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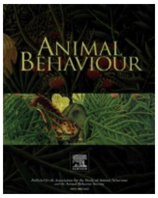

Social security: less socially connected marmots produce noisier alarm calls

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The nonlinearity and fear hypothesis predicts that the structure of alarm vocalizations will be influenced by the signaller's internal state. Specifically, stressed or otherwise more aroused individuals will produce alarm calls that are relatively more nonlinear (i.e. they sound noisier). The position of an individual in a social network can influence an individual's sense of security. More centrally located individuals may feel more secure and thus we might expect that they would produce noisier calls. Building on previous research about the influence of social relationships on an individual's sense of security, we asked whether social network position explained variation in the noisiness (quantified as Wiener entropy) and goodness of pitch of alarm calls produced by trapped yellow-bellied marmots, *Marmota flaviventer*. More socially isolated individuals, characterized by lower instrength, produced alarm calls with higher entropy and higher goodness of pitch. These isolated individuals may be more aroused because they have fewer social partners to depend on when presented with a predatory threat; therefore, they produce both noisy and potentially louder calls. Additionally, individuals with higher outcloseness produced calls with higher goodness of pitch, which may be indicative of their ability to better inform neighbours of impending threats. Overall, this study further illustrates how an individual's social network position influences the structure of its alarm calls, which could reflect how individuals perceive their current safety levels.

When threatened by predators, many animals produce vocalizations known as alarm calls. Numerous studies have shown that a variety of external and internal factors may influence both the propensity to call as well as the structure of alarm calls produced. For instance, some animals selectively produce alarm calls only during certain social situations with high predation risk. Tufted capuchin monkeys, *Cebus apella*, produced alarm calls only when kin were nearby and only after detecting snakes but not after detecting other types of predators (Wheeler, 2008). Generally, individuals may be more likely to alarm-call when they are near vulnerable offspring (Haff & Magrath, 2013) or other groupmates (Townsend, Rasmussen, Clutton-Brock, & Manser, 2012; Zaccaroni, Binazzi, Massolo, & Dessì-Fulgheri, 2013) than when alone. Internal factors can also influence whether an animal vocalizes. For example, yellow-bellied marmots, *Marmota flaviventer*, called more frequently in traps when their faecal glucocorticoid levels were higher, which suggests that physiological arousal influences the likelihood of calling (Blumstein, Patton, & Saltzman, 2006). Fewer studies have examined factors influencing alarm call structure. Marmots infected with *Eimera* parasites in their faeces produced calls with higher entropy than those infected with other parasites or no parasites (Nouri & Blumstein, 2019). The structure of other vocalizations, specifically screams and contacts calls, are known to be affected by the caller's arousal levels, as seen in captive common marmosets, *Callithrix jacchus* (Liao, Zhang, Cai, & Ghazanfar, 2018), marmots (Blumstein, Richardson, Cooley, Winternitz, & Daniel, 2008), humans (Lingle, Wyman, Kotrba, Teichroeb, & Romanow, 2012), captive piglets, *Sus scrofa* (Linhart, Ratcliffe, Reby, & Špinka, 2015), and captive zebra finches, *Taeniopygia guttata* (Soula et al., 2018).

When grouped with conspecifics or heterospecifics, or both, an individual's vulnerability to predation may decrease (Fairbanks & Dobson, 2007; Hamilton, 1971; Mady & Blumstein, 2017; Roberts,

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1996; Vine, 1971). A new line of research has also noted that social security extends beyond simply being in a group and may include an individual's position within a social network. For example, less socially integrated and poorly connected yellow-bellied marmots alarm called more than their better connected groupmates (Fuong, Maldonado-Chaparro, & Blumstein, 2015). The authors proposed that poorly connected marmots had fewer closely connected groupmates that would call and deter predators on their behalf, so when in immediate danger, they called themselves to enhance their safety. Therefore, one might argue that more socially isolated individuals are more vulnerable to predation and less secure.

