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ORIGINAL ARTICLE

Social security: social relationship strength and connectedness influence how marmots respond to alarm calls

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Abstract

Individuals vary in the number and types of social relationships they maintain. If beneficial, social relationships may reduce predation risk and thus increase an individual's sense of security. We tested this hypothesis by studying the responses of female yellow-bellied marmots (*Marmota flaviventer*) to broadcast alarm calls from unfamiliar individuals. First, we quantified affiliative interactions of animals in the field to calculate a set of social network measures. Because attributes of sociality are often correlated, we used principal component analysis to reduce our social network metrics to two unrelated factors and used the social network measure that accounted for the most variance for each principal component in further analyses. We then quantified the change in time allocated to vigilance and foraging following alarm call playback from baseline levels to the first 30 s and the second 30 s period (i.e., 31–60 s) following playback. We expected that if marmots with strong affiliative relationships felt more secure, they would forage more and allocate less time to vigilance after their immediate vigilance response to the broadcast alarm calls. Using mixed effects models that controlled for variation explained by a number of biologically important covariates and permutation tests to test the significance of social network variables, we found that marmots with a higher incloseness allocated significantly more time to vigilance in both the first and second 30 s after hearing a novel alarm call. Additionally, and while not significant (the observed parameter estimate fell between the 90 and 95% CI), marmots with a higher outstrength increased foraging in the second 30 s after hearing a novel alarm call. If we assume that time allocated to foraging is a measure of security, then marmots with strong affiliative relationships reacted more to an alarm call from a novel individual and seemingly felt more secure than their counterparts. Our results, therefore, suggest that strong social relationships increase perceptions of security and illustrate an effect of social relationships on predation risk assessment.

Significance statement

In many species, including humans, there are benefits from maintaining good social relationships. These benefits include better health and greater longevity. We studied yellow-bellied marmots, a ground-dwelling squirrel that is notable because it has variable social relationships. Capitalizing on this social variation, we found that marmots that maintain strong affiliative relationships with other marmots may indeed forage more after hearing an artificially broadcast alarm call than marmots with weaker affiliative relationships. This result suggests that marmots that are more socially connected with others in their group may feel relatively more secure, possibly because they have others that can help them assess risk, and that a benefit of maintaining strong friendly social ties is that it

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permits animals to forage more. Thus, we suggest a new way that social relationships can be beneficial: they increase perceptions of security and this ultimately may facilitate foraging.

Keywords Social network statistics · Social attributes · Predation risk · Yellow-bellied marmots · Risk assessment · Security

Introduction

Individuals vary their antipredator behavior according to social context, but most of these studies have focused on describing group size effects (Elgar 1989; Beauchamp 2008). Group size is but one of many social attributes that can be used to describe social variation (Lea and Blumstein 2011; Croft et al. 2009; Blumstein 2013), and the formal application of social network statistics in animal behavior shows that there are a variety of both direct and indirect relationships that can be quantified (Wasserman and Faust 1994; Whitehead 1995; Croft et al. 2009). Social network statistics also permit the identification of how centrally located and embedded in a group each individual is (Wey et al. 2008; Micheletta et al. 2012; Fuong et al. 2015). Indeed, a benefit of using formal social network statistics is that it permits the precise definition of a series of attributes of sociality, each of which may have specific consequences on other behaviors (Wey et al. 2008; Blumstein 2013). For example, traits calculated from a social network analysis can be used to explain foraging specializations in bottlenose dolphins (*Tursiops truncates*) (Daura-Jorge et al. 2012), aggressive fin-biting in Atlantic salmon (*Salmo salar*) (Cañon Jones et al. 2011), and the spread of obesity-driving behaviors in humans (Christakis and Fowler 2007). However, there are only a few studies that have examined how antipredator behavior is influenced by specific traits that have been calculated from social network analyses.

A recent study has shown that social relationship strength is associated with yellow-bellied marmots' (*Marmota flaviventer*) propensity to emit alarm calls (Fuong et al. 2015). Specifically, marmots in weaker and less connected social relationships were more likely to emit alarm calls when in a trap, suggesting either that isolated marmots must communicate directly to the predator because they cannot rely on conspecifics for assistance, or that they are trying to enhance their social status with their conspecifics by engaging in a potentially risky behavior.

The extent to which an individual is connected to others in its social network can be a function of both the affiliative interactions and agonistic acts that the individual participates in (Lehmann and Ross 2011). Thus, in principle, individuals could be well connected in a grooming network or a bullying network. Fewer affiliative network connections might suggest that poorly integrated individuals cannot rely on conspecifics to emit alarm calls, either as a warning notification or a deterrent directed at predators (Fuong et al. 2015). However, animals do not only produce alarm calls, they must respond to them.

