

More social female yellow-bellied marmots have enhanced summer survival

Anita Pilar Montero

Abstract

For many animals, group living is an effective strategy to mitigate predation risk and ensure survival. However, in yellow-bellied marmots (*Marmota flaviventris*), increased sociality is associated with lower female reproductive success, decreased female longevity, and increased over-winter 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 ask questions about the relationship between specific attributes of sociality and summer survival, which is almost always attributable to predation. Yearling females have enhanced survival when they have stronger social relationships and are more central in their network. Adult female survival is not associated with social network traits, but females are more likely to survive the summer if they live in larger groups. Male survival is not associated with either social network trait variation or variation in group size. These findings identify a benefit for marmot sociality and an explanation for marmot colony social structuring.

Introduction

Virtually all animals face some risk of predation and prey species must make frequent decisions and modify their behavior to mitigate individual risk (Lima 1998). Living socially may reduce predation risk through a variety of mechanisms (Alexander 1974; Beauchamp 2014). Across many study systems, predation pressure is associated with group size (Hill 1998) and individuals in larger groups have a lower average risk of predation (Sorato et al. 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 and Dill 1990; Pulliam 1973). With more individuals contributing vigilance behavior, groups can detect predators more efficiently (Dehn 1990). Confusion effects can explain the lower success rate predators experience when hunting grouped prey (Landeau and 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 behaviors (Curio 1978; Graw and 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 anti-predation benefits, are not due to group size alone and therefore group size alone fails to fully capture social complexity (Wey et al. 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). By contrast, formal social network analysis offers behavioral ecologists a suite of specific social attributes that can be used to study the costs and benefits of sociality, within the context of group dynamics and individual actors (Croft et al. 2008; Krause et al. 2007; Pinter-Wollman et al. 2014; Wey et al. 2008). Here, social groups are functionally defined as a network of individuals who regularly interact with each other (Wey and 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.

There is a growing literature that employs social network statistics to quantitatively describe social relationships in a variety of obligately social species. For instance, Barocas et al. (2011) found that in rock hyraxes (*Procavia capensis*), female longevity is positively associated with centrality, a measure of influence and connectedness within a network. These findings show that within-group relationships affect the survival of individual group members, a conclusion that would not have been possible using group size statistics alone (Barocas et al. 2011). Mann et al. (2012) discovered a relationship between social association and the use of sponges as hunting tools in Shark Bay bottlenose dolphins (*Tursiops sp.*). Female tool-users preferentially fraternized with each other and were more cliquish overall, compared to non-tool users, indicating that tool use is a cultural behavior in dolphins (Mann et al. 2012). Social network analysis also allowed Kutsukake (2006) to discover that variation in vigilance in wild chimpanzees (*Pan troglodytes schweinfurthii*) is influenced by variation in group relationship quality and strength. When less connected group members were nearby, more connected males and females increased their vigilance. These findings demonstrate that vigilance is influenced by within-group threat, stemming from within-group dynamics, in addition to predation risk (Kutsukake 2006).

Facultatively social animals, in contrast, provide an unprecedented opportunity to study the adaptive basis of sociality *itself*, through the lens of specific network statistics (Blumstein 2013). Individuals that are facultatively social exhibit phenotypic plasticity and vary their degree of social interaction according to environmental conditions (Ulijaszek et al. 1998). These animals are capable of both solitary and group living (Roux et al. 2007). Groups themselves vary tremendously in size, age and sex demographics, and social dynamics (Roux et al. 2007). These qualities give researchers the ability to compare the effects of solitary and social living, and different types of social organizations, *within the same species*. Furthermore, facultatively social animals do not have to be social, therefore the individuals that are social have either chosen, or were forced, to do so. This choice could stem from some benefits 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 et al. 2009) or social rearing of 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.

Here we focus on facultatively social yellow bellied marmots, *Marmota flaviventris* (henceforth, 'marmots'), a large, ground-dwelling, alpine squirrel (Armitage 2014). We ask whether more social marmots are more likely to survive the summer. While the majority of

mortality is over the winter (Blumstein et al. 2018), summer survival is almost entirely attributed to predation (Van Vuren 2001) so by asking this question we can determine whether specific social attributes are have an antipredator benefit.

Within marmot social groups, social cohesion is primarily determined by age class, sex, and kinship affiliation (Maldonado-Chaparro et al. 2015; Wey and Blumstein 2010). 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 and Blumstein 2010), which can differ greatly in size and sex and age class composition (Blumstein et al. 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, but about half of female yearlings remain in the natal colony (Armitage 2014). Females who are less socially embedded in their natal colony's social network are more likely to disperse (Blumstein et al. 2009), indicating that social relationships may have consequences on life history decisions.

Within the colony, related individuals interact more frequently, in both affiliative and agonistic ways (Wey and Blumstein 2010). Yearlings are more social than adults (Yang et al. 2017) and less likely to initiate agonistic interactions, although both adults and yearlings initiate and receive more interactions with others in their age class than individuals outside of their age class (Wey and Blumstein 2010). Yearlings, in particular, are important for maintaining social cohesion within a colony network because they are the primary initiators and receivers of affiliative interactions (Wey and Blumstein 2010). Marmot social interaction patterns have a strong sex-based component as well: females have more affiliative relationships than males and tend to be better integrated within the larger network (Wey and Blumstein 2010).