The nonlinearity and fear hypothesis predicts that the structure of alarm vocalizations will be influenced by the signaller's internal state (Blumstein et al., 2008; Blumstein & Recapet, 2009). Specifically, stressed or otherwise more aroused individuals will produce alarm vocalizations that contain relatively more nonlinear acoustic attributes (Fitch, Neubauer, & Herzel, 2002). These nonlinearities may be produced when aroused animals ‘overblow’ their vocal production systems. Thus, they are expected in vocalizations that are produced during more urgent or risky situations. Additionally, because nonlinear vocal attributes are irregular or harsh sounding and can be difficult to ignore (Fitch et al., 2002), sounds containing them are considered ‘noisy’ and may be difficult to habituate to (Townsend & Manser, 2011). For instance, meerkats, *Suricata suricatta*, produce alarm calls that become increasingly noisy with the imminence of predation or response urgency (Manser, 2001), which suggests that more aroused individuals produce noisier calls. Noisy vocalizations can honestly communicate arousal and capture the attention of surrounding individuals, including social partners and predators (Blesdoe & Blumstein, 2014; Blumstein et al., 2008; Blumstein & Recapet, 2009).

Because more vulnerable animals will likely be more aroused by predators and highly aroused animals tend to produce noisier calls (but see Coss, Cavanaugh, & Brennan, 2019; Wilson & Evans, 2012), we asked whether security influences alarm call structure. Specifically, do yellow-bellied marmots in different social network positions produce structurally different alarm calls? We hypothesized that alarm call structure varies with social network position, and that more socially isolated marmots would produce noisier calls to enhance their sense of security. We examined the structure of alarm calls produced by marmots when in traps, focusing specifically on the calls' Wiener entropy (hereafter, entropy) and goodness of pitch. Entropy measures how noisy or random a sound is, and goodness of pitch measures the harmonic pitch periodicity or whether a call has stacked harmonics (Tchernichovski, Nottebohm, Ho, Pesaran, & Mitra, 2000). Together, these measures allow us to assess how noisy a call is.

Yellow-bellied marmots are an ideal study species to investigate the relationship between the structure of alarm calls and social network position. They produce alarm calls that are individually distinguishable (Blumstein & Munos, 2005; Blumstein, Verneyre, & Daniel, 2004) and situationally variable (Blumstein & Armitage, 1997). Their alarm calls communicate risk, not predator type (Blumstein & Armitage, 1997); therefore, by examining the alarm calls produced in a controlled setting (i.e. in traps), we were able to focus on other potential drivers of acoustic variation (see also Blumstein & Chi, 2012). Additionally, marmots have consistent behavioural responses or personalities when trapped, and these personalities, which we measured as docility (Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013), are known to influence alarm-calling behaviour (Fuong et al., 2015). Lastly, their positions within social networks are known to influence antipredator behaviour, particularly their propensity to alarm-call (Fuong et al., 2015) and responses to alarm calls (Blumstein, Fuong, & Palmer, 2017).

METHODS

Study Subjects

From 2003 to 2014, teams of trained observers followed a population of free-living yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory, RMBL (38^{0}77^{0}N, 106^{0}59^{0}W). Observations of marmot behaviour occurred while marmots were active, from mid-April to mid-September, and during hours of peak activity, between 0700 and 1100 hours and between 1630 and 1900 hours Mountain Daylight Time (MDT). We live-trapped and observed marmots at six geographically distinct colony sites.

Live Trapping

Every other week, we set Tomahawk single-door live traps at each colony and baited traps with horse feed (Omolene 100, Ralston Purina, St Louis, MO, U.S.A.) at known burrow locations. When trapped, in-trap behaviours were recorded as subjects were transferred into canvas handling bags. These behaviours included whether the marmot tried to bite through the cage, tooth-chattered, alarm-called, struggled in trap, or failed to walk immediately into the bag. If an animal called while trapped, we recorded their alarm calls with either a Sony PCM-M1 or Marantz PMD 660 digital recorder at 44.1 kHz with 16-bit resolution sampling using Audix OM-3xb microphones (frequency response: 40 Hze20 kHz), which were placed 20e40 cm from the mouth of calling subjects.

