Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2024), 35(1), 1–9. https://doi.org/10.1093/beheco/arad104

Original Article

Social security: Does social position influence flight initiation distance?

Tali Szulanski,[a,b] Conner S. Philson,[a,c] Kenta Uchida,[d] and Daniel T. Blumstein[a,c]
[a]Rocky Mountain Biological Laboratory, Box 519, Crested Butte, CO 81224, USA, [b]Department of Biological Science, Mount Holyoke College, 50 College Street, MHC 3358, South Hadley, MA 01075, USA, [c]Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA, and [d]Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1 Chome-1-1 Yayoi, Bunkyo City, Tokyo 113-0032, Japan

Received 10 August 2023; revised 9 November 2023; editorial decision 18 November 2023; accepted 27 November 2023

Specific social relationships that individuals have with others may modulate perceptions of risk and explain variation in antipredator behavior. We asked whether and how yellow-bellied marmots' (*Marmota flaviventer*) connectivity and position in their social network explained variation in flight initiation distance (FID). We examined the relationship of both direct and indirect measures of sociality and separated models by age and sex classes to isolate the relationships for different life-history stages. Following the "social security" hypothesis, we predicted that more socially connected individuals would have a lower FID because they are less fearful. When examining all age–sex cohorts, there was a weak effect of social interaction frequency on FID: individuals in stronger relationships tolerated closer human approaches. When examining each cohort independently, we found adult male's FID was not associated with any social network measure, but female adults fled at greater distances as their number of social partners increased. Male yearlings more closely connected to their social group fled at shorter distances (only when perceived risk was high), but female yearlings experienced the opposite effect in which closer connection to others in their group led to greater FID at higher perceived risks. These results are partly consistent with the social security hypothesis in that they show that social relationships are associated with escape only at certain levels of perceived risk and for certain age and sex cohorts. Together, the results illustrate the importance of social attributes on antipredator behaviors and show how it depends on the life stage and the sex.

Key words: **antipredator behavior, flight initiation distance, *Marmota flaviventer*, social networks.**

INTRODUCTION

Group living has many benefits, such as increased access to mates and resources (Alexander 1974; Hinde 1976; Beauchamp 2014). Living socially can also reduce predation risk (Beauchamp 2014). For instance, individuals in many species decrease antipredator vigilance as group size increases, a phenomenon known as the "group-size effect" (Lima 1995). Two common models of predation risk assessment may explain the group size effect. The detection effect predicts that within a larger group, a given individual will devote less time to vigilance behavior because they can rely on other group members to detect predators (Pulliam 1973). The dilution effect predicts larger groups decrease the probability of a given individual being predated upon (Hamilton 1971; Vine 1971). Therefore, foraging species may benefit from foraging in larger aggregations or by living in larger groups to decrease their own individual antipredator assessment and response burden. However, the group size an individual lives in is one of several ways that sociality can influence risk assessment; social relationships with conspecifics within the group might also be a key factor driving antipredator behavior.

Formal social network analysis (Wasserman and Faust 1994; Wey et al. 2008) provides insights into individual social variation that cannot be explained by group size via attributes of direct and indirect social relationships (Wey et al. 2008; Brent 2015). For instance, Trinidadian guppies (*Poecilia reticulata*), under higher risk of predation, form stronger affiliative relationships with others (Heathcote et al. 2017). Therefore, an individual's sense of security may be explained not only by the size of the group they are in but also by the quantity, frequency, and overall structure of their relationships within their social network. How social network position is associated with an individual's risk assessment is not fully understood.

Flight initiation distance (FID) is the distance from an approaching object at which a prey animal decides to flee and is a

---

Address correspondence to D.T. Blumstein. E-mail: marmots@ucla.edu.

Table 1

Definition of individual-level social network measures used to quantify individual social position and connectivity

Measure	Description	References	Interpretation
Degree	Number of social partners an individual has	Wasserman and Faust 1994; Wey et al. 2008	How many individuals one interacts with
Strength	Frequency of interactions between social partners	Wasserman and Faust 1994; Wey et al. 2008	How often an individual is social
Closeness Centrality	Reciprocal of the shortest paths between the focal individual and every other individual within the group	Wasserman and Faust 1994; Wey et al. 2008; Brent 2015	Social distance of an individual to others in the group
Eigenvector Centrality	Represents how social an individual's direct social partners are	Bonacich 1987; Brent 2015	The degree to which one's status is connected to the status of their associates
Embeddedness	How well connected an individual is within their social group as a product of the connectivity of their cluster and surrounding social partners.	Moody and White 2003	How well connected an individual is

commonly used metric of predation risk assessment (Ydenberg and Dill 1986; Cooper and Blumstein 2015). Many factors explain interspecific differences in FID (e.g., body size in birds [Møller 2015], fishes [Samia et al. 2019], and lizards [Samia et al. 2016]). The number of nearby conspecifics (i.e., aggregation group size) is positively associated with increased FID in waterbirds (Møller 2015) but is not associated with FID when looking across many fish species (Samia et al. 2016). Indeed, a meta-analysis across taxa has shown an overall lack of significant effect of group size on FID, but that external factors like habitat type and internal factors like body condition explain variation in FID (Stankowich and Blumstein 2005). Yet, FID is an individual decision that animals make about fleeing. Therefore, an individual's social position and connectivity, which may be more appropriate measures of sociality than simply the number of nearby conspecifics, may influence an individual's decision to flee.

We asked whether and how social relationships and group size explained variation in FID in yellow-bellied marmots (*Marmota flaviventer*). Yellow-bellied marmots are a facultatively social mammal and have been the subject of many studies of antipredator and social behavior since 1962 (Blumstein 2013; Armitage 2014). Marmots, therefore, are a good system in which to study the relationship between social position and antipredator behavior because prior work has shown that social position influences a number of antipredator traits in relation to the social security hypothesis (i.e., stronger social relationships with conspecifics increases perceived security and thus reduces perceived predation risk; Mady and Blumstein 2017). For instance, socially isolated individuals are more likely to produce alarm calls (Fuong et al. 2015), and these calls are noisier and have higher entropy, indicating a higher state of arousal possibly because they cannot rely on conspecifics for their safety (Fuong and Blumstein 2019). Furthermore, different sex and age cohorts of marmots may assess risk differently (Blumstein and Pelletier 2005; Lea and Blumstein 2011; Mady and Blumstein 2017), and thus, social position may buffer the response to risk differently across these cohorts. For example, females in larger social groups spent less time allocated to vigilance while foraging (Mady and Blumstein 2017). Based on these findings and the social security hypothesis, we predicted that more socially connected individuals will have lower FIDs. In this study, we focused on five social network measures (Table 1) to measure how marmots' social connectivity and position within their social group influence individual risk assessment.