Given the results from the Fuong et al. (2015) study, we suggest that variation in individual sociality might also influence the intensity of an animal's response to alarm calls. Not all individuals respond to an alarm call with equivalent reactions, nor does one individual respond equivalently to all received alarm calls (Caro 2005; Micheletta et al. 2012). An individual's social position within its community of conspecifics may influence the intensity to which it may benefit from responding to calls. For instance, an individual with strong social ties is more likely to have a social bond with the caller than a less socially embedded individual. If these bonds influence the individual's assessment of caller reliability (Blumstein et al. 2004), or if these bonds provide information about the likelihood that animals will emit calls, then social relationships may not only influence perceptions of predation risk but also actual predation risk. Prior studies have shown that social status (one attribute of sociality) is associated with response to alarm calls. Often, high social status is an indication of relatively strong physical condition (Archie et al. 2012), suggesting that higher status individuals might be able to afford any costs associated with responding to a call (e.g., lost foraging time—Lea and Blumstein 2011), whereas it might be costlier for less dominant or less well-connected individuals to respond to a signal of increased risk (Gould et al. 1997; Krams 1998). Regardless, these results illustrate the possibility of a relationship between a social attribute and response to alarm calls. We explored this in more detail with social attributes other than dominance rank that are not as likely to be associated with physical condition.

We focused on a well-studied population of yellow-bellied marmots and capitalized on the response to a set of control stimuli (see also Lea and Blumstein 2011) from a series of playback experiments that were previously conducted to test specific hypotheses about the meaning of marmot alarm communication (Blumstein and Daniel 2004; Blumstein et al. 2008a, b; Blumstein and Récapet 2009; Lea and Blumstein 2011). Marmots are well suited for evaluating this hypothesis because they live in social groups of variable sizes and with sufficient variation in social attributes that enables correlates of relationship strength to be studied. Prior work has also shown that marmots modify antipredator behavior based on group size (e.g., Blumstein et al. 2004) and that marmots have an optimal matriline size (Armitage and Schwartz 2000), although for this study (as well as others that focus on social group composition), we used a different definition of group size than that used in the matriline study. Marmots also have a rich suite of antipredator behaviors that include modifying vigilance as a function of both internal state and environmental factors (Chmura et al. 2016) and the distance to their burrows (Monclús et al. 2015), emitting situationally variable alarm calls based on peripheral visibility (Blumstein and Armitage 1998; Bednekoff and Blumstein 2009), modifying call production based on their audience (Blumstein et al. 1997), and discriminating among individual callers (Blumstein et al. 2004) and different age callers (Blumstein and Daniel 2004).

For each experiment, marmots were baited to a handful of high-quality food, their baseline time allocated to foraging and vigilance was measured, and then they were exposed to four brief and rapidly paced alarm calls from an unfamiliar adult female. If having strong and connected relationships with others reduced animals' perceptions of predation risk, then we expected an attenuated response from the most socially connected marmots. Specifically, we predicted that after responding to the alarm call by looking, they would resume foraging sooner than less connected individuals. However, well-connected individuals might also be more sensitive to hearing calls because they can assess the risk conveyed in a call using prior knowledge of the caller's reliability (e.g., Blumstein et al. 2004), or prior knowledge of the caller's relationship to themselves (Pollard 2011; Kern and Radford 2016). Such prior knowledge could permit a more precise assessment of risk. In that case, we might expect that calls from a novel marmot would elicit a considerable amount of investigation because they were unable to assess the true risk of predation. Either way, we would infer that social connectedness influenced risk assessment and, hence, an individual's perception of security.

Methods

Quantifying behavior

We focused on marmots living at four distinct colonies in and around the Rocky Mountain Biological Laboratory (RMBL), located in the upper East River Valley in Gunnison County, CO, USA (38° 77′ N, 106° 59′ W). Marmots emerge from hibernation and are active from mid-April to mid-September during which time they are regularly live-trapped, weighed, marked, and have fecal samples collected. Observations occurred during these months, at peak hours of activity, in the morning and early evening (Armitage 1965). Observational, trapping, and marking methods are described in detail elsewhere (Blumstein et al. 2009).

Using an established ethogram (Blumstein et al. 2009), trained observers recorded all instances of social behavior from a distance of 20 to 150 m; distances were selected so as not to interfere with normal behavior (which varied by location based on human exposure—Li et al. 2011). For these analyses, we focused on individually identified marmots and quantified the initiator and recipient of affiliative behavior. Affiliative behaviors included greetings, sitting near each other, and play—all of these activities required one individual to approach another individual (full ethogram in Blumstein et al. 2009).

