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More social female yellow-bellied marmots, *Marmota flaviventer*, have enhanced summer survival

Anita Pilar Montero [a], Dana M. Williams [a, b], Julien G. A. Martin [c, 1], Daniel T. Blumstein [a, b, *]

[a] The Rocky Mountain Biological Laboratory, Crested Butte, CO, U.S.A.
[b] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, U.S.A.
[c] Institute of Biological & Environmental Sciences, School of Biological Sciences, University of Aberdeen, Aberdeen, U.K.

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For many animals, group living mitigates predation risk and ensures survival. However, in yellow-bellied marmots, increased sociality is associated with lower female reproductive success, decreased female longevity and increased overwinter mortality for both males and females, which raises questions about the adaptive value of sociality in this facultatively social mammal. Here we used social network analysis to examine the relationship between sociality and summer survival, which is almost always attributable to predation. Yearling females had enhanced survival when they had stronger social relationships and were more central in their network. Adult female survival was not associated with social network traits, but females were more likely to survive the summer if they lived in larger groups. Survival of yearling and adult males was not associated with either social network trait variation or variation in group size. These findings identify a potential benefit for marmot sociality and an explanation for marmot colony social structuring.
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Virtually all animals face some risk of predation. Prey species must make frequent decisions and modify their behaviour to mitigate individual risk (Lima, 1998). Living socially may reduce predation risk (Alexander, 1974; Beauchamp, 2014), and individuals in larger groups have a lower average risk of predation (Sorato, Gullett, Griffith, & Russell, 2012). Indeed, predation pressure may select for communal living in a variety of mammals (Ebensperger et al., 2012; Sorato et al., 2012; van Schaik, 1983). There are a variety of ways that group size may buffer predation risk. Through the dilution effect, predation risk is spread throughout the group. Therefore, an individual's chance of being the victim of any given attack decreases with increasing group size (Hamilton, 1971; Vine, 1971). Prey groups may also benefit from increased predator awareness and overall vigilance (Dehn, 1990; Lima & Dill, 1990; Pulliam, 1973). Confusion effects can explain the lower success rate predators experience when hunting grouped prey (Landeau & Terborgh, 1986; Neill et al., 1974); predators have difficulty differentiating between individuals in a homogenous group (Curio, 1976). In a large group, prey individuals may attempt to actively deter predators through attacking or mobbing behaviours (Curio, 1978; Graw & Manser, 2007). These effects are not mutually exclusive, and individuals living in groups may benefit from a combination of the mechanisms described above.

However, the impacts of group membership on the individual, including potential antipredation benefits, are not due to group size alone and therefore group size alone fails to fully capture social complexity (Wey, Blumstein, Shen, & Jordan, 2008). The group size approach assumes that all individuals are homogeneously affected by group membership and only indirectly considers relationships between individuals (Wey et al., 2008). However, individuals of many species are known to alter vigilance patterns, an expression of risk perception, in response to foraging group composition and relationships with conspecifics (giraffes, *Giraffa camelopardalis*: Cameron & Du Toit, 2005; chimpanzees, *Pan troglodytes*: Kutsukake, 2006). These include Croft et al.'s (2006) findings that Trinidadian guppy, *Poecilia reticulata*, females with strong social bonds are more likely to exhibit switching behaviour during risky

* Correspondence: D. T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA, 90095-1606, U.S.A.
E-mail address: marmots@ucla.edu (D. T. Blumstein).
[1] J. G. A. Martin is now at the Biology Department, University of Ottawa, Ottawa, ON K1N 9A7, Canada.

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predator inspections, suggesting that social relationships between individuals alter risk in antipredator behaviour. Formal social network analysis offers behavioural ecologists a suite of specific social attributes that can be used to study the influence of individual social position and environmental factors on individual behaviour (Croft, Krause, & James, 2008; Krause, Croft, & James, 2007; Pinter-Wollman, Hobson, Smith, Edelman, & Shizuka, 2014; Wey et al., 2008). Here, social groups are functionally defined as a network of individuals who regularly interact with each other (Wey & Blumstein, 2010). Social network statistics (such as closeness, centrality, strength, clustering, etc.), the product of social network analysis, characterize an individual's role in a social group and the qualities of the social group itself.

