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Original Article

A cost of being amicable in a hibernating mammal

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Amicable social interactions can enhance fitness in many species, have negligible consequences for some, and reduce fitness in others. For yellow-bellied marmots (*Marmota flaviventris*), a facultatively social rodent species with demonstrable costs of social relationships during the active season, the effects of sociality on overwinter survival have yet to be fully investigated. Here, we explored how summer social interactions, quantified as social network attributes, influenced marmot survival during hibernation. Using social data collected from 2002 to 2012 on free-living yellow-bellied marmots, we calculated 8 social network measures (in-degree, out-degree, in-closeness, out-closeness, in-strength, out-strength, embeddedness, and clustering coefficient) for both affiliative and agonistic interactions. We performed a principal component analysis (PCA) to reduce those attributes to 3 affiliative (connectedness, strength, and clustering) and 4 agonistic (submissiveness, bullying, strength, and clustering) components. Then, we fitted a generalized linear mixed model to explain variation in overwinter survival as a function of these social components, along with body mass, sex, age, weather conditions, hibernation group size, and hibernation group composition. We found that individuals with stronger amicable relationships were more likely to die during hibernation. This suggests that social relationships, even affiliative ones, need not be beneficial; for yellow-bellied marmots, they can even be fatal.

Key words: **connectedness, cost of sociality, hibernation, overwinter survival, social relationships, yellow-bellied marmot**

INTRODUCTION

Engaging in social interactions and the specific types of relationships that emerge from them can enhance or reduce survival in many group-living species (Alexander 1974; Krause and Ruxton 2002). Putative benefits include enhanced resource exploitation (e.g., river otters (*Lontra canadensis*), Blundell et al. 2002; striped parrotfish (*Scarus iserti*), Clifton 1990; western banded geckos (*Coleonyx variegatus*), Lancaster et al. 2006), predator defense (e.g., crested macaques (*Macaca nigra*), Micheletta et al. 2012); white-nosed coatis (*Nasua narica*), Hass and Valenzuela 2002; paper wasps (*Polistes bellicosus*), Strassmann et al. 1988; fathead minnows (*Pimephales promelas*), Chivers et al. 1995), reproductive success (e.g., Assamese macaques (*Macaca assemensis*), Schülke et al. 2010; feral horses (*Equus caballus*), Cameron et al. 2009), and longevity (e.g., chacma baboons (*Papio hamadryas ursinus*), Silk et al 2010; bovids, Bro-Jørgensen 2012). On the other hand, sociality may also increase competition for resources (e.g., Alaskan moose (*Alces alces gigas*), Molvar and Bowyer 1994); coho salmon (*Oncorhynchus kisutch*), Grand and Dill 1999), attraction to predators (e.g., elk (*Cervus elaphus*), Hebblewhite and Pletscher 2002), parasite and disease transmission (e.g., North American bison (*Bison bison*), Dobson and Meagher 1996; African lions (*Panthera leo*), Packer et al. 1999; barn swallows (*Hirundo rustica*), Shields and Crook 1987), and loss of reproductive opportunities (e.g., marmosets (*Callithrix jacchus*), Abbott 1987); meerkats (*Suricata suricatta*), Clutton-Brock et al. 1998; social spiders (*Stegodyphus dumicola*), Bilde et al. 2007).

Complex relationships and social structures can be quantified using social network analysis that has historically been used to study human populations (Wasserman and Faust 1994; Degenne and Forsé 1999; Hanneman and Riddle 2005) and, more recently, non-human populations (Lusseau and Newman 2004; Croft et al. 2008; Wey et al. 2008; Whitehead 2008). In humans, social relationships can affect an individual's health through the availability of social support, influence, and engagement; person-to-person contacts to pathogens; and access to resources (Smith and Christakis 2008). Moreover, social integration can enhance longevity (Berkman and Glass 2000; Cacioppo and Hawkley 2003; Smith and Christakis 2008) and lower mortality risks (Hu and Goldman 1990). Links between social network position and fitness have also been found in animals, such as male bottlenose dolphin calves (*Tursiops truncatus*),

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where central individuals (those with high eigenvector centrality) had higher survival (Stanton and Mann 2012), and adult rock hyrax (*Procavia capensis*), where egalitarian groups with more equal associations (those with low variance in nonaggressive centrality) lived longer (Barocas et al. 2011). Other examples can be found in cichlids (*Neolamprologus pulcher*), where individuals with higher affiliative in-degree maintained more peaceful connections, helping to facilitate dispersal to neighboring groups (Schürch et al. 2010). Furthermore, male chimpanzees (*Pan troglodytes schweinfurthii*) that participated in more aggressive coalitions (characterized by aggressive betweenness) were found to produce more surviving offspring (Gilby et al. 2013), and Barbary macaques (*Macaca sylvanus*) with more aggressive partners and lower clustering coefficients increased their individual survival probability (Lehmann et al. 2015). Likewise, in yellow-bellied marmots (*Marmota flaviventris*; herein marmots), male bullies—those that initiated more aggressive interactions—had higher reproductive success and were likely to sire more offspring (Wey and Blumstein 2012). On the other hand, nonaggressive male sleepy lizards (*Tiliqua rugosa*) that were more closely connected with females in the network had higher reproductive success (Godfrey et al. 2012).

