After the fall: A Climax Avalanche Altered Vigilance but not Social Relationships in a Wild Mammal

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ABSTRACT

Across ecosystems, disturbances drive changes in habitat composition, which alter visibility. Visibility, in turn, alters animal behavior. Climate change is expected to increase the frequency/severity of disasters, and thus understanding how such events alter animal behavior is a critical part of understanding how climate change alters the biosphere. Here, we investigate how a change in visibility brought about by a climax avalanche alters anti-predator vigilance levels and social network measures in a wild population of yellow-bellied models (*Marmota flaviventer*). We fit a series of generalized linear mixed models to examine the influence that the year being before versus after the avalanche has on the time spent being vigilant and several social network measures. We found a significant increase in anti-predator vigilance following the avalanche, while no significant changes in social network measures were detected. Our finding suggests that the obstruction of peripheral visibility brought about by the avalanche increased the marmot's perception of risk without affecting their ability to socialize.

INTRODUCTION

Ecosystems exist in a constant state of flux. Disturbances (e.g., storms, wildfires, floods, avalanches) can severely alter habitats, changing vegetation communities, landscape structure and nutrient flow (1–3). As human-caused climate change continues to occur, many environmental disturbances are expected to increase in frequency, severity, or both (4–6). As a result, understanding how organisms alter their behavior in response to major environmental disturbances is a critical part of assessing how climate change will impact the biosphere (7,8).

After disturbances, organisms face many challenges, including finding resources and shelter in a drastically altered landscape. Another potential obstacle organisms face in the wake of disturbances is a change in visibility. Disturbances may remove cover, and in doing so remove shade plants (9) or make animals more visible and vulnerable to predation (10). Alternatively, the deposition of debris may impair an organism's visibility or create cover where there was no protective cover before. Visibility plays an important role in impacting animal behavior. An animal's ability to identify objects within its environment modulates resource detection, mate choice, territoriality, and dispersion (11). African lions (*Panthera leo*) are twice as likely to make a kill in areas that are densely vegetated in comparison to open areas (12). Both male and female two-spotted gobies (*Gobisculus flavescens*) change their mating behavior in more complex habitats, with females having more difficulty comparing the sizes of displaying males, relaxing sexual selection for larger body sizes in males (13) Visibility is also important for lekking species. Male greater sage grouse (*Centrocercus urophasianus*) are more likely to lek in areas where long-range visibility is low but short-range visibility is high, possibly to decrease the chances of being spotted by a predator while making it easier for visiting females to observe their displays (14) .

In addition to the examples listed above, vigilance plays an important role in anti-predator behavior. Animals must balance tradeoffs between scanning for predators and other

fitness-enhancing behaviors, such as foraging or socializing. In many cases, visibility plays a substantial role in how animals manage these tradeoffs. For example, crimson rosellas (*Platycercus elegans*) forage more frequently in habitats where visibility is higher, potentially because foraging is safer in areas where predators are easier to detect (15). Similarly, impaired visibility increases risk perceptions in the stymphalia minnow (*Pelasgus stymphalicus*). When in more turbid conditions, minnows are less likely to emerge from an artificial structure and explore smaller regions of their environment
(16).

The extent to which an animal can clearly see plays an important role in social behavior as well. For example, mice (*Mus musculus*) can use vision alone to determine characteristics of other mice relevant to social behavior, namely sex and whether another mouse is a cage mate or a stranger (17). In addition to recognizing familiar individuals or identifying sex, many animals depend on vision to respond to social signals. For example, facial expressions are widespread among primates and other mammals (18), and anthropoid apes use gestures to communicate with one another (19). Gaze-following is widespread across various animal taxa, having been observed in bottlenose dolphins (*Tursiops sp.*), ungulates, several ratites, and red-footed tortoises (*Geochelonia carbonara*) (20–23). From this, we expect that altering the visibility of an environment may have impacts on how animals socialize. For example, an increase in visibility may increase sociality by making it easier for an animal to detect conspecifics, assess a conspecific's traits (sex, age, etc.), or clearly discern visual signals. Alternatively, organisms in an environment where they are easy to detect may withhold socializing in favor of other behaviors, such as vigilance, that reduce the chances of being detected by a predator.

Quantifying social networks is a widely used method of studying animal social behavior (24). Social network analysis defines attributes of sociality by quantifying precise metrics that can apply to either an individual's position in the network or the structure of the group network. Each social attribute may (or may not) have fitness consequences (25). Social network analysis can explore the relationship between social behavior and abiotic factors. For example, sociable weavers (*Philetairus socius*) form less cohesive social networks as temperature increases (26). When inhabiting more complex habitats, sleepy lizards (*Tiliqua rugosa*) form denser and more stable social networks (27). During cold and rainy weather, which heightens metabolic demands, common waxbills (*Estrilda astrild*) form larger and more homogeneous social networks (28). Despite numerous studies investigating how abiotic factors such as seasonality, temperature, and weather impact animal social behavior, little work has been done using social network analysis to assess the impact visibility has on social behavior.