Formal social connectedness was calculated using observations collected from 2004 to 2007 (the years that we conducted the original playback experiments) using the igraph package 0.7.0 (Csárdi and Nepusz 2006) in R 3.3.3 (R Development Core Team 2017). Social networks were restricted to include only yearling and adult females and were calculated for each geographically separated colony. We characterized each individual marmot for each year, with respect to its degree centrality, strength, closeness centrality, eigenvector centrality, and embeddedness, and ultimately for analysis, we paired these values to the corresponding year that playback data were collected. Degree centrality is simply the number of direct relationships an individual has within the social network; higher scores indicate that an individual has greater influence over the entire social network (Wey et al. 2008). Relationship strength is dependent on the frequency with which individuals interact and is calculated as the sum of the weighted relationships. While two individuals who interact a single time have very low relationship strength, individuals who interact on a daily basis have high relationship strength. Closeness centrality is a measure of how centralized one individual is within a social network relative to all other individuals and is a function of the shortest path between one individual and all other individuals in the network (Wey et al. 2008). An individual with a high closeness centrality is a key player in a social network that is well connected to other focal individuals. Eigenvector centrality is a measure of the closeness of one individual to other centralized individuals and is calculated using both direct and indirect relationships (Moody and White 2003) and is a function of the sum of an individual's associates' associates. Lastly, embeddedness is a measure of how isolatable an individual is, based on non-agonistic interactions with others. Embeddedness measures how many connections between individuals would need to be severed in order to completely isolate an individual from its social network which is in part a function of how other members of the network are connected (Blumstein et al. 2009), and was calculated following Lea et al. (2010).

All social network calculations were based on affiliative interactions. Degree and closeness centrality were calculated from directed, unweighted networks; thus, we calculated indegree, outdegree, incloseness, and outcloseness. Strength was calculated from a directed, weighted network; thus, we calculated instrength and outstrength. Eigenvector centrality and embeddedness were calculated as undirected and unweighted measures.

We quantified how female marmots responded to playback experiments that were conducted independently as part of previous work (described in Lea and Blumstein 2011). Alarm calls were digitally recorded from trapped individuals so as to control for the situation that elicited the call, and hence the degree of risk (see Lea and Blumstein 2011). Recordings were then normalized (amplitudes adjusted to 95% of peak amplitude) and edited into tracks with four alarms calls in a 2-s period. We used a total of five different exemplars and always broadcast calls from unacquainted individuals (all were adult females) to our subjects.

Subjects were baited to a location with horse feed (Omalene 300 horse feed, Ralston Purina Inc., Saint Louis, MO, USA) that was 8–12 m from the hidden speaker and ca. 1 m from a burrow entrance. Once a solitary subject was foraging on the bait, we started the alarm call playback track. For 60 s prior to playback and 60 s following the alarm call playback, marmots were video-recorded (Canon G1-1 mini-DV digital video recorder). It was not possible to record data blind because our study involved focal animals in the field. We used JWatcher 1.0 (Blumstein and Daniel 2007) to score the time subjects allocated to vigilance (looking in a quadrupedal, bipedal, or lying position), locomotion, foraging, self-grooming, social interactions, and the amount of time they were out of sight (Lea and Blumstein 2011). Our analyses focus on time allocated to foraging and vigilance because previous studies have shown that these are the most sensitive assays to this playback protocol (Lea and Blumstein 2011). The original yellow-bellied marmot playback protocol was designed to alarm subjects (all looked immediately in response to the playback), but not to scare them so much that they immediately dove into their burrows. This protocol has been used in many prior playback studies (including Blumstein and Daniel 2004; Blumstein and Récapet 2009; Blumstein et al. 2004, 2008a, b). By providing food 1 m from their burrow and not broadcasting the alarm call at very high amplitudes (which would simulate an urgent threat), all marmots looked, but almost no marmots disappeared into their burrows immediately following playback. We also note that since all subjects were foraging before playback, changes in foraging behavior are the most sensitive assay to quantify responsiveness to playback. This is because once an individual elects to not forage, it could do a number of other activities—including vigilance and locomotion. Thus, in experiments like this, the resumption of foraging after playback is an appropriate assay that should correlate with perceived risk. We subdivided the 60-s post-playback interval into two 30-s intervals for analysis and subtracted each of these intervals from the baseline interval for analysis. By doing so, we controlled for individual difference in baseline behavior. Some prior marmot studies used 15-s intervals to gain an even more nuanced view of recovery from playback (e.g., Blumstein et al. 2008a, b), but after plotting the responses in our data set, we noticed that the most variability was in the final 30-s time bin and thus conducted a formal analysis on 30-s time bins.

