Biological Conservation 315 (2026) 111718

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

The landscape of no worries? Increased recreation exposure decreases the landscape of human fear in wildlife

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ARTICLE INFO

Keywords:
Antipredator behavior
Habituation
Human disturbance
Human mobility data
Landscape of fear
Recreation impacts

ABSTRACT

Recreation's expanding footprint increasingly overlaps habitats once considered refuges from human disturbance. Yet our ability to predict wildlife responses across broad spatial scales to balance recreational opportunities and wildlife refugia remains limited. We integrated data from an experimental audio playback study quantifying antipredator responses of large mammals to recreation noise with estimates of human use derived from fine-scale GPS data from smartphone applications. We tested whether variation in responses to recreation noises was mediated by exposure history to human presence and the reliability of human-associated cues. To evaluate potential behavioral mechanisms, we compared three competing hypotheses: (a) habituation or filtering, where responses decline with increased exposure or less tolerant individuals are excluded from high-use areas; (b) sensitization, where responses intensify with greater exposure; and (c) no relationship to exposure, with responses instead reflecting individual differences or seasonal drivers. Exposure intensity strongly influenced the probability of fleeing when recreation noises were played. Fleeing behavior was 22% lower in high-use areas relative to low-use areas during the previous month, with the reduction especially pronounced in species generally more sensitive to human presence. By combining behavioral experiments with human mobility data, we scaled predictions of wildlife behavior across an expansive National Forest and revealed how recreation reshapes the landscape of fear. Our results highlight a practical framework for managing human–wildlife coexistence. Strategic spatial or temporal zoning of recreation, including densification of new trail systems, may help preserve refugia for sensitive species while sustaining recreation access.

1. Introduction

Popularity of outdoor recreation, such as hiking, mountain biking, and motorized use, has been steadily increasing in recent decades (Outdoor Foundation, 2023). This trend is expected to continue, with mountain biking participation in the U.S., for example, projected to increase by as much as 119% by 2070 (from a 2012 baseline; White et al., 2023). The growth in outdoor recreation has been especially pronounced in the U.S. Rocky Mountain region, where the infrastructure to support recreational opportunities has expanded into previously undeveloped areas (Hansen et al., 2002). Most land management agencies have multiple-use mandates that include providing opportunities for

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https://doi.org/10.1016/j.biocon.2026.111718
Received 3 September 2025; Received in revised form 18 January 2026; Accepted 22 January 2026
Available online 28 January 2026
0006-3207/Published by Elsevier Ltd.

outdoor recreation while conserving natural resources such as wildlife. Increasingly, there is concern that these two objectives may be at odds with one another. Accessing nature has been shown to have significant positive effects on human well-being (Díaz et al., 2015; Huynh et al., 2022), and yet, in a global survey of protected area managers, 55% listed outdoor recreation as a threat to biodiversity (Schulze et al., 2018).

Recreational activities, in the form of both motorized (e.g., off-highway vehicles) and non-motorized activities (e.g., hiking, biking), can negatively impact wildlife by producing sensory cues—sound, movement, and visual presence—that mimic those of predators ("risk-disturbance hypothesis"; Gill and Sutherland, 2000; Frid and Dill, 2002; Sih et al., 2010). As such, short-term antipredator behaviors to recreation exposure include behavioral responses such as vigilance and fleeing (Borkowski et al., 2006; Jayakody et al., 2008). Repeated and longer-term exposure can result in increased stress (Creel et al., 2002; Thiel et al., 2011; Piñeiro et al., 2012), temporal shifts in activity patterns to avoid human daytime use (Coppes et al., 2017; Sytsma et al., 2022), or avoidance of recreation areas altogether (Patten and Burger, 2018; Heinemeyer et al., 2019). These behavioral and physiological impacts can result in reduced foraging times (Duchesne et al., 2000; Smith et al., 2017), limited access to high-quality habitat (Ciuti et al., 2012; Dwinnell et al., 2019), and altered movement patterns (Naylor et al., 2009; Gill et al., 2024), which may collectively impact energy balance, body condition, and ultimately, fitness.

At the same time, these responses are not uniform across species or contexts. Several studies report limited or context-dependent effects of recreation (Marion et al., 2024), or argue that some negative effects are overstated (Bateman and Fleming, 2017). Sensitivity to recreational disturbance tends to increase with trophic level (Burton et al., 2024) and body size (Shamoon et al., 2018; Salvatori et al., 2024). Hunting can further modulate responses to non-lethal human recreation activities, with some studies showing that hunting pressure can either heighten sensitivity to human cues or, in some systems, decouple responses to recreation from hunting risk (e.g., Zenth et al., 2025). There is also evidence of threshold effects where levels of recreation may be tolerated up to a point (Taylor and Knight, 2003; Dertien et al., 2021). Beyond individual responses, high-use recreation areas have been linked with reduced species richness and shifts in community composition compared to areas with restricted access (Reed and Merenlender, 2008; Reed and Merenlender, 2011). In particular, high-intensity, spatially dispersed recreation may be especially impactful due to the widespread and unpredictable nature of human activity, particularly when it occurs off established trails or in unmanaged areas (Wilson et al., 2020). Collectively, these patterns indicate that recreation can reshape both individual behavior and community structure, but suggest that different forms or levels of human use elicit different responses from wildlife. Thus, discerning the connections between response and recreation types and intensity of use is critical for informing both recreation and wildlife management.

The effects of recreation on wildlife may be far-reaching because animals often hear recreationists before observing them visually. Outdoor recreation noise, even from non-motorized recreation, can travel long distances and cause auditory encounters off-trail (Gump and Thornton, 2023), resulting in behavioral and space use changes (Zeller et al., 2024). Our study expands on questions raised by Zeller et al. (2024), who were the first to examine the impacts of recreation noise on terrestrial mammals. They demonstrated that wildlife exposed to recreation noises were far more likely to flee and engage in vigilance behavior compared to control (no sound and natural sound) treatments, and that local abundance of wildlife was significantly lower at the site following a week of recreation noise treatments. However, antipredator behaviors in the study varied; the probability of fleeing was less than 30% and the average proportion of time an animal in a video displayed vigilance behavior was ~30–40% – leading to several follow-up questions (Gaynor and Green, 2024), including whether, and under what conditions, wildlife show tolerance to recreation noise.