Yellow-bellied marmots (*Marmota flaviventer*) are an ideal model system to investigate this question because a population has been studied in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO since 1962. Yellow-bellied marmots are also important prey species for a variety of predators and are facultatively social, making them an

ideal study system to investigate anti-predator vigilance and the factors influencing social behavior. During the winter of 2018/19, an avalanche deposited tones of debris (broken tree trunks, branches, and rocks) across a well-studied marmot colony, 'Marmot Meadow'. In doing so, the avalanche drastically reduced the peripheral visibility in a once open, gently sloping, subalpine meadow. Previous work has already established the importance of peripheral visibility in marmot behavior. When peripheral visibility was experimentally blocked, marmots were less vigilant within the foraging apparatus but more vigilant outside of it, and frequently moved outside of the apparatus (29). Additionally, marmots prefer to forage in areas with vegetation below shoulder height and more frequently stand on their hind feet to survey their surroundings when foraging in taller vegetation (29). Visibility is known to impact habitat use in marmots as well. The amount of debris within a given area correctly predicts whether or not a given location will be a persistent or non-persistent marmot colony, with more debris being associated with non-persistent colonies (30). As a result, the avalanche at Marmot Meadow provides a "natural experiment" to test how the antipredator and social behavior of wild mammals changes following a dramatic reduction of peripheral visibility.

We predicted that marmots would be more vigilant in the years following the avalanche, as the debris will have obstructed their peripheral vision. We predicted that social connectivity would be disrupted in the years following the avalanche, as detecting conspecifics would be more difficult.

METHODS

Study Site and Species

The yellow-bellied marmots at RMBL (38°57'N, 106°59'W; ca. 2900 m elevation) are facultatively social and harem polygynous (31). Individual marmots were routinely trapped using Omolene horse bait and Tomahawk live traps (32,33). Once trapped, marmots were given unique ear tags and marked using Nyanzol fur dye. Effectively, every resident member of each colony under study is marked and identified. Marmot Meadow is a gently sloping (< 10°) subalpine meadow bordered by aspen and spruce forests. Following the avalanche, large portions of the meadow became cluttered with fallen trees and boulders.

Metrics of Vigilance

Vigilance was calculated from 917 two-minute focal observations (34) taken from 141 animals spanning from 2002-2024 following standardized methods. Trained observers conducted two-minute focal animal samples to quantify vigilance while foraging using a simple ethogram that focused on foraging and vigilance (35). All behavioral transitions were dictated into a recording device (notes app on phone or a digital or microcassette recorder). These recordings were scored using JWatcher 1.0 (36). Additional relevant covariates were collected during the

focal observation, including the height of surrounding vegetation (low vegetation [vegetation shorter than the back of the animal] and high vegetation [vegetation taller than the back of the animal]; incline (0-10°, 10-30°, >30°); the distance (m) to the nearest burrow, and the number of conspecifics within 10 m. Observers were trained to identify these behaviors with 100% accuracy and consistently score them in JWatcher, with the correlation between the proportion time in sight between behaviors from the same focals ≥ 0.95.

Metrics of Social Behavior

Social behavior was recorded during hours of peak activity (07:00 to 11:00 h and 16:00 to 18:00 h) with trained observers notating behavior as it occurred at each of the colonies under study. Observers noted when an interaction occurred, the number of individuals involved in the interaction, the initiator and recipient, the location, and the type of interaction as described in Blumstein et al. (2009). From these data, a matrix of all affiliative interactions between individuals was constructed. Juveniles were excluded from the analysis, as juveniles interact almost exclusively with their mothers. Only social observations from the months of April-June were used, as these months are when most social activity occurs. To exclude transient individuals, data was only used from animals that have been seen five or more times. In total, social observations from 816 individuals spanning from 2003 to 2025 were used.

Social groups are defined based on space-use overlap (two different individuals being observed/trapped at the same burrow within a 1-day period. Simple-pairwise association indices were calculated using SOCPROG (Whitehead 2009, Version 2.9), and social groups were defined using a random walk algorithm in MapEquation (Csardi, 2006; Rosvall 2008; Rosvall 2009). This information was used to calculate social network measures in the R package “igraph” (Csardi, 2006, Version 2.3.3.9024).

Statistical Analysis

All analyses were conducted in R (R Core Team, 2026, Version 4.6.0). We used the packages “glmmTMB” (Brookes et al., 2017; McGillycuddy et al., 2025, Version 1.1.14) and “lme4” (Bates et al., 2015, Version 2.0-6) to run generalized linear mixed models and “performance” (Version 0.12.4; Lüdecke et al., 2021) and “DHARMa” (Version 0.4.7; Hartig, 2024) to check model assumptions.

