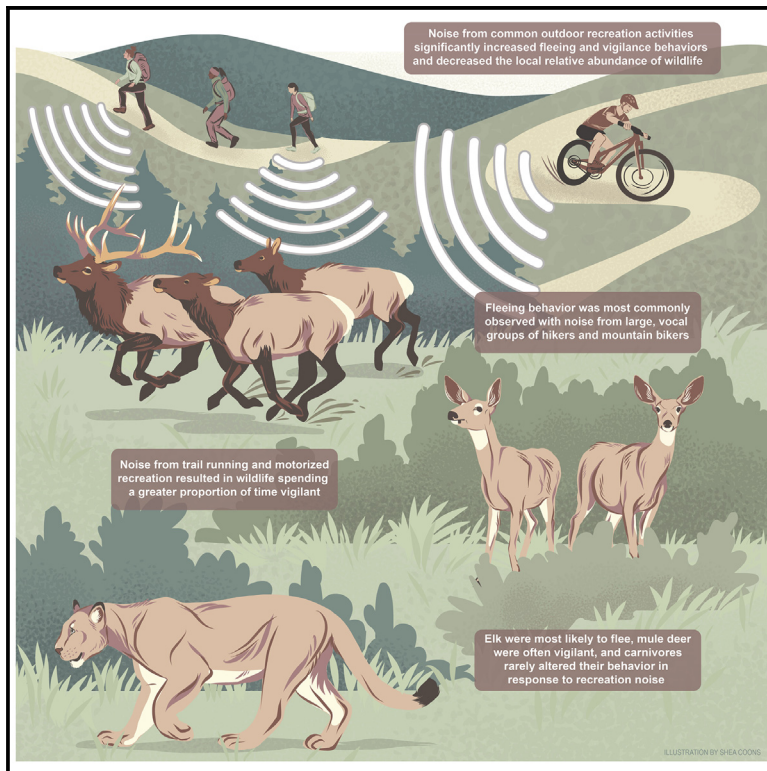


Current Biology

Experimental recreationist noise alters behavior and space use of wildlife

Graphical abstract



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In brief

Noise from recreational activities can be far reaching and have negative effects on wildlife, yet the impacts of these auditory encounters are often unobservable. Zeller et al. design an experiment to isolate the effect of recreation noise and test recreation type, group size, and vocalization presence on terrestrial wildlife.

Highlights

- Noise from human recreation may have far-reaching effects on wildlife
- We experimentally tested the effect of human recreation noises on wildlife
- Recreation noise, without any human presence, caused anti-predator responses
- Species' sensitivity varied, but large vocal groups caused the strongest responses

Report

Experimental recreationist noise alters behavior and space use of wildlife

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SUMMARY

Providing outdoor recreational opportunities to people and protecting wildlife are dual goals of many land managers. However, recreation is associated with negative effects on wildlife, ranging from increased stress hormones^{1,2} to shifts in habitat use^{3–5} to lowered reproductive success.^{6,7} Noise from recreational activities can be far reaching and have similar negative effects on wildlife, yet the impacts of these auditory encounters are less studied and are often unobservable. We designed a field-based experiment to both isolate and quantify the effects of recreation noise on several mammal species and test the effects of different recreation types and group sizes. Animals entering our sampling arrays triggered cameras to record video and broadcast recreation noise from speakers ~20 m away. Our design allowed us to observe and classify behaviors of wildlife as they were exposed to acoustic stimuli. We found wildlife were 3.1–4.7 times more likely to flee and were vigilant for 2.2–3.0 times longer upon hearing recreation noise compared with controls (natural sounds and no noise). Wildlife abundance at our sampling arrays was 1.5 times lower the week following recreation noise deployments. Noise from larger groups of vocal hikers and mountain bikers caused the highest probability of fleeing (6–8 times more likely to flee). Elk were the most sensitive species to recreation noise, and large carnivores were the least sensitive. Our findings indicate that recreation noise alone caused anti-predator responses in wildlife, and as outdoor recreation continues to increase in popularity and geographic extent,^{8,9} noise from recreation may result in degraded or indirect wildlife habitat loss.

RESULTS

We experimentally broadcast human-produced recreation noise to wildlife (Figure 1) in the Bridger-Teton National Forest, Wyoming, USA, to address the following questions.

- (1) Does recreation noise cause behavioral responses in wildlife?
- (2) Which species are more tolerant or sensitive to recreation noise?
- (3) What attributes of recreation noise (e.g., recreation type, group size, and group vocalizations) influence wildlife responses?
- (4) Does recreation noise lead to changes in relative abundance of wildlife?

We tested eight recreation noise treatments representing different recreation types (hiking, mountain biking, trail running, and off-highway vehicle [OHV] use), group sizes (small and large), and vocalization presences (talking or silent). For controls, we played back a natural sound treatment (recordings of ambient natural sounds) and a no-noise treatment.

We obtained 1,023 audio trigger events over 4,444 trap nights from the following species: mule deer (*Odocoileus hemionus*, $n = 640$), elk (*Cervus canadensis*, $n = 122$), red fox (*Vulpes vulpes*, $n = 74$), black bear (*Ursus americanus*, $n = 51$), moose (*Alces americanus*, $n = 50$), pronghorn (*Antilocapra americana*, $n = 54$), cougar (*Puma concolor*, $n = 17$), coyote (*Canis latrans*, $n = 8$), and wolf (*Canis lupus*, $n = 7$). Because of small sample sizes for cougars, coyotes, and wolves, we combined those observations into an “other carnivore” group for further analysis. The total number of

