Biological Conservation 323 (2026) 112084

Contents lists available at ScienceDirect

Biological Conservation

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

Experimentally quantifying how long recreation noise displaces mammals: Recovery over weeks to months varies by disturbance type and species tolerance

Julia N.D. Daniell [a,b], Mark A. Ditmer [c,d,*], William L. Rice [a,b], James Wilder [e], Brian D. Gerber [f], Svea Smith [g], Elizabeth Reynolds [h], Jesse R. Barber [i,j], Katherine A. Zeller [k]

[a] Department of Society & Conservation, University of Montana, 32 Campus Drive, Missoula, MT, 59812, USA
[b] Parks, Tourism, and Recreation Management Program, University of Montana, 32 Campus Drive, Missoula, MT, 59812, USA
[c] USDA Forest Service, Rocky Mountain Research Station, 240 Prospect Road, Fort Collins, CO, 80526, USA
[d] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 400 University Avenue, Fort Collins, CO, 80523, USA
[e] USDA Forest Service, Bridger-Teton National Forest, 390 N. Cache, Jackson, WY, 83001, USA
[f] U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1484 Campus Delivery, Fort Collins, CO, 80523, USA
[g] W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT, 59812, USA
[h] Department of Biological and Environmental Sciences, East Texas A&M University, Commerce, TX, 75429, USA
[i] Department of Biological Sciences, Boise State University, 1910 University Drive, Boise, ID, 83725, USA
[j] American Museum of Natural History, New York, NY, USA
[k] The Wilderness Society, 1801 Pennsylvania Ave. NW, Suite 200, Washington, DC, 20006, USA

ARTICLE INFO

Keywords:
Acoustic playback
Habituation
Mammal assemblage
Motorized recreation
Recreation ecology
Soundscape
Wildlife disturbance

ABSTRACT

Outdoor recreation is expanding across public lands, yet managers lack evidence for how long wildlife responses to recreation persist and whether response duration depends on disturbance type and frequency. Using a field-based acoustic playback experiment in the Bridger–Teton National Forest, Wyoming, USA, we isolated recreation noise from other components of human presence and quantified how long mammal detections took to return to baseline. Across 12 sites over two field seasons, we broadcast motorized and non-motorized recreation sounds at rates mimicking high- and low-use trails, paired with nature-sound controls. We quantified treatment effects as deviations from expected weekly detections at our control sites, defining time-to-return as the first week when deviations overlapped zero. Response duration differed between disturbance types. High-rate motorized playbacks produced the longest suppression: all species except mule deer did not return to baseline within our 15-week season, whereas mule deer recovered by six weeks. For high-rate non-motorized playbacks, all species except for mule deer had suppressed detections until seven weeks while mule deer detections were not different from baseline. For low-rate non-motorized playbacks, mule deer detections returned to baseline at nine weeks while all other species returned to baseline at seven weeks. Species differences indicate that apparent overall recovery can mask prolonged avoidance by less tolerant taxa. Recreation effects persisted for weeks to months and varied with disturbance type and exposure frequency, highlighting how temporal patterns of use influence wildlife responses and where recreational planning of spatial refugia or seasonal restrictions could reduce impacts on sensitive species.

1. Introduction

Assessing the impacts of outdoor recreation on wildlife is complex, as it involves factors related to recreationists, animals, management, and the environmental context (Tablado and Jenni, 2017). Wildlife responses vary with the species of wildlife, the type of recreation activity (e.g., mountain biking, hiking, off-highway vehicles), the intensity of trail-based recreation, and with how recreationists move through the landscape, such as staying on trails versus traveling off-trail (Taylor and Knight, 2003; Westekemper et al., 2018). Nonetheless, a systematic

* Corresponding author at: USDA Forest Service, Rocky Mountain Research Station, 240 Prospect Road, Fort Collins, CO, 80526, USA.
E-mail address: mark.ditmer@usda.gov (M.A. Ditmer).

https://doi.org/10.1016/j.biocon.2026.112084
Received 4 May 2026; Received in revised form 5 August 2026; Accepted 31 August 2026
0006-3207/Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

review of recreationist impacts reported that most studies in the literature (93% of 274 studies) show one or more effects on wildlife, generally negative (Larson et al., 2016). These negative effects ranged from behavioral changes, spatial and temporal avoidance, and hormonal shifts, to demographic changes such as increased mortality (Creel et al., 2002; Lewis et al., 2021). However, previous work often lacks controls for recreation type or trail-use intensity (Cardona et al., 2024) and rarely evaluates responses over time. As a result, it remains unclear whether wildlife responses are driven by recreation type, the rate of exposure, or their interaction, and whether repeated exposure leads to short-lived displacement or more persistent effects. These uncertainties limit managers' ability to determine when interventions such as visitor education, refugia, seasonal restrictions, or means of creating predictable recreation schedules are warranted.

