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ARTICLE

Animal Ecology

Investigating the relationship between antipredator behavior and human disturbance using LiDAR imagery

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Abstract

The human-built environment influences the behavior and survival of many species, but most of these studies have been conducted in urban areas. Yet, anthropogenic development may impact species differently across scales, including at the rural level. We examined whether the built environment in a rural area obstructed visibility and influenced the antipredator behaviors of yellow-bellied marmots (*Marmota flaviventer*). We collected observational and experimental data around the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA, to analyze differences in maximum running speed, antipredator vigilance, propensity to alarm call, and flight initiation distance at both undeveloped and low human density developed sites. We calculated marmot viewscapes using high-resolution light detection and ranging (LiDAR) scans of marmot colonies and conducted visibility analyses to understand how overall visibility influences antipredator behaviors. We used mixed models to analyze the relationship between antipredator behaviors, development, and visibility. Development and visibility interacted to affect marmot vigilance: Animals in developed sites with highly variable visibility allocated more time to vigilance than animals in undeveloped, highly variable visibility sites, suggesting that despite the benefits of the human shield effect, living in close proximity to humans may increase risk perceptions more than living in undeveloped areas that had a similar level of visibility. We found no association between different intensities of development and visibility with maximum running speed, alarm calling propensity, or flight initiation distance. However, we found that marmots living in areas with highly variable visibility were less likely to emit alarm calls. We conclude that visibility analyses may be effective at explaining variation in some, but not all, antipredator behaviors. Our study provides a comprehensive and mechanistic examination of the ways in which human disturbance may affect behaviors with documented fitness consequences. We encourage continued consideration and study of human disturbance's impacts on wildlife behavior at the rural scale.

KEYWORDS
antipredator behavior, human development, human disturbance, LiDAR, visibility, yellow-bellied marmot

INTRODUCTION

Human encroachment on wild spaces has left many species facing novel challenges. Important habitat is fragmented (Hostetler et al., 2009) and humans and animals are forced to coexist (Theobald, 2010). Some species are well adapted to novel pressures, such as blue birds (*Sialia sialis*; Kight & Swaddle, 2007), common voles (*Microtus arvalis*; Mazza et al., 2020), and coyotes (*Canis latrans*; Schell et al., 2018), while others cannot thrive in an urbanized ecosystem and have reduced reproductive success and survival (Halfwerk & Slabbekoorn, 2013). Behavioral plasticity is crucial to survival in a human-dominated landscape. Wildlife may alter their behaviors to avoid potentially harmful encounters with people, often through shifts to nocturnality (Gaynor et al., 2018) or changes in movement patterns (Tolhurst et al., 2008; Zong et al., 2023), which may have deleterious fitness consequences (Leblond et al., 2013). Our knowledge of these phenomena is growing at a rapid rate, but as more people move into previously undisturbed areas, it is imperative to examine other ways that disturbance may influence wildlife behavior.

Most studies related to human disturbance have focused on high density, urban ecosystems. However, it is important to consider how coexistence may change behavior across scales (Uchida et al., 2021). In relation to human density across cities, the impact of disturbance on wildlife may not be linear (Bautista et al., 2021; Rostro-García et al., 2016) and so it is crucial to consider how wildlife respond to habitat encroachment across a human density gradient. At the low density, rural level, there are distinct challenges for wildlife. Elephants (*Loxodonta africana*) exposed to many tourists in South Africa experienced elevated stress levels (Szott et al., 2020). Rural development often facilitates predation on caribou (*Rangifer tarandus*) by wolves (*Canis lupus*), likely by increasing the efficacy of wolves in locating prey (James & Stuart-Smith, 2000; Leblond et al., 2013). Black bears (*Ursus americanus*) near development experience foraging benefits such as improved body condition and greater reproductive success but also show a decline in population growth and decreased female survivorship rates, highlighting an important fitness trade-off of living near disturbance (Johnson et al., 2020). Behavioral plasticity itself may also change with disturbance (Hewes et al., 2017), which indicates that species adapted to disturbance may still change crucial behaviors over time. Thus, it is imperative that human–wildlife coexistence research continues to maintain a focus on the mechanisms of these changes to facilitate effective conservation management of at-risk species.

Human disturbance-mediated changes in visibility may be an important predictor for explaining why these behavioral changes occur. Grizzly bears (*Ursus arctos horribilis*) have been observed to select for higher road visibility while traveling and lower road visibility while resting (Parsons et al., 2021), and red deer (*Cervus elaphus*) tolerated closer distances to roads and human recreation activities in areas with less visibility (Zong et al., 2023). European badgers (*Meles meles*) tended to occupy setts in open habitats that had visibility of roads (Jenkinson & Wheater, 1998). These changes suggest that species may be experiencing different pressures in areas of varying visibility near disturbance.

The risks associated with varying visibility may have large consequences for predator–prey relationships. Crimson rosellas (*Platycercus elegans*; Boyer et al., 2006) and white-tailed deer (*Odocoileus virginianus*; Lagory, 1986) forage more and allocate less time to antipredator vigilance in areas with high visibility. In low visibility areas, purple sandpipers (*Calidris maritima*) scan their surroundings more often while turnstones (*Arenaria interpres*) increase the duration of their scans (Metcalfe, 1984). Pygmy rabbit (*Brachylagus idahoensis*) flight initiation distances (FIDs) decreased with greater concealment by vegetation, which can be attributed to decreased perceptions of risk when hidden from predators (Camp et al., 2012). Chaffinches (*Fringella coelebs*) were more vigilant and had slower response times to predators when in higher vegetation due to visual obstruction (Whittingham et al., 2004), whereas fat sand rats (*Psammomys obesus*) were less vigilant in areas of high vegetation (Tchabovsky et al., 2001). Australian magpies (*Cracticus tibicen*) relied more on conspecific alarm calls when their visibility was obstructed (Ratnayake et al., 2021).