Addressing questions concerning individual tolerance to recreation disturbance requires data on background exposure of wildlife to the temporal patterns, distribution, and intensity of human presence across meaningful ecological scales. Repeated exposure to sensory cues associated with human presence, such as recreation noises, may allow animals to perceive such activities as benign. However, mismatches between actual and perceived risk are common, and human activity can reshape the landscape of fear in ways that diverge from predation risk (Gaynor et al., 2019). For example, unpredictable or novel human cues may exaggerate fear responses and lead to costly habitat avoidance (Taylor and Knight, 2003), while predictable, repeated exposure can facilitate habituation and either better align actual predation risk or disconnect the cues from true risks (e.g., human hunters or predators; Smith et al., 2021). Whether such shifts toward reduced fear are desirable is dependent on management goals. For example, fostering safe, predictable human use (e.g., concentrating recreation on designated trails or visual barriers) such that wildlife can habituate without increased mortality risk (Weston et al., 2012; Smith et al., 2021) may be an objective in one location, whereas in systems with high hunting, poaching, or vehicle-collision risk, increased tolerance to humans may be maladaptive. Recognizing how recreation alters the landscape of fear is therefore critical for predicting wildlife responses and informing management decisions, including setting thresholds and considering buffers around sensitive life history areas during certain times of the year (e.g., breeding season). Predictive maps leveraging human mobility data (HMD), such as the one developed here, represent one potential tool for assisting managers in tailoring actions at both fine scales and across broad areas.

Incorporating static measures of infrastructure, trail systems, or recreation areas, without a measure of their dynamic usage, is often insufficient for measuring human exposure for wildlife at fine spatio-temporal scales. Numerous studies have successfully used camera trap imagery of humans to measure the intensity of recreation use coincident with wildlife occupancy and activity patterns (e.g., Suraci et al., 2021; Sytsma et al., 2022). However, like trail counters, camera traps cannot collect data beyond their limited field of view. The effectiveness of camera grids to measure exposure at broad scales is limited and cost prohibitive, particularly in areas with dispersed recreation, multiple recreation types, while highly mobile species may encounter several recreation areas. Measuring behavioral responses of wildlife to human activity at relevant spatial and temporal scales is difficult, leading to the use of novel data streams (Corradini et al., 2021; Ellis-Soto et al., 2023). Anonymized human mobility data (HMD) addresses many of these shortcomings by providing the movement data of smartphone locations at fine spatial and temporal scales and is comprised of GPS locations of users from many smartphone applications. HMD is being recognized by conservation biologists as potentially "transformative" for guiding resource management, sustainable development (Oliver et al., 2024), and wildlife management (Abernathy et al., 2025a).

To develop a more mechanistic understanding of human-induced behavioral changes, we tested whether exposure to different types and amounts of human presence was linked with wildlife tolerance for recreation noise. Importantly, because recreation exposure is persistent on many of our public lands – particularly during warmer months when many wildlife species are rearing young – wildlife responses dictate whether recreation may have long-term detrimental effects, or if wildlife habituation will mitigate initially detrimental impacts (e.g., Slauson et al., 2017; Salvatori et al., 2023). Here, we used HMD to map and quantify outdoor users and vehicles, developing metrics of exposure to human presence across a large swath of the Bridger-Teton National Forest, Wyoming, USA. Our estimates of human exposure were combined with behavioral observations of several mammal species being exposed to recreational noises from an experimental acoustic playback design (Zeller et al., 2024). To explain variation in wildlife antipredator responses to recreation recorded in Zeller et al. (2024), we considered three competing behavioral mechanisms—habituation, sensitization,

and cue unpredictability—that differ in their ecological basis and expected outcomes based on exposure history and the reliability of human-associated cues:

- *Habituation hypothesis:* antipredator responses are less likely in areas with increased exposure to human presence. Here, we predict that wildlife that are regularly exposed to human presence will associate the sensory cues accompanying recreation as benign and exhibit habituation responses to playback of recreating humans (Bejder et al., 2009).
- *Sensitization hypothesis:* antipredator responses are more likely in areas with greater exposure to human presence. Hunting for all of the mammal species considered in this study occurs within our study sites on the Bridger-Teton National Forest; therefore, wildlife that experience more human presence may struggle to differentiate true perceived threats (e.g., hunting, vehicle strikes) from benign human stimuli due to an overlap in the cues for both hunting and recreation (Kays et al., 2017). As such, individuals with more exposure to human activities may increase antipredator behaviors (i.e., sensitization).
- *Null hypothesis:* antipredator responses remain unchanged with increasing exposure to human presence. Here, there will be no detectable relationship between the response of wildlife at our experimental sites and exposure to recreationists nor vehicular traffic levels. Differences among the various types, group sizes, and human behaviors create highly unreliable cues for wildlife to pair an appropriate response, resulting in a similar frequency of antipredator behavior regardless of background exposure (Smith et al., 2021). Under this hypothesis, differences in the responses to recreational noise are either random or driven by individual personality or time of year, regardless of exposure levels.

We discuss the implications of our results and consider ways to further leverage our approach for the confluence of recreation management and biodiversity conservation.

2. Methods

2.1. Study area

The Bridger-Teton National Forest (BTNF) is situated in the northwestern corner of the state of Wyoming (USA; Fig. 1) and contains ~1.4 million hectares of National Forest System lands and >4000 km of trails. Unlike its national park neighbors, additional forms of motorized (e.g., off-highway vehicle [OHV] trail riding) and off-trail non-motorized recreation (e.g., shed hunting, big game hunting, trapping) are allowed on the BTNF. The U.S. Forest Service estimates ~2.2 million people visit the BTNF annually, but abundance is difficult to measure on National Forest lands where there are numerous unmonitored entrance points and no entrance fees. The mammal community on the BTNF includes 74 species with several large predators (grizzly & black bears [*Ursus arctos horribilis*, *Ursus americanus*], wolves [*Canis lupus*], cougars [*Puma concolor*]) and ungulates (bighorn sheep [*Ovis canadensis*], elk [*Cervus canadensis*], moose [*Alces alces*], mule deer [*Odocoileus hemionus*], pronghorn [*Antilocapra americana*]) present.