Despite their robust social groups, there is compelling evidence that increased yellow-bellied marmot sociality has serious life history consequences, rather than benefits. Blumstein et al. (2018) found that more social marmots, with stronger connections to others in their network, lived *shorter* lives. Over-winter mortality partially underlies 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 et al. 2017). More social marmots have not only shorter lives, but they have less productive lives. More social females have reduced reproductive success than less social ones (Wey and Blumstein 2012). Thus, by asking whether and how sociality is associated with summer survival, we may gain insights into the adaptive value of sociality in this facultatively social species.

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, USA. 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, socially variable, and because we had detailed information on social interactions for these colonies (Appendix A, Figure 1).

Marmots were individually identified by permanent metal ear tags and temporary marks applied to individuals' dorsal pelage, using nontoxic Nynzol-D dye. 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 (0700-1000 and 1600-1900) from mid-April to mid-September. Researchers sat 20-150 m away from the colony and used binoculars and 15-45 x spotting scopes to identify marmots and record all instances of social interactions. For the purposes of this study we focused on directed affiliative interactions, between adult and yearling males and females.

For each social group each year, and based on observed interactions between individuals seen >5 times, we constructed a matrix of social interaction for each of the four colonies, for each of the fourteen years under study. Using these matrices, and for each social group year, we calculated eleven social network statistics that we hypothesized 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 a focal individual receives and initiates interaction with. This measure represents how directly connected an individual is to others in the network (Wasserman and Faust 1994). If sociality is positively associated with summer survival, we expect that individuals with higher indegree and outdegree measures to be more likely to escape predation. Closeness centrality, measured in both incloseness (initiated interactions) and outcloseness (received interactions), is a measure of how influential a focal individual is within a network (R Core Team 2016). 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 (R Core Team 2016). Similarly, we expected that the more influential an individual is, the greater their sense of security within the network, and therefore the lower their risk of summer mortality. We expected to see the same pattern with betweenness centrality, which 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 neighbors (Newman 2010). A high degree of eigenvector centrality indicates that an individual's connections are highly connected themselves, potentially increasing an individual's security within the network and decreasing summer risk. Strength, measured in instrength (received interactions) and outstrength (initiated interactions), describes how frequently a focal individual interacts with their neighbors (Wasserman and Faust 1994). An individual with stronger relationships should have greater network security and therefore a decreased predation risk. 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). This measure of connection should, again, be positively correlated with summer survival if sociality is beneficial. 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 (Wasserman and Faust 1994) and more embedded individuals should have higher rates of summer survival. Global clustering describes the density of the network, or the degree to which a focal individual's connections are connected with each other (Barrat et al. 2004). An individual with a high degree of global clustering is embedded in a smaller, more exclusive, group within the larger network. This could have a negative effect on an individual's security, leading to greater predation risk. A more egalitarian network may increase summer survival more than a highly clustered network.

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 fourteen years of data, 75% of adult survivors were seen for the last time after 1 August. 75% 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 et al. 2009). During this time, we considered all yearlings that disappear 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 if an individual's social attributes can predict summer survival, we fitted a series of generalized linear mixed effects model with a binomial error structures. Because some social metrics were undefined for some individuals, we filtered our dataset so that each individual had a value for each network parameter. We performed separate analyses on four marmot demographic groups: adult females; yearling females; adult males; and yearling males. We split the population into these groups because individuals of different ages and sexes have different social association patterns and predation may affect these groups differently. Within each demographic group we fitted a model for each social variable. 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 and individual identity (in the adult models) as random effects. In order to get the models to converge we made a few adjustments. Using the R package *optimx*, we applied the optimizer *bobyqa* to models that failed to converge. For the adult male local clustering and betweenness models, we excluded the interaction between the social variable and predation index. For the adult female local clustering model we again excluded the interaction between the social variable and predation index. Finally, we $\log_{10}$ transformed the outcloseness variable in the yearling female model.

We calculated the predation index based on predators sighted during the social observation periods described above (Monclús 2008). For each colony, in each year, we summed the number of observation sessions during which a predator was sighted and then employed a median split to define low and high predation pressure. 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.

We evaluated the assumptions of all models graphically by examining frequency histograms and the distribution of residuals using *q,q* plots. In cases where models violated

linearity and normality assumptions, we explored whether transforming variables improved residual distributions.

Results

Overall, yearling male summer survival was unaffected by social network position and group size. However, marmots living in high predation index colonies were less likely to survive the summer survival in the local clustering model (estimate = 0.862, $p = 0.037$), and marmots living at up-valley sites were less likely to survive in five models (estimates ranged from -1.800 to -1.521, p -values ranged from 0.035 to 0.049; full model results in Appendix B)

In contrast, yearling female summer survival was heavily affected by various social networks statistics. After accounting for valley position, predation index, and group size (full model results in Appendix C), we found a significant positive effect of outdegree (estimate = 9.665, $p = 0.032$), betweenness (estimate = 17.051, $p = 0.038$), log_outcloseness (estimate = 1.300, $p = 0.047$), outstrength (estimate = 0.055, $p = 0.021$), and instrength (estimate = -1.124, $p = 0.021$). The interaction of outstrength and predation index had a significant negative effect on survival (estimate = -0.065, $p = 0.012$), such that females in higher predation sites that had higher outstrength were less likely to survive. Valley position was also significant in the instrength model.

None of the fixed effects included in the models were significant predictors of adult male summer survival (all results in Appendix D). For adult females, group size was a positive predictor of survival in three models (betweenness (estimate = 0.089, $p = 0.033$), local clustering (estimate = 0.086, $p = 0.048$), average shortest path length (estimate = 0.087, $p = 0.048$)). The interaction between a social variable and predation index was negatively associated with survival in the betweenness model (estimate = -8.819, $p = 0.030$) and average shortest path length model (estimate = -2.122, $p = 0.010$). Thus, individuals in high predation areas with high betweenness and high average shortest path length were less likely to survive. As is the case with yearling males and females, valley position had a negative effect in one model (see Appendix D). Conversely, high predation index was a positive predictor of survival in the average shortest path length model (all results in Appendix E).

