

Social security: Does social position influence flight initiation distance?

Abstract

A variety of factors can influence an individual's antipredator behavior including their group size because simply being around conspecifics may reduce predation risk. Recent work has shown that it is not just being around others, but rather the specific social relationships that individuals have with others may also modulate perceptions of risk and explain variation in a variety of antipredator behaviors. We asked whether and how yellow-bellied marmots' (*Marmota flaviventer*) position in their social network explains 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 individuals with different life histories. Following the "social security" hypothesis, we predicted that more socially connected individuals would have a lower FID. We found that the magnitude and direction to which sociality was associated with FID varied based on age and sex. When examining all age-sex cohorts there was a weak effect of strength on FID: individuals in stronger relationships tolerated closer approaches. When examining each cohort independently, we found adult male's FID was not associated with any social network measure, while female adults fled at greater distances as degree increased. Yearlings of both sexes, however, seemingly benefited from stronger social relationships, but only when perceived risk was high. These results are consistent with the social security hypothesis; the degree of social connectedness may explain variation in FID in at least some age and sex cohorts.

Keywords: antipredator behavior, flight initiation distance, *marmota flaviventer*, social networks

Introduction

Group living has many benefits, ranging from predator avoidance to increased access to resources (Alexander 1974; Hinde 1976; Beauchamp 2014). Living socially can 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 models of predation risk assessment may explain the group size effect. Detection predicts that within a larger group, a given individual will devote less time to vigilance behavior because

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they can rely on other group members to detect predators (Pulliam 1973). Dilution further explains how larger groups benefit individuals by “diluting” the risk of predation across more individuals, thus lowering 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 vigilance burden. For example, females in larger social groups dedicated less time to vigilance behaviors while foraging in wild yellow-bellied marmots (Mady & Blumstein 2017). However, group size is but one of several ways that sociality can influence risk assessment.

Formal social network analysis (Wasserman & Faust 1994; Wey et al. 2008) can provide direct insights into individual social variation that cannot be explained by group size. Social network analyses allow for the identification of specific attributes of direct and indirect social relationships that quantify social variation (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 strength and quality of the relationships within their social network.

Flight initiation distance (FID) is the distance from a predator at which a prey animal decides to flee and is a metric of predation risk assessment (Ydenberg & Dill 1986; Cooper & Blumstein 2015). Many factors explain interspecific differences in FID. Among them, body size in birds (Møller 2015), fishes (Samia et al. 2019), and lizards (Samia et al. 2016) explains substantial interspecific variation in FID. Group size is 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 & 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 group size, 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 are an ideal system in which to study the relationship of 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. 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 & Blumstein 2019). Females in larger social groups also spent less time looking while foraging (Mady & Blumstein 2017). Based on these findings and the social security hypothesis, we predicted that more socially connected individuals will have lower FIDs because of this higher sense of security within social networks.

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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). 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 five 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 (*Aquila chrysaetos*), red-tailed hawks (*Buteo jamaicensis*), Swainson's hawks (*B. swainsoni*), and goshawks (*Accipiter gentilis*) (Van Vuren 2001).

Each year virtually all of the marmots in our study site are trapped in walk-in livetraps, 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

Trained observers recorded social interactions between marmots using spotting scopes and binoculars from distances of 20 - >100 m (distances varied by group and were selected so as 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, social interactions were categorized as either affiliative or agonistic, and the initiator, recipient, and “winner” (individual who displaced another) were recorded. 79% of interactions are between identified individuals and 88% of these interactions are affiliative (Philson and Blumstein 2023). A full ethogram of behaviors can be found in Blumstein et al. (2009).

To measure the FID, a trained observer identified a subject, waited until the individual became relaxed (i.e., it was not rearing up or looking directly at the observer), and walked directly towards the marmot maintaining a 0.5-meter step per second (eg. Blumstein et al. 2004). We recorded the starting distance, distance of first look (alert distance), flight initiation distance, and the distance at which the subject disappeared into its burrow from their original position, which, in previous studies (Dumont et al. 2012) explained significant variation in FID.

Social network calculations

Social networks were built annually from 2003 to 2020 for yearlings and adults for affiliative social interactions with known recipients and initiations. Pups were excluded from networks because they primarily interact 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.