Several other factors (e.g., body condition and basal stress hormone levels) could influence responsiveness to playback and risk assessment and were ultimately modeled as fixed effects. We calculated body condition as the standardized residual of linear mixed effects models that accounted for recorded mass at the time of trap events. Variation in body mass was found to be a function of age and a covariate of days since 1 January. We used the residual from the mass recorded at the date nearest the playback as an index of body condition (see Lea and Blumstein 2011). We calculated fecal glucocorticoid metabolite levels as a baseline stress measure using a validated radioimmunoassay (for further details, see Blumstein et al. 2006; Smith et al. 2012).

Data analysis

Because attributes of sociality are often correlated (Wey and Blumstein 2012), we used principal component analysis to reduce our social network metrics to two unrelated factors. Factors were extracted with an eigenvalue > 1, and we used varimax rotation to aid in interpretation (correlation matrix of raw social attributes in Supplementary Table 1). We then used the social network measure that accounted for the most variance for each principal component in further analyses. We examined the change from baseline of time allocated to foraging and time allocated to vigilance in the first 30 s and the second 30 s following playback by fitting linear mixed effects models. Our fixed effects included individual's age class (yearling or adult), the presence of pups (i.e., females are more likely to emit calls once they have had young emerge above ground, Blumstein et al. 1997; for this analysis, pups present meant that the litter had emerged above ground regardless of the number or distance to the focal subject), the individual's body condition, the logarithm of the individual's fecal glucocorticoid metabolite levels, the sample size for a given individual (i.e., number of playback experiments conducted on a particular individual during a specific year), the colony that an individual resided in, and the two top loading social network measures (outstrength and incloseness). For all the models, we included a single random effect, the marmot's unique identity. For these analyses, we were restricted to analyzing those individuals with both playback results and social network estimates.

For social network parameters only, we compared the observed coefficient values with the posterior frequency distribution calculated from 1000 iterations of node-level pre-network permutations (Croft et al. 2011; Farine 2017). We calculated the 90 and 95% confidence intervals for each coefficient using the quantile function in the R base stats package, and considered a coefficient significant if the observed value was outside of the 95% confidence interval, and almost significant if the observed value was outside of the 90% confidence interval but within the 95% confidence interval.

All statistical calculations were completed in R 3.3.3 (R Development Core Team 2017). For principal component analysis, we used package psych version 1.6.12 (Revelle 2015). For linear mixed effects models, we used package lme4 1.1.12 (Bates et al. 2014). We calculated P values for all models using F-tests with a Kenward-Roger approximation using the package pbkrtest 0.4.7 (Halekoh and Højsgaard 2017). We produced plots of the observed social network coefficient estimates and the 90 and 95% confidence intervals using ggplot2 2.2.1 (Wickham 2009).

Our final data set contained the results from 45 playback experiments (29 to adult females, 16 to yearling females) that were conducted on 28 unique individuals with some individuals observed across multiple years. The average number of hours of observations per colony per year was 160.62 h (min 22.70 h, max 278.35 h, median 139.07 h, standard deviation 73.88 h). Using the raw social network estimates for the final set of subjects in our analyses, we extracted two principal components (Table 1). Principal component 1 was composed of outstrength, instrength, outdegree, embeddedness, and eigenvector centrality. Principal component 2 was composed of incloseness, outcloseness, and indegree. The top-loading variable for principal component 1 was outstrength, and for principal component 2 was incloseness.

Table 1 Rotated (eigenvector > 1 with varimax rotation) principal component scores from the analysis of social attributes

Social network measure	PC 1	PC 2
Outstrength	*0.90*[a]	0.13
Instrength	*0.89*	0.07
Outdegree	*0.71*	0.56
Embeddedness	*0.73*	−0.01
Eigenvector centrality	*0.63*	0.62
Incloseness	−0.18	*0.96*[a]
Outcloseness	0.12	*0.87*
Indegree	0.44	*0.64*

Italicized values indicate those social attributes used to define the principal component

[a] The top loading social network measure for that principle component

Results

The results from our linear mixed effects models and permutation tests showed that, after controlling for other potentially important variables, marmots with a higher incloseness allocated significantly more time to vigilance in both the first and second 30 s after hearing an experimentally broadcast novel alarm call (Fig. 1; Table 2). While not significant (the observed parameter estimate fell between the 90 and 95% CI), we found that marmots with a higher outstrength increased foraging after hearing a novel alarm call.