2.2. Recreation noise experimental setup and behavioral classification

We used the data collected by Zeller et al. (2024), an experimental noise playback study designed to discern whether recreation noise alone, and various characteristics of the recreationists (e.g., type, group sizes), influenced mammal behavior and space use. The experiment was conducted at 20 sites distributed across the Jackson, Blackrock, and Greys River Ranger Districts of the BTNF during 2022 (June 20th-October 9th) and 2023 (June 5th–September 26th; Fig. 1). Each site consisted of a four-camera array along game trails with speakers

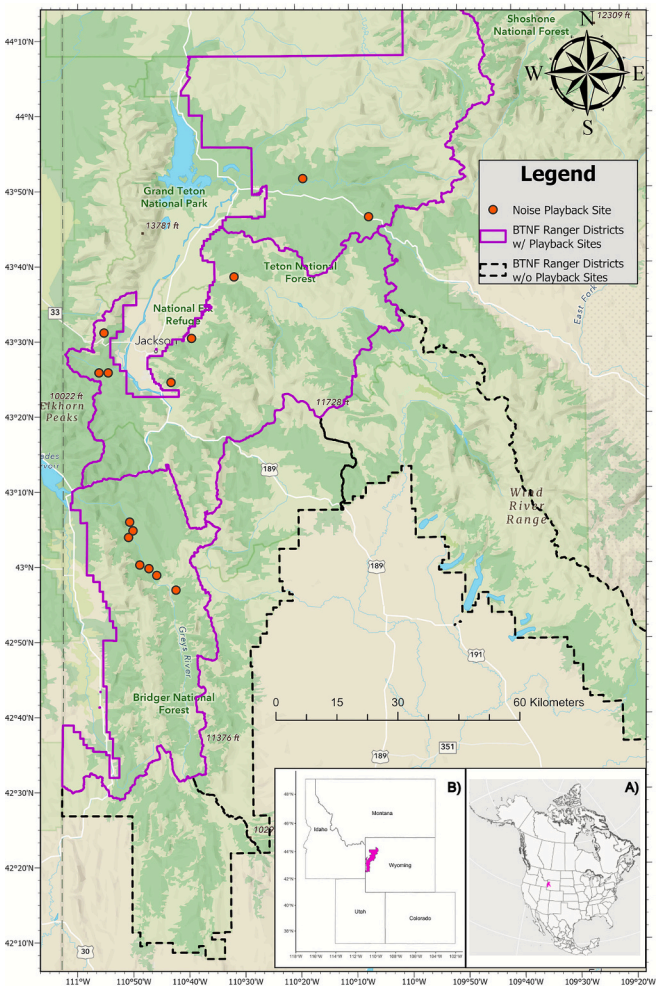

Fig. 1. Map depicting the Bridger-Teton National Forest (BTNF) with designations with ranger district boundaries. Using human mobility data within the Jackson, Blackrock, and Greys River Ranger Districts (shown in purple), we assessed how exposure to recreation and vehicles influenced the antipredator behaviors recorded in a study by Zeller et al. (2024). The locations of the 15 experimental recreation noise playback sites from Zeller et al. (2024) are shown as orange points. Inset (A) shows the entirety of the BTNF within North America and inset (B) shows the 3 ranger districts with noise playback sites within some of the western United States. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

positioned centrally to broadcast playback sounds. At each sampling site, recreation noises, control natural sounds, or no noise (null) were triggered when an animal passed by a camera trap. The recording was played by speakers placed ~20 m ahead of the animal at the same decibel level as the recreation or natural event that was recorded, and an array of other camera traps continuously monitored all subsequent behaviors. Results from Zeller et al. (2024) indicated there was no difference between wildlife responses to nature sounds vs. no sound playback; demonstrating that responses to the recreation sounds were not simply a startle response. Behavioral data, focusing on antipredator responses of fleeing and time spent vigilant during the noise playback, were classified using BORIS (Behavioral Observation Research Interactive Software), an open-source event-logging program for behavioral video analysis (v.7.13; Friard and Gamba, 2016). In addition, it was noted if the animal or groups of animals were with yearlings, which was expected to impact behavior. The U.S. Forest Service Research and Development IACUC approved the study design (permit #: 2022–007). See Supplemental Methods or Zeller et al. (2024) for more details.

2.3. Human mobility data: overview and general processing

We purchased anonymized human mobility data (HMD) to assess exposure to recreation and vehicular traffic. The data, managed by Unacast, Inc., was sourced from software development kits integrated into a wide variety of frequently used mobile applications that collect GPS locations. Data were collected from anonymized consenting users across the United States, which comply with the California Consumer Privacy Act and the European General Data Protection Regulation. The HMD is derived from various smartphone applications and sampled to maintain a generally consistent percentage of users across the United States. Estimates from Unacast Inc. suggest data are drawn from ~10–15% of total undisclosed smartphone users. By sourcing locations across a variety of smartphone applications instead of recreation only, we are able to better quantify vehicle road use, off-road motorized recreation use, and off-trail users (e.g., shed hunting) beyond the road and trail systems.

HMD does not rely on cellular service to acquire a GPS location, providing the ability to capture backcountry use in the BTNF. While some HMD sourced from other providers has shown a relative bias between urban and rural areas (Li et al., 2024), we used our data to compare relative use among backcountry sites, and we considered both the number of locations and the unique number of users. We removed HMD locations with flags suggesting potential unreliability (e.g., impossible rates of movement). We then classified HMD locations into three categories of smartphone users: 1) inside buildings, 2) vehicles, and 3) outdoor users. We considered any locations ≤20 m from a building footprint (Microsoft Building Dataset) as a user inside a building and removed them from our dataset. We classified locations ≤50 m of any public roadway (including highways to unpaved forest roads) as likely vehicular traffic (U.S. Geological Survey, 2023). This assumption may result in some foot traffic being assigned a "vehicle" classification on unpaved roads, but this percentage is small relative to motorized traffic on these roadways. Any locations not classified as on a roadway or in a building were considered outdoor users.

