitness when alarm calling. Until then, our results show that both personality traits and position in a social network influence the propensity to emit calls, and this finding should stimulate research in other systems to better understand the prevalence and nature of the response. Future studies in more social species may support the initial hypothesis that more centrally positioned individuals are more likely to emit calls.

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REFERENCES

Armitage K. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annu Rev Ecol Syst. 22:379–407.

Bartoń K. 2013. MuMIn: multi-model inference. R package version 1.10.5 [cited 2014 December 21]. Available from: http://CRAN.R-project.org/package=MuMIn.

Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1.7 [cited 2014 December 21]. Available from: http://www.r-project.org/.

Bercovitch FB, Hauser MD, Jones JH. 1995. The endocrine stress response and alarm vocalizations in rhesus macaques. Anim Behav. 49:1703–1706.

Blumstein DT. 2007. The evolution, function, and meaning of marmot alarm communication. Adv Study Behav. 37:371–402.

Blumstein DT. 2013. Yellow-bellied marmots: insights from an emergent view of sociality. Philos Trans R Soc B. 368:20120349.

Blumstein DT, Armitage KB. 1997. Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. Anim Behav. 53:143–171.

Blumstein DT, Patton ML, Saltzman W. 2006. Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. Biol Lett. 2:29–32.

Blumstein DT, Steinmetz J, Armitage KB, Daniel JC. 1997. Alarm calling in yellow-bellied marmots: II. The importance of direct fitness. Anim Behav. 53:173–184.

Blumstein DT, Wey TW, Tang K. 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. Proc R Soc B. 276:3007–3012.

Bonacich P. 2007. Some unique properties of eigenvector centrality. Soc Network. 29:555–564.

Caro T. 2005. Antipredator defenses in birds and mammals. Chicago (IL): University of Chicago Press.

Collier TC, Blumstein DT, Girod L, Taylor CE. 2010. Is alarm calling risky? Marmots avoid calling from risky places. Ethology. 116:1171–1178.

Csardi G, Nepusz T. 2006. The igraph software package for complex network research. R package version 0.7.0 [cited 2014 December 21]. Available from: http://www.r-project.org/.

Dunford C. 1977. Kin selection for ground squirrel alarm calls. Am Nat. 111:782–785.

Fox J, Weisberg S. 2011. An R companion to applied regression. 2nd ed. Thousand Oaks (CA): Sage.

Gabriel PO, Black JM. 2010. Behavioural syndromes in Steller's jays: the role of time frames in the assessment of behavioural traits. Anim Behav. 80:689–697.

Gosling SD. 2001. From mice to men: what can we learn about personality from animal research? Psychol Bull. 127:45–86.

Granovetter MS. 1973. The strength of weak ties. Am J Sociol. 78:1360–1380.

Herrera EA, Macdonald DW. 1993. Aggression, dominance, and mating success among capybara males (*Hydrochaeris hydrochaeri*). Behav Ecol. 4:114–119.

Hollander FA, Overveld TV, Tokka I, Matthysen E. 2008. Personality and nest defence in the great tit (*Parus major*). Ethology. 114:405–412.

IBM Corp. 2012. IBM SPSS statistics for Windows version 21.0. Armonk (NY): IBM Corp.

Krams I, Krama T, Igaune K. 2006. Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? J Avian Biol. 37:131–136.

Krause J, James R, Croft DP. 2010. Personality in the context of social networks. Phil Trans R Soc B. 365:4099–4106.

Lea AJ, Blumstein DT, Wey TW, Martin JG. 2010. Heritable victimization and the benefits of agonistic relationships. Proc Natl Acad Sci USA. 107:21587–21592.

Lusseau D, Newman MEJ. 2004. Identifying the role that animals play in their social networks. Biol Lett. 271:S477–S481.

Maldonado-Chaparro A, Martin JGA, Armitage KB, Oli MK, Blumstein DT. 2014. Environmentally induced phenotypic variation in wild yellow-bellied marmots. J Mammal. 95.

Maynard Smith J. 1965. The evolution of alarm calls. Am Nat. 99:59–63.

Moody J, White DR. 2003. Structural cohesion and embeddedness: a hierarchical concept of social groups. Am Sociol Rev. 68:103–127.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol. 4:133–142.

Newman MEJ. 2001. Scientific collaboration networks. II. shortest paths, weighted networks, and centrality. Phys Rev E. 64:016132.

Newman MEJ. 2004. Analysis of weighted networks. Phys Rev E. 70:056131.

Petelle MB, McCoy DE, Alejandro V, Martin JGA, Blumstein DT. 2013. Development of boldness and docility in yellow-bellied marmots. Anim Behav. 86:1147–1154.

R Development Core Team. 2014. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing [cited 2014 December 21]. Available from: http://www.R-project.org.

Réale D, Gallant BY, Leblanc M, Festa-Bianchet M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. Anim Behav. 60:589–597.

Ruhnau B. 2000. Eigenvector-centrality—a node centrality? Soc Network. 22:357–365.

Schwagmeyer PL. 1980. Alarm calling behavior of the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*. Behav Ecol Sociobiol. 7:195–200.

Shelley EL, Blumstein DT. 2005. The evolution of vocal alarm communication in rodents. Behav Ecol. 16:169–177.

Sherman PW. 1977. Nepotism and the evolution of alarm calls. Science. 197:1246–1253.

Trivers RL. 1971. The evolution of reciprocal altruism. Q Rev Biol. 46:35–57.

Vital C, Martins EP. 2009. Using graph theory metrics to infer information flow through animal social groups: a computer simulation analysis. Ethology. 115:347–355.

Wasserman S, Faust K. 1994. Social network analysis: methods and applications. Cambridge (UK): Cambridge University Press.

Wey T, Blumstein DT. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. Anim Behav. 79:1343–1352.

Wey T, Blumstein DT. 2012. Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. Behav Ecol Sociobiol. 66:1075–1085.

Wey T, Blumstein DT, Shen W, Jordán F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav. 75:333–344.

Wilson ADM, Krause S, Dingemanse NJ, Krause J. 2013. Network position: a key component in the characterization of social personality types. Behav Ecol Sociobiol. 67:163–173.

Wilson DS, Clark AB, Coleman K, Dearstyne T. 1994. Shyness and boldness in humans and other animals. Trends Ecol Evol. 9:442–446.

Woodland DJ, Jaafar Z, Knight M-L. 1980. The "pursuit deterrent" function of alarm signals. Am Nat. 115:748–753.

Zahavi A. 1995. Altruism as a handicap: the limitations of kin selection and reciprocity. J Avian Biol. 26:1–3.

Zuberbühler K, Noë R, Seyfarth RM. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. Anim Behav. 53:589–604.