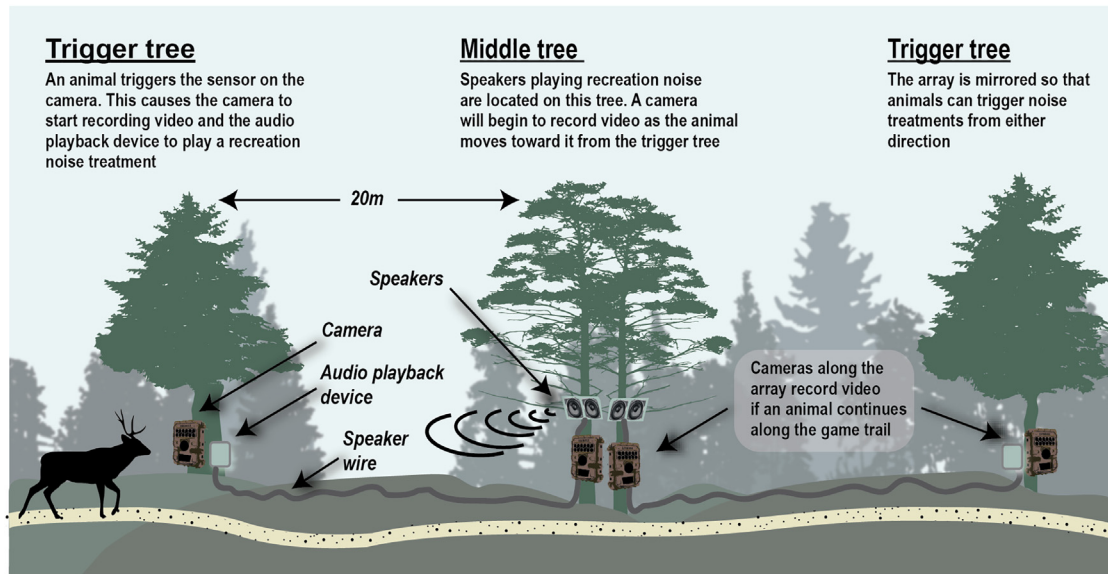


Figure 1. Sampling array design for testing the effects of human-produced recreation noise on wildlife

Each array consisted of four trail cameras, two audio playback devices, and two sets of speakers placed along a game trail. Cameras on either end of the array (trigger cameras) were connected to an audio playback device such that when the sensor on the camera was triggered it also broadcast sound from the speaker array. Additional remotely triggered cameras in the middle of the array captured continuous videos as animals moved along the game trail. See also [STAR Methods](#).

trigger events and the total number of independent captures of our focal species (i.e., total captures on trail cameras regardless of whether they initiated a trigger of a recreation treatment) are provided in [Data S1A](#) and [S1B](#).

Recreation noise alone caused negative behavioral responses in wildlife

Recreation noise resulted in significant increases in the likelihood of fleeing and vigilance behavior for wildlife relative to both control treatments ([Figure S1](#)). Wildlife were 4.7 times more likely to flee (odds ratio [OR] = 0.21, $p < 0.0001$) and were vigilant for 2.9 times longer (OR = 0.34, $p < 0.0001$) when compared to the no-noise treatment ([Figure S1](#)). Wildlife responses to natural sounds were not different from the no-noise treatment (flee, OR = 1.51, $p = 0.451$; vigilant, OR = 1.33, $p = 0.442$), indicating that wildlife perceived ambient sounds playing from the speakers differently than recreation noise, confirming our experimental design. Given this result, we collapsed the no-noise treatment and the natural sound treatment into a single control treatment for subsequent analyses.

Overall, wildlife had a higher probability of fleeing when exposed to the sounds of larger vocal groups (>4 people), regardless of recreation type, and had the lowest probability of fleeing from the sounds of small non-vocal groups of hikers ([Figure 2A](#); [Data S2A](#)). Noise from larger groups of vocal hikers resulted in the highest probability of fleeing across wildlife species ([Figure 2A](#)): 8.1 times more likely to flee compared to the control treatments (OR = 8.114, $p < 0.0001$). Large groups of vocal mountain bikers were associated with similar probabilities of fleeing as large groups of vocal hikers (OR = 0.74, $p = 0.938$; [Figure 2A](#)). The proportion of time wildlife spent vigilant echoed the probability of fleeing results for hikers and bikers, except for

small groups of non-vocal bikers, which resulted in longer times spent vigilant than the other biking treatments ([Figure 2B](#)). Wildlife spent the longest time vigilant in response to sounds of OHVs (\bar{x} = 40% of time, 95% CI [0.30–0.51]; [Figure 2B](#)) and were 3 times more likely to spend time vigilant in response to OHV noise compared to control treatments (OR = 2.99, $p = 0.020$). This was followed by small groups of non-vocal mountain bikers (\bar{x} = 38% of time, 95% CI [0.32–0.46]) and small groups of non-vocal trail runners (\bar{x} = 38% of time, 95% CI [0.26–0.51]; [Figure 2B](#)). Complete OR results are provided in [Data S2](#). The differences among recreation noise treatments for both fleeing and vigilance were largely explained by the associated decibel level (dB(A)) of the recreation activity itself. Both behavioral responses were positively associated with the mean dB(A) of the playback treatments ([Data S3](#); [Figure S2](#)).

Species had different sensitivities to recreation noise

Elk were the most sensitive to recreation noise among species in our study ([Figures 3A](#) and [3B](#)). Elk had a 47% probability of fleeing (95% CI [0.34–0.61]) upon hearing any recreation noise and were 6.9 times more likely to flee compared with the control treatments (OR = 0.144, $p = 0.0008$). Elk also spent 48% of the time vigilant (95% CI [0.41–0.68]) in response to recreation noise and spent 2.9 times longer being vigilant compared to the controls (OR = 0.348, $p = 0.0490$). Black bear and pronghorn also had relatively high fleeing probabilities, with a 40% and 26% chance of fleeing, respectively. Elk, moose, and mule deer spent longer being vigilant compared to other species ([Figure 3B](#)). Medium and large carnivores were the least responsive to recreation noise. Large carnivores had a 6% probability of fleeing in response to recreation noise ([Figure 3A](#)). Model ORs are provided in [Data S4](#). Example responses are provided in [Video S1](#).