Social network analysis has also revealed negative fitness consequences of sociality in group-living species. Potential social conflict (characterized by heterogeneity of association strength) in plural breeding degus (*Octodon degus*), for example, was negatively related to female per capita pup production (Wey et al. 2013), whereas adult female marmots with strong affiliative relationships were less likely to wean offspring (Wey and Blumstein 2012). Levels of aggression in feral goats (*Capra hircus*) were higher between individuals that spent time in relatively close proximity to each other (quantified by degree and closeness centrality; Stanley and Dunbar 2013). Similarly, Atlantic salmon (*Salmo salar*) in more aggressive groups (characterized by in-degree centrality and clustering coefficient) experienced more fin damage and gained less weight (Jones et al. 2010). Additionally, European badgers (*Meles meles*; Weber et al. 2013) and Tasmanian devils (*Sarcophilus harrisii*; Hamede et al. 2009) with central network positions had a disproportionality high contribution to the spread of transmittable disease.

Hibernating members of group-living species can acquire thermoregulatory benefits by huddling together. For instance, clustering of individuals provides thermal advantages in Indian bats (*Myotis sodalis*) by decreasing heat loss and reducing mass loss during arousal (Boyles et al. 2007), whereas in Natterer's bats (*Myotis nattereri*), huddling reduces evaporative water loss during the inactive season (Boratyński et al. 2015). It has also been suggested that overwinter aggregations in hibernating rattlesnakes (*Crotalus viridis*) may reduce heat loss and water loss (White and Lasiewski 1971). Huddling alpine marmots (*Marmota marmota*) can conserve energy by decreasing expenditure for thermoregulation. Also, because juveniles are more prone to winter mortality than adults, hibernating in groups can significantly enhance the survival of young through active warming and passive heat conductance by parents or close relatives (Arnold 1993; Allainé et al. 2000).

Although previous studies suggest that social thermoregulation during hibernation may provide energetic advantages (Gilbert et al. 2010), these benefits are not certain. In alpine marmots, torpor bouts, or periods of reduced body temperature and metabolic rate, must be synchronized for social thermoregulation to be effective; otherwise individuals are more likely to increase metabolism, fat loss, and energy expenditure (Armitage and Woods 2003). Such inefficiencies in hibernation may reduce the probability of individual overwinter survival, especially if individuals are in close proximity to one another. This can be observed in Malagasy lemurs (*Cheirogaleus medius*), where larger groups experienced less regular hibernation patterns and more frequent interruptions in torpor-arousal cycles (Dausmann and Glos 2015). Hibernation patterns can also be influenced by social group composition. In yellow-bellied marmots, the length of hibernation was reduced by 4 days with each additional male in the social group and individuals hibernating together had higher daily mass loss (Blumstein et al. 2004). And, in alpine marmots, group synchrony was impaired by the presence of yearlings, which frequently delayed warm-ups and passively gained heat from close body contact to warmer adults (Ruf and Arnold 2000). This arrangement may enhance mortality rates and be responsible for social group extinction (Arnold 1990, 1993). In addition to these social factors, environmental conditions may also play a role in the effectiveness of group thermoregulation in socially hibernating animals, including hoary marmots (*Marmota caligata*), where group overwinter survival was significantly influenced by the severity of weather conditions (Patil et al. 2013).