Social network statistics are often used to quantitatively describe social relationships in a variety of social species, but few studies have examined the influence of individual network position on antipredator behaviour. Social network analysis allowed Kutsukake (2006) to discover that variation in vigilance in wild chimpanzees (*P. t. schweinfurthii*) is influenced by variation in group relationship quality and strength. Chimpanzees often engage in aggressive within-group interactions, and when less connected group members are nearby, more connected males and females increase their vigilance (Kutsukake, 2006), suggesting an aspect of trust associated with network position. Trinidadian guppies form more differentiated and more stable social ties under high-perceived predator risk, with larger and bolder individuals, who are targeted by predators, also forming stronger social bonds (Heathcote, Darden, Franks, Ramnarine, & Croft, 2017). Yellow-bellied marmots (*Marmota flaviventer*, formerly *Marmota flaviventris*; see Wilson, Lacher, & Mittermeier, 2016) with strong affiliative relationships show increased responsiveness to novel alarm calls but, among adults, those with strong affiliative relationships return to foraging more quickly, suggesting that strong affiliative relationships act as a form of social security (Fuong et al., 2015).

Many studies of social structure have focused on obligately social animals. However, individuals in facultatively social species may exhibit phenotypic plasticity and vary their degree of social interaction according to environmental conditions or throughout their lives (Ulijaszek, Johnston, & Preece, 1998). Facultatively social animals are likely capable of both solitary and group living (Roux, Cherry, & Manser, 2007) and, thus, are more likely to exhibit plasticity in socially mediated behaviours. Facultatively social animals do not have to be social; therefore, the individuals that are social have either chosen, or were forced, to be so. This choice could stem from some benefits that individuals experience when integrated in a network. These benefits could include any of the predation risk mitigation effects described above or other advantages, such as greater reproductive success (Cameron, Setsaas, & Linklater, 2009) or help rearing young (Moehlman, 1987). Alternatively, facultatively social individuals could be forced into sociality due to ecological constraints. Emlen (1982) suggested that the interplay between two broad ecological factors determine dispersal rates: the harshness of the surrounding environment and the difference between a grouped individual's rate of successful reproduction and an independent individual's rate of successful reproduction. Thus, facultatively social animals provide an unprecedented opportunity to study the adaptive basis of sociality itself. We suggest that formal social network analyses of facultatively social species permits a more detailed understanding of the adaptive value of social structure. By focusing on facultatively social species, we may identify drivers of social life in animals that do not need to be social to survive.

Here we focus on facultatively social yellow-bellied marmots (henceforth, 'marmots'), a large, ground-dwelling, alpine squirrel (Armitage, 2014). We ask whether more social marmots are more likely to survive the summer. Marmots are harem polygynous and their social networks usually consist of a female kin group, offspring and one or a few adult males (Armitage, 2014). Marmots live in colonies that contain one or more social networks (Wey & Blumstein, 2010), which can differ greatly in size, sex and age class composition (Blumstein, Williams, Lim, Kroeger, & Martin, 2018). Adult females have litters in June and July, and pups stay in the natal colony through winter and into the following summer, at which point they are considered yearlings (Armitage, 2014). Yearlings disperse when the next litter is born; most males leave, while about half of female yearlings remain in the natal colony (Armitage, 2014).

Despite living in stable social groups, there is compelling evidence that increased sociality in yellow-bellied marmots has negative life history consequences, rather than benefits. Wey and Blumstein (2012) found that more social females, with stronger connections to others in their network, have reduced reproductive success. More social marmots also have decreased longevity; they live shorter lives (Blumstein et al., 2018). Overwinter mortality partially explains this phenomenon, given that amicable relationship strength in the summer is linked to an increased likelihood of death during the following winter's hibernation (Yang, Maldonado-Chaparro, & Blumstein, 2017). However, we do not yet understand how marmot sociality influences survival during the summer active season.

Mortality during the summer is almost entirely attributed to predation (Van Vuren, 2001), although the degree of predation pressure probably varies throughout the active season; we see more predators early in the year. By asking whether social network position is associated with summer survival, we can determine whether specific social attributes have an antipredator benefit. This will allow us to investigate the impact of social behaviour on survival, elucidating the evolutionary origins of marmot sociality. We hypothesize that individuals with higher measures of social integration and connectivity have a higher probability of summer survival because these individuals have more contact with other members of the group and therefore may have access to more information about predation risk, and/or may benefit from living with well-known conspecifics.

METHODS

We studied yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (38°57′29″N, 106°59′06″W, elevation ~2890 m), which is located in the Upper East River Valley in Gunnison County, Colorado, U.S.A. Although this population has been studied since 1962 (Armitage, 2014), we focused on data collected between 2002 and 2015 at four colony sites: Bench-River, Town, Picnic and Marmot Meadow. Bench-River and Town are lower-elevation sites and are considered 'down-valley'. Picnic and Marmot Meadow are higher-elevation sights and are considered 'up-valley'. We selected these colonies because they are geographically distinct and socially variable, and because we had detailed information on social interactions for these colonies.