METHODS

Study subjects and site

Yellow-bellied marmots have been continually studied in and around the Rocky Mountain Biological Laboratory (38°77′N, 106°59′W; ca 2872 m above sea level), Gothic, Colorado since 1962 (Armitage 2014). Yellow-bellied marmots are facultatively social mammals that form harem-polygynous matrilineal societies with at least one adult female and one dominant adult male (Armitage 2014). Marmots are active for 5 months during the summer, and during this period, 98% of mortality can be attributed to predation (Van Vuren 2001). Marmots are susceptible to a variety of aerial and terrestrial predators. Terrestrial mammalian predators include coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), American badgers (*Taxidea taxus)*, black bears (*Ursus americanus*), American martens (*Martes americana*), long-tailed weasels (*Mustela frenata*), and mountain lions (*Puma concolor*) (Van Vuren 2001). Avian predators include golden eagles (*Aguila chrysaetos*), red-tailed hawks (*Buteo jamaicensis*), Swainson's hawks (*B. swainsoni*), and goshawks (*Accipiter gentilis*) (Van Vuren 2001). Yellow-bellied marmots obligately hibernate for about 7 months from late September to mid-April (Armitage 2014).

Each year, virtually all of the marmots in our study site are trapped in walk-in live traps, fitted with unique ear tags for individual identification, and given a dorsal fur mark (with black Nyzanol dye) to aid in identification while conducting observations (Armitage 1982). These marks allow observers to record interactions between specific individuals so that individual social network measures can be calculated.

Behavioral observations

On most days, when it was not raining or snowing from mid-April to July, trained observers recorded social interactions between all age class marmots using spotting scopes and binoculars from distances of 20–100 m (distances varied by group and were selected to limit observer effects; Blumstein et al. 2009) during hours of peak marmot activity (0700–1100 hours and 1600–1800 hours). Using all-occurrence sampling, we categorized social interactions as affiliative or agonistic and recorded the initiator, recipient, and "winner" (the individual who remained and was not displaced). Some 79% of interactions were between identified individuals, and 88% of these interactions were affiliative (Philson and Blumstein 2023). A full ethogram of behaviors can be found in Blumstein et al. (2009).

To measure the FID, one trained observer identified a subject, waited until the individual was at rest (i.e., it was not rearing up or looking directly at the observer), and then walked directly toward the marmot, maintaining a consistent speed of 0.5m/s (Blumstein et al. 2004). At sites where the observer was not able to approach safely while watching the animal (due to terrain) or maintain adequate visual contact with the animal (due to high vegetation), an additional "spotter" located ≥50 m away assisted in identifying when the animal alerted and fled and communicated with the approaching observer via radio. We recorded the starting distance, alert distance (AD; the distance when the marmot starts looking at the approaching observer), flight initiation distance, and the distance between the subject's original position and the burrow they fled to (which has explained significant variation in FID; e.g., Uchida and Blumstein 2021). Since FIDs were measured multiple times from the same individual within a year, we calculated the trial number within a year to control for potential habituation. We did not conduct field observations when it was raining, excessively windy, or snowing to minimize the effects of weather conditions on marmot behavior (and because marmots were not that active during inclement weather).

Social networks

Social networks were built annually from 2003 to 2020 for yearlings and adults for affiliative social interactions (e.g., play, allogrooming, greeting, sitting) with known initiators and recipients. Pups were excluded from networks because they primarily interacted with their mother and other pups and because they emerged halfway through the active season. To exclude transient individuals, only individuals that had been seen and/or trapped more than five times on different days within the year were included in our networks. Only interactions in April, May, and June were used as this ~2.5-month timeframe is from when marmots emerge from hibernation/mate to when pups emerge from natal burrows. This is also when most social interactions occur and when we have the highest quality observational data (the growth of vegetation begins to impair observations as the summer progresses).

Because marmots often share space with a subset of all possible individuals within their colony area, social groups were determined based on space-use overlap, defined as individuals seen, trapped, or observed around/using the same burrow within the same day. Using SOCPROG (Whitehead 2009), we calculated simple-ratio pairwise association indices (Cairns and Schwager 1987), which were run through the random walk algorithm Map Equation (Csardi and Nepusz 2006; Rosvall and Bergstrom 2008; Rosvall et al. 2009) to identify social group membership.

From these groups, social networks were built, and eight social attributes (in/out degree, in/out strength, eigenvector centrality, embeddedness, and in/out closeness centrality; Table 1) were calculated using R (version 4.2.0; R Development Core Team 2023) and the package "igraph" (version 1.4.2; Csardi and Nepusz 2006). The directed measures (in and out) represent whether that measure was the receiver (i.e., in) or the initiator (i.e., out).

Statistical analyses

Our final data set consisted of 17 years and 947 observations of FID and social network data collected on 308 individuals from 112 social groups. Using "lme4" (version 1.1-33; Bates et al. 2015), we first attempted to fit generalized linear mixed-effects models with a Poisson and then negative binomial distribution, but these models did not converge and had overdispersion issues, respectively, that prevented their use. Thus, FID was log-transformed, and we fitted a linear mixed-effect model with a Gaussian distribution. All continuous variables were log-transformed in order to normalize the residuals and meet the assumptions of this model. All continuous variables were then mean-centered to facilitate model fit and comparisons among variables.