Despite some knowledge about the effects of winter social aggregation on thermoregulation and mortality, we know virtually nothing about how social relationships during the summer active season influences overwinter survival. However, the fact that there are fitness consequences of social relationships during the active season (Wey and Blumstein 2012) suggests that it is worthwhile to examine their effects during the hibernation period. We focused on a well-studied population of yellow-bellied marmots to explore how social relationships built during the active season influenced overwinter survival. In marmots, body mass and winter duration have profound effects on fitness (Armitage 2014), but social factors may also influence overwinter survival and activity for several reasons. Previous work identified a cost to direct social cohesion in these facultatively social rodents (Wey and Blumstein 2012) and that individuals are social but not cooperative (Olson and Blumstein 2010). Previous studies further identified benefits emerging from agonistic relationships (Lea et al. 2010; Wey and Blumstein 2012). From such evidence, we hypothesized that despite the potential benefits of social hibernation, affiliative social relationships in marmots may have a negative effect on overwinter survival and agonistic relationships may have a positive effect. Thus, we expected more affiliative individuals would have a greater mortality during hibernation than more socially isolated individuals, which typically engage in more agonistic interactions. Furthermore, given that yearlings are more likely to disrupt hibernation and torpor-arousal patterns of neighboring individuals (Arnold 1990, 1993; Ruf and Arnold 2000; Armitage and Woods 2003), we predicted that group composition would also play a role—specifically, amicable individuals hibernating in groups with yearlings would have higher overwinter mortality than individuals in groups without yearlings or solitary individuals. Using social network analysis, we explicitly quantified direct and indirect relationships between individuals in their social groups to investigate the influence of specific social attributes on fitness. This relationship-based approach ultimately allowed us to study the consequences of both affiliative and agonistic interactions on marmot overwinter survival.

METHODS

Study system

Yellow-bellied marmots are facultatively social, harem-polgynous sciurid rodents that form matrilines—mother:daughter:sister groups (Armitage 2014). Matrilines are typically composed of one or two females (mean size of 1.38) and defended by one or more territorial adult males (Armitage and Schwartz 2000). Colonies are defined when one or more of these kin units live in a single habitat patch. Marmots typically hibernate from September/October of one year to April/May of the following year (Armitage 2014). Some individuals hibernate alone, whereas others share burrows over winter and hibernate socially (Blumstein et al. 2004).

We studied free-living, individually marked marmots in and around the Rocky Mountain Biological Laboratory in Gothic, Colorado (38° 57′ 29″ N; 106° 59′ 06″ W), where they have been studied since 1962 (Blumstein 2013; Armitage 2014). Individuals live in 6 different colony sites, each geographically distinct and separate from the other. Marmots were studied under the University of California, Los Angeles Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and under permits from the Colorado Division of Wildlife (TR917, renewed annually).

Behavioral observations

Marmots were systematically livetrapped between 2002 and 2013. At each trapping event, we recorded their mass (in g), sex, and age category (classified as either pups [<1 year], yearlings [=1 year], or adults [≥2 years]). Yearlings are considered a separate age class because they are more socially interactive than adults (Wey and Blumstein 2012), and most males and about half of the females disperse from the natal colony as yearlings (Armitage 1991). Pups were usually caught within 1 week of emergence from their natal burrow. Individuals trapped for the first time were given a pair of numbered ear tags for unique identification. All individuals were marked (or remarked) with fur dye on their dorsal pelage for identification from observation sites.

Marmots were observed between 2002 and 2012. We quantified social interactions using an all-occurrence sampling scheme (details in Blumstein et al. 2009) throughout the active season—from mid-April to mid-September. Observations were made during periods of peak activity (0700–1000 h and 1600–1900 h mountain daylight time; Armitage 1962) (total hours observed in Supplementary Table S1) from distances that did not interfere with normal behavior (20–150 m). For each interaction, we noted the type of behavior (affiliative or agonistic), the initiator and recipient, and the time and location at which the behavior took place (Blumstein et al. 2009). Affiliative interactions are amicable or cohesive behaviors such as allogrooming, greeting, sitting in body contact and in close proximity, foraging within 1 m and play. Agonistic interactions included biting, chasing, fighting, and displacements—which were scored when one individual moved away from another following contact with or presence of another individual (detailed ethogram in Blumstein et al. 2009).

Quantifying overwinter survival

We assigned overwinter survival based on regular trapping and observation data. A marmot is considered to have survived hibernation if it was last seen or trapped after 1 August of one year and again the following spring. Those observed after 1 August, but not the following spring, were considered nonsurvivors. Any individual known to have been killed after 1 August were excluded from the analysis.

Quantifying social relationships

We assigned each resident marmot—an individual seen or trapped more than 5 times annually—to a single social group using a network approach based on space-use overlap (details in Maldonado-Chaparro et al. 2015). We then constructed affiliative and agonistic interaction matrices for the individuals of each identified social group.