The varied responses of species in response to both high and low visibility indicates that some species may perceive lower visibility as a form of concealment from predators, while obstructed visibility may hinder threat detection for others. Conversely, some prey species may perceive high visibility areas as ideal for predator detection, but others may feel overexposed to threats.

Thus, these studies are highly context-dependent and require an understanding of the focal species' life history to make conclusive statements about its risk perceptions. As such, this phenomenon must be examined in more species.

Despite the many studies that focused on visibility's influence on antipredator behavior, the mechanisms involved in these studies are not examined in conjunction with human disturbance. Prey species adapt their antipredator behaviors in response to disturbance (Frid & Dill, 2002). Human-built structures may disrupt habitat visibility to a greater extent than would the area's natural physical characteristics, which may force prey species to allocate more time to antipredator behaviors instead of longer term fitness-improving activities, such as foraging or socializing (Metcalfe, 1984). Many prior studies that focused on the intersection between visibility obstruction and antipredator behavior assessed overall visibility of a space by manually quantifying general visibility or by controlling for visibility during experiments (Arenz & Leger, 1997; Boyer et al., 2006; Fiori et al., 2018). For an observational study, it is crucial to get an accurate representation of a habitat's visibility, which can be difficult depending on the topology of the landscape.

In recent years, light detection and ranging (LiDAR) technology has become more frequently used in ecological research (Vierling et al., 2008). In regard to visibility analyses, LiDAR has become a useful and precise tool for determining how habitat structure influences wildlife behavior. By sending a signal down to the ground and measuring the time it takes for the signal to be reflected, LiDAR drones and planes can estimate the elevations of both the ground and features attached to the ground, including natural and man-made structures like trees and buildings, respectively (Wandinger, 2005). These elevations can then be used in subsequent analysis to simulate physical obstructions to visibility across a landscape. Ucero et al. (2023) used viewsheds obtained via LiDAR data to determine that male houbara bustard (*Chlamydotis undulata fuertaventurae*) display locations were dependent on habitat visibility. LiDAR imagery has been used to understand deer (Zong et al., 2023) and grizzly bear (Parsons et al., 2021) tolerance of human disturbance. There is clear utility of using LiDAR in assessing landscape visibility; however, there have been only a few studies that used this technology to understand antipredator behavior, most of which have provided evidence that species may alter their perceptions of risk in differing densities of vegetation cover (Adams et al., 2023; Frazier et al., 2025; Olsoy et al., 2015). We aim to fill an important knowledge gap in how remote sensing can aid in predicting a prey species' antipredator responses to anthropogenic disturbance, using a well-studied population of yellow-bellied marmots (*Marmota flaviventer*).

Yellow-bellied marmots, hereafter referred to as "marmots," are facultatively social, behaviorally plastic rodents that live along a wide elevational and environmental gradient (Armitage, 1986, 1991; Blumstein, 2013, 2025; Floyd, 2004; Frase & Hoffman, 1980). Individual plasticity facilitates marmot persistence in a variety of environments, including near human settlements (Uchida et al., 2021). Marmots engage in many antipredator behaviors, including vigilance while foraging, alarm calling, and fleeing from threats. Past studies of marmots have shown that they acclimate to human presence and exhibit changes in these antipredator behaviors as a result, such as heightened vigilance when a camera is pointed at them (Uchida et al., 2022), and decrease their FID when repeatedly approached (Morgan et al., 2021; Uchida & Blumstein, 2021). Further, previous studies on this system have shown that changes in visibility (Bednekoff & Blumstein, 2009; Blumstein et al., 2004; Chmura et al., 2016) and disturbance (Li et al., 2011) impact these behaviors. Thus, marmots are an ideal system to study how antipredator behaviors are influenced by human-built obstructions to visibility.

Our study aims to identify whether differences in visibility in areas of human disturbance influence a suite of antipredator behaviors, including vigilance while foraging, FID, the propensity to alarm call, and maximum running speed (MRS). We predict that in disturbed areas with low visibility, vigilance and MRS will increase, while FID and the propensity to alarm call will decrease. Compensatory vigilance provides an opportunity for marmots to avoid predation by shortening the amount of time they spend on other fitness-improving activities, such as foraging (Bednekoff & Blumstein, 2009). Conversely, predators may use decreased visibility to stalk prey more effectively, as prey may not notice predators as quickly and must flee from a shorter distance (Whittingham et al., 2004), thus decreasing FID. Marmots may also prioritize flights to safety over deterring nearby predators by alarm calling, which would result in a decrease in alarm calling propensity. Fleeing from a shorter distance may require marmots to run faster to avoid predation, which would reflect an increase in MRS (Howland, 1974). Here, we combine LiDAR imagery and over 20 years of experimental and observational data to examine how remote sensing can aid in predicting changes in antipredator behavior of a behaviorally plastic prey species.

METHODS

Study area

We studied marmots in the upper East River Valley, in and around the Rocky Mountain Biological Laboratory

(RMBL) in Gothic, Colorado (38.9592° N, 106.9898° W), from April to September of 2002–2024. 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).

Marmots inhabited up to 12 colony sites of varying size in and around RMBL. Three colony sites were considered "developed" in that they had at least one main burrow (which was defined as burrows where marmots either hibernated or slept) located underneath a human-built structure. Nine colony sites were considered "undeveloped" and had no human development nearby. Substrate and slope across and within sites were relatively variable, from completely flat and grassy to rocky slopes that in places exceeded 45°.

