

Social Security: Do Individuals in Tight-Knit Social Groups Perceive Greater Security?

Abstract

Antipredator behavior is influenced by many factors including group size. Group size effects are seen when animals in larger social groups allocate less time to antipredator vigilance while foraging, but group size alone does not capture the diversity and complexity of sociality and behavior. An individual's 'sense of security', or their perception of predation risk, is also influenced by an individual's social behavior, but it is unknown whether a group's social structure – the pattern of all social interactions in a group – could explain variation in an individual's perceptions of security. Using time allocated to vigilance during foraging and flight initiation distance (FID) as two measures of an individual's sense of security, we explored whether individual yellow-bellied marmot (*Marmota flaviventer*) in tightly connected social groups looked less while foraging and had shorter FIDs compared to individual marmots in less-connected social groups. Using linear mixed effect models, we found modest support for the Social Security Hypothesis as individuals in more socially reciprocal groups spent less time looking for predators while foraging. We found no measures of group social structure explained variation in FID. We also found that measures of the immediate environment (number of individuals within 10 meters for vigilance and distance from burrow and alert distance for FID) had effect sizes an order of magnitude greater than the social network measures, suggesting an individual's immediate environment has more of an impact on their antipredator behavior than the structure of their social group.

Keywords: group social structure, social network analysis, vigilance, flight initiation distance, antipredator behavior, yellow-bellied marmot.

Introduction

By aggregating with conspecifics, prey may decrease their risk of predation through a variety of mechanisms. Previous studies have focused on describing antipredator behavior using group size effects and have found that as group size increases, per capita risk of predation decreases. This phenomenon is known as the 'dilution effect' (Cresswell 1994). With the help of more eyes, ears, and noses to detect predators, larger groups can detect potential predation risks more quickly, known as the 'many eyes hypothesis' (Lima 1995; Pulliam, 1973). While social group size is one of many attributes that may influence risk assessment (Hill & Lee 1998), group size alone does not capture the diversity and complexity of social relationships within the group (Blumstein & Armitage 1997). When individuals aggregate, they may engage in preferential relationships with one another. Thus, groups contain individuals that vary in how they are connected with others (Hinde 1976). By using social network analysis, we can determine the intensity, frequency, and directionality (initiators and recipients of an interaction) of both direct social interactions and indirect social positions (such as who your direct social partners interact with) (Wey et al., 2008). Past studies have used social network measures to understand how individual social behavior and position influences antipredator behaviors, namely, to test the Social Security Hypothesis (Blumstein, Fuong, Palmer, 2017). The Social Security Hypothesis states that the presence of strong affiliative social relationships with conspecifics increases an individual's perceived security and reduces perceived predation risk. The presence of strong social bonds in a group improves the coordination and effectiveness of cooperative antipredator defenses such as vigilance, alarm calling, and escape (Micheletta et al., 2012; Fuong, Maldonado-Chaparro, and Blumstein, 2015; Szulanski et al. 2024).

While individual sociality and social position may be influencing antipredator behaviors, the overall connectedness and structure of the social group may also influence individual antipredator behaviors. Extending the Social Security Hypothesis to group social structure, residing in more connected and socially close groups may increase an individual's perceived security, reducing perceived predation risk. While group social structure has known fitness consequences for the individuals who reside in the group (Solomon-Lane et al. 2015; Philson, Todorov, Blumstein, 2022; Philson and Blumstein 2023a, b), no prior studies have focused on how group structure is associated with how an individual perceives risk. Because group social structure is pertinent to individual fitness, and group size has a known effect on antipredator behavior, a detailed understanding of the intricacies of group social structure is necessary to better understand individual antipredator behavior and social security.

The time an animal allocates to vigilance versus eating during spurts of foraging and flight initiation distance (FID) are often used as measures of antipredator behavior and risk assessment, as seen in mammals (Beauchamp, 2021), birds (Tätte et al. 2019), and insects (Shackleton et al., 2018). Animals detect perceived threats by allocating time to antipredator vigilance while foraging (Tyrrell and Fernández-Juricic 2015). There is abundant evidence that social living impacts vigilance while foraging. For example, the presence of non-affiliative group members increases vigilance while foraging in primates (Kutsukake 2006; Watts 1998). An individual's social position within their group also impacts their vigilance; well-connected impala (*Aepyceros melampus*) have decreased vigilance compared to their marginalized conspecifics (van Deventer and Shrader 2021). FID measures the distance at which a prey flees from an approaching threat (Ydenberg and Dill 1986). Many biological and environmental factors have been associated with FID, including body size (Weston et al. 2016), starting distance (Samia et al. 2013), and the number of neighboring individuals (aggregation size) (Shuai et al. 2024). Additionally, individual social position and connectivity has recently been shown to decrease FID (Szulanski et al. 2024).