Using the igraph package in R (Csardi and Nepusz 2015), we calculated two sets of 8 social network measures (affiliative and agonistic): in-degree, out-degree, in-closeness, out-closeness, in-strength, out-strength, embeddedness, and clustering coefficient. To quantify degree and closeness, matrices were converted to directed, unweighted networks. Degree measures the number of direct connections that an individual has (Okamoto et al. 2008). In directed networks, in-degree denotes the number of nodes that a focal individual receives interactions from and out-degree the number of nodes that a focal individual initiates interaction with. We calculated in-degree as the number of ties terminating at and out-degree as the number of ties originating from a focal individual (Wasserman and Faust, 1994). Closeness centrality corresponds to the shortest path distance from one individual to all other group members (Wey et al. 2008) and was calculated as the reciprocal sum of shortest path lengths between a focal subject and everyone else (Wasserman and Faust 1994). In-closeness measures the shortest distance from which a node can be reached from other nodes, whereas out-closeness measures the distance from which a node can reach other nodes. For strength, we used directed, weighted networks. Strength measures the magnitude of a relationship between two individuals within a group (Barthélemy et al. 2005). In-strength is calculated as the number of times an individual initiated an interaction with another individual and out-strength as the number of times an individual received the interaction (Barrat et al. 2004). For clustering coefficient and embeddedness, we used directed, unweighted networks. Embeddedness measures how deeply integrated an individual is within its social group and was quantified by identifying the number of subsets where a node is found within a network (Moody and White 2003). Clustering coefficient is a measure of the density of subgroups within a network (Wey et al. 2008). It is calculated by dividing the observed number of ties between neighbors with all possible tie combinations between those same neighbors (Wasserman and Faust 1994).

We included degree, closeness, and strength as individual measures to quantify the structural importance of individuals in social networks. Degree and strength allowed us to determine how influential an animal is based on the number of ties it has, whereas closeness allowed us to evaluate how well connected the animal is to all others. These individual measures described the potential effects that individual position within affiliative and agonistic networks can have with respect to the marmot overwinter survival. We also included clustering coefficient as an intermediate measure to assess the distribution of ties within the network. Clustering coefficient provided us a way to describe affiliative and agonistic relationships beyond a single individual by defining how densely or sparsely the network is clustered around a focal animal. Finally, we used embeddedness as a measure of an individual's integration into a social group (Blumstein et al. 2009). Whether an animal is socially connected with other members can affect its behavioral decisions during both the active and the inactive season.

Reduction of social variables

We used PCA (in the psych R package; Revelle 2015) to reduce highly correlated social network measures to smaller sets of uncorrelated social attributes. Raw social network measures for each individual in each year were used in the analysis. Components were extracted separately for both affiliative and agonistic social interaction sets based on eigenvalues >1. Varimax rotation was used to aid interpretation, and PCA scores were used for subsequent analyses.

Biological and environmental covariates

We included three biological factors in our analysis: mass on 1 August, sex, and age category. August mass is a good estimate of hibernation fat reserves, and differences in body size largely depend on sex and age category—adult males are significantly larger than females and yearlings (Armitage 2014). Sex and age category also serve as important factors when considering the overwinter survival of reproductive females because lactation and weaning of young can greatly influence individual body mass (Griffin 2008).

We included 3 climatic variables and 2 social variables to reflect the influence of environmental conditions on overwinter survival. Climatic variables included: winter mean temperature (°C), spring mean temperature (°C), and first date of bare ground (data from the RMBL weather station; 38°57′29″N, 106°59′20″W at 2900 m) from 2002 to 2013. Winter mean temperature is the average daily temperature between November and March, and spring mean temperature between March and May. First date of bare ground is the first calendar date on which there is no more snow at the RMBL Gothic town site. Social covariates included: hibernation group size (including pups) and group composition (the ratio of adults to yearlings). Hibernation group size refers to the number of resident individuals seen after 1 August in each social group. Increasing group size has been associated with reduced energy costs through higher ambient temperature in the hibernaculum (Arnold et al. 1991). Hibernation group composition is the ratio of adults to yearlings in each social group during winter. It was calculated as the proportion of yearlings relative to total group members and ranges from 0 (all adults) to 1 (all yearlings). As with hibernation group size, hibernation group composition only accounts for individuals seen after 1 August that were not otherwise known to be dead.