Behavioural Observations

Trained observers recorded marmot behaviour using 15e45 × spotting scopes and 10 × 40 × binoculars. From distances of 20e150 m, observers recorded all social interactions (ethogram in Blumstein, Wey, & Tang, 2009), indicating the initiator, recipient and winner of these interactions. Winners were defined as individuals who maintained their position after the interactions.

Preparation and Analysis of Sound Files

Each bout of in-trap calling was separated into five different 0.100 s segments or clips in Audacity 2.1.3 (Audacity Team, 2017). We selected segments with minimal background noise to avoid interfering with analyses and normalized each call to the maximum amplitude per bout segment. To determine the number of energy bands, we counted the number of harmonic bands seen in the spectrograms produced by Raven Pro 1.5 (Bioacoustics Research Program, 2017) and added one to this number. We used the Explore and Score function of Sound Analysis Pro 2011 to determine the entropy and goodness of pitch of individual call segments (Tchernichovski et al., 2000). Entropy is measured on a negative log scale, where noisier calls have entropy values closer to 0 and calls that are more pure tone have values approaching negative infinity (Fig. 1). Smaller values of goodness of pitch are seen in noisier sounds, and pure tones and larger values are seen in sounds with more harmonic stacks (Fig. 1). Calls with more harmonic stacks, and thus larger goodness of pitch, will be louder.

Docility Calculations

Using the in-trap behaviours, we calculated docility scores for each trapping event by subtracting the maximum score of 5 by the sum of numbers given from each trap behaviourdtried to bite through cage (0 ¼ no; 1 ¼ yes), tooth-chattered (0 ¼ no; 1 ¼ yes), alarm-called (0 ¼ no; 1 ¼ yes), struggled in trap (0 ¼ no; 1 ¼ yes) and immediately walked into bag (0 ¼ yes without coercion;