We asked how group social structure is associated with an individual's 'sense of security' as a potential explanation for variation in individual antipredator behavior in yellow-bellied marmots (*Marmota flaviventer*). Since 1962, the yellow-bellied marmots at and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado have been studied annually. Marmots are a well-suited system for studying antipredator behavior because they have variation in their antipredator behaviors (Armitage 2003) and social structure (Blumstein 2013), and we know how their social structure relates to their individual fitness. Namely, group social structure has been related to dispersal (Schneidman et al., 2024), overwinter survival (Philson and Blumstein, 2023), mass gain rate (Philson, Todorov, Blumstein, 2022), and reproductive success (Philson and Blumstein, 2023). Social network measures have been applied on an individual-level to study marmot social position and antipredator vigilance (Mady et al., 2017; Szulanski et al., 2024). However, how group social structure relates to individual social security has not been explored in this system, or others.

Social security in the marmots of RMBL has been previously studied in the context of alarm calling, vigilance while foraging, and flight initiation distance using individual-level, not group-level, measures of social networks. It has been shown that more socially connected marmots alarm call less often (Fuong et al. 2015), have shorter flight initiation distances (Szulanski et al.

2024), and allocate less time to vigilance during bouts of foraging (Blumstein et al. 2017; Mady et al. 2017). These findings suggest that social connectedness fosters a ‘sense of security’ in social groups. In this study, we examined six group-level measures of sociality in yellow-bellied marmots to determine the relationship between group social structure and two antipredator behaviors: vigilance and flight initiation distance.

Because social connectedness can create a ‘sense of security’, and past studies using individual-level social network measures have found a positive relationship between an individual’s social connectedness and vigilance while foraging (Mady et al. 2017), we extended this prediction to the group-level to predict that individuals residing in social groups that are more tightly connected will allocate less time to antipredator vigilance when foraging. Namely, we predicted that density, inverse average path length, inverse cut points, transitivity, and reciprocity will have a negative relationship with vigilance while centrality will have a positive relationship. Because past studies using individual-level social network measures have found that, generally, flight initiation distance decreases as individuals are more socially connected (Szulanski et al. 2024), we extended this prediction to predict that individuals in more tightly connected social groups will have shorter flight initiation distances (FIDs). Namely, we predicted that density, inverse average path length, inverse cut points, transitivity, and reciprocity will have a negative relationship with FID while centrality will have a positive relationship.

Materials and Methods

Study Site and System

We studied yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL) in and around Gothic, Colorado, USA (38°77’N, 106°59’W; ca. 2900 m above sea level). Since 1962, the marmots have been under continuous study (Blumstein 2013; Armitage 2014). Yellow-bellied marmots are a well-suited species because they are a facultatively social mammal, and the long-term dataset facilitates asking about the antipredator consequences of group structure (Blumstein, 2013). Yellow-bellied marmots are a facultative socially species, residing in social groups which may include one or more adults, yearlings, and pups (Armitage, 2014). Marmots are subject to aerial and terrestrial predation (Kelt & Van Vuren 2001), including red-tailed hawks (*Buteo jamaicensis*), golden eagles (*Aquila chrysaetos*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), American badgers (*Taxidea taxus*), black bears (*Ursus americanus*), and mountain lions (*Puma concolor*).

Marmots hibernate for about 7-8 months of the year from around mid-September to mid-April (Armitage 2014). During their active season, the marmots are trapped in walk-in Tomahawk traps and given a set of unique ear-tags and uniquely marked with dorsal furmark with a nontoxic Nyanzol-D dye (Albanil Dyestuff Corp., Jersey City, NJ, U.S.A) to distinguish individuals with a unique fur mark on their dorsal pelage for ease of observational identification from afar.

Quantifying Social Behavior

Trained observers recorded the social interactions between individual marmots from distances of 20 to 150 meters away using spotting scopes and binoculars. Behavioral data were collected during the active season (mid-April to mid-September) during hours of peak marmot activity (0700 – 1100 hours and 1600-1900 hours) six days a week, weather permitting. Observers recorded all marmot social observations and interactions that were classified as affiliative (e.g.,

foraging together, grooming, play) or agonistic (e.g., chasing, biting, fighting) (full ethogram in: Blumstein et al., 2009). The initiator and recipient of the interactions were also recorded.

Social Networks

Using these social observations on data yearlings and adults collected from 2003 to 2022, we created social networks based on affiliative social interactions because they make up approximately 88% of the social interactions (Philson & Blumstein 2022) and because we assumed that affiliative, not agonistic, interactions would increase an individual's sense of security (Wey & Blumstein 2012). We filtered our data to include only social observations collected in April, May, and June because vegetation was low allowing for accurate recording, the most social interactions occurred during this time, and yearlings had not yet dispersed.