Statistical analyses

We fitted a generalized linear mixed effects model in lme4 R package (Bates et al. 2015) using a binomial distribution (logit link function) to explore the relationship between overwinter survival and social interactions. We conducted the model selection procedure suggested by Zurr et al. (2009) whereby we removed nonsignificant terms to arrive at the minimum adequate model. First, we fitted a full model that included as fixed effects: 3 affiliative factor scores (connectedness, affiliative strength, and affiliative clustering), 4 agonistic factor scores (submissiveness, bullying, agonistic strength, and agonistic clustering), hibernation group size and composition, August mass, sex, spring and winter temperature, age category, and the interaction between mass and sex (to account for inherent variation in mass between males and females). Additionally, we included year and unique ID as random effects in all of our models (Supplementary Table S2). We checked for the significance of the interaction terms in the model and then employed a stepwise reduction approach. At each step, we identified the less significant factor (i.e. largest P values), removed this factor, and refitted the model. Then, we compared the new model results versus the previous model fitted, using the Akaike information criterion (AIC) values (corrected for small samples) of each model. We considered that we identified the minimum adequate model once the difference in the AIC values from two consecutive models was less than 2 units. Our final model included as fixed effects: 2 affiliative factor score (affiliative strength and affiliative clustering) and 4 agonistic factor scores (submissiveness, bullying, agonistic strength, and agonistic clustering), hibernation group composition, August mass, sex, spring and winter temperature, age category, the interaction between mass and sex (to account for inherent variation in mass between males and females), and the random effects of year and unique ID. All variables included in the models were scaled. The explanatory power of the model was then estimated by calculating the R^2 values (Nakagawa and Schielzeth 2013) for the model (MuMIn R package; Bartoń 2015). All analyses were implemented in R version 3.1.2 (R Core Team 2015).

RESULTS

Between 2002 and 2012, we followed a total of 1369 marmots and recorded 15,625 affiliative and 2352 agonistic interactions. After taking into account only adults and yearlings observed more than 5 times per year and seen after 1 August, our final analysis focused on 241 observations made on 135 individuals from 53 social group-years ($N = 2$–16 individuals; Supplementary Table S2). Of these 135 marmots included in our final analysis, 22 died during the winter.

From our PCA, we reduced our 8 affiliative and 8 agonistic social network measures into 2 sets of uncorrelated variables (Supplementary Tables S3–S5). We extracted 3 affiliative social components—connectedness, strength, and clustering (Table 1)—and 4 agonistic social components—submissiveness, bullying, strength, and clustering (Table 2).

After controlling for variation in body mass, sex, and age category, we found a significant negative relationship between overwinter survival and amicable relationship strength (Table 3, Figure 1). Although this relationship was driven by 3 observations of highly amicable individuals failing to survive the winter,

Table 1

Components extracted from principal component analysis of affiliative interactions within marmot social groups. Social network measures (SNMs) indicate which SNMs were included in each component. Variance explained indicates the proportion of the total variance accounted for by each affiliative component

Component	SNM	Description	Variance
Connectedness	In-degree Out-degree In-closeness Out-closeness	Extent to which individuals interact affiliatively with others.	0.389
Affiliative strength	In-strength Out-strength Embeddedness	Intensity of relationships between members based on their level of amicable interactions.	0.272
Affiliative clustering	Clustering coefficient	Extent of subgrouping within a network resulting from friendly social behavior among members	0.127

there was no reason to remove these subjects from the analysis; they were well-studied and not erroneous observations. When any of the 3 observations were removed, the results were unchanged. The removal of all 3 apparent outliers eliminated the significance of amicable relationship strength. None of the other included social network attributes explained variation in overwinter survival (Table 3). Additionally, August body mass (Figure 2) and the interaction between body mass and sex (Figure 3) also had significant

Table 2

Components extracted from principal component analysis of agonistic interactions within marmot social groups. Social network measures (SNMs) indicate which SNMs were included in each component. Variance specifies the proportion of the total variance accounted for by each agonistic component

Component	SNM	Description	Variance
Submissiveness	In-degree In-closeness	Extent to which an individual receives aggressive behavior.	0.246
Bullying	Out-degree Out-closeness	Degree to which an individual initiates aggressive behavior.	0.267
Agonistic strength	In-strength Out-strength Embeddedness	Intensity with which agonistic interactions occurs between group members	0.272
Agonistic clustering	Clustering coefficient	Density of subgroups within a network resulting from aggressive behavior among members	0.135

Table 3

Estimates and standard errors in the final generalized linear mixed model used to explain variation in overwinter survival in yellow-bellied marmots. Bold indicates significant effect. Reference values of factors indicated by square brackets

Variable	Estimate	Standard error	*Z* value	*P* value
Intercept	**2.211**	**0.965**	**2.290**	**0.022**
Affiliative strength	**–0.877**	**0.362**	**–2.426**	**0.015**
Connectedness	–0.0840	0.342	–0.246	0.806
Submissiveness	–0.206	0.366	–0.564	0.562
Bullying	0.566	0.497	1.139	0.254
Agonistic strength	0.722	0.508	1.421	0.155
Agonistic clustering	0.0543	0.348	0.156	0.876
Age category	1.742	1.156	1.508	0.132
August mass	**–2.095**	**0.698**	**–3.002**	**0.003**
Sex [male]	1.152	0.841	1.371	0.170
Hibernation group composition	0.351	0.460	0.763	0.446
Spring temperature	0.776	0.445	1.743	0.081
Winter temperature	0.704	0.524	1.343	0.179
Mass × Sex [male]	**1.488**	**0.648**	**2.296**	**0.022**