Social networks were built and eight social attributes (in/out degree, in/out strength, eigenvector centrality, embeddedness, and in/out closeness centrality) were calculated using R (version 4.2.0; R Development Core Team 2023) and the package “igraph” (version 1.4.2; Csardi & Nepusz 2006). Degree is the number of relationships that an individual has, with indegree measuring the number of relations an individual receives and outdegree measuring the number of relationships an individual initiates (Wasserman & Faust 1994; Wey et al. 2008). In/out strength calculates, respectively, the number of social interactions an individual receives or initiates. Closeness centrality (in/out closeness) measures the social distance of an individual from all other individuals within their social group. Closeness is calculated as the reciprocal of the shortest initiated or received paths between the focal individual and every other individual within a group (Wey et al. 2008). Eigenvector centrality represents how social an individual's direct social partners are (Wey et al. 2008). Finally, embeddedness measures how well connected an individual is within their social group as a product of the connectivity of their cluster and surrounding connections (Wey et al. 2008).

Statistical analyses

Our final data set consisted of 17 years and 947 observations of FID and social network data collected on 308 distinct individuals from 112 distinct 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, all continuous variables were log-transformed in order to normalize the residuals and met assumptions of a Gaussian linear mixed-effect model. All continuous variables were also mean centered to facilitate model fit and comparisons.

We originally 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 ten meters 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 (Fox &

Monette 1992; Fox & Weisberg 2019) for several of the social networks 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 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 (Dumont et al. 2012), we also wanted to examine the interactive effects of alert distance and social network measures on FID. This allows us to determine if any putative benefits of sociality are dependent upon perceived risk as measured by alert distance.

From this model that met all assumptions and included all individuals, we 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 & Blumstein 2011). Using the partR2 package (version 0.9.1; Stoffel et al. 2020), we report marginal and conditional partial R^2 values for our model. We then estimated 95% confidence intervals using 100 parametric bootstrap iterations.

Results

When examining the entire data set (Table 1a) and after controlling for significant variation FID explained by alert distance, distance to burrow, and trial number (Estimate = -0.026, SD = 0.013, $P = 0.043$), there was a significant relationship with strength (figure 1A) (Estimate = -0.104, SD = 0.053, $P = 0.050$); individual marmots that had stronger relationships tolerated closer approaches. There were no significant interactions.

When examining male yearlings alone (Table 1b), we found that as the number of individuals within 10 m increased, FID also increased (Estimate = 0.131, SD = 0.042, $P = 0.002$), but there were no other significant direct relationships with any of the other measured social attributes. However, there were some significant interactions with social attributes and alert distance. As alert distance increases and group size increased, FID decreased (figure 1C) (Estimate = -0.421,

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SD = 0.141, P = 0.004), and that as alert distance and degree increased, so did FID (figure 1D) (Estimate = 0.279, SD = 0.113, P = 0.015). In contrast, as alert distance and closeness increased, FID decreased (figure 1E) (Estimate = - 0.315, SD = 0.105, P = 0.003).

When examining female yearlings alone (Table 1c), we found that there were no direct relationships of any social measures on FID, but there were some interactions. As alert distance and group size increased, FID increased (figure 1F) (Estimate = 0.258, SD = 0.113, P = 0.024). Also in contrast to male yearlings, as alert distance and closeness increased, FID increased (figure 1G) (Estimate = 0.252, SD = 0.089, P = 0.005).

While there were no significant associations with any measured social attributes and adult male FID (Table 1d), we found that female adult FID was directly explained by degree (figure 1H): as degree increased, FID also increased (Estimate = 0.172, SD = 0.068, P = 0.012). There were no significant interactions for either adult males or females.

Table 1: Model estimates, standard error, p-value, marginal and conditional part R² for A) all age and sex cohorts; B) male yearlings; C) female yearlings; D) male adults; E) female adults. Significant p-values are in bold.