To define social groups, we calculated simple-ratio pairwise association indices based on where individuals were trapped or seen together using SOCPROG (Whitehead 2009). The resulting matrices were run through a community detection algorithm called MapEquation (Csardi and Nepusz 2006; Rosvall and Bergstrom 2008; Rosvall et al. 2009) to define social groups within colonies using the “igraph” package (Csardi and Nepusz 2006) in R (version 20.2.5; R Core Development Team 2024). In total, social networks were constructed from 42,369 affiliative social interactions between 752 unique individuals (with 549 being observed in multiple years) in 255 unique social groups across 20 years (2003-2022).

For each unique social group, we calculated six group-level social network measures to quantify social structure (Table 1) “igraph”: density, average path length, cut points, transitivity, reciprocity, and centrality (Table 1). Measures of social group connectivity included density, transitivity, cut points, and centrality. Measures of group homophily included reciprocity and inverse average path length. These six measures were selected due to relevance in human (REFs) and non-human (REFs) studies and because these measures have been explored in relation to fitness previously in this system (Philson et al. 2022; Philson and Blumstein 2023a; Philson and Blumstein 2023b; Schneidman et al. 2024). These group-level traits are also roughly extensions of individual-level social network measures used in past social security studies (Fuong et al. 2015; Mady et al. 2017; Blumstein et al. 2017; Szulanski 2024), facilitating comparison between individual and group studies of social security.

Table 1: Group-level social network measures, their descriptions, references, and predictions for their relationship with flight initiation distance (FID) and time allocated to vigilance.

Group Measure	Description	Reference	FID	Vigilance
Density	The proportion of all possible social relationships in a group that are observed.	Burt 1992; Wasserman & Faust 1994; Grund 2012	—	—
Average Path Length*	How many social links individuals are from all others in the group.	Watts & Strogatz 1998; Broder et al. 2000.	—	—

Cut Points*	A measure of social connectedness that quantifies how easily a group can fracture into two or more groups.	Wasserman & Faust 1994; Borgatti 2006.	-	-
Transitivity	Quantifies group connectedness as the proportion of connected triads in the group.	Wasserman & Faust 1994; Milo et al. 2002; Faust 2010.	-	-
Reciprocity	Measures the proportion of relationships within a group where both individuals initiate at least one interaction with each other.	Wasserman & Faust 1994; Kankanhalli et al. 2005; Squartini et al. 2013.	-	-
Centralization	Centralization quantifies if interactions flow through few (high centralization) or many (low centralization) individuals in the group.	Freeman 1979; Wasserman & Faust 1994; Kang 2007.	+	+

**The inverse of average path length and cut points is presented for interpretability (so that as values increase, all measures of connectivity can be interpreted as more connected).*

Antipredator Vigilance and Boldness

Trained observers conducted 2-minute focal observations on individual marmots during bouts of foraging. The ethogram focuses on head position and activity; vigilance is defined as the head being up; foraging is defined when the head is down and an individual ingests food (full ethogram in Blumstein et al. 2009). In addition to quantifying foraging, we also collected key contextual information: the colony, number of individuals within 10 meters, incline of the slope, substrate (stones, talus, dirt, low vegetation, or high vegetation), and the distance the marmot was to the nearest burrow while foraging (Chmura et al. 2016). All focal recordings were then scored in JWatcher 1.0 (Stankowich 2008) to quantify the mean time each individual allocated to looking versus foraging during the two-minute foraging bouts recorded across the active season.

Flight Initiation Distance

To quantify flight initiation distance (FID), a trained observer walked at a constant speed of 0.5 m/s directly towards a marmot at rest until the marmot fled (Blumstein et al. 2004). We recorded the starting distance from the marmot to the observer, the alert distance from the marmot to the observer (when the marmot looked towards the observer but did not flee), and the flight initiation distance (when the marmot began to move away from the approaching observer). Additionally, we also recorded the following environmental data shown to be important in explaining variation in FID (Stankowich and Blumstein 2005; Shuai et al. 2024): initial behavior, number of marmots within 10 meters, slope of terrain and escape, substrate, and the marmot's distance from a burrow during the trial.

Statistical Methods

To explore the relationship between group social structure and the time individuals allocated to vigilance, we fit a linear mixed effects model using the package “lme4” (Bates et al. 2015). The following fixed effects were included in the model: number of individuals within 10 meters, sex (female or male), age class (yearling or adult), social group size (i.e., social network size) and the six social network measures. Year, colony, and marmot ID were included as random effects. We log transformed alert distance, distance to burrow, number of individuals within 10 meters, group size, reciprocity, cut points, and centralization to meet model assumptions and we then standardized all numeric fixed effects. This initial model had high VIF values ($VIF > 6$) for density and average path length. A correlation matrix for all numeric fixed effects found that density and inverse average path length were highly correlated ($r = 14.167$). Thus, we removed inverse average path length from our model because density was more central to the Social Security Hypothesis than average path length. The model without average path length did not have multicollinearity issues and met all other assumptions of a linear mixed effects model and is reported in Table 2. This model for vigilance had 2,625 total observations consisting of 529 unique individuals across 133 unique social groups across 20 years.