Frequent experience with human activity can lead wildlife to habituate to outdoor recreationists (Bejder et al., 2009; Blumstein, 2016; Ditmer et al., 2026). For managers, understanding whether responses attenuate through time is important because it influences expectations for where, when, and how recreation is concentrated across the landscape. This apparent behavioral tolerance can be associated with reduced costs of antipredator responses or access to benefits in human-used areas (i.e., "human shields"; Berger and Cassidy, 2024), but it may also elevate risk through reduced fear responses and increased potential for human-wildlife conflict (Blumstein, 2016). Despite broad evidence that human recreation affects wildlife, most studies emphasize short-term or localized responses, and comparatively few quantify how responses attenuate through time (Larson et al., 2016; Marion et al., 2020). Therefore, managers and ecologists often lack empirical estimates of the time course of animal displacement under repeated exposure, making it difficult to anticipate whether impacts to space use and habitat availability are brief, cumulative, or periodic. Here, we address this gap by experimentally manipulating soundscapes to synthesize the sounds of human recreationists, creating low- and high-use trail conditions to test whether mammals habituate over time to the presence of people recreating in natural areas.

Anthropogenic noise can influence animal behavior, distribution, reproductive success, and the structure of ecological communities at broad spatial scales (Beale and Monaghan, 2004). Road ecology research, including "phantom road" experiments, has demonstrated that wildlife respond negatively to road noise even in the absence of vehicles (McClure et al., 2013; Ware et al., 2015). Distinguishing noise from other disturbance sources remains challenging due to limitations in assessing acoustic detection thresholds in free-ranging animals (Buxton et al., 2017). However, Zeller et al. (2024) explicitly evaluated recreation-noise effects on terrestrial mammals using a field-based acoustic playback design. This experimental approach isolated sound from other dimensions of recreation (e.g., visual presence, movement, scent), which provided stronger inference about noise-specific effects.

Zeller et al. (2024) observed that wildlife abundance at their sampling locations was roughly 1.5 times lower in the week following any recreation-noise treatment relative to control conditions, but variation in antipredator behavior (e.g., vigilance, fleeing) suggested that mediating factors such as predictability and background human presence may influence responses. Furthermore, Ditmer et al. (2026) examined the latter by pairing anonymized human mobility data (HMD; cellular data) with the data of Zeller et al. (2024) and found that wildlife showed a reduced tendency to flee from recreation noise and spent less time vigilant in areas where human use was high. Together, these studies motivate a focused investigation into whether wildlife exhibit habituation to recreation-related noise and the time scales over which such changes can emerge. Whether such responses weaken with continued exposure over time, and whether attenuation depends on the rate of exposure, remains largely untested.

Here, we used a field-based acoustic playback experiment to test how long it takes mammal detections to return to baseline levels after recreation-noise disturbance. Over the 2024 and 2025 summer seasons, we measured mammal site use (camera detections) across 12 sites within four deployment areas across the Bridger-Teton National Forest (Wyoming, USA) under experimentally manipulated soundscapes. Treatments included motorized recreation (ATVs and off-road 4 × 4 vehicles) and non-motorized recreation (vocal hikers/cyclists) broadcast at rates approximating high- and low-use trails. Within each deployment area, we spatially matched recreation-noise treatment sites with a nature-sound control (e.g., birdsong). We estimated the treatment effects of recreation activity as the difference in mammal detections through time from the expected number of detections at the baseline nature-sound control sites. Further, we quantified the time-to-return as the first week when the 95% confidence intervals for predicted deviations overlapped zero, a pattern operationally consistent with reduced avoidance, whether via habituation or compositional filtering, to repeated recreation-noise exposure (Bejder et al., 2009). We also quantified daily temporal dynamics by comparing daytime broadcast ("playback on") versus nighttime non-broadcast ("playback off") periods to determine if temporal shifts in site use occurred. Because higher-frequency broadcasts created more regular temporal exposure, we predicted they would be experienced as more predictable than low-frequency broadcasts. When recreation was predictable, we predicted that wildlife would habituate more rapidly under high-rate playbacks, whereas if intermittent cues are perceived as less predictable, low-rate playbacks should produce stronger early avoidance and slower attenuation (Smith et al., 2021). Finally, because vocal non-motorized recreationist groups elicited strong antipredator responses in prior work (Zeller et al., 2024), we expected equal or greater initial suppression under a non-motorized soundscape, with the possibility that this contrast depends on trail use frequency.