Some of our biologically meaningful covariates also explained variation in playback response (Table 2). Marmots with higher fecal glucocorticoid metabolite levels decreased vigilance in the first 30 s after playback. Marmots with recently emerged pups increased time allocated to foraging in the first 30 s and tended ($0.1 < P < 0.05$) to increase time allocated to foraging in the second 30 s following the alarm call.

Discussion

Predation pressure and experience with predators can have an immediate effect on social dynamics (Voelkl et al. 2016) and the social interactions that underlie collective behavior (Ioannou et al. 2017). A recent experimental study showed that fear of predation modifies guppies' (*Poecillia reticulata*) fine-scale social structure (Heathcote et al. 2017). Thus, we should expect that something in addition to simply group size may be an important determinate of an individual's perceptions of security. Importantly, social attributes quantified using social network analyses might be a promising way to understand more precisely how sociality might enhance security. The results of our study of yellow-bellied marmots suggest some important ways that an individual's position within a social network influences their sense of security.

Closeness centrality is a measure of how quickly an individual can reach everyone in the network; it describes the distance of a node to all others in the network via the fewest number of indirect ties. We found that individuals with more conspecifics affiliatively and closely connected to them were more vigilant after they heard an alarm call from a novel marmot. This may reflect the surprise of hearing a novel caller. Indeed, marmots are able to discriminate individuals based solely on their alarm calls (Blumstein and Daniel 2004) and may do so because individuals may differ in the reliability when they call (Blumstein et al. 2004). In addition, many species are able to discriminate neighbors from strangers (e.g., Falls 1982), and this result suggests that this ability is in part a function of how closely connected to other group members they are. Future studies manipulating novelty are clearly warranted.

However, this was not the only social network trait that may influence how marmots responded to alarm calls. We have suggestive evidence that marmots with greater outstrength—those that directed more affiliative behavior to others—also foraged more. We acknowledge that we are less confident in this conclusion because our estimate fell between the 90 and 95% confidence intervals generated from the very conservative permutation test. Nevertheless, the increase in foraging was most pronounced in adults, who presumably had more time to develop social relationships, in the second 30-s time bin following playback. This increase in foraging