For FID, we fit another linear mixed effects model nearly identical to our model for vigilance. Our fixed effects were the following: alert distance, distance to burrow, number of individuals within 10 meters, group size, and our six social network measures. We included year, colony, and marmot ID as random effects as well. To meet our model’s assumptions, we log transformed alert distance, distance to burrow, number of individuals within 10 meters, group size, reciprocity, cut points, and centralization. We removed average path length as well because of its high correlation with density ($r = 8.685$). The model without average path length is reported in Table 3. Our model for FID had 850 total observations between 299 unique individuals across 91 unique social groups.

Results

We found no statistically significant relationship between affiliative group social network measures and FID (Table 3). We found that alert distance, distance to burrow, and trial number were positively statistically significant for FID. Our model explained 58.6% of the marginal variance in FID, and 72.36% of the conditional variance. For vigilance, we found that reciprocity had a negative statistically significance relationship (i.e., individuals in more socially reciprocal groups spent less time looking for predators), while no other measures of group social structure did (Table 2). In addition to reciprocity, we found that the number of individuals within 10 meters and group size were negatively statistically significant with vigilance. This model explained 4.66% of the marginal and 22.9% of the conditional variance in vigilance.

Table 2: Estimates, standard errors, t-values, p-values, and marginal and conditional part R^2 values for the fixed effects of the linear mixed models for vigilance.

Fixed Effects	Estimate	Standard Error	t-value	p-value	Marginal Partial R^2	Conditional Partial R^2
Intercept	0.360	0.021	16.969	<0.001	4.66% (3.39% - 7.32%)	22.89% (15.48% - 31.80%)
Group Size	-0.016	0.007	-2.362	0.0183	0.41% (0% - 3.19%)	18.65% (10.74% - 27.99%)

Number w/in 10m	-0.020	0.003	-5.890	<0.001	1.27% (0% - 4.05%)	19.51% (11.70% - 28.77%)
Density	0.021	0.011	1.836	0.067	0.25% (0% - 3.03%)	18.49% (10.55% - 27.85%)
Transitivity	-0.005	0.008	-0.589	0.556	0.02% (0% - 2.79%)	18.25% (10.30% - 27.64%)
Reciprocity	-0.016	0.007	-2.382	0.018	0.13% (0% - 2.90%)	18.36% (10.42% - 27.74%)
Cut Points*	-0.008	0.006	1.508	0.132	0.16% (0% - 3.08%)	18.54% (10.61% - 27.90%)
Centralization*	-0.006	0.005	-1.110	0.267	0.05% (0% - 4.05%)	18.40% (10.46% - 27.77%)

**Indicates log transformation was done to better meet model assumptions*

Table 3: Estimates, standard errors, t-values, p-values, and marginal and conditional part R² values for the fixed effects of the linear mixed models for FID.

Fixed Effects	Estimate	Standard Error	t-value	p-value	Marginal Partial R ²	Conditional Partial R ²
Intercept	3.126	0.109	28.690	<0.001	58.60% (52.98% - 65.61%)	72.36% (68.24% - 76.96%)
Alert Distance*	0.648	0.026	24.722	<0.001	44.38% (39.03% - 51.48%)	58.14% (53.16% - 63.76%)
Distance to Burrow*	0.155	0.022	7.022	<0.001	2.42% (0% - 9.36%)	16.18% (7.93% - 25.14%)
Number w/in 10m*	0.026	0.020	1.309	0.191	0.09% (0% - 9.36%)	13.86% (5.38% - 23.02%)
Group Size*	0.030	0.053	0.561	0.575	0.05% (0% - 9.32%)	13.82% (5.34% - 22.99%)
Density	0.011	0.086	0.124	0.899	0.01% (0% - 9.28%)	13.77% (5.29% - 22.95%)
Transitivity	0.068	0.048	1.423	0.155	0% (0% - 9.10%)	13.58% (5.08% - 22.78%)
Reciprocity*	-0.059	0.044	-1.340	0.182	0.38% (0% - 9.63%)	14.15% (5.70% - 23.29%)
Cut Points*	-0.055	0.034	1.610	0.108	0% (0% - 9.07%)	13.55% (5.0% - 22.75%)
Centralization*	0.039	0.036	1.081	0.280	0% (0% - 0.926%)	13.76% (5.13% - 22.82%)
Trial Number	-0.030	0.014	-2.240	0.025	0% (0% - 9.14%)	13.63% (5.13% - 22.82%)

**Indicates log transformation was done to better meet model assumptions*

Discussion

Overall, we found modest support for the Social Security Hypothesis at the group-level in vigilance, but no support at the group-level in our findings for FID. This is surprising because affiliative social relationships at the individual-level in this system have been shown to relate to both FID and vigilance (Mady et al. 2017; Szulanski 2024). For vigilance, there was a

statistically significant negative association with reciprocity, suggesting that individuals residing in more egalitarian groups (in which individuals initiate interactions with one another more equally) allocate less time towards vigilance behavior and perceive less risk than individuals residing in less socially reciprocal groups. In other study systems, reciprocal interactions between individuals across a group has been shown to be related to cooperative antipredator response behaviors (McGhee et al. 2013; Taborsky and Riebli, 2020). Future research in this system could determine the relationship between egalitarian social groups and antipredator responses such as alarm calling, vigilance, and escape in yellow-bellied marmots.