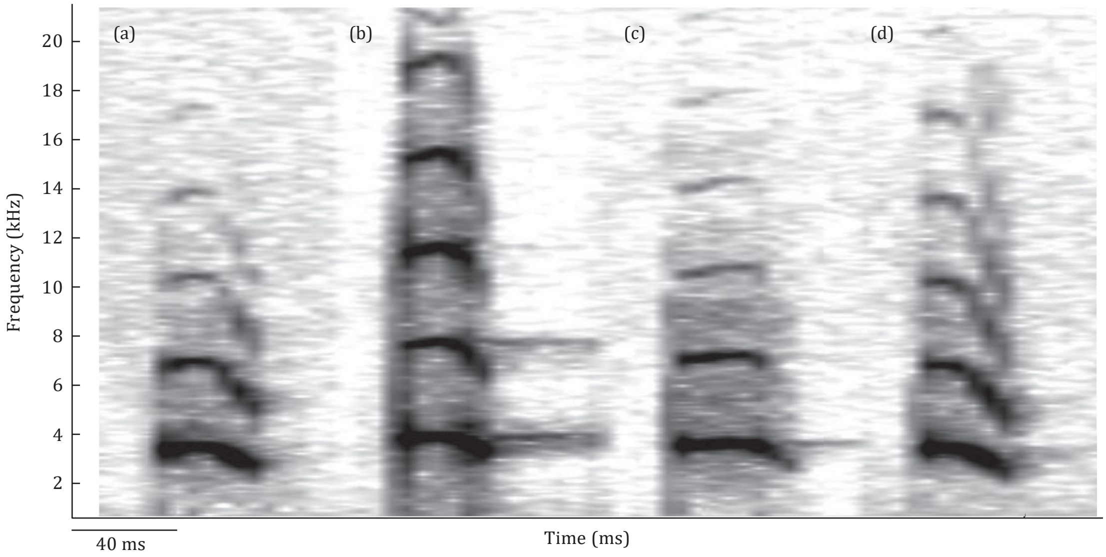

Figure 1. Spectrograms of alarm calls with (a) low entropy, (b) high entropy (i.e. noisier), (c) low goodness of pitch and (d) high goodness of pitch. The spectrograms illustrating differences in entropy (a, b) have similar goodness of pitch values, and the spectrograms illustrating differences in goodness of pitch (c, d) have entropy values similar to (a). Spectrograms were prepared using Raven Pro 1.5 with Hann filter, fast Fourier transformation (FFT) size 512, sampling rate 44.1 kHz, 54% brightness and 55% contrast.

1 ¼no) (Petelle et al., 2013). Lower docility scores indicate less docile individuals, while higher docility scores indicate more docile individuals (Reale, Gallant, Leblanc, & Festa-Bianchet, 2000).

Social Network Calculations

We calculated individual social network position of each yearling and adult individual in each colony from 2003 to 2014. To avoid the inclusion of transient individuals, we calculated networks using individuals only if they were seen and/or trapped at least five times on different days within a year. Because yellow-bellied marmots live in matrilines and male and female life histories differ (Armitage, 2014), we calculated male and female networks separately. We used affiliative interactions (allogroom, forage 1: m apart, greet, sit <1 m apart, play, and sniff anogenital region) to construct the affiliative social matrix and corresponding social network for each colony site and year (Blumstein et al., 2009). Using these networks, we calculated nine social network measures for each individual: degree (in/out), strength (in/out), closeness centrality (in/out), betweenness centrality, eigenvector centrality and embeddedness. Degree is a directed, unweighted measure and represents the number of direct relationships for each individual (Wasserman & Faust, 1994). Strength is a directed, weighted measure that considers the time spent associated and frequency of interactions between individuals, and is calculated as the sum of the edge weights (Brent,2015; Wey, Blumstein, Shen, & Jordan, 2008). Closeness centrality (hereafter, incloseness or outcloseness) is a directed, unweighted measure that is calculated using the reciprocal of the sum of the shortest path lengths between individuals (Wasserman & Faust, 1994; Wey et al., 2008). Betweenness centrality is an undirected, unweighted measure of the number of shortest paths that connect all individuals within the network and pass through the focal individual (Ruhnau, 2000). Eigenvector centrality is an undirected, weighted measure calculated as the first eigenvector, which is proportional to the sum of the centralities of individuals with whom the focal individual is directly connected (Csardi & Nepusz, 2006). Lastly, embeddedness is an undirected, unweighted measure calculated using the cohesive substructures of the social network (Moody & White, 2003). All calculations were conducted in package igraph 1.0.1 (Csardi & Nepusz, 2006) in *R* 3.3.3 (R Core Team, 2017).

After individual social network measures were calculated, we performed a principal components analysis to reduce the number of correlated network measures. We combined data for all males and females and then reduced our set of nine social network measures (indegree, outdegree, instrength, outstrength, incloseness, outcloseness, betweenness centrality, eigenvector centrality and embeddedness) to two uncorrelated network measures by selecting the top-loading variable of each principal component (extractions based on eigenvalue >1 with varimax rotation) using *R* package psych 1.7.5 (Revelle, 2015).

Statistical Analysis

To determine whether alarm call structure was influenced by social relationships, we fitted linear mixed effects models (LMM; Gaussian distribution) with response variables as entropy and natural log-transformed goodness of pitch. For both models, we included the fixed effects as colony, individual's sex, age class (yearling or adult), docility, time of day (AM/PM), alarm call segment duration (ms), number of energy bands in the call segment, interaction between duration and energy bands, square root-transformed outcloseness (highest loading measure of principal component 1) and natural log-transformed instrength (highest loading measure of principal component 2), and the random effects as the marmot's unique identity, year and bout number in a given year. All of these variables could influence the structure of an individual's alarm call. Sex, age and individual identity are known to differ consistently among alarm calls produced by different marmots (Blumstein & Munos, 2005). Docility is known to influence alarm-calling behaviour (Fuong et al., 2015) and may also influence alarm call structure. Because alarm calls were recorded at different times of day and there may be diurnal variation in the propensity to call, we also considered whether calls were recorded during the AM or PM period. Lastly, we included call duration and number of energy bands to further control for potentially confounding factors in call structure that could influence our ability to assess differences in entropy and goodness of pitch. We standardized the continuous response variables (entropy, goodness of pitch) and covariates (docility, duration, number of energy bands, outcloseness, instrength) by subtracting the mean and dividing by the standard deviation to allow for comparison of the effects of the regression coefficients (Schielzeth, 2010).