To identify whether vigilance significantly increased following the avalanche, we fitted a generalized linear mixed model. Our dependent variable was the proportion of time allocated to vigilance during a given focal observation. Fixed effects included: whether the year was before 2019, age class, the angle and substrate of terrain, number of conspecifics within 10 m, and predator index. Predator index was calculated as a binary variable (high versus low) according to whether the number of predators at a colony was above or below the median number of predator observations per colony across every colony each year (37,38). The model was fitted with a beta distribution using a ‘logit’ link function and a ziformula = ~1.

To determine if social network measures significantly changed following the avalanche, we fitted a series of generalized linear mixed models. Strength and embeddedness were fit with Type II negative binomial distributions; betweenness, density, transitivity, and reciprocity were fit with ordered beta regression models; and cut points was fit using a Poisson distribution. For individual-level network traits, fixed effects included whether the year was before 2019, sex, age, predator index, and group size, and random effects included year and marmot ID. For group-level social network measures, fixed effects included whether the year was before 2019, predator index, and group size; we included year as a random effect for all measures except for cut points.

RESULTS

Vigilance

Our results reveal that anti-predator vigilance while foraging significantly increased following the avalanche (Table 1).

Sociality

The results of our social network analysis did not reveal any significant association between the effects of the avalanche for either individual (Table 2) or group level (Table 3) social network traits.

DISCUSSION

The increase in vigilance after following a climax avalanche is consistent with our predictions and supports our hypothesis that the avalanche obstructed visibility by depositing debris. This is consistent with earlier work done in yellow-bellied marmots and other prey species showing that blocking peripheral vision leads to an increase in perceptions of risk (29,39–41).

The importance of this finding extends beyond marmots. As disturbances become more common due to climate change, visibility may change across ecosystems. Since the amount of time an animal spends being vigilant (as opposed to foraging) could conceivably impact its fitness, changes to visibility could have larger effects on the population structure of wild animals. Better understanding how wildlife change their vigilance following disturbances may have conservation value. Captive animals raised for conservation purposes are often at an increased risk of predation, and anti-predator training prior to release increases vigilance levels and foraging efficiency (42). The fact that animals perceive predation risk differently depending on visibility may help guide decision making regarding appropriate levels of anti-predator training and inform site selection.

The lack of any observed change in social network values is not consistent with our hypothesis that the obstruction of peripheral visibility would decrease marmot sociality, nor is it consistent with a substantially larger analysis across all colonies that showed that visibility was

associated with social network structure (Adler and Blumstein in review). Two possible explanations exist for the lack of any observed significant changes in social network measures: either our sample sizes were too small to detect significant differences, or marmot social networks are robust to environmental changes. Given that this study only focused on a single colony, while the Adler and Blumstein analysis focused on XX colonies, it is quite possible that we were underpowered to detect small effects. The latter option is consistent with some research showing that social network analysis metrics can remain stable even in the face of disturbance (i.e., individuals being isolated from one another before being reunited in a novel environment) (43). Avalanches are a natural occurrence in the areas occupied by yellow-bellied marmots, and natural selection may have favored the evolution of stable social networks in the face of these common occurrences. If marmot social networks are indeed robust to reductions in visibility caused by avalanches, it becomes an open question as to why anthropogenic obstructions to visibility alter social behavior while natural obstructions to visibility do not.

As climate change continues to generate more severe weather events, understanding the limits to disturbance of animal social networks is critical to understanding how climate change will affect the biosphere. Social behavior often has consequences for animal fitness and thus changes to social networks could have widespread consequences to wild populations . That animal social networks may be sensitive to some levels of disturbance but not others may have important management implications. Assessing how much disturbance is necessary to significantly impact social network measures may impact decision making surrounding activities that could impact sensitive species.

CONCLUSION:

We found that changes in peripheral visibility brought about by environmental disturbances have the potential to significantly affect the behavior of wild animals. Debris deposited by a climax avalanche obstructed visibility at a well-studied colony of yellow-bellied marmots, resulting in significant increases to their anti-predator vigilance but not social network measures, which may suggest that climate disturbances may selectively influence fitness-related behaviors.

TABLES AND FIGURES

Table 1. The results of the generalized linear mixed model explaining variation in the proportion of time an individual spent being vigilant while foraging.