Marmots were individually identified by permanent metal eartags and temporary marks applied to individuals' dorsal pelage, using nontoxic Nyanzol-D dye (Greenville Colorants, Jersey City, NJ, U.S.A.). Individuals were marked and tagged during trapping, according to procedures described in Armitage (1982). Trained observers conducted near-daily observations during periods of peak activity (0700e1000 h and 1600e1900 h) from mid-April to mid-September. Researchers sat 20e150 m away from the colony and used binoculars and 15e45× spotting scopes to identify marmots and record all instances of social interactions. For the purposes of

this study, we focused on directed affiliative interactions (N ¼6,222) between known individuals.

To examine affiliative interactions, we first compiled all social interactions between individuals seen at least five times per year between 2002 and 2015. We then constructed social interaction matrices for each year for the four colony sites listed above. Using these matrices, we calculated 11 social network statistics for each social group year that we hypothesized had directional relationships between sociality and longevity: indegree, outdegree, incloseness, outcloseness, betweenness centrality, eigenvector centrality, instrength, outstrength, average shortest path length, local clustering and global clustering.

Indegree and outdegree, respectively, calculate the number of individuals that a focal individual receives and initiates interaction with. These measures represent how directly connected an individual is to others in the network (Wasserman & Faust, 1994). Closeness centrality, measured as both incloseness and outcloseness, is a measure of how influential a focal individual is within a network. It is calculated as the sum of the reciprocal of the shortest path length between the focal individual and all other individuals in the network (Wasserman & Faust, 1994). Betweenness centrality measures centrality by calculating the proportion of shortest path lengths between all other pairs of the individuals within the network that include the focal individual (Wey et al., 2008). Eigenvector centrality also measures an individual's connectedness and takes into account the indirect effect of relationships that occur between a focal individual's neighbours (Newman, 2010). A high degree of eigenvector centrality indicates that an individual's connections are themselves highly connected. Strength, measured as instrength and outstrength, describes how frequently a focal individual interacts with its neighbours (Wasserman & Faust, 1994). Average shortest path length is calculated as the average number of individuals between a focal individual and another individual in the network (Newman, 2010). It describes how efficiently the members of a network can connect with other members (Newman, 2010). Due to this definition, a larger value is interpreted as being less social. To characterize the cliquishness of a network, clustering calculations divide the actual relationships formed by a focal individual by the total number of possible relationships (Wey et al., 2008). Local clustering describes the embeddedness of a focal individual within its social group (Wasserman & Faust, 1994). Global clustering describes the density of the network, or the degree to which a focal individual's connections are connected with each other (Barrat, Barthelemy, Pastor-Satorras, & Vespignani, 2004). An individual with a high degree of global clustering is embedded in a smaller, more exclusive, group within the larger network.

We predicted that measures indicating that an individual was more central or embedded in their social group (e.g. high degree closeness, betweenness centrality, eigenvector centrality, strength and local clustering and low average shortest path) would have higher summer survival. Central individuals have contact with more members of the group and thus have access to more antipredator information. High measures of global clustering, which would indicate smaller, more exclusive groups, would be negatively correlated with survival because individuals would have less access to antipredator information.

We based calculations of summer survival on the date of last sighting for adults and yearlings that were known to survive the summer. After pooling all 14 years of data, 75% of adult survivors were seen for the last time after 1 August. Seventy-five per cent of yearling survivors were seen for the last time after 10 August. Therefore, we considered any yearling or adult seen after 1 or 10 August, respectively, to have survived the summer. To control for yearling dispersal, we included a 20-day blackout period, 10 days before and 10 days after the date of first litter emergence at each colony for each year (Blumstein, Wey, & Tang, 2009). During this time, we considered all yearlings that disappeared to have dispersed, rather than having been predated. Additionally, we considered the few individuals who were last seen before 1 and 10 August, respectively, but who reappeared in successive years, to have survived the summer.