All models were fitted using *R* package lme4 1.1e18 (Bates, Mächler, Bolker, & Walker, 2015). Each variable included in the model has possible biological significance, and we selected models using likelihood ratio tests (LRT) and the drop1 function (setting test ¼ 'Chisq'). We examined the normality of random effects using package sjplot 2.3.3 (Lüdecke, 2016). We obtained *P* values and the variance explained by the random effects using package lmerTest 2.0e33 (Kuznetsova, Brockhoff, & Christensen, 2016). We then fitted a linear model of the observed response variables (entropy, goodness of pitch) as a function of the predicted values of the final models to calculate the adjusted R^2 for each model (Nakagawa & Schielzeth, 2013).

Ethical Note

Marmots were studied under protocols approved by the Animal Use and Care Committees of the University of California Los Angeles and the RMBL (UCLA Protocol No. 2001-191-01, RMBL protocol No. 1, both renewed annually) and under permits from the Colorado Division of Wildlife (TR917 issued annually). Animals were recorded in live-traps. In the morning, traps were set before marmots emerged from their sleeping burrows and checked up to 3 h later before it got too hot. All traps were closed down during the heat of the day and if it was not too hot in the afternoon, we set traps and checked them no more than 3 h later. Handling was briefdwe weighed all subjects, checked eartags and tagged new animals, checked fur marks, remarked individuals if required, collected blood from nonpups if it was the first time they were trapped that week, and collected faeces from all subjects. Most animals were fully processed and released into their burrows within 10e15 min. Animals were not harmed from this routine trapping and handling.

RESULTS

Our final data set contained 523 segments of 108 bouts of alarm calling from 57 individuals (yearlings and adults) over 12 years. Thirty-two unique females produced 353 alarm call segments and 25 unique males produced 170 alarm call segments. Twenty-seven of these individuals were recorded only as adults and produced 248 alarm call segments, 26 individuals were recorded only as yearlings and produced 165 alarm call segments and four individuals were recorded as both yearlings and adults throughout the study period and accounted for 110 of the alarm call segments (80 as adults, 30 as yearlings).

We extracted two principal components from a data set containing nine social network measures for all 57 individuals (Table 1). Principal component 1 accounted for 47% of variance, and principal component 2 accounted for 27% of variance, with the principal components analysis yielding results similar to Fuong et al. (2015) and Blumstein et al. (2017). The top-loading variable of principal component 1 was outcloseness and the top-loading variable of principal component 2 was instrength.

Table 1
Rotated (varimax rotation) principal component (PC) scores from the principal component analysis

Social network measure	PC 1	PC 2
Outcloseness	0.92	0.14
Incloseness	0.91	0.23
Indegree	0.90	0.33
Outdegree	0.82	0.43
Eigenvector centrality	0.76	0.20
Betweenness	0.41	0.22
Instrength	0.41	0.83
Outstrength	0.41	0.82
Embeddedness	0.07	0.78

The first two principal components were extracted from a single analysis of nine social network measures for all 57 individuals. Bold values indicate the top-loading social network measure for that principal component.

We then used likelihood ratio tests to determine which potentially confounding factors to use in our final models (Table 2). We included the following fixed effects: colony, age, docility, time of day, duration, number of energy bands, square root-transformed outcloseness, natural log-transformed instrength and the interaction between duration and energy bands. Duration, number of energy bands and the interaction between duration and energy bands were retained because they were significant in model selection, while the other fixed effects were retained primarily because they could be biologically relevant to alarm call structure.