Discussion

The effect of sociality on summer survival varies for different age and sex demographic groups in fundamentally different ways. Female yearlings and adults mitigate predation risk through group living, the former through maintaining relationships between individuals, and the later through group size itself. For males, both yearling and adult, social association does not reduce the likelihood of predation during the 4-5 month long summer active season.

Yearling females seemingly benefit the most from maintaining specific types of social relationships. Individuals with more connections (outdegree) and stronger relationships (outstrength, instrength), with a more central role in the larger network (betweenness, outcloseness), are more likely to survive the summer. However, sociality benefits are also influenced by the degree of predation in a given area. For example, although outstrength is generally beneficial, in areas of high predation, somewhat

paradoxically, it has a negative effect on survival. This may suggest a cognitive costs of maintaining social relationships (Blumstein 1998). Although an individual's relationships are generally beneficial, 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. Maintaining some social relationships likely demand more attention and time than others. It may not be cognitively costly to have activities directed at oneself (indegree), but to figure out how to maximize an indirect relationship—like outcloseness—may require basing decisions about whom to interact with based on knowledge of who that individual interacts with. And acquiring that information may be costly both in time and cognitive ability.

The benefits that yearling females accrue from social relationships echo Blumstein et al.'s (2009) finding that more integrated female yearlings are more likely to remain in the natal colony during dispersal, increasing their chance of survival by up to 16% (Van Vuren & Armitage 1994). Blumstein et al. found that an yearling female's embeddedness in addition to their direct interactions best predicted dispersal patterns. These are the same social statistics that best predict summer survival. It is possible that social integration increases yearling female survival in multiple ways: more social individuals are less likely to be predated upon in the beginning and end of the active season and, during periods of pup emergence, are more likely to remain in the natal colony. In this way, yearling females have more to gain in investing in social relationships, compared to other demographic groups.

By contrast, allopatric adult females mitigate predation risk, not through their relationships, but through group living itself. Group size has a strong impact, and individuals who live in large groups are more likely to survive the summer. These results are similar to a recent study which found that adult females in larger groups devoted less time to vigilance and more time to foraging (Mady & Blumstein 2017). Here, as with our current results, group size has a more important effect for adult females than does social network position. Such a finding suggests that for adults, the benefits of aggregation accrue through dilution. Despite the positive effect of group size, there is evidence that social relationships negatively impact adult female summer survival. In high predation environments, betweenness and average shortest path length have a negative impact on survival. Both, because they describe indirect social relationships, may require time or be cognitively costly to maintain if they force individuals to divert attention away from antipredator vigilance. Thus, individuals may attempt to negotiate the trade-offs between the energetic costs of maintaining relationships and the benefit of large group predation dilution.

Yearling males do not mitigate predation risk through social factors but their summer survival is influenced by predation risk and valley position (which, in some years, is also associated with predation risk). Given that 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. Yearling males may be functionally less social than their female counterparts or they may engage in the same amount of social behavior without reaping the same rewards. The comparison between yearling female and male social behavior represents a fruitful avenue for future research.

For adult males, none of the predictors we included in the models (social statistics, predation index, valley position, group size, and the interaction between social statistics and predation index) were significant. Although this demographic is our smallest cohort, and our analysis may be underpowered, 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 longevity. Paradoxically, however, the males with the greatest reproductive success are those that live the longest. That said, more dominant males, who exhibit higher degrees of bullying behavior, have higher reproductive success (Blumstein 2013), and for males, agonistic relationships may be more important in their quest to maximize fitness than the affiliative relationships we studied here.

The discovery that females 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 adults interactions decrease attachment (Wey and 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 only benefit from group size; they have no motivation to invest in the relationships themselves. By continuing to live in groups, but growing more anti-social over time (Wey and Blumstein 2010), adult females can reap the anti-predator rewards of group living while expending less energy and attention on non-beneficial interactions. Additionally, more related females engage in more amicable behavior toward 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).

Previous work has found marmot sociality to be costly (decreased longevity (Blumstein et al. 2018), increased winter mortality (Yang et al. 2017), decreased reproductive fitness (Blumstein 2013)) but this study provides strong evidence that individuals 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 behavior rather than due to ecological constraints. A yearling female individual's likelihood of survival is heavily influenced by the individual's relationships and the relationships of others in the network. We know that group size can affect an individual's level of perceived risk by altering the individual's sense of security (Fuong et al. 2015, Mady & Blumstein 2017). Here, an individual's sense of security is directly related to the security the individual actually experiences. These findings have important implications for understanding how security is achieved and maintained, and how perceptions of security translate to real risk. These questions can be effectively addressed by studying yellow-bellied marmot populations but have the potential to contribute to a greater understanding of allopatric species social behavior in general.

Finally, this study introduces the concept of cognitive costs and finds evidence for the phenomenon in the form of decreased survival when social relationships are strong and predation index is high. In this study system, social marmots are affected by direct, indirect,

and network social consequences: three different levels of social impact that marmots may track. Our findings indicate that maintaining some types of social relationships are seemingly more costly than others. Measures of centrality and relationship strength have negative impacts in a more demanding environment. Therefore, we predict that there is a limit on maintaining complex social relationships in yellow-bellied marmots. This hypothesis is applicable to many systems, but it would be particularly interesting to look at these sort of costs in more social species, for example primates.