To determine whether an individual's social attributes can predict summer survival, we fitted a series of generalized linear mixed effects models with binomial error structures. Because some social metrics were undefined for some individuals, we filtered our data set to include only individuals who had a value for all network parameters. We also excluded all pups from the models. As a result, there were three colony-years (Picnic, 2003, 2005; Town, 2002) that were not represented in the models. We calculated the predation index based on the number of predators sighted during the marmot observation sessions described above (Monclús, Tiulim, & Blumstein, 2011). For each colony, in each year, we summed the number of observation sessions during which a predator was sighted and determined the median number of predator sightings across all colonies and all years. We then employed a median split to define low and high predation pressure: colony-years (i.e. Picnic, 2002) above the median were considered 'high predation' and colony-years below the median were considered 'low predation'. This metric has been successfully used in prior studies and captures the variation in predation pressure in a biologically relevant way for our system (Monclús et al., 2011; Pinho, Ross, Reese, & Blumstein, 2019). These calculations provide a yearly colony predation index that is relative to all other colonies in all other years. To calculate group size, we used a community detection algorithm that calculated possible interacting individuals based on overlapping colony use (Blumstein et al., 2009).

We performed separate analyses on four marmot demographic groups: adult females (N ¼185); yearling females (N ¼129); adult males (N ¼47); and yearling males (N ¼53). We split the population into these groups because individuals of different ages and sexes have different social association patterns and predation risk may affect these groups differently. Within each demographic group, we fitted a separate model for each social variable. This avoids collinearity problems due to correlated social traits, making interpretation of these results easier than that for results obtained by selecting a subset of variables or reducing dimensionality with principal component analysis (PCA). In addition to the focal social variable, models included age (in the adult models), valley position, predation index, group size and a social variable*predation index interaction term as fixed effects and year as a random effect. In the adult models, individual identity was also included as random effect. Some models failed to converge. For these we used the 'bobyqa' optimizer from the R package 'optimx' (Nash, 2014). For the adult male local clustering and betweenness models, we additionally excluded the interaction between the social variable and the predation index, which allowed the models to converge. For the adult female local clustering model, we again excluded the interaction between the social variable and the predation index. Finally, we log-transformed the outcloseness variable in the yearling female model to achieve a normal distribution of outcloseness values.

Ethical Note

All procedures were approved under research protocol ARC 2001-191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually, as well as annual permits issued by the Colorado Division of Wildlife (TR-519). After trapping, individuals were released immediately at the

trap location. Marmots were in traps no longer than 2e3 h, and typically for much less time. Traps were shaded with vegetation on warm days. Marmot handling was brief (typically 5e15 min depending upon the data to be collected), and marmots were not injured during handling. All marmots were handled while inside a conical cloth-handling bag to reduce stress. We swabbed ears with alcohol before tagging individuals to reduce the chance of infection. Observations were conducted at distances chosen to not overtly affect marmot behaviour.

RESULTS

Overall, yearling male summer survival was unaffected by social network position and group size (Tables 1 and 2, Supplementary material 1). However, yearling males in colonies with a higher predation index were less likely to survive the summer in the local clustering model (estimate = −3.880, z = −2.481, P = 0.013), and yearling males living at Picnic and Marmot Meadow were less likely to survive in the outdegree (estimate = −1.537, z = −1.996, P = 0.046), betweenness (estimate = −1.521, z = −1.964, P = 0.050), incloseness (estimate = −1.529, z = −1.981, P = 0.048), local clustering (estimate = −1.800, z = −2.088, P = 0.037) and eigenvector centrality (estimate = −1.610, z = −2.108, P = 0.035) models.

In contrast, yearling female summer survival was heavily affected by various social network statistics (Tables 1 and 2, Supplementary material 2). We found a significant positive effect of outdegree (estimate = 9.665, z = 2.142, P = 0.032), betweenness (estimate = 17.051, z = 2.080, P = 0.038), outcloseness (estimate = 1.300, z = 1.986, P = 0.047), instrength (estimate = −1.124, z = −2.695, P = 0.021) and outstrength (estimate = 0.055, z = 2.308, P = 0.021). The interaction of outstrength and predation index had a significant negative effect on survival (estimate = −0.065, z = −2.505, P = 0.012), such that females in higher predation sites that had higher outstrength were less likely to survive. Valley position also had a significant negative effect on survival (estimate = −1.124, z = −2.316, P = 0.021) in the instrength model. Neither predation index nor group size was a significant predictor of survival in any of the models.