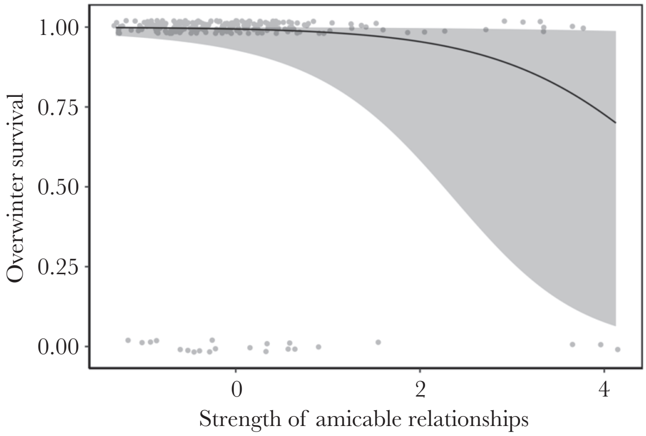

Figure 1

Relationship between overwinter survival and affiliative strength in yellow-bellied marmots. Gray area represents 95% confidence interval. Dots are observed values (jittered for better visibility). The *x*-axis plots the scaled values of affiliative strength.

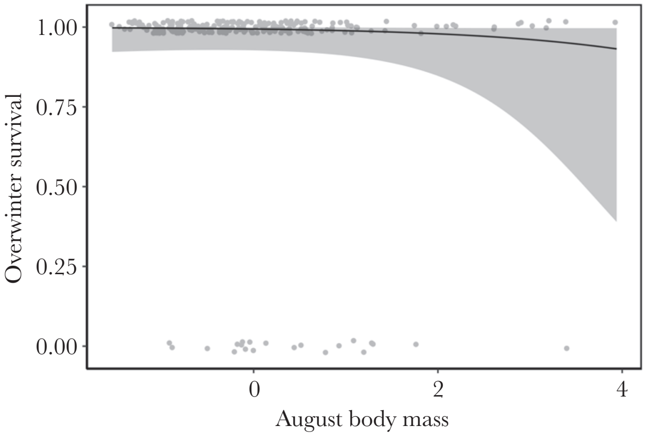

Figure 2

Relationship between overwinter survival and August body mass in yellow-bellied marmots. Gray area represents 95% confidence interval. Dots are the observed values (jittered for better visibility). The *x*-axis plots the scaled values of August body mass.

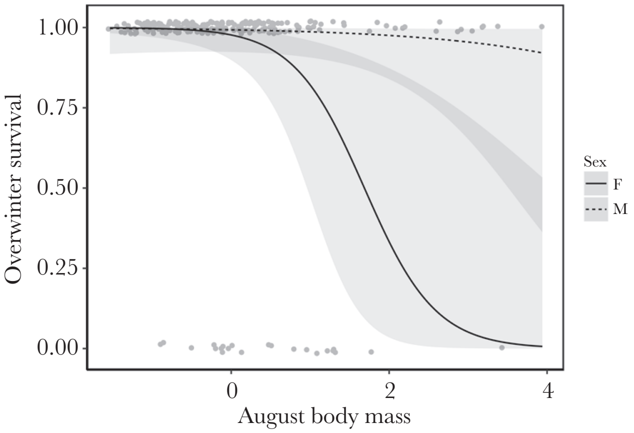

Figure 3

Relationship between overwinter survival and August body mass in yellow-bellied marmots, with respect to sex. Gray area represents 95% confidence interval. Dots are the observed values (jittered for better visibility). Dotted lines are males; solid lines are females. The *x*-axis plots the scaled values of August body mass.

negative effects on overwinter survival, whereas sex, age category, group size, and measures of group composition had none (Table 3). Our random effect of year was not significantly different from 0 (0.963 ± 95% CI: 0.000–1.949), and ID explained 0% of the variation. Overall, fixed factors explained 48.5% of the variance in the model, whereasboth fixed and random effects accounted for 60.1% of the variance.

DISCUSSION

Affiliative strength

We found that affiliative social interactions were significantly associated with marmot overwinter survival; marmots with stronger amicable relationships were less likely to survive than those with weaker relationships. This result supported our expectation that affiliative social behaviors during the summer months would have a negative impact on the survival of individuals over the inactive winter season.