Additionally for vigilance, social group size and the number of individuals within 10 meters of the focal individual had a statistically significant negative association. The group size association supports the “dilution effect”, which states that individuals in larger groups allocate less time to vigilance while foraging. More individuals within 10 meters while foraging having a negative association with time spent looking for predators suggests that foraging aggregation size and the immediate surroundings of an individual may have a greater impact on antipredator risk assessment behavior than group social structure. While no measures of group social structure were statistically significant for FID, three fixed effects were. Alert distance and distance to burrow were found to have a statistically significant positive association with FID. That is, the closer the observer started walking towards an animal and the further an individual was from their burrow, the more quickly the individual fled (as seen in Blumstein et al. 2005). This suggests that the environmental context and immediate surroundings of an individual may have a larger influence on antipredator escape behavior than social group structure when approached by a threat. The negative association between FID and trial number suggests repeated trials of flushing marmots has a modest habituation effect on the animals, with FID decreasing with more trials. In this system, it has been shown that animals subject to repeated trials of FIDs and exposure to human disturbance will tolerate closer human approach (Uchida & Blumstein 2021).

Taking both models together, our results suggest that environmental and contextual factors have a stronger effect on their antipredator escape and risk assessment behavior. How many individuals are nearby, how close the threat starts to approach from, and how many past FID trials has a larger effect (as measured by the semi-partial marginal R^2 's) and stronger relationship (as measured by the estimates) with antipredator escape behavior than any measure of group social structures. For vigilance, the number of neighbors surrounding a foraging individual.

Taking models separately, FID and time allocated to vigilance, while both useful metrics of antipredator behavior, are fundamentally different in their contexts within the predatory sequence. The time an individual allocates to vigilance represents the response to the ambient environment during foraging (Lima & Bednekoff 1999; Armitage & Salsbury 2016), whereas the decision to flee reflects the response to more immediate threats, such as an approaching predator (Lima & Bednekoff 1999). Thus, perhaps an animal's group social structure is less informative and supportive when being approached by a threat than it is when foraging with no active threat present. Our finding of a measure of group social structure (reciprocity) being associated with vigilance and not FID perhaps aligns with this thinking.

It can be difficult to generalize antipredator results across taxa. Prior studies have found that many contextual factors associated with FID are species-specific. For example, aggregation size and repeated exposure to human disturbance (habituation) have been shown to have conflicting results with FID. Increased aggregation size may increase FID, supporting the many eyes hypothesis (Morelli et al. 2019), and decrease FID, supporting the dilution effect (Braumoh et al. 2018; Ardila-Villamizar et al. 2022). Habituation can occur in repeated trials of FIDs, and individuals that are flushed repeatedly have decreased FIDs over time (Uchida & Blumstein 2021). Additionally, animals in urban areas decrease their responsiveness to humans due to repeated exposure to harmless humans (Uchida et al. 2019). However, habituation is not consistent across all taxa: human disturbance from increased hunting activity has increased the FID in wild reindeer (*Rangifer tarandus*). Another contextual factor with significance to FID is the distance a prey is from their burrow, which has been shown to have a large, positive effect on FID: animals far from their refuge fled at greater distances and perceived risk increases by 43% when prey are far away from burrows (Stankowich & Blumstein 2005). This further suggests that risk perception is less influenced not by the presence of strong social bonds, but by the prey's environment (as we observe here).

In summary, we found that group social structure is not associated with antipredator escape decisions. Additionally, group social structure is only modestly associated with antipredator risk assessment behaviors, with reciprocal social groups allocating less time to antipredator vigilance. Despite our somewhat surprising results (given that past studies in the system have found significant results for both FID and vigilance with individual-level social network measures), this study provides a valuable addition to analysis of group social structure and antipredator risk assessment and escape decisions. Namely, it has increased our understanding of the role of environmental context and group social structure. Because individual-level social network statistics have been used so heavily in this system to study antipredator behavior, analysis at the group level is critical for a holistic understanding of the causes of variation in antipredator behaviors with both individual and group-level analysis.

References

- Ardila-Villamizar, Melissa, et al. "Fear in Urban Landscapes: Conspecific Flock Size Drives Escape Decisions in Tropical Birds." *Royal Society Open Science*, vol. 9, no. 11, 2022, p. 221344, <https://doi.org/10.1098/rsos.221344>.
- Armitage, K. B. "Behavioral Responses of Yellow-Bellied Marmots to Birds and Mammals." *Oecologia Montana*, vol. 12, no. 1–2, Dec. 2003, pp. 15–20, <https://om.vuvb.uniza.sk/index.php/OM/article/view/163>.
- Armitage, Kenneth B. *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*. 1st ed., Cambridge University Press, 2014, <https://doi.org/10.1017/CBO9781107284272>.