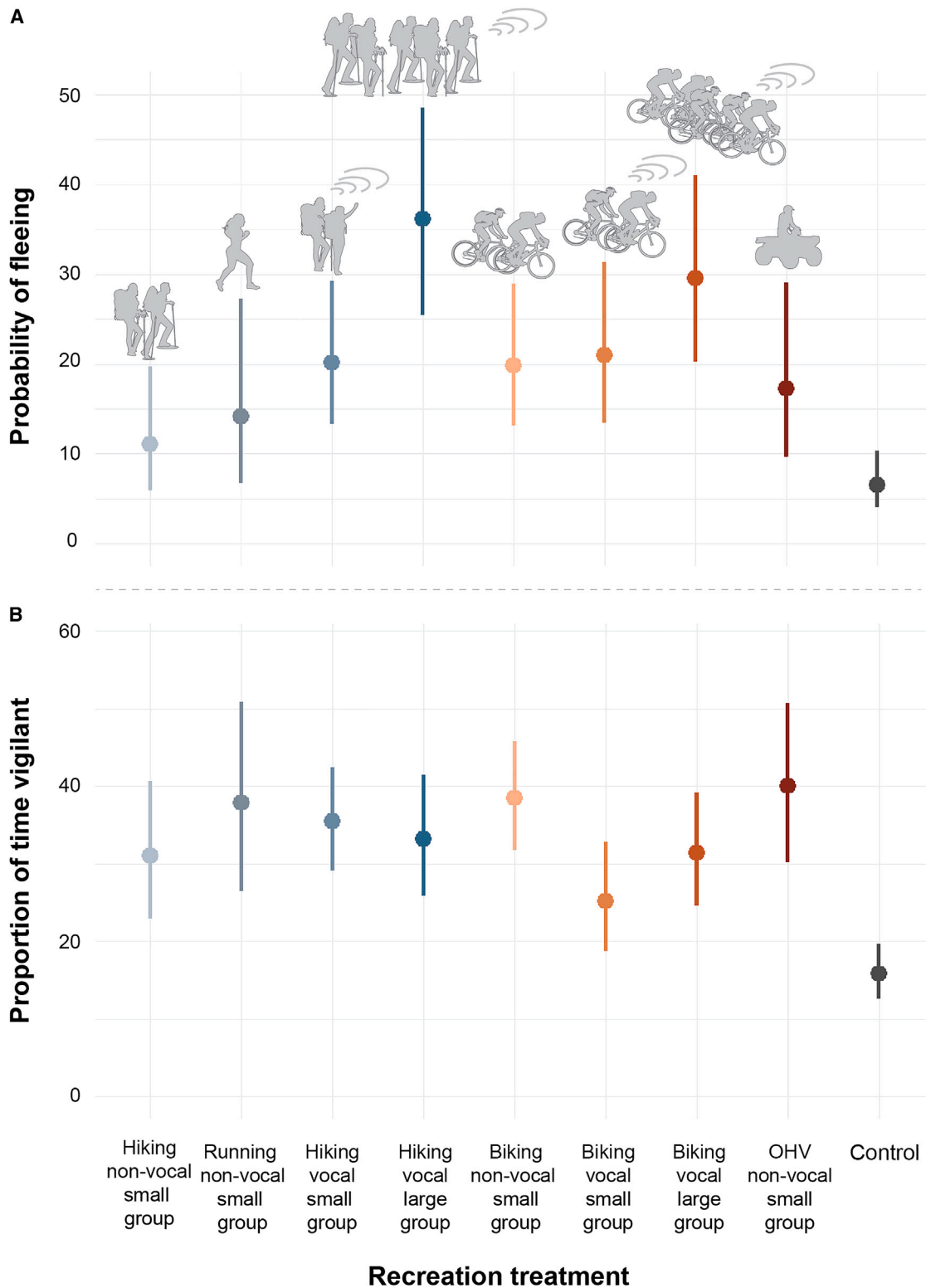


Figure 2. Wildlife fleeing and vigilance responses to recreation noise treatments

Probability of fleeing (A) and proportion of time spent vigilant (B) as a function of the recreation sounds broadcast in this study. “Biking” refers to mountain biking and OHV stands for off-highway vehicle. Plots show predicted means and 95% confidence intervals. Non-overlapping confidence intervals indicate statistically significant differences between treatments. The “Control” treatment was a combination of our natural sounds and no-noise treatments. See also [Figures S1](#) and [S2](#), [Data S2](#) and [S3](#), and [Video S1](#).