2.4. Variable creation

We created two response variables based on antipredator responses: 1) a binary (0/1) measure of whether or not there was fleeing behavior within an event, and 2) the proportion of time an individual(s) spent vigilant during an event throughout the time the animal was present in the video. We considered an event to contain fleeing behavior if any single animal within the video fled when subjected to the recreation noise (for herds, this typically meant the entire herd fled). Information on non-HMD variables can be found in the Supplemental Methods. Using the HMD filtered to the boundaries of the BTNF, we calculated metrics for the number of unique smartphone users by counting the number of unique anonymized IDs (each phone is assigned an anonymous ID) and the total number of smartphone locations collected around each sampling site at three spatial scales (1 km, 3 km, 5 km) and four temporal scales for both vehicle and outdoor user classifications (e.g. Fig. 2). We assumed each user in the HMD was carrying a single device. See Supplemental Methods for information on the scales selected and handling of outliers. We scaled the data within each sampling year to account for any potential annual bias in data sampling, which allowed us to assess relative human use around each site.

2.5. Statistical modeling, effects plots, and mapped predictions

Logistic models describing the probability of fleeing contained additive effects for all base variables (Day of Study, Precipitation, Wind, Sun Position, With Young, Noise Treatment [see Supplemental Methods for full description]) and included random intercepts for the sampling site and the observer of the animal behaviors. We fit these models using the package 'glmmTMB' (Brooks et al., 2017). For each multi-species model, we included all base model variables and included a single HMD-based measure at a time. HMD derived variables differed based on 1) whether they measured vehicle users or outdoor users, 2) the spatial buffer around each experimental site for including cell phone locations (i) 1 km, ii) 3 km, or iii) 5 km) and, 3) the temporal scale for inclusion prior to the observation at the experimental site (i) 7 days prior, (ii) 30 days prior (1 month), (iii) from the beginning of the experiment within

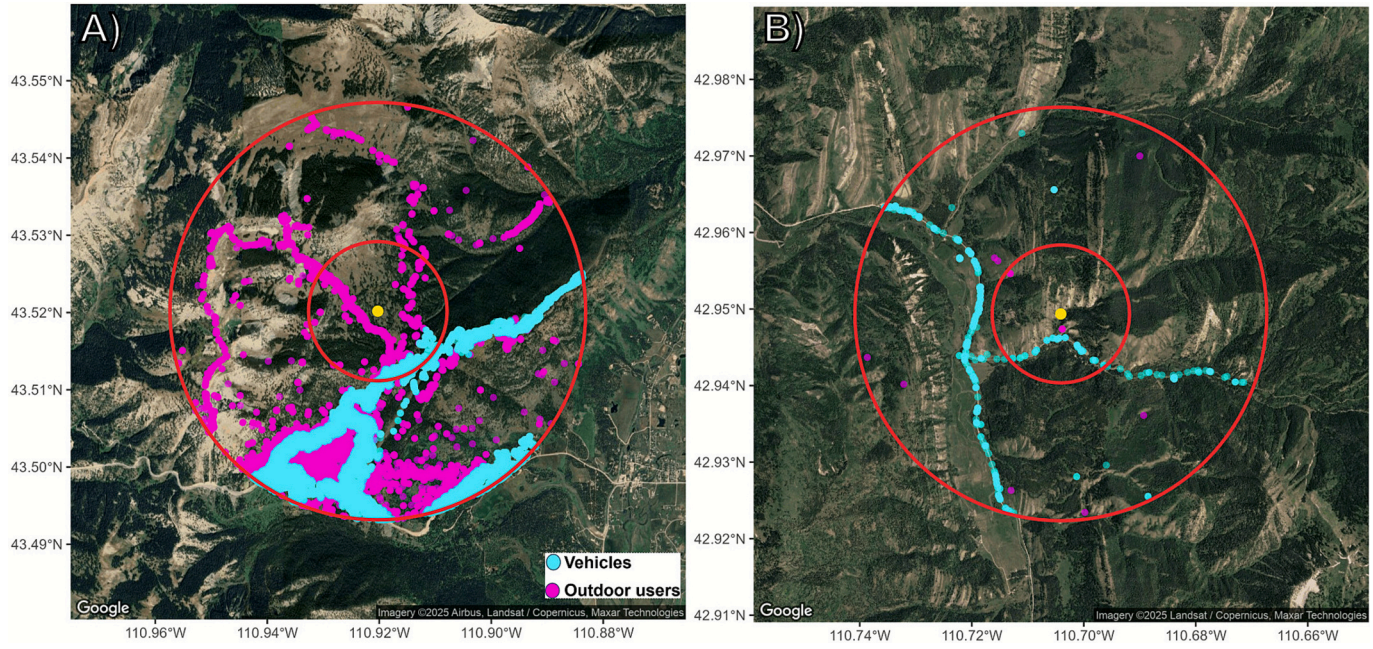

Fig. 2. Locations of anonymized smartphone users, classified as either outdoor users or vehicles, shown at multiple spatial scales around sites near A) Teton Pass/Philip's Ridge site on the Jackson District and B) Blind Bull Creek on the Greys River District of the Bridger-Teton National Forest. The center yellow point indicates the sample site, while the inner circle contains locations within 1 km of the sampling site. The second circle shows locations that were within 3 km. Our analysis also considered a 5 km spatial buffer as well. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

each year (i.e., totals since season start to event date), and (iv) the total for the entirety of the experiment within each year (i.e., annual totals during the period the noise experiment was conducted). Finally, we represented 4) all these metrics based on whether we counted the raw number of cell phone locations or only counts of unique cell phones. We chose the temporal scales to represent very recent, moderate (i.e., to reduce the influence of recent weather events which may impact recreation or traffic use), and longer-term average scales of use. We considered including paired HMD-metrics at a given spatial and temporal scale, based on either total cell locations or unique users, for both our estimates of vehicles and outdoor users. However, counts of locations and unique users were highly positively correlated across spatio-temporal scales between vehicle and outdoor users (max $r = 0.7$). We included each HMD variable as either linear or using natural cubic spline (with 2 degrees of freedom; to assess non-linear relationships) fits and compared all models using BIC.