We first fitted a model with the fixed effects of in/out degree, in/out strength, eigenvector centrality, embeddedness, and in/out closeness centrality, alert distance, distance to burrow, number of individuals within 10 m of the focal individual, group size, age class (yearling or adult), sex, and trial number. Individual ID and year were included as random effects. However, as the variance inflation factor (VIF; calculated using the package "car"; version 3.1-2; Fox and Monette 1992; Fox and Weisberg 2019) for several of the social network measures were >7, we elected to fit only the undirected measures (degree, strength, eigenvector centrality, embeddedness, and closeness in addition to the other fixed effects). This model had a VIF of 8.57 for degree and a correlation matrix revealed a degree was highly correlated with embeddedness (0.919). Because the degree is a direct network measure and embeddedness includes indirect relationships, we opted to exclude embeddedness from calculations. Thus, the final set of social network measures used were degree, strength, closeness, and eigenvector centrality (alert distance, distance to burrow, number of individuals within ten meters of the focal individual, group size, age class, sex, and trial number were maintained as fixed effects).

Because there is a strong positive correlation between alert distance and FID (Blumstein 2010; Cooper and Blumstein 2014), and because "best practice" suggests that AD should be included as a variable in FID models (Blumstein et al. 2015), we also fitted five interaction effects of alert distance and each social measure (group size, degree, strength, closeness, and eigenvector centrality) on FID. Formally, support for the social security hypothesis could come from significant main effects or significant interactions. Significant interactions would show that putative benefits of sociality were dependent on perceived risk as estimated by alert distance (i.e., individuals with longer alert distances assessed a greater risk of predation than those with shorter alert distances). And this too could be consistent with the social security hypothesis (Mady and Blumstein 2017). Because we expected that there is a strong positive relationship between alert distance and FID (Cooper and Blumstein 2014), we would infer that animals felt more secure with stronger relationships if, at large alert distances (i.e., greater perceived risks), they tolerated a closer approach. This would be seen if there was a negative interaction estimate.

From this model that met all assumptions and included all individuals, we also fitted four additional models subdivided by age–sex cohort (yearling males, yearling females, adult males, adult females) because each cohort has distinct life histories that warrant individual exploration (Lea and Blumstein 2011). These models each met all assumptions and included the following sample sizes: yearling males = 206 observations of 108 unique individuals across 16 years; yearling females = 258 observations of 121 unique individuals across 16 years; adult males = 75 observations of 29 unique individuals across 12 years; and adult females = 408 observations of 101 unique individuals across 17 years. Using the partR2 package (version 0.9.1; Stoffel et al. 2020), we report marginal and conditional partial and semi-partial R^2 values for our model. We then estimated 95% confidence intervals using 100 parametric bootstrap iterations. While the social security hypothesis makes no

Table 2

Model estimates, standard error, *P*-value, marginal and conditional semi-partial R^2 for (A) all age and sex cohorts; (B) male yearlings; (C) female yearlings; (D) male adults; (E) female adults

A) All age and sex cohorts	Estimate	Standard error	*P*-value	**Marginal partial R^2 (%)**	**Conditional partial R^2 (%)**
Model	3.147	0.059	**<0.001**	62.56 (58.92–66.10)	71.57 (68.95–74.39)
Alert distance	0.671	0.024	**<0.001**	50.45 (46.77–54.44)	59.46 (56.27–62.67)
Distance to burrow	0.144	0.022	**<0.001**	2.66 (0–10.63)	11.67 (5.41–18.66)
No. within 10 m	0.013	0.019	0.491	0.06 (0–8.21)	9.07 (2.63–16.26)
Social group size	0.034	0.058	0.561	0.010 (0–8.25)	9.11 (2.68–16.31)
Degree	0.076	0.049	0.121	0.55 (0–8.68)	9.57 (3.16–16.72)
Strength	−0.104	0.053	**0.05**	0.87 (0–8.97)	9.88 (3.5–17.02)
Closeness	0.048	0.044	0.281	0 (0–8.14)	9 (2.55–16.2)
Eigenvector centrality	0.012	0.042	0.775	0 (0–8.01)	8.86 (2.4–16.07)
Age class [Yearling]	0.073	0.052	0.159	0.64 (0–8.75)	9.65 (3.25–16.8)
Sex [Male]	−0.048	0.054	0.381	0.05 (0–8.21)	9.06 (2.62–16.26)
Trial number	−0.026	0.013	**0.043**	0 (0–8.09)	8.93 (2.49–16.14)
Alert distance × social group size	0.044	0.056	0.434	0.16% (0–8.31)	9.17 (2.74–16.36)
Alert distance × degree	0.006	0.045	0.888	0% (0–8.31)	8.98 (2.54–16.18)
Alert distance × strength	−0.036	0.045	0.426	0.06% (0–8.21)	9.07 (2.63–16.26)
Alert distance × closeness	0.03	0.045	0.499	0.21 (0–8.35)	9.22 (2.79–16.4)
Alert distance × eigenvector centrality	−0.006	0.035	0.852	0 (0–8.13)	8.98 (2.53–16.18)

B) Male yearlings	Estimate	Standard error	*P* value	**Marginal partial R^2 (%)**	**Conditional partial R^2 (%)**
Model	3.087	0.093	**<0.001**	72.86 (68.02–77.6)	73.7 (69.83–79.59)
Alert distance	0.714	0.068	**<0.001**	25.15 (16.09–34.72)	25.99 (19.21–40.4)
Distance to burrow	0.129	0.045	**0.004**	0.96 (0–13.32)	1.8 (0–20.33)
No. within 10 m	0.131	0.042	**0.002**	1.28 (0–13.6)	2.12 (0–20.58)
Social group size	0.275	0.127	**0.035**	0.73 (0–13.12)	1.57 (0–20.13)
Degree	−0.161	0.111	0.151	0.14 (0–12.6)	0.98 (0–19.65)
Strength	0.257	0.163	0.116	0.11 (0–12.58)	0.95 (0–19.63)
Closeness	0.11	0.095	0.247	0.24 (0–12.69)	1.08 (0–19.73)
Eigenvector centrality	−0.222	0.125	0.078	0.72 (0–13.11)	1.56 (0–20.13)
Trial number	−0.045	0.032	0.156	0.14 (0–12.6)	0.98 (0–19.65)
Alert distance × social group size	−0.421	0.141	**0.003**	1.68 (0–13.96)	2.52 (0–20.91)
Alert distance × degree	0.28	0.113	**0.015**	1.61 (0–13.89)	2.45 (0–20.85)
Alert distance × strength	0.013	0.151	0.932	0 (0–12.47)	0.83 (0–19.53)
Alert distance × closeness	−0.315	0.105	**0.003**	1.88 (0–14.13)	2.72 (0–21.08)
Alert distance × eigenvector centrality	−0.114	0.113	0.314	0.08 (0–12.55)	0.92 (0–19.61)