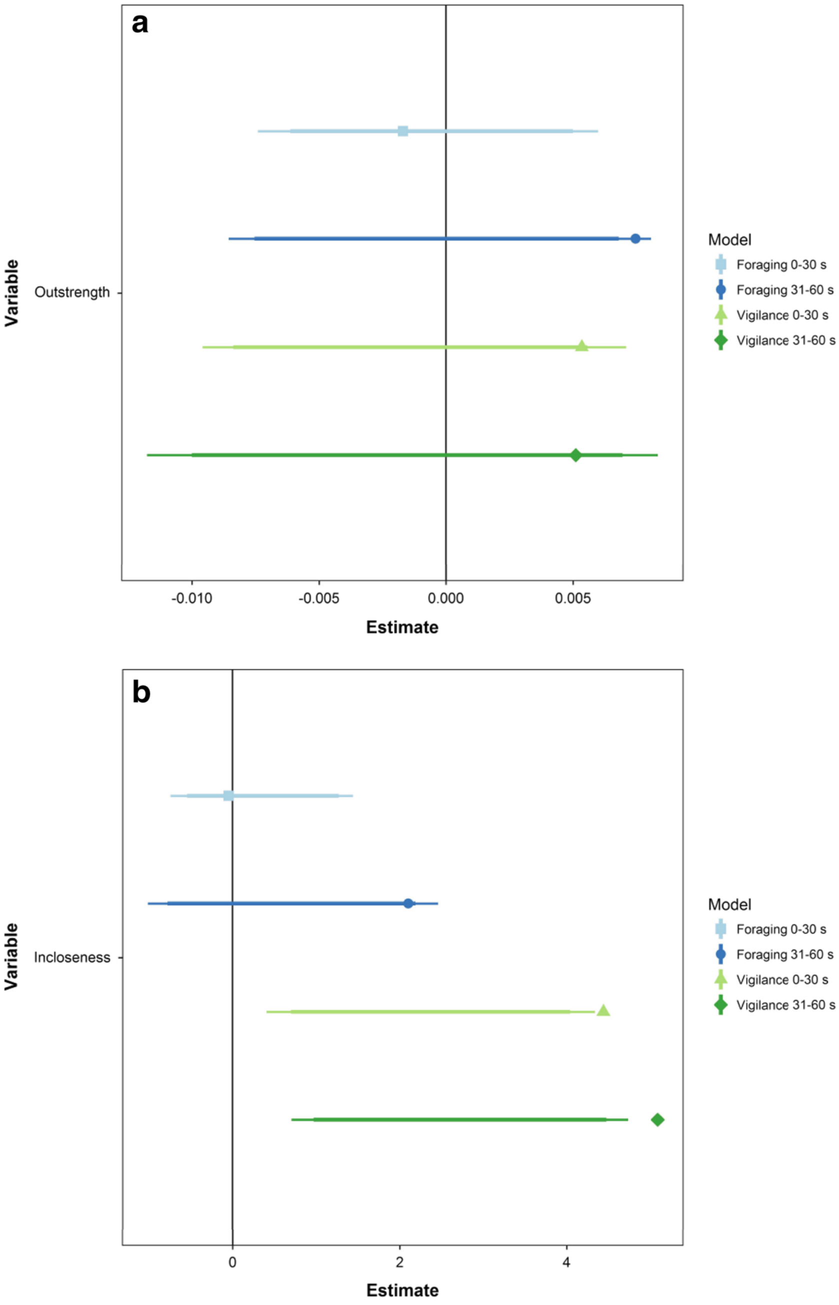

Fig. 1 Observed coefficient estimates of **a** outstrength and **b** instrength from linear mixed effects models following 1000 permutations of network data (permutation details in text). Thinner lines represent the 95% CI, and thicker lines represent the 90% CI. Points that do not overlap with the 95% CI were considered significant, and points that do not overlap with the 90% CI but do overlap with the 95% CI were considered almost significant

may reflect a greater perception of safety or security from having well-established affiliative relationships with others or could reflect a greater perception of competition. Future studies are warranted to clarify the importance of this result.

Nevertheless, both of these results illustrate the value of using social network statistics to study how animals perceive safety—and indeed how specific relationships with their conspecifics might afford safety. This might be referred to as social security. Marmots are an appropriate system in which to study social security because of their social plasticity, and the increase in time allocated to foraging is an appropriate metric of response in our experimental assay given prior work on antipredator behavior and response to alarm calls in this well-studied system. Thus, our current results demonstrate that having established affiliative social relationships, above and beyond simply being associated with other conspecifics, influences how marmots respond to alarm calls and more broadly demonstrates that social relationships influence risk perception.

Prior work showed that less “popular” marmots (those with fewer direct affiliative interactions) were more likely to emit alarm calls (Fuong et al. 2015). In addition, prior work showed that marmots in weaker social relationships called at higher rates when in traps, which Fuong et al. (2015) interpreted as

Table 2 Linear mixed effects models explaining variation in the transformed change in the proportion of time allocated to foraging and vigilance in the first 30 s (i.e., 0–30 s) and second 30 s following playback (i.e., 31–60 s)

		0–30 s: foraging			0–30 s: vigilance			31–60 s: foraging			31–60 s: vigilance		
	Variable	Estimate (SE)	*t*	*P*	Estimate (SE)	*T*	*P*	Estimate (SE)	*t*	*P*	Estimate (SE)	*t*	*P*
Fixed effects	(Intercept)	0.192 (0.470)	0.409	0.685	0.748 (0.756)	0.990	0.330	− 0.061 (0.593)	− 0.102	0.919	0.897 (0.732)	1.226	0.229
	Outstrength	− 0.001 (0.004)	− 0.365	0.718	0.005 (0.005)	1.003	0.324	0.007 (0.004)	1.792	0.082	0.005 (0.005)	0.991	0.329
	Incloseness	− 0.025 (1.256)	− 0.020	0.984	*4.442 (1.995)*	*2.227*	*0.033*	2.106 (1.564)	1.347	0.187	*5.091 (1.930)*	*2.637*	*0.013*
	Age (yearling)	0.077 (0.100)	0.767	0.448	− 0.260 (0.146)	− 1.773	0.086	− 0.117 (0.115)	− 1.020	0.315	− 0.230 (0.142)	− 1.625	0.114
	log(Cort)	− 0.261 (0.213)	− 1.224	0.229	*− 0.661 (0.323)*	*− 2.043*	*0.049*	− 0.237 (0.254)	− 0.935	0.357	− 0.605 (0.313)	− 1.933	0.062
	Body condition	− 0.042 (0.044)	− 0.958	0.345	0.098 (0.068)	1.455	0.156	0.001 (0.053)	0.015	0.989	− 0.036 (0.065)	− 0.545	0.590
	Sample size	0.014 (0.031)	0.456	0.651	0.069 (0.047)	1.482	0.148	− 0.020 (0.037)	− 0.534	0.597	− 0.022 (0.045)	− 0.486	0.630
	Pups (yes)	*0.275 (0.067)*	*4.112*	*< 0.001*	− 0.086 (0.118)	− 0.726	0.473	0.259 (0.093)	2.787	0.009	− 0.042 (0.115)	− 0.367	0.716
	Colony (horse mound)	0.085 (0.271)	0.312	0.757	*− 0.883 (0.404)*	*− 2.185*	*0.036*	0.087 (0.317)	0.275	0.785	*− 1.382 (0.391)*	*− 3.531*	*0.001*
	Colony (marmot meadow)	− 0.157 (0.230)	− 0.681	0.500	− 0.500 (0.342)	− 1.460	0.154	0.125 (0.268)	0.466	0.644	− 0.289 (0.331)	− 0.872	0.390
	Colony (river-bench)	− 0.085 (0.228)	− 0.373	0.712	− 0.213 (0.361)	− 0.590	0.559	0.231 (0.283)	0.815	0.421	0.094 (0.350)	0.268	0.790
	Variable	Variance	SD		Variance	SD		Variance	SD		Variance	SD	
Random effects	Individual ID	0.022	0.150		0.000	0.000		0.000	0.000		0.000	0.000	