Vigilance is a muted antipredator response relative to the act of fleeing, which requires a higher energy expenditure. We 1) assumed that the factors that elicited a fleeing response in some should also be associated with vigilance and 2) wanted to see if there was a tradeoff between the behaviors using the same variables. As such, using the same covariates as the top model describing the probability of a fleeing event, we fit a beta regression model with the proportion of time vigilant during an event as the response variable. Vigilance proportions of 0.0 and 1.0 were converted to 0.01 and 0.99, respectively, to fit the model. For the model describing the proportion of time spent vigilant, we again tested the linear and natural cubic spline fits for the HMD metric from the top model describing fleeing probability. Our goal was to determine how our measures of human presence impacted the mammal community across our sites. We treated responses from all large-bodied species as representing a community-level response and included a random intercept for experimental site to account for differences in overall detection and local conditions among sites. For both our top models describing fleeing probability and the proportion of time vigilant, we ran species-specific models based on our top models using observations from elk, mule deer and carnivores (cougars, wolves, and coyotes). We chose to assess how these species, or species groups, responded specifically because they represented the most different responses to recreation noise in Zeller et al. (2024). Elk were the most responsive and likely to flee while mule deer and large carnivores were the least (See Supplemental Methods for additional details). We calculated effect sizes when recreation noises were present (Noise Treatment = "Recreation Sounds") using the 'emmeans' R package (Lenth, 2023). All analyses were conducted using R (R Core Team, 2024). We created a predictive surface of fleeing from our top model to map wildlife behavior as a function of recreation across 3 districts of the BTNF (see Supplemental Methods for additional details).

3. Results

During the summers of 2022–2023, our sampling sites recorded 4444 trap nights and obtained 913 audio trigger events of wildlife exposures to either recreation noise or null treatments. Behavioral information regarding whether an individual fled, and the proportion of time spent vigilant, was classified into unique event sequences for 640 mule deer (*Odocoileus hemionus*), 122 elk (*Cervus canadensis*), 74 red fox (*Vulpes vulpes*), 51 black bear (*Ursus americanus*), 50 moose (*Alces americanus*), 54 pronghorn (*Antilocapra americana*), and a combined predator category consisting of 17 cougars (*Puma concolor*), 8 coyotes (*Canis latrans*), and 5 gray wolves (*Canis lupus*). The number of HMD locations varied greatly among our sampling sites (Fig. 2). For example, the Blind Bull Creek site, at the southern extent of our study area on the Greys River District, received minimal vehicular traffic (daily maximum HMD locations: 1 km = 14; 3 km = 124; 5 km = 215) and even fewer HMD locations associated with outdoor use (daily maximum HMD locations: 1 km = 1; 3 km = 2; 5 km = 6). In contrast, the Philip's Ridge site in the heavily recreated Jackson District had large amounts of both vehicles (daily maximum HMD locations: 1 km = 271; 3 km = 11,909; 5 km = 31,794) and outdoor users (daily maximum HMD locations: 1 km = 551; 3 km = 884; 5 km = 1457).

All top three models incorporated the measure of unique counts of outdoor users at the 3 km radius spatial scale, with the top model using the temporal scale of the previous 30-day count (Table 1). The 3 km spatial scale was the most supported – the top 14 models, and 19 of the 23 models that ranked higher than the base-only model, had HMD data at the 3 km scale. Models using metrics with unique cellphone users outperformed those with counts of all raw cell phone locations (the top 3 ranked models and 7 of the top 10 included unique user count metrics) and models that included outdoor user metrics outperformed those with vehicle count estimates (all of the top 10 ranked models and 16 of the 23 that outperformed the base model included outdoor user metrics) despite the generally high positive correlation between them. The top models concurred for most human activity aspects except for temporal scale, although most top models included either the monthly or summer to date measures.

Based on the top model describing the probability of fleeing, wildlife were less likely to flee from our noise playbacks if greater numbers of unique outdoor smartphone users were in the area during the previous 30 days (HMD for the 3 km radius and 30-day temporal scales, linear fit; $\beta = -0.62$; 95% CI = −0.92, −0.33; $p < 0.001$; Tables 1 & 2; Fig. 3A). Wildlife fleeing probability was far greater when recreation sounds were played relative to the null treatments ($\beta = 1.41$; 95% CI = 1.06, 1.75; $p < 0.001$; Table 2). If exposed to any recreation noise, wildlife with the least exposure to outdoor users were predicted to flee 26.3% (95% CI = 17.6%, 37.5%) of the time. In contrast, wildlife living in areas with the greatest amounts of outdoor use were predicted to flee in just 4.3% (95% CI = 1.7%, 10.8%) of exposures. Consequently, spatial predictions from our top model illustrate the elevated tolerance for outdoor human presence closer to towns and associated trail systems throughout our study area (Fig. 4). More daylight was also associated with elevated fleeing probability ($\beta = 0.01$; 95% CI = 0.00, 0.01; $p = 0.03$; Table 2).

Wildlife spent less time vigilant and were more likely to flee if they experienced few outdoor users (Fig. 3B; Table 2). The non-linear fit suggests that wildlife also spent less time vigilant when they were exposed to higher amounts of outdoor users (Fig. 3B). Compared to the null treatment, exposure to recreation noise was the only other significant variable (Table 2).

3.1. Species-specific responses

Elk were far less likely to flee in times and areas where exposure to outdoor users was highest ($\beta = -0.73$; 95% CI = −1.21, −0.25; $p < 0.01$; Supp. Table 1) – a reduction from 40 to 45% probability of fleeing in areas with the least outdoor user exposure to 5–7% in areas with the most exposure (Supp. Fig. 1). Mule deer showed a negative association between outdoor user exposure and fleeing probability (Mule Deer: $\beta = -0.19$; 95% CI = −0.49, 0.12; $p = 0.23$; Supp. Table 1). The carnivore group only occurred in times and places with low outdoor user exposure (range of scaled recreationist counts: carnivores = −0.49 to −0.28; mule deer & elk = −0.49–2.92). For both, the effect sizes were small, and the large variation in responses among mule deer, and low sample sizes for carnivores resulted in large confidence intervals that overlapped zero for the measure of exposure in both models (Supp. Fig. 1, Supp. Fig. 2). Like the combined species model, elk vigilance time was shortest at both the lowest and greatest outdoor user exposure levels (Supp. Fig. 2). Mule deer and carnivore vigilance levels were not influenced by outdoor user exposure (Supp. Figs. 1 & 2; Supp. Table 2).