C) Female yearlings	Estimate	Standard error	*P* value	**Marginal partial R^2 (%)**	**Conditional partial R^2 (%)**
Model	3.309	0.084	**<0.001**	65.43 (57.26–71.86)	74.46 (69.96–81.9)
Alert distance	0.635	0.054	**<0.001**	33.74 (23.29–43.25)	42.76 (36.23–53.88)
Distance to burrow	0.118	0.04	**0.004**	1.57 (0–15.68)	10.6 (0.61–26.4)
No. within 10 m	0.008	0.038	0.83	0.04 (0–14.41)	9.07 (0–25.11)
Social group size	0.03	0.145	0.837	0 (0–14.23)	8.86 (0–24.94)
Degree	0.035	0.119	0.772	0.11 (0–14.46)	9.14 (0–25.17)
Strength	−0.291	0.151	0.056	1.94 (0–15.98)	10.96 (1.02–26.71)
Closeness	0.053	0.112	0.64	0 (0–14.23)	8.86 (0–24.94)
Eigenvector centrality	0.212	0.119	0.078	0.15 (0–14.5)	9.18 (0–25.21)
Trial number	−0.029	0.025	0.252	0 (0–13.8)	8.34 (0–24.5)
Alert distance × social group size	0.258	0.113	**0.024**	2.23 (0–16.22)	11.26 (1.35–26.96)
Alert distance × degree	−0.148	0.098	0.134	1.3 (0–15.45)	10.32 (0.3–26.17)
Alert distance × strength	0.146	0.119	0.221	0.89 (0–15.11)	9.91 (0.01–25.83)
Alert distance × closeness	0.252	0.089	**0.005**	3.41 (0–17.2)	12.43 (2.68–27.95)
Alert distance × eigenvector centrality	−0.035	0.104	0.736	0.01 (0–14.38)	9.03 (0–25.09)

D) Male adults	Estimate	Standard error	*P* value	**Marginal partial R^2 (%)**	**Conditional partial R^2 (%)**
Model	3.073	0.146	**<0.001**	51.47 (36.98–68.75)	69.14 (63.78–88.65)
Alert distance	0.403	0.097	**<0.001**	20.68 (7.39–43.54)	38.35 (35.18–70.22)
Distance to burrow	0.114	0.07	0.113	2.87 (0–30.51)	20.55 (15.76–60.02)
No. within 10 m	−0.025	0.066	0.705	0.52 (0–28.92)	18.19 (12.9–58.68)
Social group size	−0.216	0.243	0.381	0.07 (0–29.04)	18.38 (13.12–58.78)
Degree	0.097	0.104	0.619	0 (0–28.24)	17.2 (11.69–58.11)
Strength	−0.398	0.266	0.146	0.66 (0–29.01)	18.33 (13.07–58.76)
Closeness	−0.208	0.174	0.239	3.94 (0–31.23)	21.61 (17.01–60.64)

Table 2. Continued

D) Male adults	Estimate	Standard error	P value	**Marginal partial R^2 (%)**	**Conditional partial R^2 (%)**
Eigenvector centrality	0.142	0.169	0.412	0 (0–26.82)	15.1 (9.14–56.9)
Trial number	−0.012	0.045	0.791	0.22 (0–28.71)	17.89 (12.54–58.51)
Alert distance × social group size	−0.502	0.27	0.068	0 (0–24.84)	12.15 (5.56–55.21)
Alert distance × degree	0.187	0.192	0.334	0 (0–26.2)	14.17 (8.02–56.37)
Alert distance × strength	−0.407	0.292	0.169	0 (0–27.47)	16.06 (10.31–57.45)
Alert distance × closeness	−0.277	0.169	0.107	0 (0–25.16)	12.63 (6.14–55.49)
Alert distance × eigenvector centrality	0.279	0.22	0.211	3.71 (0–31.08)	21.39 (16.76–60.51)

E) Female adults	Estimate	Standard error	P value	**Marginal partial R^2 (%)**	**Conditional partial R^2 (%)**
Model	3.107	0.063	**<0.001**	65.15 (59.71–70.25)	72.67 (69.15–77.07)
Alert distance	0.703	0.04	**<0.001**	38.39 (31.87–45.1)	45.91 (41.17–53.3)
Distance to burrow	0.14	0.032	**<0.001**	0.19 (0–9.67)	7.71 (0–19.72)
No. within 10 m	−0.056	0.028	**0.05**	0.36 (0–9.83)	7.89 (0–0.08–19.87)
Social group size	0.054	0.075	0.476	0.27 (0–9.74)	7.79 (0.03–19.79)
Degree	0.172	0.068	**0.012**	1.64 (0–11)	9.17 (1.08–20.99)
Strength	−0.128	0.07	0.068	1.18 (0–10.58)	8.7 (0.57–20.59)
Closeness	0.066	0.061	0.275	0 (0–9.46)	7.48 (0–19.52)
Eigenvector centrality	−0.016	0.059	0.781	0.03 (0–9.53)	7.55 (0–19.58)
Trial number	0.006	0.018	0.732	0.04 (0–9.54)	7.57 (0–19.59
Alert distance × social group size	−0.089	0.079	0.259	0.56 (0–0–10.01)	8.09 (0.18–20.05)
Alert distance × degree	0.114	0.065	0.082	0.4 (0–9.87)	7.93 (0.1–19.91)
Alert distance × strength	−0.133	0.068	0.051	0.95 (0–10.37)	8.48 (0.38–20.39)
Alert distance × closeness	−0.062	0.068	0.363	0.07 (0–9.56)	7.59 (0–19.62)
Alert distance × eigenvector centrality	0.002	0.053	0.973	0 (0–9.5)	7.53 (0–19.56)

Significant P-values are in bold.

direct predictions about how social relationships explain variation in AD (as a dependent variable), we include these analyses in the Supplementary Material.