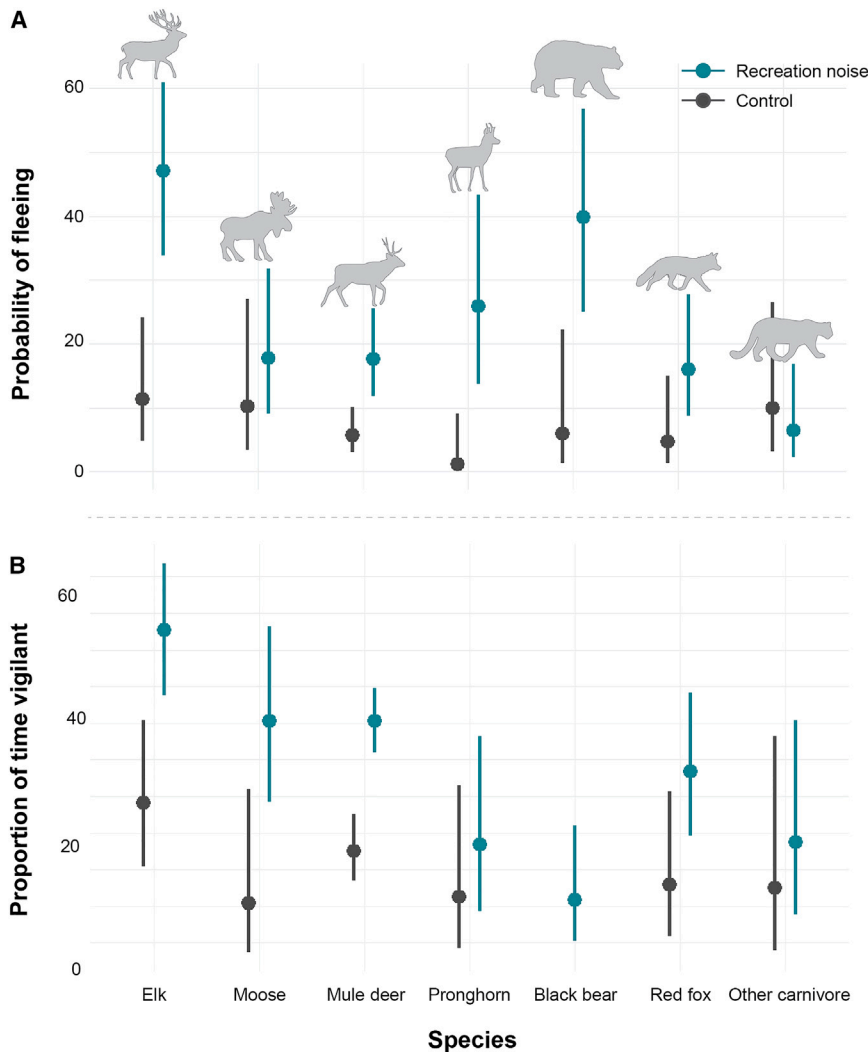


Figure 3. Species-specific behavioral responses to recreation noise

Probability of fleeing (A) and proportion of time spent vigilant (B) in response to recreation sounds broadcast for each species in our study. Plots show predicted means and 95% confidence intervals. “Other carnivore” refers to a large carnivore group consisting of cougars, coyotes, and wolves. Black bear does not have results for the control for vigilance behavior due to lack of data. See also [Data S4](#) and [Video S1](#).

Recreation noise alone caused a decrease in the site abundance of wildlife

We broadcast sounds on a weekly schedule and found abundance of wildlife at our sampling sites was 1.5 times lower the week following the deployment of any recreation noise treatment compared with the controls (OR = 1.53, $p = 0.0001$). When examining site use in response to different recreation noise treatments, we found there were 1.7 times fewer animal encounters when noise from large groups of vocal bikers (OR = 0.578, $p = 0.0457$) or vocal hikers (OR = 0.594, $p = 0.0457$) was being broadcast compared with the controls.

DISCUSSION

The sounds people generate during outdoor recreation activities cause strong anti-predator responses in wildlife in the absence of actual humans. This finding aligns with other studies showing negative effects of anthropogenic noise on

Group size and vocalizations were important attributes of recreation noise treatments

There was no difference in the probabilities of fleeing and proportions of time spent vigilant in response to noise from different recreation types (i.e., hikers, mountain bikers, and OHV drivers; [Figures 4A](#) and [4B](#); [Data S5A](#) and [S5B](#)), but wildlife did have differing responses to group size and human vocalization ([Figures 4C–4F](#)). Wildlife were twice as likely to flee in response to noise from larger group sizes of recreationists compared with noise from smaller group sizes (OR = 2.11, $p < 0.0001$; [Figure 4C](#)) and 6.8 times more likely to flee in response to larger groups compared to the control treatments (OR = 6.80, $p < 0.0001$). While larger recreationist group sizes tended to increase the probability that an individual would flee, overall vigilance time increased during exposure to noise from smaller groups compared to larger groups ([Figure 4D](#); [Data S5C](#) and [S5D](#)), highlighting the tradeoff between fleeing and vigilance behaviors. When recreationists were not vocal, wildlife were 1.7 times less likely to flee from the game trail (OR = 0.567, $p = 0.0001$; [Figure 4E](#); [Data S5E](#)).

wildlife.^{10–12} Our experimental playback approach allowed us to decisively isolate human-created noise as a key driver of animal response to recreationists. Unlike common opportunistic recreation studies, ours is the first to quantify responses to human-produced recreation noise based on recreation type, group size, vocalization presences, and wildlife species—critical information for improved management of both human and natural systems. We found negative behavioral and site use responses to recreation noise, and given the spatial reach of propagating sound, our findings indicate that these negative impacts likely reach beyond the location of trails, increasing the spatial footprint of recreation impacts. Critically, we observed negative behavioral and site use responses with extremely low levels of recreation.¹³ For example, the maximum number of times our triggered system broadcast recreation noise during a 2-week period was 21, which is equivalent to approximately 1.5 recreation events per day. As outdoor recreation opportunities continue to expand, and as more people engage in these activities, high-quality habitats may be degraded and result in indirect habitat loss for wildlife due to sensory pollution. The salience of this finding is