4. Discussion

Given the increasing recreational use of important wildlife habitats, it is critical to determine the degree to which wildlife can tolerate

Table 1
Description of human mobility data metrics from the top four models (based on BIC) describing fleeing probability of wildlife exposed to recreation noise treatments within the Bridger-Teton National Forest in northwestern Wyoming (USA). The base model, with no human mobility data variable, is listed after the top four models.

HMD measure	User type	Spatial scale - HMD	Temporal scale - HMD	HMD fit	Degrees of freedom	BIC	Delta BIC	Model rank
Unique users	Outdoor user	3 km	30 Day	Linear	10	1855.4	0	1
Unique users	Outdoor user	3 km	Summer to date	Natural cubic splines	11	1857.5	2.2	2
Unique users	Outdoor user	3 km	Summer average	Natural cubic splines	11	1860.2	4.9	3
Total locations	Outdoor user	3 km	Summer to date	Linear	10	1860.3	4.9	4
None - base model only	NA	NA	NA	NA	9	1872.6	17.2	21

Table 2
Model output from the top model – determined by BIC - describing fleeing probability of wildlife exposed to recreation noise treatments on the Bridger-Teton National Forest in northwestern Wyoming (USA), and the associated output from the same model fit to the proportion of time spent vigilant.

Response	Variable	Estimate	95% CI	z value	*p*-Value
Fleeing probability	Intercept	−2.68	(−3.27, −2.09)	−8.91	<0.001
	Noise treatment: recreation sounds	1.41	(1.06, 1.75)	7.96	<0.001
	Day of study	0.03	(−0.1, 0.15)	0.42	0.68
	Scaled unique outdoor user count	−0.62	(−0.92, −0.33)	−4.18	<0.001
	Precipitation	−0.84	(−2.51, 0.84)	−0.98	0.33
	Wind	0.01	(−0.02, 0.04)	0.74	0.46
	Sun position	0.01	(0, 0.01)	2.20	0.03
	With young	−0.26	(−0.77, 0.25)	−0.99	0.32
Proportion time vigilant	Intercept	−1.50	(−1.75, −1.25)	−11.83	<0.001
	Noise treatment: recreation sounds	0.64	(0.53, 0.75)	11.32	<0.001
	Day of study	−0.05	(−0.1, 0)	−1.85	0.06
	Scaled unique outdoor user count, spline 1	1.65	(0.52, 2.78)	2.85	<0.001
	Scaled unique outdoor user count, spline 2	−0.10	(−0.64, 0.43)	−0.37	0.71
	Precipitation	0.41	(−0.11, 0.94)	1.55	0.12
	Wind	−0.01	(−0.02, 0)	−1.13	0.26
	Sun position	0.00	(0,0)	−0.68	0.50
	With young	−0.02	(−0.21, 0.17)	−0.22	0.83

recreational disturbance. The likelihood that wildlife displayed antipredator responses to audio playback noises of recreationists was mediated by the level of exposure to outdoor recreation within the area. This finding supports the habituation hypothesis, that antipredator responses decrease with increasing exposure to human presence, and is consistent with either habituation to repeated recreation exposure or filtering of the least tolerant individuals (Wat et al., 2020), similar to other anthropogenic disturbance (Dwinnell et al., 2019). Thus, repeated human exposure appears to either reduce the "landscape of fear" – the spatial variation in antipredator behavior driven by differences in predation risk and response (Gaynor et al., 2021), or to filter the mammal community based on individual tolerance levels. In our combined-species model, animals in areas with the greatest exposure to recreation had a 22% lower probability of fleeing in response to recreational sounds than animals in areas with the least exposure. Patterns of vigilance were more nuanced: across most of the exposure gradient, wildlife tended to spend more time being vigilant in areas where fleeing from recreational sounds was less likely. However, individuals in the areas with the greatest exposure to recreation had both the lowest probability of fleeing and spent less time being vigilant, consistent with a relaxation of antipredator responses. The reduction in antipredator behavior was greater for species more sensitive to human presence, such as elk (Zeller et al., 2024). In contrast, more tolerant species still exhibited a declining probability of fleeing with increased recreation exposure, but the decline was negligible (e.g., mule deer). Our measures of human presence, derived from anonymized smartphone locations (HMD), enabled us to scale up our model and derive spatially explicit predictions of behavioral tolerance, the "landscape of no worries" (i.e., predicted probability of fleeing when hearing recreation noises), across three districts of the Bridger-Teton National Forest (~672,000 ha). Regardless of the mechanism for the support of the habituation hypothesis (i.e., habituation, filtering of less tolerant individuals, or a process where both occur such that individuals are filtered and the remaining become habituated), our findings demonstrate that human presence in the form of recreation alters the expected antipredator profiles of wildlife present in an area. Our approach offers a new framework for coupling behavioral ecology with recreation ecology, which has important implications for understanding behavioral adaptation to human stimuli and informing recreation planning and management.

Many land managers have mandates to balance public demands for recreational opportunities while maintaining wildlife habitat quality. Discerning the relationship between tolerance and recreation exposure, and the capacity to develop spatially explicit predictions of antipredator behaviors, is an important first step for planning and proactive recreation management for wildlife issues. On one hand, species and individuals that are more tolerant or habituated to recreation may benefit because they avoid increased energy expenditures from fleeing human presence (Wang et al., 2017; Uchida and Blumstein, 2021) or lost foraging time associated with the trade-off of vigilance behavior (Shannon et al., 2014; Smith et al., 2021). In addition to accessing high-value forage in human-disturbed areas, where productivity or supplemental food sources may exceed that of nearby natural environments (Fedriani et al., 2001), individuals may gain protection from competitors or predators less tolerant of human presence (predator shield hypothesis; Berger, 2007; Muhly et al., 2011). However, inherently greater tolerance and habituation can carry long-term ecological risks through inappropriate behavioral responses to real threats – such as predators, human hunting, or vehicle strikes – while tolerance of humans may increase risk of human-wildlife conflict (Geffroy et al., 2015; Smith et al., 2021). Recreation may also reduce carrying capacity, with only the most tolerant individuals using the habitat (Rowland et al., 2000; Samia et al., 2015). Indeed, Zeller et al. (2024) found mammal abundance to be 1.5 times lower the week following exposure to recreation noise sounds. Importantly, this study found that the large carnivores recorded by Zeller et al. (2024) were only present at sites with some of the least exposure to human recreation.