RESULTS

When examining the entire data set (Table 2A), our model explained 62.56% of the marginal variance in FID and 71.57% of the conditional variance. After controlling for statistically significant variation in FID explained by alert distance ($B = 0.671$, SD = 0.024, $P < 0.001$), distance to burrow ($B = 0.144$, SD = 0.022, $P < 0.001$), and trial number ($B = -0.026$, SD = 0.013, $P = 0.043$), there was a modestly significant relationship with strength ($B = -0.104$, SD = 0.053, $P = 0.050$; Figure 1A): individual marmots that had more frequent social interactions with their social partners tolerated closer human approaches. There were no significant interactions (Table 2A).

When examining male yearlings alone (Table 2B), our model explained 72.86% of the marginal variance in FID and 73.7% of the conditional variance. We found that as the number of individuals within 10 m ($B = 0.131$, SD = 0.042, $P = 0.002$) and social group size ($B = 0.275$, SD = 0.127, $P = 0.035$; Figure 1B) increased, male yearlong FID also increased. There were no other significant direct relationships with any of the other measured social attributes. There were significant interactions with social attributes and alert distance. As alert distance increased and group size increased, FID decreased ($B = -0.421$, SD = 0.141, $P = 0.004$), and as alert distance and degree increased, so did FID ($B = 0.279$, SD = 0.113, $P = 0.015$). In contrast, as alert distance and closeness increased, FID decreased ($B = -0.315$, SD = 0.105, $P = 0.003$).

When examining female yearlings alone, the model explained 65.43% of the marginal and 74.56% of the conditional variance. We found no direct relationships of any social measures on FID but did find key significant interactions (Table 2C). As alert distance and group size increased, FID increased ($B = 0.258$, SD = 0.113, $P = 0.024$). In contrast to male yearlings, as female yearlings' alert distance and closeness increased, FID also increased ($B = 0.252$, SD = 0.089, $P = 0.005$).

While there were no significant associations with any measured social attributes and adult male FID (Table 2D; $R^2_m = 51.47\%$, $R^2_c = 69.14\%$), we found that female adult FID was directly associated with degree: individuals with more social partners fled at greater distances ($B = 0.172$, SD = 0.068, $P = 0.012$; Figure 1C). The adult female model explained 65.15% of the marginal and 72.67% of the conditional variance. There were no significant interactions for either adult males or females.

DISCUSSION

Overall, there was modest support for the hypothesis that an individual's network position was associated with risk assessment when analyzing all cohorts together. There was a modestly significant negative association between strength and FID (Figure 1A; Table 2A), suggesting that marmots with increased frequency of affiliative relationships may have felt less threatened by human approach and thereby may rely on conspecifics for an increased sense of security. As expected from prior work in this system (Runyan and Blumstein 2004; Blumstein et al. 2015), alert distance and distance to burrow were positively associated with FID, and there was a negative association between trial number and FID, suggesting that marmots habituated to repeated experimental approaches (Uchida and Blumstein 2021). However, when we separated our analyses by sex and age classes because prior work has shown that these different cohorts assess risk differently (Blumstein and Pelletier 2005; Lea and Blumstein 2011; Mady and Blumstein 2017), we found that social position affected marmots in a variety of different ways.

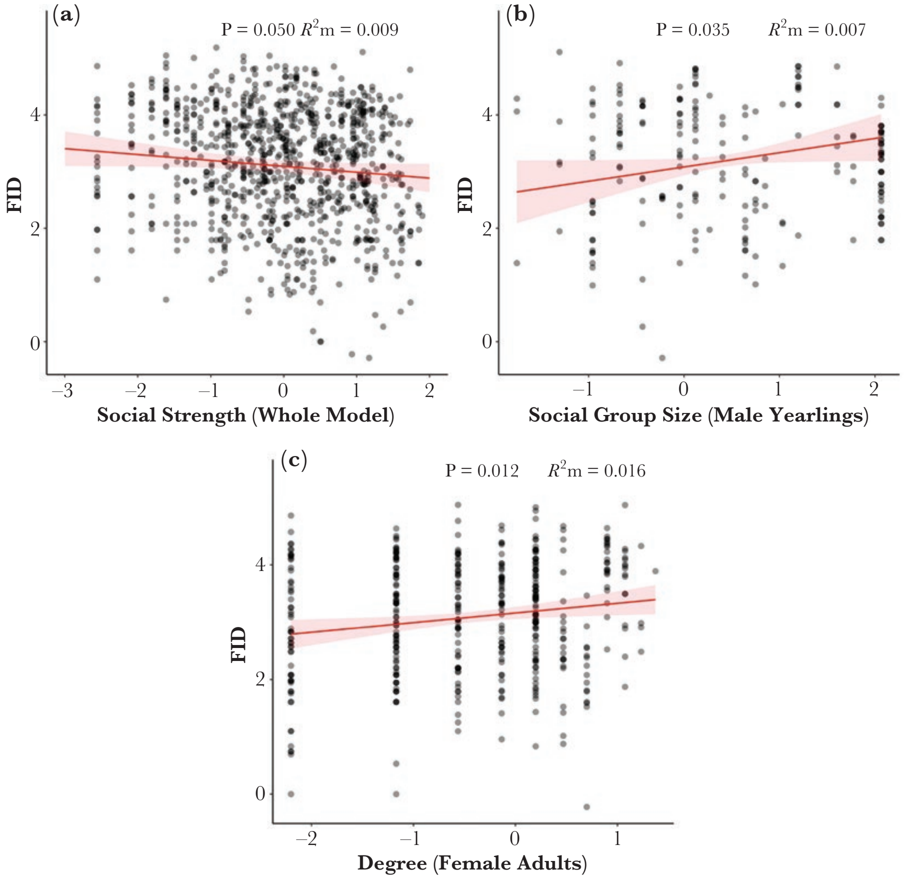

Figure 1
Main effects for social network measures (plotted as marginal effects with 95% CI) explaining statistically significant variation in log transformed flight initiation distance observed for (A) strength in all age and sex cohorts, (B) group size in male yearlings, and (C) degree in female adults. Degree, strength, and group size were log-transformed before being standardized. Figure was generated with R package "sjPlot" (version 2.8.14; Lüdecke 2023). Darker points indicate more overlaid data, whereas lighter points indicate less overlaid data.