References

Alexander RD. 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5 325-383.

Armitage KB. 1982. Yellow-bellied marmot. In: CRC Handbook of Census Methods for Terrestrial Vertebrates (Ed. by D. E. Davis), pp. 148-149. Boca Raton, Florida: CRC Press.

Armitage KB. 1991. Factors affecting corticosteroid concentrations in yellow-bellied marmots. *Comparative Biochemical Physiology* 98A(1), 47-54.

Armitage KB. 2014. Marmot Biology. Cambridge, United Kingdom: University Printing House.

Barocas A, Llany A, Koren L, Kam M, Geffen E. 2011. Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS ONE* 6(7).

Barrat A, Barthélemy M, Pastor-Satorras R, Vespignani A. 2004 The architecture of complex weighted networks. *Proc. Natl Acad. Sci. USA* 101, 3747 – 3752.

Beauchamp G. 2014. Social Predation: How Group Living Benefits Predators and Prey. London, England: Academic Press.

Blumstein DT. 2013. Yellow-bellied marmots: insights from an emergent view of sociality. *Phil Trans R Soc B* 368.

Blumstein DT, Wey TW, Tang K. 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc. R. Soc.* 10.

Blumstein DT, Williams DM, Lim AN, Kroeger S, Martin JGA. 2018. Strong social relationships are associated with decreased longevity in a facultatively social mammal. *Proc. R. Soc. B* 285.

Cameron EZ, Setsaas TH, Linklater WL. 2009. Social bonds between unrelated females increase reproductive success in feral horses. *PNAS* 106(33), 13850-13853.

Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23(4) 194-201.

Croft DP, Krause J, James R. 2008. Exploring animal social networks. Princeton, New Jersey: Princeton University Press.

Curio, E. 1976. The Ethology of Predation. New York: Springer Verlag.

Curio, E. 1978. The adaptive significance of avian mobbing. *Zeitschrift für Tierpsychologie*, 48, 175-183.

Dehn MM. 1990. Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology* 26(5) 337-342.

Ebensperger LA, Sobrero R, Quirici V, Castro RA, Tolhuysen LO, Vargas F, Burger JR, Quispe R, Villavicencio CP, Vásquez RA, Hayes LD. 2012. Ecological drivers of group living in two populations of the communally rearing rodent, *Octodon degus*. *Behavioral Ecology and Sociobiology* 66(2) 261-274.

Emlen ST. 1982. The evolution of helping. I. An ecological constraints model. *The American Naturalist* 119(1).

Fuong H, Maldonado-Chaparro A, Blumstein DT. 2015. Are social attributes associated with alarm calling propensity? *Behavioral Ecology* 26(2) 587-592.

Graw, B. & Manser, M. B. 2007. The function of mobbing in cooperative meerkats. *Animal Behaviour* 74, 507-517.

Hamilton, WD. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, 295-311.

Hill RA. 1998. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology* 245(4), 447-456.

Krause J, Croft DP, James R. 2007. Social network theory in the behavioral sciences: potential application. *Behavioral Ecology Sociobiology* 62 15-27.

Kutsukake N. 2006. The context and quality of social relationships affect vigilance behavior in wild chimpanzees. *Ethology* 112(6) 581-591.

Landeau L & Terborgh J. 1986. Orridy and the 'confusion effect' in predation. *Animal Behavior* 34(5), 1372-1380.

Lima SL. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27, 215-290.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68(4) 619-640.

Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology* 10 945-956.

Mady RP & Blumstein DT. 2017. Social security: are socially connected individuals less vigilant? *Animal Behavior* 134 79-85.

Maldonado-Chaparro AA, Hubbard L, Blumstein DT. 2015. Group size affects social relationships in yellow-bellied marmots (*Marmota flaviventris*). *Behavioral Ecology* 26(3) 909-915.

Mann J, Stanton MA, Patterson EM, Bienenstock EJ, Singh LO. 2012. Social networks reveal cultural behavior in tool-using dolphins. *Nature Communications* 3, 980.

McNamara JM, Houston AI, 1986. The common currency for behavioural decisions. *American Naturalist* 127 358-378.

Moehlman PD. 1987. Social organization in jackals: The complex social system of jackals allows the successful rearing of very dependent young. *American Scientist* 75(4), 366-375.

Monclús R, Rödel HG. 2008. Different Forms of Vigilance in Response to the Presence of Predators and Conspecifics in a Group-Living Mammal, the European Rabbit. *Ethology* 114(3) 287-297.

Newman MEJ. 2010 Networks: an introduction. Oxford, UK: Oxford University Press.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D. 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology*, 25(2), 242-255.

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, 38, 419-422

Quenette, PY. 1990. Functions of vigilance in mammals: a review. *Acta Oecologica*, 11, 801-818.

R Core Team. 2016. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Roux AL, Cherry MI, Manser MB. 2007. The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Animal Behavior* 75, 943-949.

Russel AF, Brotherton PNM, McIlrath GM, Sharpe LL, Clutton-Brock TH. 2003. Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behavioral Ecology* 14(4), 486-492.

Scrimgeour, G. J.. and Culp, J. M. 1994. Foraging and evading predators: The effect of predator species on a behavioural trade-off by a lotic mayfly. *Oikos* 69, 71-79.