Trapping and quantifying running speed

We baited Tomahawk live traps with horse feed (Omolene 100 horse feed; Ralston Purina) and set them near burrow entrances each morning before marmots emerged and in the afternoon on days when it was not too hot (>23°C) and at times when it was not snowing or raining. Traps were checked within 3 h of being set or earlier depending on temperature. Individuals were transferred into canvas handling bags, where they were given a unique symbol and were marked on their dorsal side with Nyanzol nontoxic fur dye to be seen from a distance (see *Observational methods* below). These symbols remain on the marmot's dorsal side until they molt in late July to early August (Mills et al., 2024), at which time they are trapped and re-marked. They were also given ear tags with unique four- to five-digit numbers on each ear. Sex and reproductive status were scored (on a 1–6 scale; for males: non-scrotal or scrotal [1–2]; for females: nipples present to lactating [3–6]).

MRSs were quantified each year from mid-May to early September. After an animal was processed in its handling bag, it was released and chased back to its burrow. Using a digital stopwatch, we recorded the time it took for the marmot to run a distance. A flag was dropped once the marmot started running quickly, and a second flag was dropped before it turned, entered its burrow, or moved onto a different incline or substrate. The distance between the flags was the timed interval, and we recorded the time and the distance run. We excluded runs that were not straight or those that were <1.5 s because such runs have a higher likelihood of error (Blumstein, 1992). We measured the incline in degrees and the substrate of the path taken by the individual. Substrate was categorized as either low vegetation (below marmot shoulder height) and dirt, stones and talus, or high vegetation (at or above marmot shoulder height).

Observational methods

From mid-April to early September, we conducted near daily behavioral observations at peak activity hours (07:00–11:00 and 16:00–18:00) (Armitage, 1962) with binoculars or a spotting scope at sufficient distances (20–150 m) from the focal marmot to avoid disturbance (Blumstein et al., 2009). Individuals were identified using unique fur marks.

Observers were trained to listen for marmot alarm calls during observation sessions. It was often difficult to locate the caller as calling bouts often lasted for only a few seconds; in these cases, we could not always confirm which individual called with certainty. To reduce any bias caused by this uncertainty, we only recorded calling bouts where the individual had been confidently identified.

Two-minute focal observations were conducted on identified individuals while foraging. The observer dictated into a recording device whether the individual was quadrupedal or bipedal foraging (later combined for analyses), quadrupedal or bipedal looking (later combined for analyses), locomoting, or out of sight (Blumstein et al., 2004). Observers scored the date of the focal, substrate (same categorizations as MRS), and number of other individuals within 10 m of the focal individual. Recordings were scored in JWatcher 1.0 (Blumstein & Daniel, 2007). Focal observations that were <60 s were excluded to account for any behavioral changes that may have ended the foraging session early and to ensure an accurate estimate of time allocation across behaviors.

Experimental methods

FID was recorded from mid-May to early September. We focused on solitary individuals that were relaxed (not alerting to our presence) and identified them using their dorsal fur marks. The trained observer dropped a flag to mark the location that the researcher began the experiment, whereupon they walked at a pace of 0.5 m/s in a straight line towards the focal individual and dropped flags along their path when they observed the individual alert to their presence (look in their direction) and when the individual fled. The observer then measured the distance from the first flag to the third flag to measure starting distance and the second flag to the third flag to measure FID. We also recorded the distance of the individual from the nearest burrow when it fled and substrate type (same categories as MRS). For FID experiments where the individual was too far away to see alerting and running with the naked eye, we sometimes used a "spotter" who communicated to the person walking by radio when the focal marmot alerted and fled.

Geospatial methods

Many marmot burrows are used across years and generations (Barash, 1989; Svendsen, 1976) with many occupied intermittently within and across years. In the summer of 2024, we collected precise (~60 cm) GPS coordinates of frequently used burrows across each colony using a Trimble Catalyst GNSS system (Trimble, Westminster, Colorado, USA). To quantify burrow use at each colony, we summed the number of times individuals were trapped at each burrow from 2002 to 2024. We applied a median split and burrows above the median were considered frequently trapped. Although we attempted to obtain GPS coordinates for all burrows of interest, one colony (Picnic) had multiple burrows that were categorized as above the median that had not been used for many years and thus were grown over and difficult to find. We excluded any of these burrows that we were not confident we could identify. However, the Picnic colony had 33 identifiable burrows (the most of any colony in our study), which was sufficient to accurately represent burrow distribution and use for our visibility analysis. These data across all colony sites were later concatenated into a shapefile for analysis.

Visibility analyses were conducted in ArcGIS Pro (Version 3.3) using the coordinate system "WGS 1984 UTM Zone 13N." We used a digital surface model (DSM) from the RMBL Spatial Data Platform that was created during a 2018 LiDAR flight across the Upper East River Valley of Colorado (Breckheimer, 2020; Chadwick et al., 2020; Goulden et al., 2020). We uploaded shapefiles of each colony's burrow coordinates as point layers. We used the Viewshed 2 tool (ESRI, 2025a) to perform the visibility analysis for each colony. For Viewshed parameters, analysis type was set as "Observers" and a unique observer–region relationship table was created for each analysis. For observer parameters, observer offset was 0.30 m, or the estimated height of a marmot's eyes standing and looking quadrupedally (Blumstein et al., 2006). The outer radius was set as a 3-D distance of 10 m. In a post hoc analysis, we also ran the Viewshed analysis with distances of 50, 100, 200, and 400 m, but determined that 10 m was a satisfactory distance because we are interested in examining how marmots assess immediate threats, which are typically observed from a close distance. Results of the Viewshed 2 analyses were exported using first the Raster to Polygon tool (uncheck "simplify polygons"; ESRI, 2025b) and then the Table to Excel tool (ESRI, 2025c). This process outputs count data of the number of 1-m^2 raster cells within the specified radius that are visible to an observer at a given burrow. We used this count data to calculate the mean visibility and the CV in visibility across each colony to represent the standard visibility and the variability in visibility throughout our study area, respectively. One of our colony sites ("Cliff") was small and only had one burrow included in analyses; thus, this colony's visibility could not be included in the CV measures.