- Armitage, K. B., and C. M. Salsbury. "Pattern and Variation of the Time Budget of Yellow-Bellied Marmots." *Ethology Ecology & Evolution*, vol. 28, no. 3, July 2016, pp. 329–65, <https://doi.org/10.1080/03949370.2015.1059894>.
- Bates, Douglas, et al. "Fitting Linear Mixed-Effects Models Using Lme4." *Journal of Statistical Software*, vol. 67, Oct. 2015, pp. 1–48, <https://doi.org/10.18637/jss.v067.i01>.
- Beauchamp, Guy, et al. "A Meta-Analysis of the Group-Size Effect on Vigilance in Mammals." *Behavioral Ecology*, edited by Amanda Ridley, vol. 32, no. 5, Oct. 2021, pp. 919–25, <https://doi.org/10.1093/beheco/arab048>.
- Blumstein, Daniel T., and Kenneth B. Armitage. "Does Sociality Drive The Evolution Of Communicative Complexity? A Comparative Test With Ground-Dwelling Sciurid Alarm Calls." *The American Naturalist*, vol. 150, no. 2, 1997, pp. 179–200, <https://doi.org/10.1086/286062>.
- Blumstein, Daniel T., et al. "Inter-specific Variation in Avian Responses to Human Disturbance." *Journal of Applied Ecology*, vol. 42, no. 5, 2005, pp. 943–53, <https://doi.org/10.1111/j.1365-2664.2005.01071.x>.
- Blumstein, Daniel T., et al. "A Test of the Multipredator Hypothesis: Yellow-Bellied Marmots Respond Fearfully to the Sight of Novel and Extinct Predators." *Animal Behaviour*, vol. 78, no. 4, 2009, pp. 873–78, <https://doi.org/10.1016/j.anbehav.2009.07.010>.
- Blumstein, Daniel T. "Yellow-Bellied Marmots: Insights from an Emergent View of Sociality." *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 368, no. 1618, May 2013, p. 20120349, <https://doi.org/10.1098/rstb.2012.0349>.
- Blumstein, Daniel T., et al. "Social Security: Social Relationship Strength and Connectedness Influence How Marmots Respond to Alarm Calls." *Behavioral Ecology and Sociobiology*, vol. 71, no. 10, Sept. 2017, p. 145, <https://doi.org/10.1007/s00265-017-2374-5>.

- Braimoh, Bukola, et al. "Managing Human Disturbance: Factors Influencing Flight-Initiation Distance of Birds in a West African Nature Reserve." *Ostrich*, vol. 89, no. 1, Jan. 2018, pp. 59–69, <https://doi.org/10.2989/00306525.2017.1388300>.
- Chmura, Helen E., et al. "Assessing the Sensitivity of Foraging and Vigilance to Internal State and Environmental Variables in Yellow-Bellied Marmots (*Marmota Flaviventris*).” *Behavioral Ecology and Sociobiology*, vol. 70, no. 11, Nov. 2016, pp. 1901–10, <https://doi.org/10.1007/s00265-016-2195-y>.
- Cresswell, Will. "Flocking Is an Effective Anti-Predation Strategy in Redshanks, *Tringa Totanus*.” *Animal Behaviour*, vol. 47, no. 2, Feb. 1994, pp. 433–42, <https://doi.org/10.1006/anbe.1994.1057>.
- Csardi, G., & Nepusz, T. (2006). The Igraph Software Package for Complex Network Research. *InterJournal, Complex Systems*, 1695, 1-9.
<http://igraph.org>
- Fuong, H., et al. "Are Social Attributes Associated with Alarm Calling Propensity?" *Behavioral Ecology*, vol. 26, no. 2, Mar. 2015, pp. 587–92, <https://doi.org/10.1093/beheco/aru235>.
- Hill, R. A., and P. C. Lee. "Predation Risk as an Influence on Group Size in Cercopithecoid Primates: Implications for Social Structure.” *Journal of Zoology*, vol. 245, no. 4, 1998, pp. 447–56, <https://doi.org/10.1111/j.1469-7998.1998.tb00119.x>.
- Hinde, R. A. "Interactions, Relationships and Social Structure.” *Man*, vol. 11, no. 1, 1976, pp. 1–17, <https://doi.org/10.2307/2800384>.
- Kelt, Douglas A., and Dirk H. Van Vuren. "The Ecology and Macroecology of Mammalian Home Range Area.” *The American Naturalist*, vol. 157, no. 6, 2001, pp. 637–45, <https://doi.org/10.1086/320621>.