- Sorato E, Gullett PR, Griffith SC, Russell AF. 2012. Effects of predation risk on foraging behavior and size: adaptations in a social cooperative species. *Animal Behavior* 84, 823-834
- Ulijaszek SJ, Johnston FE, Preece MA. 1998. Growth and Natural Selection. In: The Cambridge Encyclopedia of Human Growth and Development. Cambridge, United Kingdom: Cambridge University Press.
- Van Schaik CP. 1983. Why Are Diurnal Primates Living in Groups? *Behavior* 87(1) 120-144.
- Van Vuren DH. 2001. Predation on yellow-bellied marmots (*Marmota flaviventris*). *The American Midland Naturalist* 145(1), 94-100.
- Van Vuren D, Armitage KB. 1994. Survival and dispersing of philopatric yellow-bellied marmots: what is the cost of dispersal? *OIKOS* 69: 179-181.
- Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology*, 30, 405-422.
- Wasserman S, Faust K. 1994 Social network analysis: methods and application. New York, NY: Cambridge University Press.
- Wey T, Blumstein DT, Shen W, Jordan F. 2008. Social network analysis of animal behavior: a promising tool for the study of sociality. *Animal Behavior* 75, 333-344.
- Wey TW, Blumstein DT. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour* 79, 1343-1352.
- Wey TW, Blumstein DT. 2012. Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behavioral Ecology* 66, 1075-1085
- Yang WJ, Maldonado-Chaparro AA, Blumstein DT. 2017. A cost of being amicable in a hibernating mammal. *Behavioral Ecology* 28(1), 11-19.
- Zurr A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology in R. New York: Springer.

Appendix A

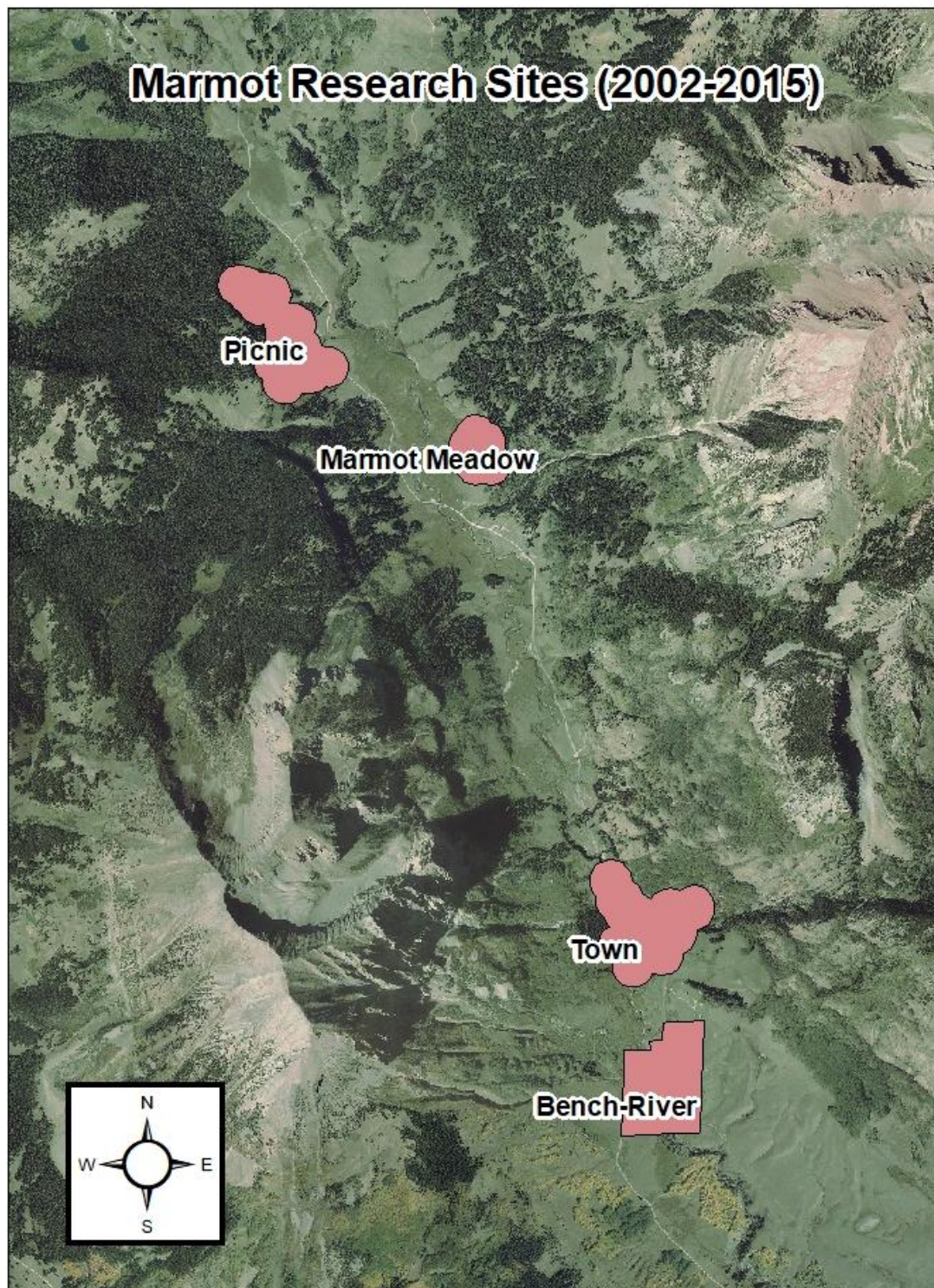


Figure 1. Map of marmot research sites in the East River Valley, Gunnison, Co from 2002 to 2015.