Our results indicate the complex adaptive values of group living across life stages.

Many prior studies have shown that by foraging or living in a group, predation risk is reduced (Hamilton 1971; Vine 1971; Pulliam 1973; Lima 1995). For example, when aggregating while foraging, individuals decrease their risk of predation because there is a higher probability of predator detection (Pulliam 1973), and more individuals dilute the risk (Ydenberg and Dill, 1986). Studies like these explain the adaptive value of grouping in many species. However, direct and indirect individual social relationships with others may influence risk assessment and flight response (Heathcote et al. 2017). Our study was somewhat consistent with the social security hypothesis by showing social relationships may have adaptive value in that under high perceived predation risk, marmots varied their FID in ways that suggested that they benefited from having certain strong relationships.

Vigilance and escape behaviors are traded off with foraging efficiency (Makowska and Kramer 2007). Therefore, individuals with weaker social relationships may benefit from escaping sooner when predation risk is high because they might spend more time and energy independently assessing risk, whereas individuals who are more socially connected might benefit from "trusted" companions and be able to continue engaging in their current behavior before escaping. However, and importantly, we found these associations between risk assessment and social attributes vary with age and sex. This indicates that the effect of social position on individuals' risk assessment is conditional and not straightforward.

Interestingly, the only cohort with a significant direct relationship between social group size and FID were male yearlings (Figure 1B; Table 1B). This positive relationship between group size and FID might support the "many eyes" hypothesis (Pulliam 1973). In addition, male yearlings are recipients of agonistic behavior from adult males (Armitage 2014), and the frequency of agonistic interactions likely increases with group size (Blumstein et al. 1999). Receiving more agonistic interactions in larger groups may cause male yearlings to be in a heightened state of vigilance (Lea and Blumstein 2011; Armitage 2014) and, therefore, may be associated with general wariness and flee at greater distances as social group size increases. Male yearlings also had a positive relationship between FID and the number of individuals in their immediate vicinity. This indicates that with more individuals looking for predators in their vicinity, either male yearlings perceive an increased risk of predation or the response of other individuals caused individuals to flee at greater distances. However, the interpretation of these main effects should be tempered because variation in male yearling FID was also explained by a number of significant interactions between alert distance and social network measures. These interactions suggest that FID was not only explained by social connectedness but also the degree of perceived risk (measured by alert distance) and that there were some social antipredator benefits when perceived risk was relatively high. In other words, individuals with longer alert distances may assess a greater risk of predation than those with shorter alert distances. At high alert distances, male yearlings in larger social groups and those socially closer to others in their group tolerated comparatively closer human approaches, suggesting a benefit present only at relatively high perceived risks. These results are consistent with the social security hypothesis but only at relatively high perceived risk levels. Yet, male yearlings with more social partners fled at greater distances when perceived risk was high, suggesting specific social attributes influence antipredator responses in different ways.

While there was no significant main effect (associations between FID and individual social network measures) detected in female yearlings, the interactions suggest that they do not benefit in the same way as yearling males. Female yearlings in larger social groups and who are socially closer to others in their group fled at greater distances with increased perceptions of risk. While not consistent with the social security hypothesis, it does illustrate that social relationships may modulate risk assessment. If female yearlings that were socially closer to others in the larger groups fled sooner and therefore lost more opportunity to forage, they may be less efficient at gaining mass and may pay a cost with respect to overwinter survival (but see Blumstein et al. 2023).

Adult females with more conspecifics within 10 m tolerated a closer human approach (Table 1E). This finding is consistent with detection and dilution models of antipredator vigilance (Hamilton 1971; Vine 1971; Pulliam 1973; Lima 1995) because individuals may rely on conspecifics to alert them to predators. Thus, adult females with more individuals in their immediate surroundings may be able to detect and respond to predators sooner. However, and importantly, adult females had a significant and positive main effect between their number of social partners and FID (Figure 1C). While adult females may benefit from the group-size effect (Mady and Blumstein 2017) and from living in matrilines (Armitage 1991; Wey and Blumstein 2010), prior work has also shown that they experience the costs of social relationships. For instance, adult female marmots with more frequent affiliative social interactions have lower reproductive success (Blumstein 2013). Bottlenose dolphins (*Tursiops* sp.), another facultatively social species, also do not have higher reproductive success in larger groups, yet they experience increased competitive costs from being gregarious (Mann et al 2000). Thus, if anything, both marmots and dolphins seem to be more wary when in stronger relationships. This could be interpreted as a cost, but it could also be interpreted as a form of enhanced wariness because they are mostly surrounded by kin (Armitage 2014), and by fleeing, they may also stimulate relatives to escape to safe locations. More work will be required to determine the adaptive value of social relationships in varying group sizes, with varying social connectivity, and under varying predation risk.

Adult males' assessments of risk were not associated with any social network measures. While adult males engage in primarily agonistic interactions (Armitage 2014), their presence is nonetheless important in affiliative network structures (Zenth et al. 2023). Therefore, despite contributing to affiliative networks, adult males seemingly do not obtain antipredator benefits from their affiliative interactions. In contrast, adult male fallow European fallow deer (*Dama dama*) in larger groups reduced vigilance (Pecorella et al. 2019), whereas adult male Przewalski's gazelles (*Procapra przewalskii*) in larger groups did not reduce vigilance (Shi et al. 2011). Therefore, the role of sociality on antipredator behavior in adult males is likely to vary by species.

Social network measures as main effects had a very modest relationship with FID, thus not providing unambiguous direct support for our main predictions. This may reflect the urgency associated with escape decision—the nature of your social relationships or social position may not matter in a life-or-death situation. Furthermore, an individual's social relationship and position may not provide enough immediate information when facing a risky situation, especially when these social partners may not be within eyesight during a risky situation, such as when approached by potential threats. Rather, we show that social network measures become important to escape decisions for some marmot cohorts and only at certain levels of risk. This suggests that social connectedness modulates tolerance for human approach but only at relatively high (for yearling males) or low (for yearling females) perceived levels of risk.