Other variables

Predation index

During observation periods, researchers noted any sightings of predators that were seen or heard at the colony sites. The species observed, time, and location of sightings were recorded. The predation index was calculated as the proportion of predator sightings to the number of observation sessions at each colony per year. We used a median split to classify the predation index as "high" (at or above the median) or "low" (below the median; Monclús et al., 2011).

Valley position

Colonies were located on an elevational gradient. The higher elevation "up" valley sites typically experience harsher weather and a later start to the growing season than the relatively lower elevation "down" valley sites, with consequences for the total time individuals can forage across the growing season (Armitage, 2014). Therefore, we considered any colonies located at higher elevation as "up valley" and all colonies at relatively lower elevation as "down valley."

Development status

Colonies that had at least one burrow included in the analysis located underneath a human-built structure, such as a residence or research facility, were considered "developed" sites. All other colonies were considered "undeveloped." All developed sites contained built structures prior to the start of the study, and all undeveloped sites remained undeveloped for the entirety of the study.

Colony size

Colony size was determined as the total number of yearling and adult individuals living at a colony site between April and July each year, as this was before most yearlings dispersed and new juveniles emerged (Armitage, 2003; Downhower & Armitage, 1981).

Statistical analysis

All data manipulation and statistical analyses were conducted in R (Version 4.4.1; R Core Team, 2024). We centered and scaled all continuous independent variables using the "scale" function (R Core Team, 2024). We used the packages lme4 (Version 1.1-35.5; Bates et al., 2015), lmerTest (Version 3.1-3; Kuznetsova et al., 2017), and glmmTMB (Version 1.1.11; Brooks et al., 2017; McGillycuddy et al., 2025) to run linear mixed models and generalized linear mixed models and the packages performance (Version 0.12.4; Lüdecke et al., 2021) and DHARMa (Version 0.4.7; Hartig, 2024) to check model assumptions. Variance inflation factors (VIFs) for all models were less than five.

Are there differences in visibility across development status?

We ran permutation tests with 1000 iterations using the packages lme4 and lmerTest to determine whether mean visibility and the CV of visibility differed across development statuses (after transforming the visibility covariates and still failing to meet the assumptions of linear mixed models). For each permutation test, we included visibility as our dependent variable and development status as a main effect with colony as a random effect.

We compared models with the Akaike information criterion (AIC; Akaike, 1973) to determine whether to use models using mean visibility or the CV of visibility. Since our CV of visibility dataset did not include the "Cliff" colony and thus had fewer overall observations than the mean visibility dataset, we excluded all observations from the "Cliff" colony when we performed model selection.

Is maximum running speed affected by visibility and development?

We fitted a linear mixed model to explain variation in MRS. To avoid a ratio-correlation problem (Blumstein, 1992), we modeled log-transformed run time as our dependent variable. The AIC value for mean visibility at 10 m (−1020.7) was lower than that of the CV of visibility (−1020.4; Table 1). Thus, fixed effects included mean visibility at 10 m, age class (juvenile, yearling, or adult), valley position, predation index, development status, sex (male or female), distance run, substrate (Blumstein et al., 2004), incline of the run (Blumstein, 1992), and trial number (to control for potential habituation; Blumstein et al., 2015). We included an interaction between mean visibility at 10 m and development status to explain human impact on visibility. Random effects included colony, marmot identity, and year. Our dataset included 783 unique observations from 486 individuals collected over 23 years.

Is vigilance while foraging affected by visibility and development?

We fitted a zero-inflated generalized linear mixed model to explain variation in time allocation to vigilance while foraging. We modeled the total proportion of time allocated to vigilance as our dependent variable. Fixed effects included the CV in visibility at 10 m (Table 1), age class (juvenile, yearling, or adult), valley position, predation index, development status, sex (male or female), the number of other individuals within 10 m of the focal individual (Blumstein et al., 2004), substrate, incline (Chmura et al., 2016), and day of year. We included an interaction between the CV of visibility at 10 m and development status to explain human impact on visibility. Random effects included colony, marmot identity, and year. We used the beta family with a "logit" link function. Our dependent variable fell within the range [0, 1), so we accounted for zero-inflation using "ziformula = ~1." Our dataset included 3029 unique observations from 669 individuals collected over 23 years.

Is alarm calling propensity impacted by visibility and development?

We excluded individuals that were not observed alarm calling in a given year. In doing so, we modeled whether

TABLE 1 Akaike information criterion (AIC) values for each model, comparing models using either mean visibility at 10 m or the CV of visibility at 10 m.