Our findings align with those of Suraci et al. (2021), who found that individuals within a given species exhibited a dichotomous response to direct human presence – suggestive of a filtering effect. Discerning whether habituation through time or whether less tolerant individuals were filtered out from more high-use recreation areas is not within the scope of our analysis. Future studies could consider combining behavioral response videos with individual identification, thus providing a

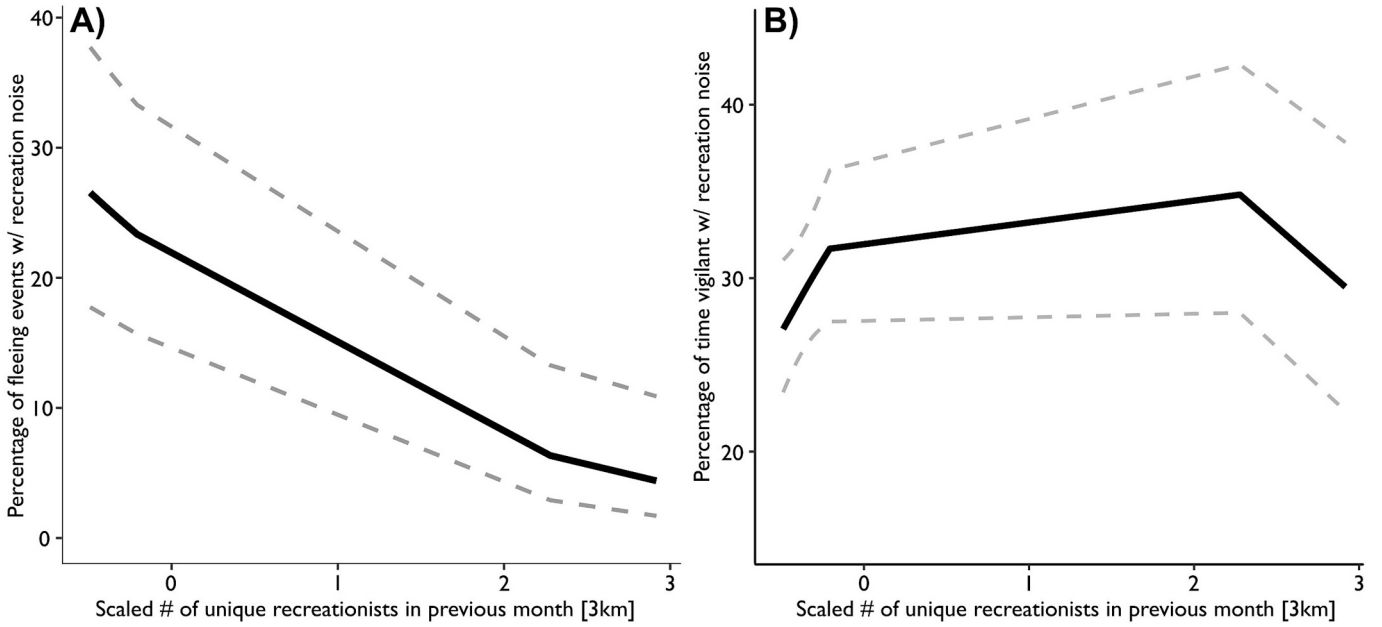

Fig. 3. Effects plots showing the predicted probability of (A) fleeing and (B) time spent vigilant when exposed to recreation noise based on the amount of exposure to counts of outdoor users (scaled values of users within a given year) at a 3 km radius spatial buffer and 30-day temporal scale across all species. Panel (A) is based on the top-fitting model for fleeing probability. The top model was refit with the proportion of time as the response variable, and we considered and included a natural cubic spline for the measure of outdoor users.

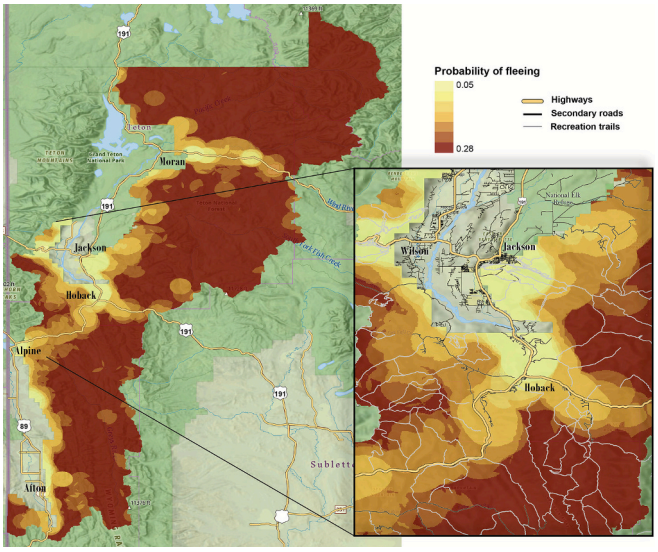

Fig. 4. Mapping the predicted tolerance, based on our top model, to recreation noise of wildlife based on exposure to the metric describing counts of unique outdoor users occurring at 3 km radius buffer and 30 days around each point in a 100 m resolution grid overlaid on the Jackson, Blackrock and Greys River Districts of the Bridger-Teton National Forest. Mapped predictions shown here represent recreation activity levels associated with August 15th, 2023.

powerful longitudinal means to assess changes in individual behaviors through time and test whether a subset of individuals do not return to locations where recreation noises are broadcast. It is important to consider the continuum of tolerance for human presence and species-specific differences. As our species-specific models also highlighted, while all species showed higher tolerance with exposure, elk exhibited the most extreme change—a ~35% reduction in fleeing from low to high recreation use.