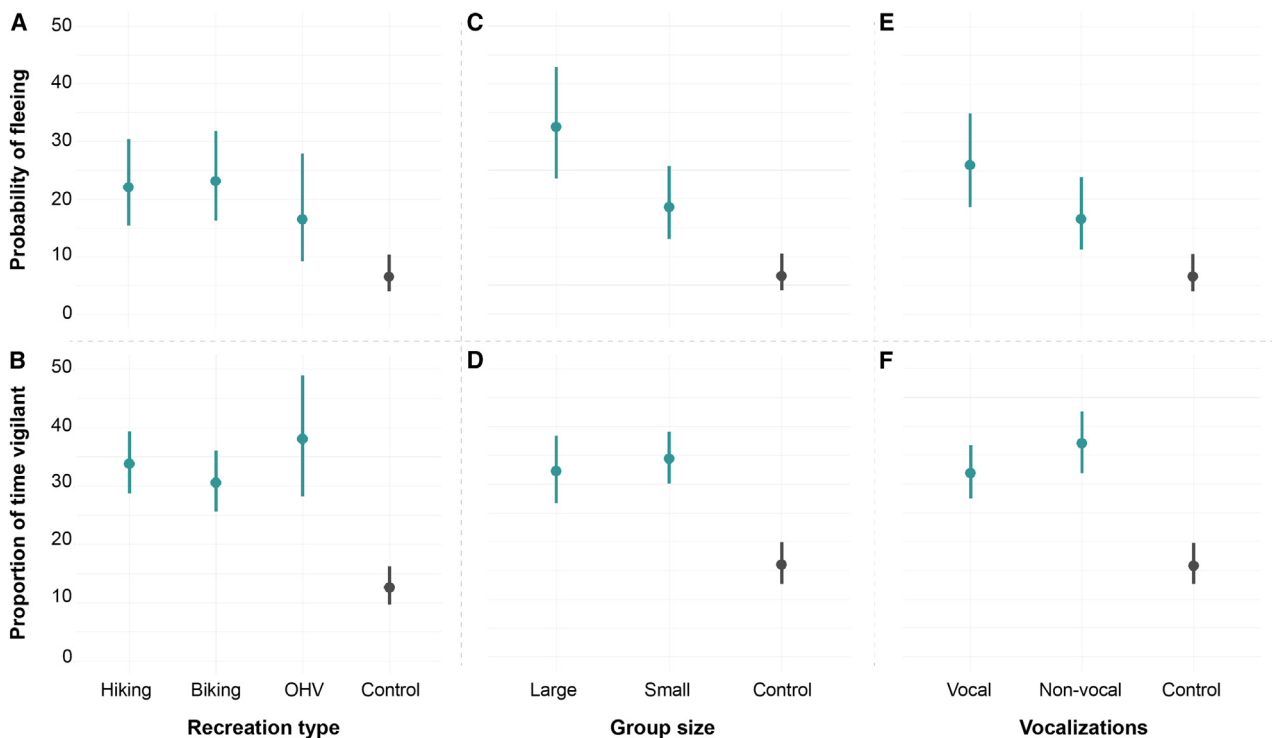


Figure 4. Wildlife fleeing and vigilance responses to recreation type, group size, and vocalizations

Probability of fleeing (top row) and proportion of time spent vigilant (bottom row) in response to recreation type (left column), group size (middle column), and group vocalizations (right column) for all species in our study. Plots show predicted means and 95% confidence intervals. Non-overlapping confidence intervals indicate statistically significant differences between treatments. The “Control” treatment included natural sounds and no-noise treatments. See also [Data S5](#) and [Video S1](#).

underscored as emerging forms of visitor use monitoring reveal an expanding footprint of recreational use beyond designated recreation trails into off-trail environments.^{14,15}

The strength of responses from mammal species differed based on the recreation noise treatment. Playback of large vocal recreation groups caused the highest probabilities of fleeing among species in our study, while small non-vocal groups of hikers resulted in the lowest probabilities. Though the large groups of mountain bikers had the highest average sound level of our recreation treatments (59 dB(A)), the average sound level for the large groups of hikers, which caused the highest probability of fleeing, was 53 dB(A), which was lower than other recreation treatments such as the OHV treatment (54 dB(A)) and small groups of non-vocal mountain bikers (55 dB(A)). This suggests sound level alone is not the only factor to which animals are responding. Other characteristics of recreation noise appear to also be driving behavioral responses of wildlife. For example, OHV use, trail running, and small groups of non-vocal mountain bikers resulted in the longest proportion of time spent vigilant among wildlife.¹⁶ These treatments represented noise from some of the faster moving recreationists and were characterized by an abrupt ramp up and decline in sound energy, suggesting moving speed of the recreationists may also have an effect on wildlife response.^{17,18} Because of the speed of these recreation types, the length of these recordings was shorter than those of other recreation types, indicating duration of the noise may also be contributing to wildlife responses. Despite the different

qualities of the recreation noises, in general, we found that as sound level increased so did the probability of fleeing and proportion of time spent vigilant. We did not observe a threshold in responses to sound level, indicating that anti-predator behavior is likely to increase with increasing intensity of recreation noise beyond the levels tested in our study.

Interestingly, we found that noise associated with different recreation types (e.g., hiking, mountain biking, and OHV driving) may not be as important a predictor as noise from different group sizes or vocalizations in eliciting fleeing or vigilance responses of wildlife.⁴ Though other studies have found non-motorized activities had more negative effects on wildlife than motorized activities, those results may be a result of wildlife experiencing both auditory and visual stimuli.^{19,20} Our findings, which showed that noise from larger, more vocal groups elicits a stronger negative response in wildlife, are consistent with previous literature,^{21–24} though most studies with these findings have been conducted on birds, further highlighting the importance of these results for mammals.

We found some species were more sensitive to recreation noise than others. Elk were the most sensitive species in terms of both probability of fleeing and proportion of time spent vigilant. Studies have found elk increased travel time and avoided recreation trails in response to OHV, mountain biking, and hiking use—both on and off trail^{16,17,25,26}—and in some cases, approaching hikers reduced elk fecundity when calving.⁶ However, in other studies, elk use of areas has been shown to be positively

correlated with recreation sites,²⁷ indicating scale and frequency of recreation use, as well as habituation, may be important factors in parsing out recreation effects on this species. The high probability of fleeing we observed for black bear and pronghorn may result in shifts of habitat use away from recreation-adjacent areas, as has been observed in other studies.^{13,28,29} Though moose and mule deer had lower probabilities of fleeing than elk, black bear, and pronghorn, both have been shown to avoid areas with human recreation in other studies.^{27,30} However, moose have also been shown to select for areas of human presence,^{13,27} presumably as a human shield effect from predators,³¹ indicating risk-reward tradeoffs and that responses to recreation noise may be situation dependent.