None of the fixed effects included in the models were significant predictors of adult male summer survival (Tables 1 and 2, Supplementary material 3). For adult females, summer survival was unaffected by social network position (Tables 1 and 2, Supplementary material 4). However, group size was a positive predictor of survival in three models (betweenness: estimate = 0.089, z = 2.128, P = 0.033; local clustering: estimate = 0.086, z = 1.977, P = 0.048; average shortest path length: estimate = 0.087, z = 1.974, P = 0.048). The interaction between a social variable and the predation index was negatively associated with survival in the betweenness model (estimate = −8.819, z = −2.171, P = 0.030) and in the average shortest path length model (estimate = −2.122, z = −2.571, P = 0.010). Thus, individuals in high predation areas with high betweenness and high average shortest path length were less likely to survive. Valley position had a negative effect in the betweenness model (estimate = −1.275, z = −1.983, P = 0.048). Conversely, high predation index was a positive predictor of survival in the average shortest path length model (estimate = −4.262, z = 2.189, P = 0.029).

DISCUSSION

The effect of sociality on summer survival varied for different age and sex groups in fundamentally different ways. While we identified associations between network traits and outcomes, because some social network traits were correlated, our study should be viewed as somewhat exploratory. Yearling males do not appear to mitigate predation risk through social relationships and, in some cases, may even experience decreased summer survival when they are more embedded in their networks in areas of high predation. Given that virtually all yearling males disperse, regardless of social embeddedness (Blumstein et al., 2009), individuals may be less motivated to invest in social relationships because they are ineligible for the compounded benefit of reduced predation and reduced likelihood of dispersal.

By contrast, yearling females with more connections and stronger relationships, with a more central role in the larger network, are more likely to survive the summer. The benefits that yearling females accrue from social relationships echo Blumstein et al.'s (2009) finding that more central female yearlings who engage in more direct interactions are more likely to remain in the natal colony during dispersal, increasing their chance of survival by up to 16% (Van Vuren & Armitage, 1994). Therefore, it is possible that social integration increases yearling female survival in multiple ways: more social individuals are less likely to be depredated at the beginning and end of the active season and, during periods of pup emergence, they are more likely to remain in the natal colony. In this way, yearling females have more to gain by investing in social relationships, compared to other demographic groups. Yearling females may be functionally more social than their male counterparts or they may engage in the same amount of social behaviour while reaping greater rewards.

For adult males, none of the predictors we included in our models were significant. These findings prompt questions about what contributes to variation in adult male summer survival. It is clear that the advantage of group living for males is to maximize reproductive success (Armitage, 2014), rather than to maximize

Table 1
Summary of the prediction direction and outcome result of the influence of each social network statistic on summer survival in four different ageesex classes

Social attribute	Prediction	Yearling male	Yearling female	Adult male	Adult female
Indegree	þ	0	0	0	0
Outdegree	þ	0	þ	0	0
Betweenness	þ	0	þ	0	0
Incloseness	þ	0	0	0	0
Outcloseness	þ	0	þ	0	0
Eigenvector centrality	þ	0	0	0	0
Instrength	þ	0	þ	0	0
Outstrength	þ	0	þ	0	0
Local clustering	þ	0	0	0	0
Global clustering	–	0	0	0	0
Average shortest path	–	0	0	0	0

þ indicates a significantly positive effect on summer survival; - indicates a significantly negative effect on summer survival; 0 indicates no significant effect. Detailed results in text.

Table 2
Values range for each social network statistic and group size in all years, by colony

Social attribute	River	Town	Marmot Meadow	Picnic
Indegree	0.025e0.353	0.030e1	0e0.941	0.02e0.643
Outdegree	0.032e0.6	0.030e1	0.030e0.824	0.02e0.409
Betweenness	0e0.599	0e0.667	0e0.522	0e0.487
Incloseness	0.025e0.435	0.030e1	0.031e0.944	0.02e0.310
Outcloseness	0.033e0.435	0.030e1	0.032e0.472	0.02e0.184
Eigenvector centrality	0e1	0e1	0e1	0e1
Instrength	1e127	1e74	2e209	1e149
Outstrength	1e109	1e59	1e135	1e127
Local clustering	0e1	0e1	0e1	0e1
Global clustering	0e0.712	0e0.933	0e0.735	0.229e0.646
Average shortest path	1.05e2.995	1e2.879	1.394e3.198	1.581e3.774
Group size	1e27	1e29	1e17	1e34

longevity. That said, more dominant males, who exhibit higher degrees of bullying behaviour, have higher reproductive success (Wey & Blumstein, 2012), and for males, agonistic relationships may be more important in their quest to maximize fitness than the affiliative relationships studied here. Importantly, however, this is our smallest demographic group (marmots live in female matrilines), and our analysis may therefore be underpowered.