Based on our findings, there were critical distinctions in how to best measure the dynamic human footprint for this research (Ellis-Soto et al., 2023). In regards to scale, our results show that shorter-term and smaller spatial extents may not adequately capture exposure for large, mobile, mammals in a meaningful way. The short-term measures (e.g., 7-days prior to experimental noise exposure) could be biased by factors influencing visitation, such as weather more or less conducive for recreation, while small spatial scales (e.g., 1 km in our study), may not capture the true exposure level of species with larger home ranges. Despite the positive correlation between them, the measures of outdoor recreation exceeded those of vehicles in explaining the probability of antipredator behaviors. This finding is not surprising given that more of the behavioral responses recorded in Zeller et al. (2024) were based on exposure to non-motorized recreation noise (~75%), and wildlife exposed to larger groups of vocal hikers and bikers more consistently exhibited a fleeing response relative to OHV noises. Importantly, HMD included off-trail users, which would otherwise be missed by trail counters, and is especially important in U.S. National Forests where various off-trail activities (e.g., shed hunting, fishing, hunting) regularly occur. In fact, off-trail recreation is increasing (Mangold et al., 2024), expanding into backcountry (Filazzola et al., 2022; Rice et al., 2019; Venter et al., 2023), and causing acute wildlife impacts (Marion, 2019), including ungulates (Westekemper et al., 2018; Neumann et al., 2010).

Altering the dynamics of the ecology of fear through interventions may help managers address situations where wildlife either exhibit overly bold behavior around people or show strong antipredator responses to recreation in populations of conservation concern (Gaynor et al., 2021). For instance, the clear pattern of increased wildlife tolerance in areas of high recreation suggests opportunities for spatial or temporal zoning and increasing the density of new trail systems instead of expanding their outer footprints. Managers may reduce broader-scale disturbance by creating concentrated, predictable, high-impact recreation in areas where wildlife has shown greater tolerance. Conversely, maintaining limited human use of other areas can act as a critical refuge for sensitive species or less tolerant individuals. In addition, future studies may want to consider the relationship between recreation exposure during various critical life stages (e.g., calving or denning), which could be paired with temporal recreation closures or limits to group sizes/activities (Larson et al., 2016; Abernathy et al., 2025a).

Thus, management programs should prioritize people-based data (Abernathy et al., 2025a) and avoid relying solely on measures of infrastructure (e.g., trail and road density) or vehicle activity (e.g., annual average daily traffic measures) when developing their own predictions of recreation exposure and consequent impacts to wildlife.

Several additional questions and limitations of this research are worth noting. The primary assumption, forming the backbone of much of the interpretation of our findings, was that antipredator behaviors were the only clear indication of a response to recreational noise. However, several studies have detected physiological stress responses to external stimuli with little to no observable behavioral reactions (e.g., Culik et al., 1990; Ditmer et al., 2015). Future work could test whether the spatial predictions from the landscape of no worries reflect differing stress levels across the landscape using stress hormones (e.g., Shipley et al., 2022), or pair GPS collars with physiological biologgers to detect acute stress responses (Ditmer et al., 2015) or increased chronic stress (Støen et al., 2015) with the recreation exposure gradient. Although HMD provided estimates of recreationist presence (both on and off trail) and vehicle activity, several limitations remain. For instance, while HMD captures relative use and patterns (Abernathy et al., 2025b), it is unreliable for estimating temporal changes in abundance, a primary reason we scaled estimates within each year, preventing testing of threshold effects generalizable across space and time. While it is possible to have classified likely recreation types of unique users with the HMD (Abernathy et al., 2025a), there is currently no obvious method of discerning recreation group sizes nor especially recreationist behavior (e.g., amount of human talking), which were found by Zeller et al. (2024) to be key factors increasing fleeing behavior. Here, we did not conduct a formal field validation of HMD in our study area, but previous work indicates that mobile device-based measures provide sufficiently reliable indices of relative human use for landscape-scale inference, while recognizing that they may under- or over-represent absolute visitation in some locations (Liang et al., 2022; Sergeyev et al., 2025).

Connecting the prevalence of antipredator behavior to recreation exposure provides a novel behavioral lens to the growing field of recreation ecology and the growing concerns about the impacts of recreation's burgeoning geographic extent and intensifying footprint (Schulze et al., 2018). Our framework, which leveraged HMD and experimental playback data is scalable to other landscapes, species, and contexts, particularly where managing wildlife-human conflict is a management priority. The ability to develop spatially explicit maps of behavioral responses to recreation can assist managers in making decisions that benefit the recreation-seeking public and provide refuge for less tolerant species and individuals. Mapping and considering how planning and management decisions may ultimately influence the behavioral tolerance landscape could become a foundational tool for zoning, conservation prioritization, and wildlife management policy. Multidisciplinary approaches, such as the one used here that integrate behavioral, recreation, and spatial ecology to meet conservation planning needs, offer a pathway forward for improving adaptive management of public lands.

CRediT authorship contribution statement

Mark A. Ditmer: Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Katherine A. Zeller:** Writing – review & editing, Visualization, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Heather N. Abernathy:** Writing – review & editing, Methodology, Data curation, Conceptualization. **James Wilder:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition. **Ashley Egan:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition. **Julia N.D. Daniell:** Writing – review & editing, Investigation. **Jesse R. Barber:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **William L. Rice:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition. **Michael K. Schwartz:** Writing – review & editing, Supervision, Resources, Conceptualization. **George Wittemyer:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors have no conflicts of interest to report.

Acknowledgements

We thank the two anonymous reviewers for their thoughtful feedback and suggestions. This research was supported by the Greater Yellowstone Coordinating Committee, USDA Forest Service, Rocky Mountain Research Station, and the Aldo Leopold Wilderness Research Institute. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111718.

Data availability

Data and code used for the final models and figure outputs associated with this work are archived at Zenodo (https://doi.org/10.5281/zenodo.15610783).

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