- Kutsukake, Nobuyuki. "The Context and Quality of Social Relationships Affect Vigilance Behaviour in Wild Chimpanzees." *Ethology*, vol. 112, no. 6, 2006, pp. 581–91, <https://doi.org/10.1111/j.1439-0310.2006.01200.x>.
- Lima, Steven L. "Back to the Basics of Anti-Predatory Vigilance: The Group-Size Effect." *Animal Behaviour*, vol. 49, no. 1, Jan. 1995, pp. 11–20, [https://doi.org/10.1016/0003-3472\(95\)80149-9](https://doi.org/10.1016/0003-3472(95)80149-9).
- Lima, Steven L., and Peter A. Bednekoff. "Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis." *The American Naturalist*, vol. 153, no. 6, June 1999, pp. 649–59, <https://doi.org/10.1086/303202>.
- Mady, Rachael P., and Daniel T. Blumstein. "Social Security: Are Socially Connected Individuals Less Vigilant?" *Animal Behaviour*, vol. 134, Dec. 2017, pp. 79–85, <https://doi.org/10.1016/j.anbehav.2017.10.010>.
- McGhee, Katie E., et al. "Reciprocal Behavioral Plasticity and Behavioral Types during Predator-Prey Interactions." *The American Naturalist*, vol. 182, no. 6, 2013, pp. 704–17, <https://doi.org/10.1086/673526>.
- Micheletta, Jérôme, et al. "Social Bonds Affect Anti-Predator Behaviour in a Tolerant Species of Macaque, *Macaca Nigra*." *Proceedings of the Royal Society B: Biological Sciences*, vol. 279, no. 1744, Oct. 2012, pp. 4042–50, <https://doi.org/10.1098/rspb.2012.1470>.
- Morelli, Federico, et al. "Contagious Fear: Escape Behavior Increases with Flock Size in European Gregarious Birds." *Ecology and Evolution*, vol. 9, no. 10, 2019, pp. 6096–104, <https://doi.org/10.1002/ece3.5193>.
- Philson, Conner S., et al. "Marmot Mass Gain Rates Relate to Their Group's Social Structure." *Behavioral Ecology*, edited by Amanda Ridley, vol. 33, no. 1, Feb. 2022, pp. 115–25, <https://doi.org/10.1093/beheco/arab114>.

- Philson, Conner S., and Daniel T. Blumstein. "Emergent Social Structure Is Typically Not Associated with Survival in a Facultatively Social Mammal." *Biology Letters*, vol. 19, no. 3, 2023, p. 20220511, <https://doi.org/10.1098/rsbl.2022.0511>.
- Philson, Conner S., and Daniel T. Blumstein. "Group Social Structure Has Limited Impact on Reproductive Success in a Wild Mammal." *Behavioral Ecology*, edited by Amanda Ridley, vol. 34, no. 1, Feb. 2023, pp. 89–98, <https://doi.org/10.1093/beheco/arac102>.
- Pulliam, H. Ronald. "On the Advantages of Flocking." *Journal of Theoretical Biology*, vol. 38, no. 2, 1973, pp. 419–22, [https://doi.org/10.1016/0022-5193\(73\)90184-7](https://doi.org/10.1016/0022-5193(73)90184-7).
- Rosvall, M., et al. "The Map Equation." *The European Physical Journal Special Topics*, vol. 178, no. 1, 2009, pp. 13–23, <https://doi.org/10.1140/epjst/e2010-01179-1>.
- Rosvall, Martin, and Carl T. Bergstrom. "Maps of Random Walks on Complex Networks Reveal Community Structure." *Proceedings of the National Academy of Sciences*, vol. 105, no. 4, Jan. 2008, pp. 1118–23, <https://doi.org/10.1073/pnas.0706851105>.
- Samia, Diogo S. M., et al. "Do Animals Generally Flush Early and Avoid the Rush? A Meta-Analysis." *Biology Letters*, vol. 9, no. 2, Apr. 2013, p. 20130016, <https://doi.org/10.1098/rsbl.2013.0016>.
- Schneidman, Sara A., et al. "Extending the Social Cohesion Hypothesis: Is Group Social Structure Associated with Dispersal in Yellow-Bellied Marmots (*Marmota Flaviventer*)?" *Current Zoology*, edited by Zhi-Yun Jia, Jan. 2024, p. z0ae002, <https://doi.org/10.1093/cz/z0ae002>.
- Shackleton, Kyle, et al. "Organization Enhances Collective Vigilance in the Hovering Guards of *Tetragonisca Angustula* Bees." *Behavioral Ecology*, vol. 29, no. 5, Sept. 2018, pp. 1105–12, <https://doi.org/10.1093/beheco/ary086>.

Shuai, Ling-Ying, et al. "A Meta-Analysis of the Relationship between Flock Size and Flight Initiation Distance in Birds." *Animal Behaviour*, vol. 210, Apr. 2024, pp. 1–9, <https://doi.org/10.1016/j.anbehav.2024.01.013>.