Compared with other species in our study, carnivores had the weakest behavioral response to recreation noise. Large carnivores responded no differently to recreation noise than to our control treatments, suggesting they may not be negatively affected by recreation noise.³² This contrasts with findings from other studies that found negative responses by carnivores to human voices and concluded that those responses were borne out of a fear of humans as a “super predator.”^{11,12,33} Two of those studies conducted their experiments at resource use areas (kill sites or watering holes), which may be situations that evoke stronger responses to human presence than walking along game trails. Though carnivores in our study had a weak behavioral response to recreation noise, they may still have been experiencing physiological effects that we were unable to observe. For example, higher stress hormone levels have been found in wolves in response to snowmobile recreation,² and though few behavioral changes were observed, acute increases in heart rates were documented in black bears in response to unmanned aerial vehicles.³⁴ Therefore, lack of an obvious behavioral response may not equate to lack of response, and our results are likely underrepresenting the breadth of effects of recreation noise.

Our study confirmed that noise from recreation activities alone can reduce wildlife abundance at local sites. We were unable to differentiate whether decreases in site abundance were the result of avoidance at smaller scales where animals may locally alter their use of areas to avoid recreation noise or larger scales where animals may shift their within-home range use to other areas,^{29,35} or even change their home range extents in response to recreation noise.^{36,37} These findings indicate recreation noise, even at low levels, may cause avoidance of habitats, which may limit access to resources and result in indirect habitat loss for species.^{5,13,36} These recreation noise-induced shifts in space use may also cause community-level changes in wildlife and species interactions by reducing the occurrence and density of some species on the landscape.^{38,39} While it is unclear to what extent habituation may counter the negative effects of recreation noise in terms of wildlife space use through time, habituation of native ungulates may only occur in areas where they are not hunted.^{3,16} It is also currently unclear how the frequency of recreation may influence responses of wildlife.

Most recreation studies on wildlife to date have been opportunistic and therefore could not control for several critical factors such as different recreation types, group sizes, and vocalizations. Though we were able to successfully conduct an experiment with controls, we were unable to assess responses to

recreation noise on trail systems regularly used by people. This allowed us to examine responses to novel recreation noise environments but did not allow us to examine habituation³²—a critical next step. More studies that employ experimental designs like ours are needed. For example, studies in different study areas and with different species would help reach generalizable conclusions. In addition, studies that employ different recreation treatments, assess noise effects at different distances, or identify potential cascading effects on energy budgets, fecundity, and survival⁴⁰ would help gain a full understanding of recreation noise effects on wildlife.

Outdoor recreation such as hiking, mountain biking, and motorized use has been steadily increasing, both in the number of people that participate in these activities and the number of days of participation.^{8,9} Most land management agencies have multiple use mandates that include providing opportunities for outdoor recreation while conserving natural resources such as wildlife. Data from studies such as this can help managers discern how increasing recreation may be affecting the wildlife communities in their area as well as individual species that are of conservation or management concern. These data can also be used to predict the effects of management restrictions like recreation group size, activity zoning, and temporary closures of areas, or the effect zones of building new trails. Importantly, these data can also help recreation managers set thresholds for recreation-related noise (e.g., group size restrictions) and guide the design of related direct (e.g., regulations and restrictions) and indirect (e.g., educational signage to reduce noise) management actions to help stay within these thresholds.⁴¹ However, in areas where best safety practices suggest recreating in larger groups and making noise (e.g., grizzly bear habitat⁴²), managers may consider alternative management strategies that, for example, target the type or quality of noise (e.g., noise that alerts but does not startle wildlife) or restrict recreationists to stay on designated trails.

Wildlife can be highly plastic, and recent studies examining changes associated with COVID-19-related closures have documented higher use of sites by species when closures to humans were implemented.^{43,44} Other studies have found that asking people to produce less noise while recreating, thereby reducing sound levels and concomitant effects on wildlife, creates a soundscape equivalent to fewer people.²³ This is just one example of a management action that can reduce the negative effects of recreation noise on wildlife. It is clear that particular attention paid to the sensory impacts of human recreation in naturally quiet, undeveloped areas—typically considered high-quality habitat and refugia from human disturbance—may be critical to balancing land management mandates while ensuring otherwise intact habitat remains available to wildlife.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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 - Materials availability
 - Data and code availability

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- METHOD DETAILS
 - Sampling arrays
 - Recreation noise treatments
 - Behavior classification
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.05.030>.

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AUTHOR CONTRIBUTIONS

M.A.D. and K.A.Z. conceived of the study design with input from J.R.B. and J.R.S. Resources were acquired by K.A.Z. Audio playback devices and software were created by J.P. and C.A.W. Experiment was implemented by K.A.Z. and M.A.D., with input from J.W., A.E., and D.D., and was executed by N.P. Analyses were performed by K.A.Z. and M.A.D. K.A.Z. led the writing and all co-authors contributed to review and editing.

DECLARATION OF INTERESTS

Prefabricated BoomBox boards/kits used in this study can be obtained from FreakLabs (owned by J.P. and C.A.W.). However, the information necessary for building upon the hardware and software is available [here](#) and [here](#).

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STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|--|--|---|
| Deposited data | | |
| Behavioral data used in the statistical analyses | This paper | https://doi.org/10.6084/m9.figshare.25328743 |
| Relative abundance data used in the statistical analyses | This paper | https://doi.org/10.6084/m9.figshare.25328743 |
| Software and algorithms | | |
| R version 4.3.1 | The R Foundation for Statistical Computing | https://cran.r-project.org/mirrors.html |
| RStudio Version 2023.06.2–561 | RStudio | https://rstudio.com/products/rstudio/download/ |
| BORIS software environment, v.7.13.9 | Behavioral Observation Research Interactive Software | https://www.boris.unito.it/ |
| BoomBox software | Freaklabs | https://github.com/freaklabs/BoomBox |
| Other | | |
| Visual Crossing Weather Data | Visual Crossing | https://www.visualcrossing.com/ |

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Katherine Zeller (Katherine.zeller@usda.gov).