Some prior studies have shown different associations between agonistic and affiliative networks and analyzed traits (Brent et al. 2014; Hirsch et al. 2012; Wey and Blumstein 2012). Here, we focused on affiliative relationships for two reasons. First, there are many more affiliative observations than agonistic interactions (affiliative observations account for 88% of all observed social interactions in this system; Philson and Blumstein 2023). Second, the social security hypothesis is focused on the benefits of social relationships, and thus, we focused on presumably beneficial social interactions. Yet, it is also worthwhile to assess how agonistic-based social network measures are associated with antipredator behavior in the future.

Overall, while we did not find strong evidence that affiliative social relationships explained variation in the full data set, we did find that these relationships were potentially important modulators of risk in more vulnerable individuals, specifically yearlings. This indicates that there is more to security than group size alone. Social structure and demography are important modulators of risk assessment. The opposing relationships for some social network measures within and between life-history groups further emphasize the value of quantifying specific social attributes and the nuances of social relationships. We must also consider that fleeing at larger distances may not be a cost but perhaps is a benefit. Detecting and fleeing from a predator at greater distances may mean that the cost of escape is reduced despite the trade-off with time allocated to other activities. Regardless of the complex effects of predator detection and avoidance, we show individual social connectivity and position play a role in modulating antipredator behavior, adding detail and nuance to the social security hypothesis. Future studies exploring FID should incorporate measures of sociality into their experiments and analysis, as well as the demographic and life-history stages of the individuals. Future work could also explore the relationship between different attributes of sociality and risk assessment.

SUPPLEMENTARY MATERIAL

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

Data were collected with permission from Colorado Parks and Wildlife (TR917, renewed annually) and under the UCLA Institutional Animal Care and Use protocol 2001-191-01 (renewed annually). We thank Julien Martin for managing the database and the many previous marmoteers who have collected these data. We also thank the Rocky Mountain Biological Laboratory for staff and logistical support.

FUNDING

T.S. was an REU Fellow supported by the Rocky Mountain Biological Laboratory (NSF DBI-1755522). C.S.P. was supported by the University of California Los Angeles, American Society of Mammalogists, the Animal Behavior Society, and Rocky Mountain Biological Laboratory. K.U. was supported by Japan Society for the Promotion of Science Overseas Research Fellowship and the KAKENHI JP22KJ0721. D.T.B. was supported by the National Geographic Society, the University of California Los Angeles (Faculty Senate and Division of Life Sciences), an RMBL research fellowship, and the U.S. National Science Foundation (NSF IDBR-0754247 and DEB-1119660 and 1557130 to D.T.B., as well as DBI 0242960, 07211346, 1226713, and 1755522 to R.M.B.L.).

AUTHOR CONTRIBUTIONS

Tali Szulanski (Formal analysis [Supporting], Investigation [Supporting], Writing—original draft [Lead], Writing—review & editing [Equal]), Conner S. Philson (Conceptualization [Equal], Formal analysis [Lead], Investigation [Equal], Supervision [Equal], Writing—review & editing [Equal]), Kenta Uchida (Conceptualization [Equal], Investigation [Equal], Methodology [Equal], Writing—original draft [Supporting], Writing—review & editing [Equal]), and Daniel Blumstein (Conceptualization [Equal], Formal analysis [Supporting], Funding acquisition [Lead], Investigation [Equal], Methodology [Lead], Project administration [Equal], Supervision [Lead], Writing—original draft [Supporting], Writing—review & editing [Equal])

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Szulanski et al. (2023).

Handling Editor: Aliza le Roux

REFERENCES

Alexander RD. 1974. The evolution of social behavior. Annu Rev Ecol Syst. 5(1):325–383.

Armitage KB. 1982. CRC handbook of census methods for terrestrial vertebrates. Boca Raton, Florida, USA: CRC Press.

Armitage KB. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annu Rev Ecol Syst. 22(1):379–407.

Armitage KB. 2014. Marmot biology: sociality, individual fitness, and population dynamics. Cambridge, UK: Cambridge University Press.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Soft. 67(1):1-48. http://www.jstatsoft.org/v67/i01/

Beauchamp G. 2014. Social predation: How group living benefits predators and prey. London, UK: Academic Press.

Blumstein DT. 2010. Flush early and avoid the rush: a general rule of antipredator behavior? Behav Ecol. 21(3):440–442.

Blumstein DT. 2013. Yellow-bellied marmots: insights from an emergent view of sociality. Philos Trans R Soc London Ser B. 368(1618):20120349.

Blumstein DT, Evans CS, Daniel JC. 1999. An experimental study of behavioural group size effects in tammar wallabies, *Macropus eugenii*. Anim Behav. 58(2):351–360.

Blumstein DT, Pelletier D. 2005. Yellow-bellied marmot hiding time is sensitive to variation in costs. Can J Zool. 83(2):363–367.

Blumstein DT, Runyan A, Seymour M, Nicodemus A, Ozgul A, Ransler F, Im S, Stark T, Zugmeyer C, Daniel JC. 2004. Locomotor ability and wariness in yellow-bellied marmots. Ethology. 110(8):615–634.

Blumstein DT, Samia DSM, Stankowich T, Cooper WE Jr. 2015. Best practice for the study of escape behaviour. In: Cooper WE Jr., Blumstein DT, editors. Escaping from predators: an integrative view of escape decisions. Cambridge: Cambridge University Press. p. 407–419.

Blumstein DT, Sanchez M, Philson CS, Bliard L. 2023. Is flight initiation distance associated with longer-term survival in yellow-bellied marmots, *Marmota flaviventer*? Anim Behav. 202(2023):21–28.

Blumstein DT, Wey TW, Tang K. 2009. A test of the social cohesion hypothesis: Interactive female marmots remain at home. Proc Biol Sci. 276(1669):3007–3012.

Bonacich P. 1987. Power and centrality: a family of measures. AJS. 92(5):1170–1182.

Brent LJ. 2015. Friends of friends: are indirect connections in social networks important to animal behaviour? Anim Behav. 103(2015):211–222.