Appendix B

Yearling Male Generalized Linear Mixed Effects Model Outputs

Indegree Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	3.21199	1.16670	2.753	0.0059*
Indegree	-1.14791	2.76235	-0.416	0.6777
Valley_Position_UpValley	-1.51978	0.78144	-1.945	0.0518
Predator_Index_High	-1.00234	1.12160	-0.894	0.3715
Group Size	-0.06414	0.04711	-1.362	0.1733
Indegree:Predator_Index_High	-6.04375	7.10034	-0.851	0.3947

Indegree Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Outdegree Fixed Effect

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2.60579	1.16538	2.236	0.0254*
Outdegree	2.16528	4.02929	0.537	0.5910
Valley_Position_UpValley	-1.53686	0.76991	-1.996	0.0459*
Predator_Index_High	-0.44235	1.21828	-0.363	0.7165

Group Size	-0.06383	0.04756	-1.342	0.1796
Outdegree:Predator_Index_High	-6.66506	5.85280	-1.139	0.2548

Outdegree Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Betweenness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	3.00715	1.15929	2.594	0.00949*
Betweenness	-0.19524	3.65244	-0.054	0.95737
Valley_Position_UpValley	-1.52110	0.77468	-1.964	0.04959*
Predator_Index_High	-1.39192	0.97549	-1.427	0.15361
Group Size	-0.06222	0.04680	-1.329	0.18372
Betweenness:Predator_Index_High	-4.86706	9.36797	-0.520	0.60338

Betweenness Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Outcloseness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2.74913	1.19107	2.308	0.0210*
Outcloseness	1.66784	6.14994	0.271	0.7862
Valley_Position_UpValley	-1.45358	0.77427	-1.877	0.0605
Predator_Index_High	-0.77468	1.25487	-0.617	0.5370
Group Size	-0.05969	0.04648	-1.284	0.1991
Outcloseness:Predator_Index_High	-8.04489	11.03094	-0.729	0.4658

Outcloseness Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Incloseness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2.31489	1.22195	1.894	0.0582
Incloseness	5.38458	7.60409	0.708	0.4789
Valley_Position_UpValley	-1.52933	0.77189	-1.981	0.0476*
Predator_Index_High	-0.22801	1.28044	-0.178	0.8587
Group Size	-0.05600	0.04652	-1.204	0.2287
Incloseness:Predator_Index_High	-13.26286	12.11328	-1.095	0.2736

Incloseness Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Local Clustering Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	5.36604	1.67098	3.211	0.00132*
Local_Clustering	-7.26695	3.74340	-1.941	0.05223
Valley_Position_UpValley	-1.79956	0.86200	-2.088	0.03683*
Predator_Index_High	-3.88019	1.56381	-2.481	0.01309*
Group Size	-0.07804	0.05603	-1.393	0.16369
Local_Clustering:Predator_Index_High	8.10199	4.23424	1.913	0.05569

Local Clustering Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Global Clustering Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	5.04803	2.62770	1.921	0.0547

Global_Clustering	-4.36788	4.32962	-1.009	0.3131
Valley_Position_UpValley	-1.26910	0.84541	-1.501	0.1333
Predator_Index_High	-0.92204	3.37981	-0.273	0.7850
Group Size	-0.06762	0.05029	-1.345	0.1787
Global_Clustering:Predator_Index_High	-0.85840	6.14994	-0.140	0.8890

Global_Clustering Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Average Shortest Path Length Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2.33427	2.04076	1.144	0.253
Average_Shortest_Path_Length	0.24768	0.81065	0.306	0.760
Valley_Position_UpValley	-1.38252	0.87167	-1.586	0.113
Predator_Index_High	0.04135	2.55227	0.016	0.987
Group Size	-0.06482	0.04708	-1.377	0.169
Average_Shortest_Path_Length:Predator_Index_High	-0.70408	1.07996	-0.652	0.514

Outdegree Random Effects

Groups Name	Variance	Std. Dev.
-------------	----------	-----------

Year (Intercept)	0	0
------------------	---	---

Eigenvector Centrality Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	3.14196	1.21672	2.582	0.00981*
Eigenvector_Centrality	-0.20885	1.65159	-0.126	0.89937
Valley_Position_UpValley	-1.61009	0.76367	-2.108	0.03500*
Predator_Index_High	-1.34324	1.16245	-1.155	0.24788
Group Size	-0.06096	0.04677	-1.304	0.19241
Eigenvector_Centrality:Predator_Index_High	-0.71387	2.14207	-0.333	0.73894

Outdegree Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Outstrength Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	3.224399	1.071878	3.008	0.00263*
Outstrength	-0.012520	0.018922	-0.662	0.50819
Valley_Position_UpValley	-1.502245	0.783354	-1.918	0.05515

Predator_Index_High	-1.525213	1.072341	-1.422	0.15493
Group Size	-0.046889	0.054560	-0.859	0.39012
Outstrength:Predator_Index_High	-0.006759	0.027435	-0.246	0.80541

Outstrength Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Instrength Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	3.41915	1.07398	3.184	0.00145*
Instrength	-0.02193	0.02192	-1.001	0.31696
Valley_Position_UpValley	-1.45220	0.78982	-1.839	0.06597
Predator_Index_High	-1.42388	0.96043	-1.483	0.13820
Group Size	-0.06495	0.04853	-1.338	0.18078
Instrength:Predator_Index_High	-0.03623	0.05473	-0.662	0.50796

Instrength Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	1.356e-16	1.165e-08

Appendix C

Yearling Female Generalized Linear Mixed Effects Model Outputs

Indegree Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.20608	0.75121	-0.274	0.784
Indegree	5.44602	3.30154	1.650	0.099
Valley_Position_UpValley	-0.62616	0.44260	-1.415	0.157
Predator_Index_High	-0.83528	0.95166	-0.878	0.380
Group_Size	0.02160	0.02819	0.766	0.443
Indegree:Predator_Index_High	2.60985	4.56446	0.572	0.567