P values were calculated with a Kenward-Roger approximation. Please note that this table does not describe the results of the permutation tests on the social network measures. Reference levels for categorical variables were: Age (adults), Pups present (no), and Colony (Gothic townsite). Italic indicates significant values of fixed effects (marmot identity was entered as a random effect). The final dataset included 45 playback experiments (29 to adult females, 16 to yearling females) that were conducted on 28 unique individuals with some individuals observed across multiple years

consistent with the hypothesis that isolated marmots direct their calls to predators to discourage attack because of increased vulnerability. Such results are consistent with the hypothesis that more isolated individuals are more responsible for their own safety and cannot rely on others to mediate risk. Here, we have shown that individuals that direct more affiliative activities to others are able to resume foraging sooner after hearing alarm calls.

Our results thus show that the degree to which animals interact affiliatively with others may be associated with their perception of risk and security. We expect this to be a general phenomenon found in other social animals. Additionally, the effects of sociality per se, rather than group size (Elgar 1989; Beauchamp 2008), dominance (Waite 1987; Elgar 1989), or body condition (Bachman 1993), can influence risk assessment and security, and the precise way that it does requires more detailed study. Such studies should be integrative (Blumstein et al. 2010; Hofmann et al. 2014; Taborsky et al. 2015) in that they should measure and account for proximate drivers of responses (such as glucocorticoid levels), and they should include precise measures of social relationships. Social network analyses provide a rich set of specifically defined social attributes (e.g., Blumstein 2013) to choose from. Future studies of even more social species will be revealing.

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Compliance with ethical standards

Ethical approval The research was in compliance with ethical guidelines and the current laws of the USA. Marmots were studied under protocols approved by the UCLA and the RMBL Animal Use and Care Committees and under permits issued annually by the Colorado Division of Wildlife.

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

Data availability statement The datasets during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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CORRECTION

Correction to: Social security: social relationship strength and connectedness influence how marmots respond to alarm calls

Daniel T. Blumstein[1,2] · Holly Fuong[1,3,4] · Elizabeth Palmer[1]

Correction to: Behavioral Ecology and Sociobiology https://doi.org/10.1007/s00265-017-2374-5

Unfortunately, there was an error in the R script which led to the incorrect labeling of two social network measures. Throughout the article, instances of 'instrength' and 'outstrength' should be switched.

Page 1, replace the following line in the abstract:

"marmots with a higher outstrength increased foraging" with
"marmots with a higher instrength increased foraging"

Page 4, replace the following line in the methods:

"social network measures (outstrength and incloseness)" with
"social network measures (instrength and incloseness)"

Page 5, replace the following line in the methods:

"The top-loading variable for principal component 1 was outstrength, and for principal component 2 was incloseness" with
"The top-loading variable for principal component 1 was instrength, and for principal component 2 was incloseness"

Page 5, replace the following line in the results:

"we found that marmots with a higher outstrength increased foraging" with
"we found that marmots with a higher instrength increased foraging"

Table 1 should be printed as shown below.