Unlike in many other social species, where enduring and consistent relationships have documented benefits during hibernation, stronger amicable relationships may decrease overwinter survival in marmots for several reasons related to thermal energetics. Studies of alpine marmots (Arnold 1990) have shown that body temperature carefully tracks hibernation bouts (Ortmann and Heldmaier 2000) and benefits can only occur when there is tight synchrony in the timing of torpor bouts. Indeed, decreased synchrony often counteracts increased insulation of group huddling, leading to greater mass loss (Armitage 2007). Thus, it is possible that the observed reduction in overwinter survival is the result of asynchronous hibernation bouts for otherwise socially bonded marmots. These disruptions would, in turn, lead to higher energy consumption (Armitage et al. 2003) and might be responsible for animals failing to survive the winter. This is an empirically testable hypothesis that requires implanted temperature monitors to evaluate. In contrast, less socially integrated marmots may be more inclined to avoid sleeping in close proximity to other group members, and although they may hibernate in the same burrow, they may be more isolated. Unfortunately, little is known about the dynamics and structure of marmot hibernacula, as many are located in rocky areas that cannot be excavated (Armitage 2014). Future studies are required to describe the details of hibernation location and synchrony in free-living yellow-bellied marmots.

If sociality and amicability are so costly for fitness in both summer and winter, why is the variation for these phenotypes still maintained in this population? In marmots, stronger affiliative relationships could help promote social hibernation, which has been suggested to possibly maintain social cohesion among matriline members and juveniles (Armitage 2014). Hibernating together, but not in close proximity, could also provide energetic and reproductive advantages. Older animals, especially adult males, are the first to emerge and will unplug the frozen burrow. If this is energetically costly, this activity will conserve fat reserves and could enhance postemergence survival as well as permitting females more energy to allocate for reproduction. Males may also be able to better associate with and monopolize connected females upon emergence (Blumstein et al. 2004). This complex balance of costs and benefits not only drives the continued selection of amicable behavior but also has important implications for population dynamics and conservation. Anthropogenic disturbances can reduce the time allocated to social behavior (Pollard and Blumstein 2008), but it is increasingly necessary to understand the role relationships play in hibernation and its overall impact on fitness.

Other social attributes

The absence of a relationship between overwinter survival and all other social attributes, such as popularity and social cohesion, suggests that it is only the strength of relationships, and not the number of social partners, the density of subgroups, nor the number of individuals in a group, that significantly affects survival. It is possible that measures such as degree or clustering exhibit negligible influence on survival during hibernation because such relationships do not encourage individuals to hibernate socially or in close proximity to one another. In the case of our marmot population at RMBL, affiliative relationship strength could be regarded as a measure of the preference for individuals to associate. Thus, group members that make stronger, more frequent connections may be more inclined to sleep together during hibernation and participate in greater levels of energy-saving behaviors, such as huddling. Consequently, the activity of one marmot would be expected to have more influence on the torpor patterns of a neighbor. In contrast, because marmots are facultatively social hibernators (Armitage 2014) and live in groups due to demographic chance and ecological constraints (Blumstein 2013), burrow mates may naturally hibernate farther apart from each other or hibernate alone. Thus, agonistic interactions, which promote dispersive behavior as opposed to cohesive behavior, may influence hibernation burrow or chamber choice.

Composition of hibernation groups

Contrary to our predictions, we found no relationship between hibernation group composition and overwinter survival in yellow-bellied marmots. Individuals hibernating in groups with yearlings did not vary significantly in overwinter survival. This finding contrasts previous marmot studies where the presence of yearlings was found to significantly reduce group synchrony and be disadvantageous for adults (Arnold 1990, 1993; Ruf and Arnold 2000; Armitage and Woods 2003). Assuming stronger affiliations increase overwinter mortality as a result of greater cohesive behavior, it may be that the negative influence of yearlings in hibernating groups is overshadowed by the overall impact of huddling between highly bonded individuals. If marmots with stronger amicable relationships hibernate in closer proximity than normal, then higher rates of disturbance and asynchrony between these individuals are also more likely, regardless of the sex or age of the participating members. Consequently, greater energy expenditure and body mass would result irrespective of whether the involved marmots were yearlings or not. Although these juveniles, which experience increased lags between arousals (Armitage and Woods 2003), may intensify the amount of energy and fat loss in their hibernating neighbors, their presence does not seem to have as large of an impact as previously thought.