Indegree Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0.0003158	0.01777

Outdegree Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.36534	0.70365	-0.519	0.6036
Outdegree	9.66525	4.51210	2.142	0.0322*
Valley_Position_UpValley	-0.59189	0.45316	-1.306	0.1915

Predator_Index_High	-0.79999	0.95275	-0.840	0.4011
Group_Size	0.01646	0.02930	0.562	0.5741
Outdegree:Predator_Index_High	2.70730	6.50956	0.416	0.6775

Outdegree Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Betweenness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.24815	0.68709	-0.361	0.7180
Betweenness	17.05138	8.19861	2.080	0.0375*
Valley_Position_UpValley	-0.78244	0.48867	-1.601	0.1093
Predator_Index_High	0.46549	0.58611	0.794	0.4271
Group_Size	0.06245	0.03524	1.772	0.0764
Betweenness:Predator_Index_High	-12.85128	8.68583	-1.480	0.1390

Betweenness Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0.4487	0.6699

Log_Outcloseness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	4.17462	1.89913	2.198	0.0279*
Log_Outcloseness	1.29990	0.65470	1.986	0.0471*
Valley_Position_UpValley	-0.68281	0.45272	-1.508	0.1315
Predator_Index_High	-1.66488	2.31737	-0.718	0.4725
Group_Size	0.03500	0.02983	1.173	0.2407
Log_Outcloseness:Predator_Index_High	-0.52764	0.86442	-0.610	0.5416

Indegree Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0.04076	0.2019

Incloseness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.14015	0.66168	0.212	0.832
Incloseness	4.65447	4.27021	1.090	0.276
Valley_Position_UpValley	-0.67342	0.44444	-1.515	0.130
Predator_Index_High	-0.27631	0.73574	-0.376	0.707
Group_Size	0.03654	0.02941	1.242	0.214

Incloseness:Predator_Index_High	0.83949	5.73802	0.146	0.884
---------------------------------	---------	---------	-------	-------

Incloseness Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0.05782	0.2405

Local Clustering Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	1.05857	0.79661	1.329	0.184
Local_Clustering	-1.56605	2.46429	-0.636	0.525
Valley_Position_UpValley	-0.57479	0.44483	-1.292	0.196
Predator_Index_High	-0.77883	0.92139	-0.845	0.398
Group_Size	0.03518	0.03104	1.133	0.257
Local_Clustering:Predator_Index_High	2.52567	3.10517	0.813	0.416

Local Clustering Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0.1749	0.4182

Global Clustering Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
--	----------	------------	---------	----------

(Intercept)	0.06455	1.11139	0.058	0.954
Global_Clustering	1.00371	2.08763	0.481	0.631
Valley_Position_UpValley	-0.52300	0.43034	-1.215	0.224
Predator_Index_High	-1.90216	1.78579	-1.065	0.287
Group_Size	0.03493	0.02811	1.243	0.214
Global_Clustering:Predator_Index_High	2.74012	3.18815	0.860	0.390

Global Clustering Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Average Shortest Path Length Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.42517	1.02729	0.414	0.679
Average_Shortest_Path_Length	0.03924	0.40299	0.097	0.922
Valley_Position_UpValley	-0.32268	0.46140	-0.699	0.484
Predator_Index_High	1.49435	1.40067	1.067	0.286
Group_Size	0.03052	0.02917	1.046	0.295
Average_Shortest_Path_Length: Predator_Index_High	-0.73103	0.57358	-1.274	0.202

Average Shortest Path Length Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0.07432	0.2726

Eigenvector Centrality Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.75139	0.60635	1.239	0.215
Eigenvector_Centrality	0.40245	0.75813	0.531	0.596
Valley_Position_UpValley	-0.56868	0.45177	-1.259	0.208
Predator_Index_High	-0.69365	0.65335	-1.062	0.288
Group_Size	0.01562	0.03189	0.490	0.624
Eigenvector_Centrality: Predator_Index_High	1.05190	1.09176	0.964	0.335

Eigenvector Centrality Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0.2254	0.4748

Outstrenght Fixed Effect

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.09484	0.55282	-0.172	0.8638

Outstrength	0.05473	0.02371	2.308	0.0210*
Valley_Position_UpValley	-0.83832	0.46248	-1.813	0.0699
Predator_Index_High	1.00207	0.58464	1.714	0.0865
Group_Size	0.02932	0.02874	1.020	0.3075
Outstrength:Predator_Index_High	-0.06496	0.02593	-2.505	0.0122*

Outstrength Random Effects

Groups Name	Variance	Std. Dev.
Year (Intercept)	0	0

Instrength Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.23435	0.58093	-0.403	0.68665
Instrength	0.05507	0.02043	2.695	0.00703*
Valley_Position_UpValley	-1.12397	0.48538	-2.316	0.02058*
Predator_Index_High	0.83511	0.68150	1.225	0.22042
Group_Size	0.02104	0.02906	0.724	0.46907
Instrength:Predator_Index_High	-0.04239	0.02324	-1.824	0.06817

Instrength Random Effects

Groups Name	Variance	Std. Dev.
-------------	----------	-----------

Year (Intercept)	0.01886	0.1373
------------------	---------	--------

Appendix D

Adult Male Generalized Linear Mixed Effects Model Outputs

Indegree Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-2.158738	4.006720	-0.539	0.590
Indegree	0.512183	3.101309	0.165	0.869
Valley_Position_UpValley	1.650468	1.083833	-1.523	0.128
Predator_Index_High	-0.178545	1.486778	-0.120	0.904
Group_Size	-0.005869	0.058564	0.100	0.920
Age	1.799573	1.675552	1.074	0.283
Indegree:Predator_Index_High	-9.515466	10.691659	-0.890	0.373