Marmots with lower instrength produced alarm calls with higher entropy (*P* ¼ 0.002) after controlling for colony, sex, docility, duration, number of energy bands, time of day and the interaction between duration and energy bands (R^2_{adj} ¼ 0.633; R^2_{adj} without social network measures ¼ 0.626; Table 3). The variance accounted for by the random effects were 36.2% for unique identity, 8.6% for year and 40.8% for bout number in a given year.

Additionally, marmots that had higher outcloseness (*P* ¼ 0.006) and marmots that had lower instrength (*P* ¼ 0.016) produced calls with higher goodness of pitch after controlling for docility, duration, number of energy bands, time of day and the interaction between duration and energy bands (R^2_{adj} ¼ 0.722; R^2_{adj} without social network measures ¼ 0.708; Table 3). The variance accounted for by the random effects were 65.6% for unique identity, 7.8% for year and 41.6% for bout number in a given year.

DISCUSSION

Social network position is associated with alarm call structure in ways that are consistent with the nonlinearity and fear hypothesis. Specifically, more socially isolated marmots with lower instrength produced noisier calls than their more socially integrated counterparts. These results support previous research showing that socially isolated callers are more wary of their surroundings (Fuong et al., 2015; Mady & Blumstein, 2017). Vocalizations with higher entropy are typically indicative of a highly aroused individual (Blumstein et al., 2008; Liao et al., 2018; Manser, 2001), and therefore we infer that marmots with lower instrength were less secure in their groups. Instrength is a particularly appropriate measure for assessing how isolated an individual is from the rest of

Table 2
Selection of fixed effects for the final models using likelihood ratio tests (LRT; drop1 function, option ¼ 'Chisq')

	Entropy		Goodness of pitch	
	LRT	*P*	LRT	*P*
Colony	12.393	0.030	6.188	0.288
Age	0.937	0.333	0.182	0.670
Docility (std)	13.984	<0.001	10.496	0.001
Time of day (AM/PM)	5.578	0.018	20.890	<0.001
Outcloseness (sqrt) (std)	2.166	0.141	5.430	0.020
Instrength (log) (std)	9.281	0.002	3.058	0.080
Sex: energy bands (std)	<0.001	0.989	2.942	0.086
Duration (std) : energy bands (std)	17.459	<0.001	7.767	0.005

We included all significant fixed effects and all fixed effects that were possibly biologically relevant (even if not significant) in the final models. We included the same fixed effects in the models for both entropy and goodness of pitch. Bold variables indicate those that were included as fixed effects in final models; (sqrt) ¼ square root-transformed; (log) ¼ natural log-transformed; (std) ¼ standardized.

Table 3
Fixed effects that explain the variation in alarm call structure (entropy or goodness of pitch)

	Entropy		Goodness of pitch	
	Estimate (SE)	*P*	Estimate (SE)	*P*
Intercept	-0.546 (0.818)	0.508	-1.404 (0.987)	0.161
Colony (Boulder)	-0.685 (0.868)	0.434	0.150 (1.090)	0.891
Colony (Gothic town)	-0.457 (0.815)	0.577	1.183 (1.008)	0.246
Colony (Marmot Meadow)	0.690 (0.813)	0.400	0.885 (1.008)	0.384
Colony (Picnic)	-0.167 (0.784)	0.832	0.984 (0.963)	0.312
Colony (River Bench)	0.237 (0.785)	0.764	1.381 (0.964)	0.158
Sex (M)	-0.407 (0.194)	0.042	-0.352 (0.244)	0.155
Age class (yearling)	0.137 (0.160)	0.394	0.112 (0.176)	0.526
Docility (std)	-0.193 (0.049)	<0.001	-0.180 (0.047)	<0.001
Duration (ms) (std)	0.154 (0.055)	0.005	0.227 (0.051)	<0.001
Energy bands (std)	0.443 (0.048)	<0.001	0.218 (0.044)	<0.001
Time of day (PM)	0.204 (0.091)	0.025	0.381 (0.083)	<0.001
Outcloseness (sqrt) (std)	0.130 (0.096)	0.181	0.290 (0.100)	0.006
Instrength (log) (std)	-0.196 (0.063)	0.002	-0.150 (0.062)	0.016
Duration (std) : energy bands (std)	0.171 (0.037)	<0.001	0.123 (0.033)	<0.001