Winter and spring temperature

Despite previous marmot studies that have suggested the importance of weather conditions on overwinter survival (Arnold 1993; Armitage et al. 2003), our results do not support these observations. Lower winter temperatures, for example, were thought to promote higher overwinter survival, possibly because colder conditions are often associated with a greater snowpack (Rebetez 1996). This prevents burrows from dropping below the optimal thermoneutral zone (2 °C to 6 °C; Armitage and Woods 2003). Additionally, because burrow temperature is mainly dependent on soil temperature (Nikol'skii 2002), snow cover may also help keep hibernacula at the ideal microclimate by preventing the soil from freezing (Armitage 2014). Low burrow temperature can increase metabolic heat production or complete arousal from hibernation (Arnold 1993), such as was observed in alpine marmots, where metabolism increased linearly at ambient temperatures below 5° C (Arnold et al. 1991; Ortmann and Heldmaier 1992). Sparse winter snow, on the other hand, can increase burrow temperature and cause hibernating marmots to reach higher body temperatures than would be energetically efficient, resulting in unstable metabolic rates and greater exhaustion of fat reserves (Armitage 2014). On the other hand, spring temperature can affect factors such as habitat and food availability. Lower spring temperatures may force individuals to exert considerably greater metabolic resources to cope with the colder environment (Armitage 2007), whereas higher temperatures can result in earlier snow melt and less snow cover. In such circumstances, marmots would have a longer active, growing period to reproduce and prepare for the next hibernation cycle.

The contrast between previous findings and our results might be due to a difference in the scale of our weather variables. In this study, spring and winter temperatures were calculated as the average temperature over a specified number of months. Our temperature measures represented overall weather conditions for each season and did not account for monthly seasonal variations. Thus, our analysis may have identified different effects of weather on overwinter survival had we used a finer scale of measurement.

August body mass

Larger body mass is generally associated with greater fat reserves, more efficient energy conservation during hibernation, and for many species, like woodchucks (*Marmota monax*), increased overwinter survival (Zervanos et al. 2013). Surprisingly, we found that August body mass had a negative impact on the survival of hibernating marmots. This negative relationship between body mass and overwinter survival might be explained by the hibernation optimization hypothesis, which postulates that torpor expression in hibernating mammals is a trade-off between the benefits of energy conservation and the costs of metabolic depression (Humphries et al. 2003a). Accordingly, individuals with larger fat reserves are predicted to rely less on torpor during hibernation to avoid the physiological costs of prolonged torpor, including oxidative stress, reduced immunocompetence, and neuronal tissue damage (Humphries et al. 2003a). The hibernation optimization hypothesis has been observed in fat-storing hibernators such as little brown bats (*Myotis lucifugus*; Boyles et al. 2007) and eastern chipmunks (*Tamias striatus*; Humphries et al. 2003b). Thus, the fattest marmots probably arouse more often, or for longer periods, especially during the early part of the winter. This is likely to not only influence their own survival but also influence the survival of other individuals in the group. This hypothesis warrants further detailed investigation. Alternatively, socially connected animals may be able to forage more efficiently and thus had a higher August body mass; in which case, they were able to lose more mass and still survive. If so, the relationship between overwinter survival and body mass may simply reflect the benefits of social relationships during the summer. Finally, this result could be explained by the temporal difference between our body mass estimates (early August) and when the marmots first entered hibernation (mid-September). It is possible that in some instances, heavier animals were more likely to be predated upon during this period and that body mass reflects active-season mortality as opposed to overwinter mortality. We think this has a small effect on the data set, however, because animals known to have been killed after 1 August were excluded from the study.

Interaction between sex and August body mass

Interestingly, although it appears that individuals with more body mass have greater mortality during hibernation, this effect is stronger in female marmots. This suggests that heavier females are more likely to die overwinter than heavier males. One possible explanation for this dichotomy relates to social behavioral differences between the sexes. Although both males and females participate in amicable behaviors, females are more actively social overall (Armitage 2003). As a result, females, especially those that engage in stronger amicable interactions, may not only forage more efficiently, resulting in greater mass gain, but also be more likely to aggregate together during hibernation. Such groupings could lead to disrupted torpor bouts between burrow mates, which, as established previously, are a possible reason as to why closely bonded individuals are more likely to die overwinter. Thus, the negative effects of body mass may be more pronounced in females and less in males because females are naturally more amicably social.

Implications

Regardless of the precise mechanism, our results highlight the fact that social relationships need not be beneficial; for yellow-bellied marmots, strong affiliative bonds may even have negative consequences for survival. Overall, this study provides insight into the complexities of animal social behavior and hibernation. Future studies, on both obligately social and faculatively social animals, are required to develop a better understanding of the costs and benefits of sociality on hibernation survival. By identifying the importance of social relationships on survival, we are in a better position to develop models that connect individual behavioral decisions with ecological outcomes (Sutherland 1996). Such individual-based models will help us link environmental drivers with behavior, behavioral mechanisms with demography, and ultimately, will help us develop a more mechanistic understanding of population persistence.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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