Analysis	Mean visibility at 10 m	CV of visibility at 10 m
Maximum running speed	−1020.7	−1020.4
Vigilance while foraging	−2612.7	−2617.0
Alarm calling propensity	3450.5	3446.2
Flight initiation distance	421.67	424.71

our fixed effects impacted variation in alarm calling across known individuals, rather than whether they directly decreased or increased an individual's propensity to call. We also excluded pups from this analysis as they are only active for a short period of the season and thus their alarm calling propensity may be artificially decreased. We fitted a generalized linear mixed model to explain variation in the propensity to alarm call. We modeled the number of calling bouts per individual over a given year as our dependent variable. Fixed effects included the CV in visibility at 10 m (Table 1), age class (yearling or adult), valley position, predation index, colony size, development status, and sex (male or female). We included an interaction between the CV of visibility at 10 m and development status to explain human impact on visibility. Random effects included colony, marmot identity, and year. We set an offset since the log-transformed total time each colony was observed per year and used the "bobyqa" optimizer with 1,000,000 maximum iterations. Our dataset included 814 unique observations from 442 individuals collected over 23 years.

Is FID impacted by visibility and development?

We fitted a linear mixed model to explain variation in FID. We modeled the log-transformed FID distance as our dependent variable. Our fixed effects included age class (juvenile, yearling, or adult), valley position, predation index, sex (male or female), the distance from the burrow of the individual at the time of flight (Blumstein et al., 2004), day of year, and trial number. We included a three-way interaction between mean visibility at 10 m (Table 1), development status, and square root-transformed starting distance of the observer from the focal individual to explain human impact on visibility. Random effects included colony, marmot identity, and year. Our dataset included 1478 unique observations from 507 individuals collected over 19 years.

RESULTS

Visibility did not differ as a function of development status

Neither mean visibility nor the CV of visibility differed as a function of development status, developed or undeveloped (mean visibility: permutation $p = 0.884$; CV of visibility: permutation $p = 0.999$; Table 2).

TABLE 2 Results from the permutation tests to determine whether there were differences in mean visibility and the CV of visibility between developed and undeveloped sites.

Visibility metric	Permutation *p*
Mean visibility	0.884
CV of visibility	0.999

Maximum running speed was not influenced by visibility and development

The interaction between mean visibility at 10 m and development status did not have a significant effect on run time (Table 3). However, distance run (estimate = 0.107, $p < 0.001$) was positively associated with run time. Marmots ran more quickly on low vegetation/dirt as seen through the negative significant relationship with run time (estimate = −0.031, $p = 0.017$). No other variables explained significant variation in MRS.

Vigilance while foraging increased in developed areas with highly variable visibility

In the vigilance model, the interaction between the CV of visibility at 10 m and development status was associated with time allocated to vigilance; vigilance increased in developed sites with highly variable visibility and increased in undeveloped sites with low variability in visibility (estimate = −0.290, $p = 0.003$; Table 4; Figure 1). Juveniles were less vigilant than adults (estimate = −0.430, $p < 0.001$). Marmots were also less vigilant as the number of individuals within 10 m increased (estimate = −0.090, $p < 0.001$). Compared to high vegetation, marmots were more vigilant when foraging in low vegetation/dirt and stone/talus substrates (vegetation/dirt: estimate = 0.135, $p < 0.001$; stone/talus: estimate = 0.218, $p < 0.002$). No other variables explained significant variation in vigilance.

Alarm calling propensity was negatively influenced by visibility, but not by the interaction between visibility and development

The interaction between the CV of visibility at 10 m and development status did not have a significant effect on alarm calling propensity (Table 5). Yearling age class had a significant negative relationship with alarm calling propensity (estimate = −0.316, $p < 0.001$). Additionally,

TABLE 3 Results from the linear mixed model explaining variation in maximum running speed.

Fixed effects	Estimate	SE	*p*
Mean visibility × development status (undeveloped)	−0.018	0.012	0.166
Age class (juvenile)	−0.003	0.013	0.799
Age class (yearling)	0.001	0.015	0.945
Valley position (up)	0.003	0.014	0.863
Predation index (low)	0.008	0.012	0.775
Sex (male)	−0.010	0.009	0.297
Distance run	**0.107**	**0.005**	**<0.001**
Slope	0.004	0.004	0.345
Substrate (low vegetation/dirt)	**−0.031**	**0.013**	**0.017**
Substrate (stone/talus)	−0.010	0.017	0.564
Trial number	<−0.001	0.004	0.973
Mean visibility	0.012	0.008	0.244
Development status (undeveloped)	0.033	0.016	0.099

Note: Results in boldface are considered statistically significant ($p < 0.05$). The model includes 486 individuals from 12 colonies across 23 years, for a total of 783 unique observations. Reference classes are developed for development status, adults for age, down valley for valley position, high predation index, females for sex, and high vegetation for substrate. Variance for the random effects are as follows: marmot ID, <0.001; colony, <0.001; year, 0.002.

TABLE 4 Results from the zero-inflated generalized linear mixed model explaining variation in time allocation to vigilance while foraging.

Fixed effects	Estimate	SE	*p*
CV of visibility × development status (undeveloped)	**−0.290**	**0.099**	**0.003**
Age class (juvenile)	**−0.430**	**0.059**	**<0.001**
Age class (yearling)	−0.037	0.035	0.301
Valley position (up)	−0.067	0.127	0.598
Predation index (low)	0.065	0.043	0.130
Sex (male)	−0.037	0.036	0.296
No. individuals within 10 m	**−0.090**	**0.015**	**<0.001**
Substrate (low vegetation/dirt)	**0.135**	**0.037**	**<0.001**
Substrate (stone/talus)	**0.218**	**0.070**	**0.002**
Angle (10–30°)	−0.028	0.034	0.412
Angle (>30°)	−0.072	0.053	0.171
Day of year	<0.001	0.020	0.978
CV of visibility	0.115	0.083	0.168
Development status (undeveloped)	**−0.439**	**0.153**	**0.004**