Indegree Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0

Log_Outdegree Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.69796	6.02920	-0.116	0.9078
Log_Outdegree	2.09297	1.98492	1.054	0.2917
Valley_Position_UpValley	-1.97967	1.29039	-1.534	0.1250
Predator_Index_High	-9.93408	5.56776	-1.784	0.0744 .
Group_Size	0.03524	0.06905	0.510	0.6098
Age	3.16678	2.26181	1.400	0.1615
Log_Outdegree:Predator_Index_High	-4.00681	2.45746	-1.631	0.1030

Log_Outdegree Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0

Betweenness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.21737	3.14207	-0.387	0.698
Betweenness	3.53788	9.96360	0.355	0.723
Valley_Position_UpValley	-1.66873	1.11373	-1.498	0.134
Predator_Index_High	-0.77447	1.15555	-0.670	0.503

Group_Size	0.01517	0.06077	0.250	0.803
Age	1.17158	1.29137	0.907	0.364

Betweenness Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0

Outcloseness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.564959	3.537031	-0.442	0.658
Outcloseness	1.417683	4.920665	0.288	0.773
Valley_Position_UpValley	-1.651317	1.117967	-1.477	0.140
Predator_Index_High	0.116522	1.998074	0.058	0.953
Group_Size	0.003858	0.057930	0.067	0.947
Age	1.492144	1.445743	1.032	0.302
Outcloseness:Predator_Index_High	-15.307109	25.606238	25.606238	0.550

Outcloseness Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0

Year	0	0
------	---	---

Incloseness Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.736828	3.230813	-0.538	0.591
Incloseness	6.751800	10.421873	0.648	0.517
Valley_Position_UpValley	-1.689660	1.092562	-1.546	0.122
Predator_Index_High	0.048726	1.579216	0.031	0.975
Group_Size	0.004968	0.057850	0.086	0.932
Age	1.251166	1.252186	0.999	0.318
Incloseness: Predator_Index_High	-9.992657	12.773136	-0.782	0.434

Incloseness Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0

Local Clustering Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	2.90453	4.08493	0.711	0.4771

Local_Clustering	-5.03540	2.93380	-1.716	0.0861
Valley_Position_UpValley	-3.25953	1.76374	-1.848	0.0646
Predator_Index_High	-1.22447	1.09673	-1.117	0.2642
Group_Size	0.05218	0.06700	0.779	0.4361
Age	0.51131	1.26803	0.403	0.6868

Local Clustering Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0

Global Clustering Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.095511	8.863969	0.011	0.991
Global Clustering	-3.730941	14.557183	-0.256	0.798
Valley_Position_UpValley	-1.193488	1.201382	-0.993	0.321
Predator_Index_High	-1.277256	8.461079	-0.151	0.880
Group_Size	-0.002882	0.060919	-0.047	0.962
Age	1.569226	1.420486	1.105	0.269

Global_Clustering: Predator_Index_High	0.370110	15.689651	0.024	0.981
---	----------	-----------	-------	-------

Indegree Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0

Average Shortest Path Length Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.903769	3.597088	-0.529	0.597
Average_Shortest_Path_Length	0.701541	0.988686	0.710	0.478
Valley_Position_UpValley	-2.373403	1.480691	-1.603	0.109
Predator_Index_High	-0.557387	2.978795	-0.187	0.852
Group_Size	0.007866	0.057394	0.137	0.891
Age	1.152782	1.264508	0.912	0.362
Average_Shortest_Path_Length: Predator_Index_High	-0.200183	1.201416	-0.167	0.868

Average Shortest Path Length Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0

Year	0	0
------	---	---

Eigenvector Centrality Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.960588	4.314816	-0.454	0.650
Eigenvector_Centrality	-0.239644	1.936327	-0.124	0.902
Valley_Position_UpValley	-1.651668	1.091041	-1.514	0.130
Predator_Index_High	-0.765278	1.551504	-0.493	0.622
Group_Size	0.003162	0.057574	0.055	0.956
Age	1.841118	1.777652	1.036	0.300
Eigenvector_Centrality: Predator_Index_High	-1.389246	2.943804	-0.472	0.637

Eigenvector Centrality Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0

Outstrength Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-5.35912	6.40769	-0.836	0.403

Outstrength	-0.01371	0.02382	-0.576	0.565
Valley_Position_UpValley	-1.44787	1.10057	-1.316	0.188
Predator_Index_High	-0.80409	1.59012	-0.506	0.613
Group_Size	0.01424	0.06677	0.213	0.831
Age	3.63729	3.05714	1.190	0.234
Outstrength: Predator_Index_High	-0.03866	0.04842	-0.798	0.425

Outstrength Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0

Instrength Fixed Effects

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.6664324	3.9980514	-0.417	0.677
Instrength	-0.0230605	0.0294547	-0.783	0.434
Valley_Position_UpValley	-1.5676028	1.1652883	-1.345	0.179
Predator_Index_High	-0.9709871	1.4750623	-0.658	0.510
Group_Size	-0.0007646	0.0622384	-0.012	0.990
Age	1.9957710	1.7618422	1.133	0.257

Instrength: Predator_Index_High	-0.0649633	0.0880789	-0.738	0.461
------------------------------------	------------	-----------	--------	-------

Instrength Random Effects

Groups Name	Variance	Std. Dev.
Uid	0	0
Year	0	0