



## Social security: are socially connected individuals less vigilant?



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### ARTICLE INFO

#### Article history:

Received 7 October 2016

Initial acceptance 6 November 2016

Final acceptance 12 September 2017

MS. number: A16-00883R4

#### Keywords:

antipredator behaviour

security

social attribute

social network

vigilance

yellow-bellied marmot

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

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

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

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

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

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

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

## METHODS

### *Study Site and Species*

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

### *Behavioural Observations*

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

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

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

### *Social Network Measures*

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

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

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