Adult females seemingly mitigate predation risk not through their social relationships but through group living itself. Individuals who live in large groups are more likely to survive the summer. Our results are similar to those of another recent study in which adult females in larger groups devoted less time to vigilance and more time to foraging (Mady & Blumstein, 2017). Such a finding suggests that for adult females, the benefits of aggregation accrue through dilution, detection, or a combination of the two. Both of these tactics are at play in the antipredator group formations of Columbian ground squirrels, *Urocitellus columbianus* (Fairbanks & Dobson, 2006), plains zebra, *Equus quagga* (Schmitt, Stears, Wilmers, & Shrader, 2014), and Rocky Mountain elk, *Cervus elaphus* (Childress & Lung, 2003), although detection may have a greater influence than dilution in the latter two species. Further research is needed to disentangle the effects of dilution versus detection in marmot populations.

The discovery that females, but not males, benefit from group living during the active season provides an explanation for the ways in which marmot colonies are socially structured. It is widely recognized that female relationships, particularly those initiated by yearlings, bond social groups together (Blumstein, 2013). It follows that males would be less involved in group structuring because they do not benefit from affiliative relationships. Among females, yearlings support network attachment through affiliation, and agonistic interactions by adults decrease attachment (Wey & Blumstein, 2010). Yearling females have a vested interest in creating strong social ties because it increases their chance of summer survival. In contrast, adult females, who only benefit from group size, have no motivation to invest in the relationships themselves. By continuing to live in groups, but growing more antisocial over time (Wey & Blumstein, 2010), adult females can reap the antipredator rewards of group living while expending less energy and attention on nonbeneficial interactions. Additionally, more closely related females engage in more amicable behaviour towards each other (Blumstein, 2013). If the individuals initiating or receiving interactions are yearlings, our findings introduce a robust mechanism for kin selection, as proposed by Wey and Blumstein (2010).

However, social benefits are also influenced by the degree of predation in a given area. Although outstrength is generally beneficial for yearling females, in areas of high predation, somewhat paradoxically, it has a negative effect on survival. A similar effect exists for adult females, who are negatively impacted by high measures of betweenness and average shortest path length in high predation environments. This may suggest a cognitive cost of maintaining social relationships (Blumstein, 1998). In a high predation context, paying too much attention to maintaining cognitively costly relationships may divert attention away from antipredator vigilance. To properly understand the importance of such a putative cognitive cost, we must quantify the costs of different types of social relationships and their information processing demands. Some social relationships most likely require more attention and time to maintain than others. For example, it may be less cognitively costly to have activities directed at oneself, but maximizing indirect relationships may require basing interaction decisions on knowledge of who other individuals in the group interact with. Acquiring that information may be costly both in time and cognitive ability.

In this study system, marmots are seemingly influenced by direct, indirect and group-level social consequences: three different levels/types of social relationships that marmots may track. Given the established relationship between group size and social complexity, wherein species with larger and more stable groups are better able to manage social relationships (David-Barrett & Dunbar, 2013), there may be a limit, imposed by group size, on maintaining complex social relationships in yellow-bellied marmots. More generally, the proposed cognitive costs of sociality and network monitoring seen in marmots, along with David-Barrett and Dunbar's (2013) theory of group size and processing power, may help to explain why complex sociality has not evolved in all species.

Previous work has found marmot sociality to be costly in the form of decreased longevity (Blumstein et al., 2018), increased winter mortality (Yang et al., 2017) and decreased reproductive fitness (Blumstein, 2013), but the results of the present study suggest that females benefit from their social groups and social relationships in tangible ways. The relationship between increased summer survival and sociality supports the theory that marmots are social because they benefit from the behaviour rather than simply due to ecological constraints. We know that group size can affect an individual's level of perceived risk, or sense of security (Fuong, Maldonado-Chaparro, & Blumstein, 2015; Mady & Blumstein, 2017). Here, an individual's sense of security is directly related to the security that the individual actually experiences. This is particularly true for yearling females whose individual likelihood of survival is heavily influenced by their relationships as well as the relationships of others in the network. These findings have important implications for understanding how security is achieved and maintained, and how perceptions of security translate to actual risk and survivorship. These questions can be effectively addressed by studying yellow-bellied marmot populations but have the potential to contribute to a greater understanding of social behaviour

in general. It is therefore possible that relationship-mediated social security is a more general phenomenon. Using social network analysis, which produces precise and specifically defined social statistics, future studies can determine to what extent social security affects perceived risk and survivorship in species across a broad range of social types.

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Declarations of Interest

None.

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Supplementary Material

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