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)
n within 10m	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 x social group size	0.044	0.056	0.434	0.16% (0-8.31)	9.17 (2.74-16.36)
Alert distance x degree	0.006	0.045	0.888	0% (0-8.31)	8.98 (2.54-16.18)
Alert distance x strength	-0.036	0.045	0.426	0.06% (0-8.21)	9.07 (2.63-16.26)
Alert distance x closeness	0.03	0.045	0.499	0.21 (0-8.35)	9.22 (2.79-16.4)
Alert distance x 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)
n within 10m	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 x social group size	-0.421	0.141	0.003	1.68 (0-13.96)	2.52 (0-20.91)
Alert distance x degree	0.28	0.113	0.015	1.61 (0-13.89)	2.45 (0-20.85)
Alert distance x strength	0.013	0.151	0.932	0 (0-12.47)	0.83 (0-19.53)
Alert distance x closeness	-0.315	0.105	0.003	1.88 (0-14.13)	2.72 (0-21.08)
Alert distance x 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)
n within 10m	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 x social group size	0.258	0.113	0.024	2.23 (0-16.22)	11.26 (1.35-26.96)
Alert distance x degree	-0.148	0.098	0.134	1.3 (0-15.45)	10.32 (0.3-26.17)
Alert distance x strength	0.146	0.119	0.221	0.89 (0-15.11)	9.91 (0.01-25.83)
Alert distance x closeness	0.252	0.089	0.005	3.41 (0-17.2)	12.43 (2.68-27.95)
Alert distance x 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 (%)
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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)
n within 10m	-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)
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 x social group size	-0.502	0.27	0.068	0 (0-24.84)	12.15 (5.56-55.21)
Alert distance x degree	0.187	0.192	0.334	0 (0-26.2)	14.17 (8.02-56.37)
Alert distance x strength	-0.407	0.292	0.169	0 (0-27.47)	16.06 (10.31-57.45)
Alert distance x closeness	-0.277	0.169	0.107	0 (0-25.16)	12.63 (6.14-55.49)
Alert distance x 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)
n within 10m	-0.056	0.028	0.05	0.36 (0-9.83)	7.89 (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 x social group size	-0.089	0.079	0.259	0.56 (0-0-10.01)	8.09 (0.18-20.05)
Alert distance x degree	0.114	0.065	0.082	0.4 (0-9.87)	7.93 (0.1-19.91)
Alert distance x strength	-0.133	0.068	0.051	0.95 (0-10.37)	8.48 (0.38-20.39)
Alert distance x closeness	-0.062	0.068	0.363	0.07 (0-9.56)	7.59 (0-19.62)
Alert distance x eigenvector centrality	0.002	0.053	0.973	0 (0-9.5)	7.53 (0-19.56)

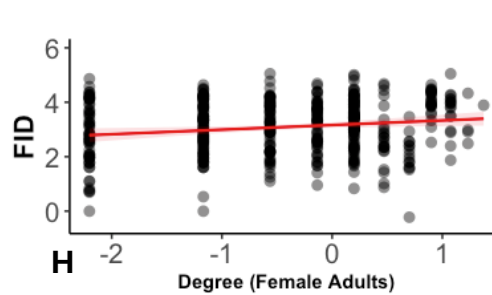
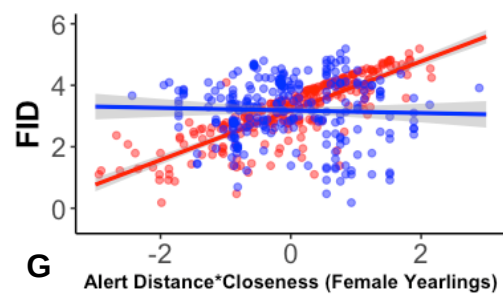
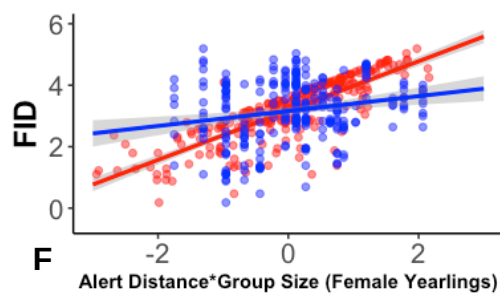
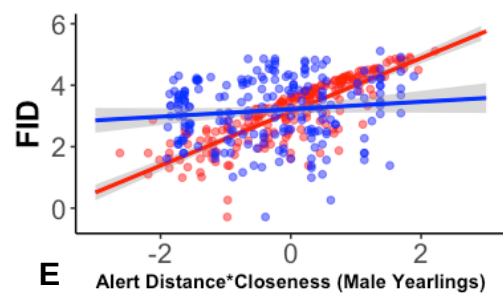
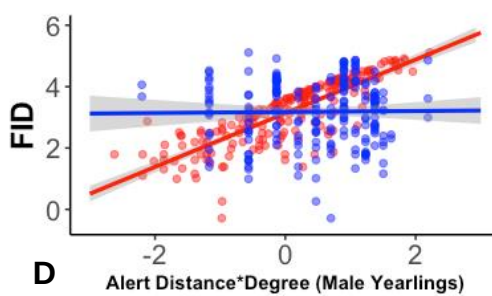
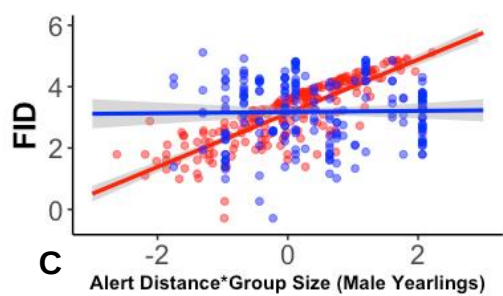
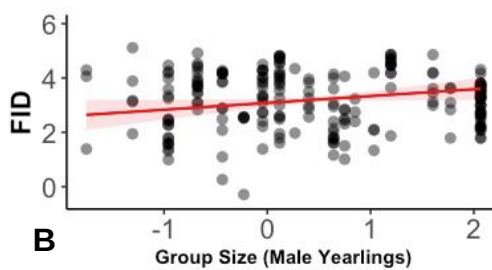
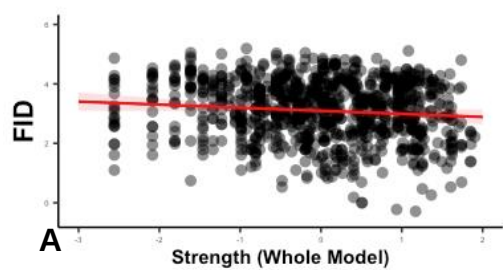