Note: Results in boldface are considered statistically significant ($p < 0.05$). The model includes 669 individuals from 11 colonies across 23 years, for a total of 3029 unique observations. Reference classes are developed for development status, adults for age, down valley for valley position, high predation index, females for sex, high vegetation for substrate, and 0–10° for angle. Variance for random effects is as follows: marmot ID, 0.039; colony, 0.015; year, 0.016.

predation index had a negative effect on the propensity to alarm call (estimate = −0.215, $p = 0.005$). No other variables explained significant variation in alarm calling. We also performed a post hoc analysis where we removed the interaction effect and only included the CV of visibility and found that, in addition to the significant fixed effects, in areas of highly variable visibility, individuals' propensities to alarm call decreased (estimate = −0.27, $p = 0.001$; Table 6; Figure 2).

Flight initiation distance was not influenced by visibility and development

The interaction between the mean visibility at 10 m, development, and starting distance did not have a significant effect on FID (Table 7). Compared to adults, yearlings (estimate = 0.049, $p = 0.013$), but not juveniles (estimate = 0.041, $p = 0.167$), fled at greater distances. Marmots living with lower predator exposure fled at greater distances (estimate = 0.052, $p = 0.022$), as did marmots farther from their burrow when the FID experiment started (estimate = 0.051, $p < 0.001$). Marmots tolerated closer approaches as the season progressed (day of year: estimate = −0.001, $p = 0.027$), and the number of trials within a year increased (estimate = −0.020, $p = 0.018$). No other variables explained significant variation in FID.

DISCUSSION

Neither mean visibility nor variability in visibility was significantly different across development status as we measured it. However, this may be attributed to environmental characteristics, such as trees or boulders, acting as natural obstructions to visibility in a way that was similar to the low-density human-built structures. Thus, our subsequent analyses did not assume that development altered visibility; instead, they were designed to interpret whether being in a developed area and having low mean

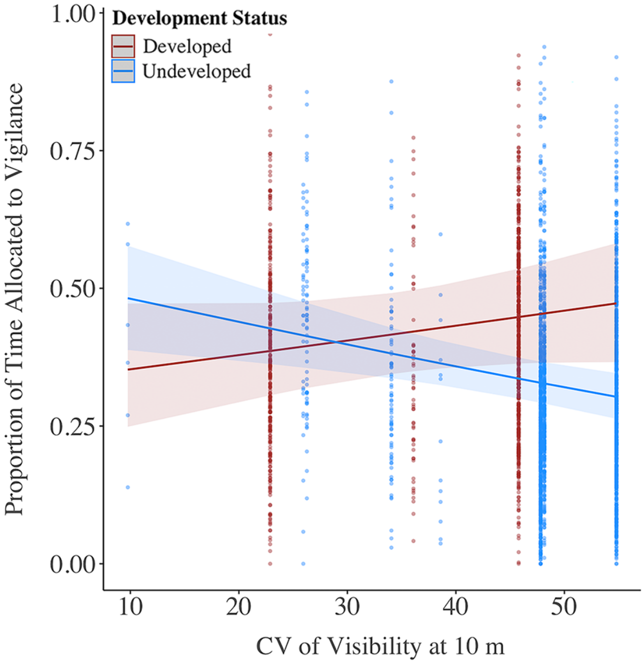

FIGURE 1 The relationship between the CV of visibility, development status, and time allocation to vigilance.

TABLE 5 Results from the generalized linear mixed model explaining variation in alarm calling propensity.

Fixed effects	Estimate	SE	*p*
CV of visibility × development status (undeveloped)	−0.016	0.186	0.933
Age class (yearling)	**−0.316**	**0.060**	**<0.001**
Sex (male)	−0.056	0.074	0.449
Valley position (up)	−0.079	0.220	0.720
Predation index (low)	**−0.215**	**0.077**	**0.005**
Colony size	−0.027	0.038	0.477
CV of visibility	−0.258	0.159	0.104
Development status (undeveloped)	0.228	0.273	0.403

Note: Results in boldface are considered statistically significant ($p < 0.05$). The model includes 442 individuals from 11 colonies across 23 years, for a total of 814 unique observations. Reference classes are developed for development status, adults for age, down valley for valley position, high predation index, females for sex, and high vegetation for substrate. Variance for random effects are as follows: marmot ID, 0.1609; colony, 0.045; year, 0.071.

visibility—or highly variable visibility—interacted to influence antipredator behavior.

Visibility in developed areas is selectively associated with antipredator behavior; marmots in disturbed areas with more variable visibility increased the time they allocated to vigilance while foraging. However, the interaction between visibility and development status was not associated with MRS, the propensity to emit alarm calls, or FID, signifying that these antipredator behaviors may be more influenced by other factors than visibility and development.

TABLE 6 Results from the post hoc analysis explaining variation in alarm calling propensity in relation to visibility, but not development status.

Fixed effects	Estimate	SE	*p*
CV of visibility	**−0.270**	**0.084**	**0.001**
Age class (yearling)	**−0.317**	**0.060**	**<0.001**
Sex (male)	−0.057	0.073	0.436
Valley position (up)	0.060	0.188	0.749
Predation index (low)	**−0.204**	**0.077**	**0.008**
Colony size	−0.027	0.039	0.486

Note: Results in boldface are considered statistically significant ($p < 0.05$). The model includes 442 individuals from 11 colonies across 23 years, for a total of 814 unique observations. Reference classes are adults for age, down valley for valley position, high predation index, females for sex, and high vegetation for substrate. Variance for random effects are as follows: marmot ID, 0.158; colony, 0.053; year, 0.071.