Table 1 Rotated (eigenvector >1 with varimax rotation) principal component scores from the analysis of social attributes

Social network measure	PC 1	PC 2
Instrength	**0.90***	0.13
Outstrength	**0.89**	0.07
Outdegree	**0.71**	0.56
Embeddedness	**0.73**	−0.01
Eigenvector centrality	**0.63**	0.62
Incloseness	−0.18	**0.96***
Outcloseness	0.12	**0.87**
Indegree	0.44	**0.64**

Bold values indicate those social attributes used to define the principal component
*Indicates the top loading social network measure for that principle component

Page 5, replace the following sentence in the discussion:

"We have suggestive evidence that marmots with greater outstrength—those that directed more affiliative behavior to others—also foraged more" with
"We have suggestive evidence that marmots with greater instrength—those that received more affiliative interactions from others—also foraged more"

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Table 2 Linear mixed effects models explaining variation in the transformed change in the proportion of time allocated to foraging and vigilance in the first 30 s (i.e., 0–30 s) and second 30 s following playback (i.e., 31–60 s)

		0–30 s: foraging			0–30 s: vigilance			31–60 s: foraging			31–60 s: vigilance		
	Variable	Estimate (SE)	*t*	*P*	Estimate (SE)	*t*	*P*	Estimate (SE)	*t*	*P*	Estimate (SE)	*t*	*P*
Fixed effects	(Intercept)	0.192 (0.470)	0.409	0.685	0.748 (0.756)	0.990	0.330	−0.061 (0.593)	−0.102	0.919	0.897 (0.732)	1.226	0.229
	Instrength	−0.001 (0.004)	−0.365	0.718	0.005 (0.005)	1.003	0.324	0.007 (0.004)	1.792	0.082	0.005 (0.005)	0.991	0.329
	In−closeness	−0.025 (1.256)	−0.020	0.984	**4.442 (1.995)**	**2.227**	**0.033**	2.106 (1.564)	1.347	0.187	**5.091 (1.930)**	**2.637**	**0.013**
	Age (yearling)	0.077 (0.100)	0.767	0.448	−0.260 (0.146)	−1.773	0.086	−0.117 (0.115)	−1.020	0.315	−0.230 (0.142)	−1.625	0.114
	log(Cort)	−0.261 (0.213)	−1.224	0.229	**−0.661 (0.323)**	**−2.043**	**0.049**	−0.237 (0.254)	−0.935	0.357	−0.605 (0.313)	−1.933	0.062
	Body condition	−0.042 (0.044)	−0.958	0.345	0.098 (0.068)	1.455	0.156	0.001 (0.053)	0.015	0.989	−0.036 (0.065)	−0.545	0.590
	Sample size	0.014 (0.031)	0.456	0.651	0.069 (0.047)	1.482	0.148	−0.020 (0.037)	−0.534	0.597	−0.022 (0.045)	−0.486	0.630
	Pups (yes)	**0.275 (0.067)**	**4.112**	**<0.001**	−0.086 (0.118)	−0.726	0.473	0.259 (0.093)	2.787	0.009	−0.042 (0.115)	−0.367	0.716
	Colony (horse mound)	0.085 (0.271)	0.312	0.757	**−0.883 (0.404)**	**−2.185**	**0.036**	0.087 (0.317)	0.275	0.785	**−1.382 (0.391)**	**−3.531**	**0.001**
	Colony (marmot meadow)	−0.157 (0.230)	−0.681	0.500	−0.500 (0.342)	−1.460	0.154	0.125 (0.268)	0.466	0.644	−0.289 (0.331)	−0.872	0.390
	Colony (river−bench)	−0.085 (0.228)	−0.373	0.712	−0.213 (0.361)	−0.590	0.559	0.231 (0.283)	0.815	0.421	0.094 (0.350)	0.268	0.790
	Variable	Variance	SD		Variance	SD		Variance	SD		Variance	SD	
Random effects	Individual ID	0.022	0.150		0.000	0.000		0.000	0.000		0.000	0.000	

P-values were calculated with a Kenward-Roger approximation. Please note that this table does not describe the results of the permutation tests on the social network measures. Reference levels for categorical variables were: Age (adults), Pups present (no), and Colony (Gothic townsite). Bold indicates significant values of fixed effects (marmot identity was entered as a random effect). The final dataset included 45 playback experiments (29 to adult females, 16 to yearling females) that were conducted on 28 unique individuals with some individuals observed across multiple years

The first sentence of the caption for Fig. 1 should read:

"Observed coefficient estimates of A) instrength and B) incloseness from linear mixed effects models following 1000 permutations of network data (permutation details in text)." Additionally, the y-axis of Fig. 1a should read "instrength" instead of "outstrength".

Table 2 should be printed as shown here.

We thank Ivo Seitz and Steven Marty for bringing the issue to our attention. The correction does not influence the interpretation of the published findings.

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