Figure 1: Variables explaining significant variation in log10 transformed flight initiation distance observed for: A) group size in male yearlings, B) the interaction between alert distance and group size in male yearlings, C) the interaction between alert distance and degree in male yearlings, D) the interaction between alert distance and closeness in male yearlings, E) strength in all age and sex cohorts, F) the interaction between alert distance and group size in female yearlings, G) the interaction between alert distance and closeness in female yearlings, and H) degree in female adults. Data plotted were standardized raw data (independent variables were log transformed before being standardized) with 95% confidence bands. Darker points indicate overlapping data.

Discussion

Overall, there was support for the hypothesis that an individual's network position was associated with risk assessment when analyzing all cohorts together; there was a nearly significant association between strength and FID, indicating that marmots with increased frequency in their affiliative relationships may have felt less threatened by human presence and thereby may rely on conspecifics for an increased sense of security. As expected from prior work in this system (Runyan & 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 & Blumstein 2021). However, when we separated our analyses by sex and age, because prior work has shown that these different cohorts assess risk differently (Blumstein & Pelletier 2005; Lea & Blumstein 2011; Mady & Blumstein 2017), we found that social position affected marmots in a variety of different ways.

Interestingly, the only cohort with a significant direct relationship between social group size and FID were male yearlings (table 1B). Male yearlings are recipients of agonistic behavior from adult males (Armitage 2014), and agonistic interactions will therefore increase as group size increases (Blumstein et al. 1999). Receiving more agonistic interactions in larger groups may cause male yearlings to be in a heightened state of vigilance (Lea & 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 their immediate group size, defined as the number of individuals within 10 m (table 1B).

This can be explained for the same reasons; male yearlings around more individuals may expect to experience more agonistic interactions. However, the interpretation of these main effects should be tempered because male yearlings also had a number of significant interactions between alert distance and social network measures. These interactions suggest that relative risk (as measured by alert distance) influenced their perception of others and there were some benefits when perceived risk was relatively high. At high alert distances, those yearlings in larger social groups, with higher degree, and those that had greater closeness with others in their group tolerated, in relatively closer approaches suggesting a benefit present only at relatively high perceived risks. All of these results support the social security hypothesis, but only at relatively high perceived risk levels.

While there was no significant main effect detected in female yearlings, the interactions suggest that they too may benefit from being in larger groups as well as having greater closeness, but only at high levels of perceived risk.

Adult females with more conspecifics within 10 m tolerated closer approach (Table 1E). This is a finding 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 to predators, thus they are able to detect and respond to predators sooner. However, and importantly, adult females had a significant and positive main effect between degree and FID. While adult females may benefit from the group-size effect (Mady & Blumstein 2017) and from living in matrilineal groups (Armitage 1991; Wey & Blumstein 2010), prior work has also shown that they experience costs of social relationships. For instance, adult female marmots with higher affiliative strength experience lower reproductive success (Blumstein 2013). Bottlenose dolphins (*Tursiops sp.*), another facultatively social species, also do not enjoy higher reproductive success in larger groups, yet they experience increased competitive costs from being gregarious (Mann et al 2000). Thus, if anything, they 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 (REFS). More work will be required to determine the adaptive value of this intriguing result.

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

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contributing to affiliative networks, adult males seemingly do not obtain antipredator benefits from their affiliative interactions. In contrast, fallow deer (*Dama dama*) adult males in larger groups (and presumably therefore having increased social interactions) did experience decreased vigilance behavior (Pecorella et al. 2019). Adult males of another ungulate, Przewalski's gazelle (*Procapra przewalskii*), did not have lower vigilance in larger groups (Shi et al. 2011).

Therefore, the role of sociality on vigilance in adult males varies by species.

While we did not find strong evidence that 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. Overall, we found limited support for group-size effecting vigilance. However, when we fit models for individual demographic groups, we found varying effects of sociality on vigilance. This indicates that not group size, but the social structure of said group, as well as demography, are important modulators of risk assessment behaviors. This result is promising for future studies examining demographic differences in antipredator behavior and human tolerance.

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