Materials availability

This study did not generate new materials.

Data and code availability

- Data for behavioral analysis and site use analysis are available here: <https://doi.org/10.6084/m9.figshare.25328743>
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Our sampling procedure involved remotely triggered trail cameras that recorded videos of wildlife that entered our sampling arrays. Species of wildlife that frequently encountered our sampling arrays included mule deer, elk, red fox, black bear, moose, pronghorn, cougar, coyote, and wolf (Data S1). We obtained U.S. Forest Service Research and Development IACUC approval for both years of the study.

METHOD DETAILS

Our study was conducted in the Bridger Teton National Forest in Wyoming, USA over two summer field seasons in 2022 (June 20th–October 9th) and 2023 (June 5th–September 26th). In 2022, we had eight sampling sites, four in the Jackson Ranger District and four in the Grey's River Ranger District. In 2023, we had 12 sampling sites, four in the Jackson, two in the Blackrock, and six in the Grey's River Ranger Districts. Sites were selected based on maximizing encounter rates of medium to large mammals. District Wildlife Biologists were consulted to identify areas with high wildlife use and site placement required the presence of a well-used game trail with fresh sign. Two of the sites in the Jackson Ranger District were used in both 2022 and 2023, while three of the sites in the Grey's River Ranger District were used in both years. We retained sites in 2023 if they had relatively high sample sizes in 2022. Sampling sites were placed at least 2 km away from one another (\bar{x} = 9 km).

Sampling arrays

Sampling arrays were placed on game trails at an average distance of 650 m from recreation trails. Each array consisted of four camera traps and two audio playback devices called ‘BoomBoxes’⁴⁵ placed on trees along a game trail (Figure 1). There were two trigger cameras, one at each end of the array, positioned to capture animals approaching the array from either side. Two middle cameras and the two pairs of BoomBox speakers were placed ~19 m (17–21 m) away from the trigger cameras in the center of the array, with the middle cameras positioned to capture an animal as it moved along the game trail from the trigger cameras so that an animal’s movements and behavior were fully captured as it moved through the array (Figure 1). We placed the speakers at this distance from the trigger trees because we did not want to evoke a startle response from wildlife, rather we wanted the recreation noises to play at a far enough distance from the trigger cameras to simulate realistic wildlife encounters along trail systems while allowing for the noise to reach the outer trigger camera. We also recorded recreation treatments (see below) so that the recording began before the noise could be heard and naturally ramped up in volume as the recreationists approached the recorder to create realistic noise cues. Trigger cameras (Reconyx Hyperfire 2 Professional Covert Infrared) were programmed to record 90 s video. Middle camera models were either Reconyx Hyperfire 2 Professional Covert Infrared or Reconyx Hyperfire 2 Covert Infrared, and programmed to record 10 s videos. See Video S1 for examples.

Trigger cameras were modified to connect to the BoomBoxes by soldering a connector wire to the passive infrared motion sensor on the camera circuit boards. BoomBoxes were located at the trigger tree and were connected to 17–21 m lengths of speaker wire so that speakers could be placed in the middle of the sampling array. Speaker wires were threaded through wire conduit to protect from the elements and from damage by wildlife.

Recreation noise treatments

We tested eight recreation noise treatments that represented different recreation types, recreation group sizes, and vocalizations (silent or talking; Data S3A). Given various constraints on our first field season we were not able to deploy the full array of recreation treatments over both seasons and were only able to run the experiment in 2022 with five of the recreation treatments (Data S3A). Furthermore, these constraints prevented us from being able to run the full factorial of recreation treatments for each reaction type, group size, and vocalization. Therefore, we selected the eight treatments we thought were the most common recreation events.

Recreation noises were recorded on recreation trails around Missoula, Montana, Fort Collins, Colorado, and Jackson, Wyoming. Recordings were made with a Zoom H4nPro portable recorder with a Deadcat windshield over the microphones. The recorder was attached to a tripod placed approximately three feet off the ground and two feet off the trail. The recorder was set to record in stereo with a WAV48kHz/24 bit format. Recordings began before noise could be heard and continued until the recreationists had passed and the noise had faded. The decibel level (dB(A)) of the recreation noise was simultaneously tracked with a Mic-W (i436) microphone attached to either an iPhone or iPad and recorded with the SmarterNoise app. SmarterNoise graphed the dB(A) continuously throughout the recording and provided information such as the mean, minimum, and maximum dB(A) levels of each recording. We used the dB(A) level information to match the dB(A) levels from the recorded recreation noise to the noise being played back through the BoomBox speakers in the field. We counted the number of recreationists in each group as we recorded the noise.

Recordings were grouped into recreation treatments and edited with Audacity software, v3.3.2. Due to BoomBox requirements, the recordings could not be longer than the video recordings from the trigger cameras, limiting recordings to 90 s. We edited recordings to remove long silent periods before the sound could be heard and in some cases we incorporated a fade out for 3 s at the end of the recordings to meet the 90 s requirement. Recordings were 21 s to 90 s in length (Data S3A). One recreation treatment was deployed at a site for either two weeks (2022) or one week (2023), with treatments rotating through the sites during a season. For each recreation treatment we had at least three different recordings that the BoomBox was programmed to cycle through sequentially. For example, at the first trigger, the BoomBox would play recording #1 of that treatment, at the second trigger, recording #2 would be played, at the third trigger, recording #3 would be played, at the fourth trigger recording #1 would be played, etc. Using multiple recordings helped to ensure the animal response was due to a specific recreation treatment and not a spurious attribute of a particular recording.