Brent LJ, Chang SW, Gariépy JF, Platt ML. 2014. The neuroethology of friendship. Ann N Y Acad Sci. 1316(1):1–17.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Anim Behav. 35(5):1454–1469.

Cooper Jr WE, Blumstein DT. 2014. Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. Behav Ecol. 25(1):44–52.

Cooper WE Jr, Blumstein DT, editors. 2015. Escaping from predators: an integrative view of escape decisions. Cambridge, UK: Cambridge University Press.

Csardi G, Nepusz T. 2006. The igraph software package for complex network research. Int J Complex Systems. 1695. https://igraph.org

Fox J, Monette G. 1992. Generalized collinearity diagnostics. J Am Stat Assoc. 87(417):178–183.

Fox J, Weisberg S. 2019. An R companion to applied regression. 3rd ed. Thousand Oaks, California, USA: Sage.

Fuong H, Blumstein DT. 2019. Social security: less socially connected marmots produce noisier alarm calls. Anim Behav. 160(2019):171–177.

Fuong H, Maldonado-Chaparro A, Blumstein DT. 2015. Are social attributes associated with alarm calling propensity? Behav Ecol. 26(2):587–592.

Hamilton WD. 1971. Geometry for the selfish herd. J Theor Biol. 31(2):295–311.

Heathcote RJP, Darden SK, Franks DW, Ramnarine IW, Croft DP. 2017. Fear of predation drives stable and differentiated social relationships in guppies. Sci Rep. 7(1):41679.

Hinde RA. 1976. Interactions, relationships and social structure. Man. 11(1):1–17.

Hirsch BT, Stanton MA, Maldonado JE. 2012. Kinship shapes affiliative social networks but not aggression in ring-tailed coatis. PLoS One. 7(5):e37301.

Lea AJ, Blumstein DT. 2011. Age and sex influence marmot antipredator behavior during periods of heightened risk. Behav Ecol Sociobiol. 65(8):1525–1533.

Lima SL. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim Behav. 49(1):11–20.

Lüdecke D. 2023. Package "sjstats." Statistical functions for regression models. Version 2.8.14. https://cran.r-project.org/web/packages/sjstats/index.html

Mady RP, Blumstein DT. 2017. Social security: are socially connected individuals less vigilant? Anim Behav. 134(2017):79–85.

Makowska IJ, Kramer DL. 2007. Vigilance during food handling in grey squirrels, *Sciurus carolinensis*. Anim Behav. 74(1):153–158.

Mann J. 2000. Female reproductive success in bottlenose dolphins (*Tursiops sp.):* life history, habitat, provisioning, and group-size effects. Behav Ecol. 11(2):210–219.

Møller AP. 2015. Birds. In: Cooper, WE Jr, Blumstein DT, editors. Escaping from predators. Cambridge, UK: Cambridge University Press. p. 88–112.

Moody J, White DR. 2003. Structural cohesion and embeddedness: a hierarchical concept of social groups. Am Sociol Rev. 68(1):103–127.

Pecorella I, Fattorini N, Macchi E, Ferretti F. 2019. Sex/age differences in foraging, vigilance and alertness in a social herbivore. Acta Ethol. 22(1):1–8.

Philson CS, Blumstein DT. 2023. Emergent social structure is typically not associated with survival in a facultatively social mammal. Biol Lett. 19(3):20220511.

Pulliam HR. 1973. On the advantages of flocking. J Theor Biol. 38(2):419–422.

R Development Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/

Rosvall M, Axelsson D, Bergstrom CT. 2009. The map equation. Eur Phys J Spec Top. 178:13–23.

Rosvall M, Bergstrom CT. 2008. Maps of random walks on complex networks reveal community structure. Proc Natl Acad Sci USA. 105(4):1118–1123.

Runyan AM, Blumstein DT. 2004. Do individual differences influence flight initiation distance? J Wildl Manag. 68(4):1124–1129.

Samia DSM, Bessa E, Blumstein DT, Nunes JACC, Azzurro E, Morroni L, Sbragaglia V, Januchowski-Hartley FA, Geffroy B. 2019. A meta-analysis of fish behavioural reaction to underwater human presence. Fish Fish. 20(5):817–829.

Samia DSM, Blumstein DT, Stankowich T, Cooper WE. 2016. Fifty years of chasing lizards: new insights advance optimal escape theory: fifty years of chasing lizards. Biol Rev Camb Philos Soc. 91(2):349–366.

Shi J, Li D, Xiao W. 2011. Influences of sex, group size, and spatial position on vigilance behavior of Przewalski's gazelles. Acta Theriol. 56(1):73–79.

Stankowich T, Blumstein DT. 2005. Fear in animals: a meta-analysis and review of risk assessment. Proc Biol Sci. 272(1581):2627–2634.

Stoffel MA, Nakagawa S, Schielzeth H. 2020. partR2: Partitioning R2 in generalized linear mixed models. PeerJ. 9:e11414.

Szulanski T, Philson CS, Uchida K, Blumstein DT. 2023. Social security: Does social position affect flight initiation distance? Behav Ecol. https://osf.io/8ja6b/

Uchida K, Blumstein DT. 2021. Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance. Behav Ecol. 32(4):668–678.

Van Vuren DH. 2001. Predation on yellow-bellied marmots (*Marmota flaviventris*). Am Midl Nat. 145(1):94–100.

Vine I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. J Theor Biol. 30(2):405–422.

Wasserman S, Faust K. 1994. Social network analysis: methods and applications. Cambridge, UK: Cambridge University Press.

Wey T, Blumstein DT, Shen W, Jordan F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav. 75(2):333–344.

Wey TW, Blumstein DT. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. Anim Behav. 79(6):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. Behav Ecol Sociobiol. 66:1075–1085.

Whitehead H. 2009. SOCPROG programs: analysing animal social structures. Behav Ecol Sociobiol. 63(5):765–778.

Ydenberg RC, Dill LM. 1986. The economics of fleeing from predators. Adv Study Behav. 16:229–249.

Zenth F, Maldonado-Chaparro AA, Solis A, Gee S, Blumstein DT. 2023. The (surprising) importance of males in a matrilineal society: behavioural insights from a topological knockout study. Anim Behav. 201(2023):63–72.