Marmots at disturbed sites with highly variable visibility were more vigilant than individuals in undisturbed sites that had similar variability of visibility. This may indicate that living in proximity to humans, combined with highly dynamic environmental visibility, may increase individual risk perceptions enough to outweigh the benefits of the human shield effect (Herrera, 2024). Species may adjust their responses to threats depending on their prior exposure to human disturbance (Tablado & Jenni, 2017). For example, gopher tortoises (*Gopherus polyphemus*) in human-dominated areas reacted faster to potential threats than did those in less human-dominated areas (Bateman et al., 2014). It is worth noting, however, that marmots near our developed sites are typically more tolerant of human presence, possibly due to compensatory vigilance (Uchida & Blumstein, 2021). Thus, further study is required to fully understand both the mechanisms that drive time allocation to vigilance in disturbed areas and whether living in proximity to human development can directly drive changes in prey risk perception.

Conversely, marmots at undisturbed sites with more consistent visibility exposure may be at greater risk than those in disturbed sites with similar cover. Undeveloped sites with consistent visibility—in particular, consistently high visibility—may leave marmots more vulnerable to predation, which may explain why time allocation to vigilance significantly increased at these sites. Time allocated to vigilance in high visibility areas varies across species (Quenette, 1990); white-tailed deer (Lagory, 1986) reduce their time allocation to vigilance in highly visible sites, whereas fallow deer (*Dama dama*; Schall & Ropartz, 1985)

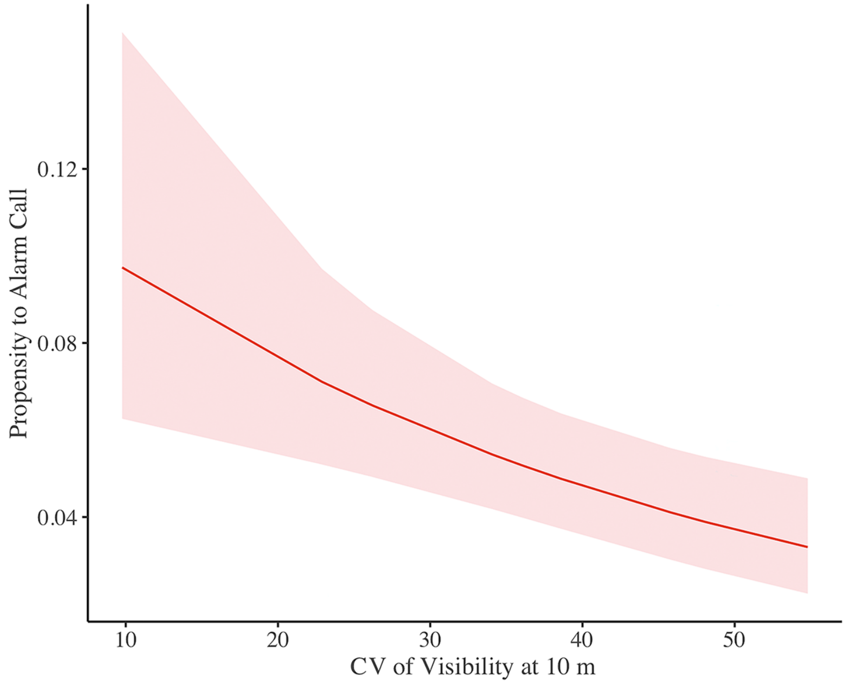

FIGURE 2 The relationship between the CV of visibility and the propensity to alarm call using the number of individual alarm calling bouts and a log offset for total observation time to represent alarm calling propensity.

increase vigilance. Obligate hibernators, like the yellow-bellied marmot, must gain sufficient mass during the growing season to survive harsh winters (Humphries et al., 2002). If individuals are allocating different amounts of time to vigilance based on their proximity to development, they may have divergent likelihoods of overwinter survival, an important fitness consequence. It is important to continue studying this phenomenon to better identify the mechanisms as to how human disturbance and visibility modulate antipredator behavior.

Visibility and development status may not be relevant to a marmot's instantaneous risk assessment, in that during the MRS experiments, the perceived threat was very close, requiring individuals to make immediate decisions on running velocity. This requirement may explain why we did not find a significant impact of visibility and developmental status on MRS. Additionally, running at top speed is energetically expensive (Blumstein et al., 2015) but may be essential for immediate survival when in a high-risk situation. Therefore, neither disturbance nor visibility levels may impact the individual's decision to flee at top speed. Energy expenditure may also explain our finding that running greater distances increased run time, which means that the marmots ran at a slower velocity. Marmots may run more slowly to avoid exerting excessive energy when they need to run longer distances. This is notable because running a greater distance necessarily implies that marmots are further from safety and are exposed to greater predation risks. Further study is needed to better understand how yellow-bellied marmots optimize their escape velocity.

Living in close proximity to people may provide a similar threat level to that of undeveloped areas. A notable observation is that for at least half the study period, one or more red foxes (*Vulpes vulpes*) inhabited our most developed Gothic town site. As such, the threat of predation in this site may be similar to that of our undeveloped sites. An additional explanation may be that individuals are habituated to human presence and thus are not tangibly affected by disturbance, resulting in them behaving similarly to how they would in an undisturbed environment. Our FID results reflect this habituation, as individuals allowed closer approaches as the number of trials increased, which is consistent with previous study in this system (Uchida & Blumstein, 2021).