We also recorded and employed background nature noise in our experiment to act as a control. This allowed us to test whether wildlife were responding to the recreation noises being played and not just to any sound playing from the speakers. In 2022, recreation treatments were deployed and arrays were checked by field technicians every two weeks. During this time, camera storage cards and batteries were replaced and the recreation noises were changed. In 2023, arrays were checked and noises were changed weekly. We also incorporated ‘no noise’ weeks into the noise schedule for each site where no sounds were played from the speakers as an additional control.

Behavior classification

Videos with false trigger events were filtered out as well as videos with birds or mammals smaller than a fox. Videos with animals at a trigger camera for more than 5 s were identified and matched with videos of the same animal from other cameras in the array, if present. We required the animal to be in the frame for at least 5 s to account for the slight lag in triggering the BoomBox noise. The video or group of videos were classified as an ‘event’. Events were then imported into the BORIS software environment, v.7.13.9 for behavioral classification.⁴⁶ Two researchers (Zeller and Dittmer) independently classified behaviors from all events to account for any bias by using only one classifier. Classifiers were blinded from the recreation treatment and behaviors were classified with the video sound off so as not to bias classifications. Behaviors were classified into one of the following categories: vigilant

(head raised, alert, listening), feeding (actively eating vegetation), walking (moving unperturbed, but not feeding or engaged in other relaxed behavior), reverse course (reversal of previous trajectory of movement), fleeing (fast exit of the camera frame in any direction), social (interactions among animals), trot or run (moving faster than a walking pace, but not as spontaneous or fast as fleeing), camera curious (sniffs, nudges, rubs against camera), bedding/resting (laying down), and other (other behavior not captured by one of the predefined classes).

Behaviors were classified for the continuous duration of the videos. For example, when a video was started, the behavior at the start was identified and carried through until the viewer identified a change in behavior, at which time, the first behavior was stopped and the new behavior was started. This process continued through the duration of all videos in an 'event' and included 'out of frame' time where animal behavior could not be observed. This process allowed us to account for each second in all videos and identify not only behaviors that occurred during a trigger event, but also the proportion of time an animal spent in each behavioral state while in the camera frame. For each event, the following information was also entered into the BORIS software environment: species, number of individuals, if rain and/or wind were observed in video, if individual(s) were with young, and which cameras in addition to the trigger camera were deployed.

QUANTIFICATION AND STATISTICAL ANALYSIS

All analyses were conducted in R software.⁴⁷ We assumed vigilance and flight behavior were anti-predator responses to hearing recreation noise,^{48–52} so we focused on those two behavioral classifications. Both proportion of time vigilant and probability of fleeing were modeled with binomial mixed models using the *glmmTMB* function from the 'glmmTMB' R package.⁵³ Each behavior was modeled as a function of recreation noise treatment, Forest Service district, day of study, precipitation amount (mm), wind speed (kph), sun position (angle above or below the horizon), and whether an animal was with offspring. We also included site and observer as random effects to account for site-level differences, classifier bias, and repeat observations. Forest service district was included due to the differences in recreation use among the districts. The two northern districts experience a lot of hiking and mountain biking use and very little OHV use while the southern district experiences frequent OHV use, and very infrequent non-motorized use. Day of study was calculated from June 1st of each year and was included to account for wildlife acclimation to noise over the course of each season as well as seasonal variations. Hourly rain and wind data obtained from nearby weather stations via [visualCrossing \(https://www.visualcrossing.com/\)](https://www.visualcrossing.com/) were matched with the observations. We used data from four weather stations in the study area and matched the data from each weather station to the closest site and time stamp. Sun position was included to account for time of day differences in responses, and animals with offspring were included to account for possible differences in behavioral responses when young were present. For all models, the global model was run, significant main effects were identified with the *Anova* function from the 'car' R package,⁵⁴ and those main effects were carried forward to the final models.

To answer our first question, "Does recreation noise cause behavioral responses in wildlife?", we ran three models. First, we collapsed all recreation treatments and all species into a single model and compared recreation noise against the natural sounds and no noise treatments. In the next model, we separated the recreation treatments. We also ran a model with the mean dB(A) of the noises as the main predictor variable. For our second question, "Which species are more tolerant or sensitive to recreation noise?", we collapsed recreation treatments and separated species. For our third question, "What attributes of recreation noise (e.g., recreation type, group size, group vocalizations) influence wildlife responses?", we ran three models. First, we collapsed all hiking and running treatments into a 'hiking' type, we collapsed all mountain biking treatments into a 'biking' type, and we kept OHV as its own separate treatment. Then, we collapsed all small groups together and all large groups together. OHV treatments were not included in these models. Third, we collapsed the treatments by whether they were vocal or non-vocal. For this question, we ran the models for all species together and for each species separately.

To answer our fourth question, "Does recreation noise lead to changes in local site use of wildlife?", we first identified when any of our focal species were captured on any camera in our arrays and considered that an observation. We required observations to be 20 min apart from one another to be counted as independent observations. We then summed the number of observations across all species for each sampling week at a site and ran two Poisson regressions with the *glmer* function from the 'lme4' R package.⁵⁵ First, we modeled species counts as a function of if any recreation noise (binary) was played at a site the previous week. We modeled number of individuals as a function of the recreation noise treatment played the week prior to allow time for wildlife to experience the noise and respond to it. Second, we modeled species counts as a function of which recreation treatment was deployed the previous week. For both models we included the week of sampling season as a main effect to account for wildlife acclimation to noise over the course of each season and for seasonal variations, and site as a random effect. The count data were slightly over-dispersed, therefore, we then re-ran the models using a negative binomial distribution with the *glmer.nb* function from the 'lme4' R package. For all models we identified significant contrasts and calculated effect sizes with the 'emmeans' R package.⁵⁶