Bold indicates significant *P* values. (sqrt) ¼ square root-transformed; (log) ¼ natural log-transformed; (std) ¼ standardized.

the group because it is based on the frequency of interactions that an individual receives as opposed to interactions that an individual initiates. Future research is warranted to determine whether social isolation is directly associated with increased predation risk.

Socially isolated marmots may be producing noisier calls for several nonmutually exclusive reasons. First, as proposed above and in the nonlinearity and fear hypothesis (Blumstein et al., 2008; Blumstein & Recapet, 2009), these individuals could simply be more aroused and possibly more likely to ‘overblow’ their vocal production system. Second, some alarm calls function to deter predators (Woodland, Jaafar, & Knight, 1980; Zuberbühler, Jenny, & Bshary, 1999), and one might predict that noisier, harsher calls should better deter predators if they are more detectable and easier to locate. Alarm calls could honestly signal to predators the quality of the calling prey (Laiolo, Tella, Carrete, Serrano, & Lopez, 2004). Socially isolated marmots may not be able to depend on others to call on their behalf and thus must produce calls themselves to deter predators; producing a noisier call should increase their probability of survival, particularly if it is more detectable by predators. Future research should evaluate predator responses to marmot alarm calls of varying entropy, which is difficult to do in this system. Third, because noisy calls attract more conspecific attention (Blumstein & Recapet, 2009; Townsend & Manser, 2011), socially isolated individuals may be producing noisy calls to increase their status. Although marmots generally avoid producing alarm calls in risky situations (Collier, Blumstein, Girod, & Taylor, 2010), active participation in group defence could enhance social status, which could in turn improve fitness.

Outcloseness describes how quickly the focal individual can influence all other individuals in its network (Wey et al., 2008). Marmots are known to respond differently to alarm callers based on their reliability (Blumstein et al., 2004), identity, age and sex (Blumstein & Munos, 2005), and therefore listeners can alter their response based on who is calling. We found that individuals with higher outcloseness also produced alarm calls that had a higher goodness of pitch, even after normalizing call segments to the same amplitude and controlling for the number of energy bands and call duration. Both the number of energy bands and duration were positively correlated with both a call's entropy and goodness of pitch. This result is consistent with more scared animals producing louder and longer calls. Although entropy was not influenced by the callers' outcloseness, differences in goodness of pitch could inform listeners of the predator threat, and callers with high outcloseness should be most able to inform others of an impending threat. Blumstein and Chi (2012) suggested that calls with a higher goodness of pitch might be more articulated, but they are also probably louder, which could be a mechanism to better get an urgent message across. While not consistent with the nonlinearity and fear hypothesis, increasing goodness of pitch, but not entropy, as a function of outcloseness suggests that social relationships influence alarm call structure.

Because docility has been linked to the propensity for marmots to alarm call (Fuong et al., 2015), we considered how docility may influence alarm call structure. By definition, more docile animals call less frequently than their less docile counterparts (Petelle et al., 2013). More docile individuals should be more accustomed to being handled in traps. Thus, they are less aroused in traps and produce less noisy alarm calls.

Overall, this study illustrates how an individual's social network position influences its alarm call structure. Individuals that received fewer interactions from others were more socially isolated and produced noisier alarm calls when they were in immediate dangerda finding that is consistent with the nonlinearity and fear hypothesis. An individual's sense of security may alter how it responds to threatening situations and influences alarm call structure.

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