In addition to habituation, FID may not have been impacted by visibility due to the nature of our data collection methods. Most FID trials began from far distances (mean starting distance = 61.2 m), and so visibility in the direct vicinity of the individual may not be as important in decision-making as other environmental factors. Future analyses may benefit from determining a relative visibility value for each FID experiment based on starting distance, rather than using a standard, predetermined radius. The large sample size of our dataset, combined with a lack of access to the precise GPS locations of individuals at the start of each experiment, makes this methodology infeasible for our longitudinal study, but may be useful in other systems.

TABLE 7 Results from the linear mixed model explaining variation in flight initiation distance.

Fixed effects	Estimate	SE	*p*
Mean visibility × development status (undeveloped) × start distance	−0.008	0.021	0.685
Age class (juvenile)	0.041	0.030	0.167
Age class (yearling)	**0.049**	**0.020**	**0.013**
Valley position (up)	0.121	0.061	0.089
Predation index (low)	**0.052**	**0.023**	**0.022**
Sex (male)	−0.035	0.020	0.081
Distance from burrow	**0.051**	**0.008**	**<0.001**
Day of year	**−0.001**	**0.049**	**0.027**
Mean visibility	0.061	0.040	0.209
Development status (undeveloped)	0.017	0.067	0.809
Start distance	**0.262**	**0.020**	**<0.001**
Mean visibility × development status (undeveloped)	**−0.156**	**0.050**	**0.028**
Mean visibility × start distance	<0.001	0.016	0.959
Development status (undeveloped) × start distance	−0.033	0.023	0.145
Trial number	**−0.022**	**0.009**	**0.018**

Note: Results in boldface are considered statistically significant ($p < 0.05$). The model includes 507 individuals from 11 colonies across 19 years, for a total of 1478 unique observations. Reference classes are developed for development status, adults for age, down valley for valley position, high predation index, females for sex, and high vegetation for substrate. Variance for random effects is as follows: marmot ID, 0.017; colony, 0.004; year, 0.003.

We also found no significant association between visibility and developmental status on the propensity to alarm call. However, our post hoc analysis, which found that the CV of visibility as a fixed effect was negatively associated with alarm calling propensity, may provide insight on the mechanisms that dictate alarm calling propensity. As variation in visibility increased, marmots alarm called less. High variation in visibility may signify a riskier environment, in that highly dynamic environments may make it more difficult for individuals to see approaching threats. Further, alarm calling can be costly—by remaining outside of the burrow to warn others of approaching danger, the caller may be at higher risk of predation (Blumstein, Adler, & Uy, 2025). If predators are able to make closer approaches before being seen, this compounded risk may lead to individuals fleeing to safety sooner instead of alarm calling. A recent study found that the propensity to alarm call in marmots, regardless of the purpose of the call, is a heritable trait (Blumstein, Velasquez, et al., 2025), but we know that much of the variation in the propensity to call remains to be explained. The decision whether to alarm call may not be affected by whether individuals inhabit a disturbed space. Given the lack of differences in visibility across developed and undeveloped sites, risk assessments may be impartial to human occupancy.

Future studies may benefit from employing a different metric for development. Our definition of a developed environment was chosen to match our hypothesis that built structures altered visibility. However, other quantifiable measures, such as pedestrian traffic or recreation types, may better represent the disturbance level of our sites. Other measures, such as bicycle presence, have been used in short-term studies within our system (Li et al., 2011), but due to the lack of available data across the entire study period we were unable to use other metrics to define development, which may have affected our outcomes.

Vulnerability to predation risk may also depend on habitat structure. Compared to situations when they were in high vegetation, in the models we fitted, marmots were more vigilant and ran faster in low vegetation/dirt substrates and stone/talus substrates, the latter result being consistent with Blumstein et al.'s findings (2004). This contradicts previous studies that found marmots to be more vigilant in taller vegetation and when their peripheral vision was obstructed (Bednekoff & Blumstein, 2009; Chmura et al., 2016). This may be related to higher risk of predation when individuals are more exposed, which would also explain the faster running speeds observed. In previous cases, cover can be interpreted as being more obstructive for marmots and preventing them from detecting predators, resulting in higher vigilance in obstructed areas. Our results suggest that cover may be protective—prey are shielded from predators, which provides them enough security to be less vigilant. Degus (*Octodon degus*; Vásquez et al., 2002) in open habitat increased their vigilance and the speed and duration of their bursts of intermittent locomotion. While our study did not consider time allocation to locomotion, it may be an important factor in understanding the true impact of habitat types on antipredator behavior.

CONCLUSIONS

Our use of remote sensing data contributes a novel approach to analyzing how landscape characteristics may influence wildlife behavior. We have shown that small-scale development, acting through its effects on visibility, may be selectively associated with variation in antipredator behavior. Interestingly, our comprehensive visibility analysis demonstrated that variation in visibility alone may also selectively affect antipredator behavior. It is likely that other prey species may be impacted by decreased visibility, including in relation to conspecific communication, sociality, habitat selection, or movement throughout a landscape, all of which have fitness consequences (Alves et al., 2013; Beauchamp and Blumstein, 2015; Kulik et al., 2012; Mayor et al., 2009; Sabol et al., 2020). Future studies should continue to disentangle the complicated impacts of urbanization on prey species across developmental scales and visibility gradients.

AUTHOR CONTRIBUTIONS

Katie A. Adler: Conceptualization; data collection; data analysis; visualization; funding acquisition; writing—original draft; writing—review and editing. **Daniel T. Blumstein:** Conceptualization; data collection; data analysis; funding acquisition; writing—review and editing. Both authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Center for Open Science's OSF repository: https://osf.io/m93zf/.

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