Solomon-Lane, Tessa K., et al. "Agonistic Reciprocity Is Associated with Reduced Male Reproductive Success within Haremic Social Networks." *Proceedings of the Royal Society B: Biological Sciences*, vol. 282, no. 1811, July 2015, p. 20150914, <https://doi.org/10.1098/rspb.2015.0914>.

Stankowich, Theodore, and Daniel T. Blumstein. "Fear in Animals: A Meta-Analysis and Review of Risk Assessment." *Proceedings of the Royal Society B: Biological Sciences*, vol. 272, no. 1581, Dec. 2005, pp. 2627–34, <https://doi.org/10.1098/rspb.2005.3251>.

Stankowich, T. "Quantifying Behavior the JWatcher Way. Daniel T. Blumstein and Janice C. Daniel." *Integrative and Comparative Biology*, vol. 48, no. 3, June 2008, pp. 437–39, <https://doi.org/10.1093/icb/icn005>.

Szulanski, T., Philson, C., Uchida, K., & Blumstein, D. (2023b, December 23). Social Security: Does social position influence flight initiation distance? *Behavioral Ecology* Volume 35, Issue 1, January/February 2024, arad104, <https://doi.org/10.1093/beheco/arad104>

Taborsky, Michael, and Thomas Riebli. "Coaction vs. Reciprocal Cooperation Among Unrelated Individuals in Social Cichlids." *Frontiers in Ecology and Evolution*, vol. 7, Jan. 2020, <https://doi.org/10.3389/fevo.2019.00515>.

Tätte, Kunter, et al. "Antipredator Function of Vigilance Re-Examined: Vigilant Birds Delay Escape." *Animal Behaviour*, vol. 156, Oct. 2019, pp. 97–110, <https://doi.org/10.1016/j.anbehav.2019.08.010>.

Tyrrell, Luke P., and Esteban Fernández-Juricic. "Sensory Systems and Escape Behavior." *Escaping From Predators*, edited by William E. Cooper, Jr and Daniel T. Blumstein, 1st ed.,

Cambridge University Press, 2015, pp. 322–42,
<https://doi.org/10.1017/CBO9781107447189.013>.

Uchida, Kenta, and Daniel T. Blumstein. “Habituation or Sensitization? Long-Term Responses of Yellow-Bellied Marmots to Human Disturbance.” *Behavioral Ecology*, edited by Ulrika Candolin, vol. 32, no. 4, Aug. 2021, pp. 668–78, <https://doi.org/10.1093/beheco/arab016>.

Uchida, Kenta, and Daniel T. Blumstein. “Habituation or Sensitization? Long-Term Responses of Yellow-Bellied Marmots to Human Disturbance.” *Behavioral Ecology*, edited by Ulrika Candolin, vol. 32, no. 4, Aug. 2021, pp. 668–78, <https://doi.org/10.1093/beheco/arab016>.

van Deventer, Anita, and Adrian M. Shrader. “Predation Risk and Herd Position Influence the Proportional Use of Antipredator and Social Vigilance by Impala.” *Animal Behaviour*, vol. 172, Feb. 2021, pp. 9–16, <https://doi.org/10.1016/j.anbehav.2020.11.019>.

Watts, David P. “A Preliminary Study of Selective Visual Attention in Female Mountain Gorillas (Gorilla Gorilla Beringei).” *Primates*, vol. 39, no. 1, Jan. 1998, pp. 71–78,
<https://doi.org/10.1007/BF02557744>.

Whitehead, Hal. “SOCPROG Programs: Analysing Animal Social Structures.” *Behavioral Ecology and Sociobiology*, vol. 63, no. 5, 2009, pp. 765–78, <https://doi.org/10.1007/s00265-008-0697-y>.

Weston, M. A., et al. “A Review of Flight-Initiation Distances and Their Application to Managing Disturbance to Australian Birds.” *Emu - Austral Ornithology*, vol. 112, no. 4, 2012, pp. 269–86,
<https://doi.org/10.1071/MU12026>.

Wey, Tina, et al. “Social Network Analysis of Animal Behaviour: A Promising Tool for the Study of Sociality.” *Animal Behaviour*, vol. 75, no. 2, Feb. 2008, pp. 333–44,
<https://doi.org/10.1016/j.anbehav.2007.06.020>.

Wey, Tina W., and Daniel T. Blumstein. “Social Attributes and Associated Performance Measures in Marmots: Bigger Male Bullies and Weakly Affiliating Females Have Higher Annual

Reproductive Success.” *Behavioral Ecology and Sociobiology*, vol. 66, no. 7, July 2012, pp. 1075–85, <https://doi.org/10.1007/s00265-012-1358-8>.

Ydenberg, R. C., and L. M. Dill. “The Economics of Fleeing from Predators.” *Advances in the Study of Behavior*, vol. 16, Elsevier, 1986, pp. 229–49, [https://doi.org/10.1016/S0065-3454\(08\)60192-8](https://doi.org/10.1016/S0065-3454(08)60192-8).