Fixed Effects	Estimate	Std. Error	Z Value	P Value
Intercept	-0.689	0.161	-4.270	**1.96e-5**
Year (Before 2019)	-0.261	0.132	-1.969	**0.049**
Sex	-0.020	0.060	-0.325	0.745
Age Class (Juvenile)	-0.334	0.082	-4.039	**5.38e-05**
Age Class (Yearling)	0.168	0.065	2.569	**0.010**

Predator Index	0.021	0.100	0.210	0.834
Angle	0.033	0.061	0.541	0.588
Substrate (low vegetation/dirt)	0.222	0.062	3.557	**3.75e-4**
Substrate (stone/talus)	0.224	0.163	1.372	0.169965
Number within 10m	-0.067	0.019	-3.445	**5.70e-4**

Note: Results in boldface are considered statistically significant. Reference classes are female for sex, adult for age class, high for predator index, and high vegetation for substrate. Variance for the random effects are: 0.01631 for marmot ID and 0.03035 for year.

Table 2. The results of the general linear mixed models explaining the variation in individual social network measures

		Intercept	Year (Before 2019)	Sex (Male)	Age (years)	Predator Index	Group Size
Degree	Estimate	1.333	0.232	0.088	-0.01976	-0.08929	-0.04292
	Std. Error	0.290	0.220	0.050	0.01225	0.19661	0.01816
	df	26.395	19.077	149.577	120.26300	18.61603	10.97798
	t value	4.590	1.057	1.738	-1.613	-0.454	-2.363
	P-value	**9.61e-05**	0.304	0.084	0.1093	0.6550	**0.0376**
Strength	Estimate	2.747	0.484	0.375	-0.13874	0.23834	0.08120
	Std. Error	0.632	0.505	0.116	0.02654	0.45116	0.03591
	Z value	4.347	0.958	3.230	-5.229	0.528	2.261
	P-Value	**1.38e-05**	0.338	**01.24e-03**	**1.71e-07**	0.59730	**0.02374**
Closeness	Estimate	4.270e-01	-4.779e-02	-1.122e-03	3.681e-03	-9.292e-02	8.144e-04
	Std. Error	1.037e-01	6.836e-02	1.318e-02	3.222e-03	5.989e-02	7.684e-03
	df	2.66e+01	2.161e+01	1.303e+02	1.356e+02	1.852e+01	2.213e+01
	t value	4.119	-0.699	-0.085	1.142	-1.552	0.106
	P-value	**3.3e-04**	0.492	0.93229	0.25529	0.13769	0.91655
Betweenness	Estimate	-1.037	-0.065	-0.-2357	0.08422	0.13073	-0.05713
	Std. Error	0.24425	0.14208	0.12598	0.03155	0.11870	0.01422
	Z value	-4.247	-0.454	-0.187	2.669	1.101	-4.017
	P-Value	**2.16e-05**	0.6497	0.8516	**0.0076**	0.2707	**5.89e-05**

Note: Results in boldface are considered statistically significant. Reference classes are female for sex, adult for age, and high for predator index. Variances of random effects were 0.001 for marmot ID, 0.070 for colony, and 0.120 for year for degree; 2.826e-09 for marmot ID, 2.082e-01 for colony, and 7.621e-01 for year for strength; 0.001 for marmot ID, 0.021 for marmot ID, and 0.001 for year for closeness; and 1.749e-02 for marmot ID, 2.687e-12, and 1.972e-12 for year for betweenness.

Table 3 The results of the general linear mixed models explaining variation in group-level social network measures.

		Intercept	Year (Before 2019)	Group Size	Local Predator Index
Density	Estimate	0.60414	0.43770	-0.08037	-0.35591
	Std. Error	0.57722	0.43111	0.03684	0.39662
	Z Value	1.047	1.015	-2.182	-0.897
	P-Value	0.2953	0.3100	**0.0291**	0.3695
Transitivity	Estimate	0.91262	0.25693	-0.01769	-0.22223
	Std. Error	0.54920	0.34142	0.04029	0.30622
	Z Value	1.662	0.752	-0.439	-0.726
	P-Value	0.0966	0.4517	0.6605	0.4680
Degree Assortativity	Estimate	-0.771075	0.137566	0.046460	0.099619
	Std. Error	0.137673	0.097152	0.009402	0.085476
	df	19.461366	15.765168	7.117784	15.561304
	t value	-5.601	1.416	4.942	1.165
	P-Value	**1.94e-05**	0.17623	**0.00159**	0.26139
Reciprocity	Estimate	1.295441	0.005037	-0.008978	0.029492
	Std. Error	0.577818	0.452435	0.034093	0.395518
	Z Value	2.242	0.011	-0.263	0.075
	P-Value	**0.025**	0.991	0.792	0.941
Cut Points	Estimate	-0.13653	-0.58977	0.04956	-0.05665
	Std. Error	0.69740	0.42689	0.05281	0.42771
	Z Value	-0.196	-1.382	0.938	-0.132
	P-Value	0.845	0.167	0.348	0.895

Note: Results in boldface are considered statistically significant. Reference classes were after 2019 for year (before 2019) and high for predator index. Variances of year, our only random effect, were, for each of the different network measures: 0.482 for density, 0.151 for transitivity, 0.015 for degree assortativity, and 0.458 for reciprocity.

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