2. Methods

2.1. Study area description

We conducted this study in the Bridger–Teton National Forest (Wyoming, USA) within the Greater Yellowstone Ecosystem, a landscape that contains a diverse community of medium- to large-bodied mammals amid substantial, spatially heterogeneous recreation use (USFS Bridger-Teton NF, 2021). The forest supports both motorized (e.g. ATVing, dirt biking) and non-motorized recreation (e.g., hiking, mountain biking, shed hunting, hunting, trapping), and use intensity varies from heavily visited front-country areas to comparatively low-use backcountry settings. This range of recreation contexts made it well suited for testing how mammal communities respond to different recreation soundscapes and whether responses attenuate through time. The U.S. Forest Service estimates that approximately 2.2 million people visit the Bridger–Teton National Forest annually, although visitation is difficult to quantify precisely on National Forest lands with many unmonitored access points (USFS Bridger-Teton NF, 2021). We conducted fieldwork on the Jackson Ranger District, which surrounds the town of Jackson, WY on the east, south, and west sides and is one of six districts within the Bridger-Teton National Forest.

2.2. Research design and site selection

We designed our study to isolate the effects of human recreationist sounds from other aspects of recreation (e.g., movement, scent, dropped food) on mammal detections through time. Our study was conducted across four deployment areas within the Jackson Ranger District, each containing three sites (one nature-sound control and two recreation-noise treatment sites), for a total of 12 sites. Our goal was to quantify whether, and for how long, mammal communities were displaced by motorized versus non-motorized recreation sounds broadcast at high versus low frequencies. We estimated treatment effects by comparing observed weekly detections at playback sites with expected detections from a baseline model fit to all control sites. To standardize local

conditions, we spatially paired control sites within each deployment area.

We recorded ambient nature sounds for our control and the sounds of human recreationists for our treatments, in areas with comparable habitats to our study sites. We calibrated recordings using the *SmarterNoise* mobile application (Rogard, 2024) to ensure playback levels matched real-world decibel levels of recreational activity (Maier, 2001). To reduce potential confounding factors, we recorded sounds in settings free from other noise sources such as aircraft or road traffic. We grouped the recordings into three types: 1) nature (e.g., ambient natural sound as a control); 2) non-motorized recreation (groups of 5 or more recreationists either hiking or mountain biking while also speaking within the group); and 3) motorized recreation (off-highway vehicles; both ATVs and off-road 4 × 4 vehicles). We obtained multiple recordings of each noise and used three different recordings per noise, selected at random, for field playback broadcasts (McGregor, 2000). We chose large vocal groups of bikers or hikers to represent the non-motorized treatment because Zeller et al. (2024) reported the strongest and most frequent antipredator responses of wildlife exposed to these types of recreationists. We kept the use of motorized recreation recordings consistent with Zeller et al. (2024), which were comprised of one to two vehicles.

We broadcast recordings using acoustic playback devices (APDs; *BoomBoxes* - Freaklabs) at selected field sites (Fig. 1). We selected deployment areas based on the potential to maximize detections of medium- to large-bodied mammals, with candidate deployment areas identified in consultation with BTNF wildlife biologists. Within each deployment area, we selected three study sites that met the following fine-scale selection criteria: 1) along a game trail, 2) evidence of high wildlife activity (e.g., scat, tracks), 3) away from sources of established human noise (sites were placed an average of 650 m from roads and maintained trails), 4) sufficient trees for mounting cameras and playback devices, and 5) topography that maximized line-of-sight conditions.

Among the four deployment areas chosen—Hoback Canyon, Gros Ventre, Mosquito Creek, and North Fall Creek—we randomly assigned each deployment area a recreation type, either motorized or non-motorized. Within each deployment area, we then randomly assigned one of the three sites as the nature-sound control and the other two as recreation-noise sites. Because recreation type was assigned by deployment area, inference about motorized versus non-motorized effects relied on replication across areas and years, not independent site-level assignment within a season. We randomly assigned different playback rates at the recreation-noise sites, one high-rate site with playbacks every 3 min and one low-rate site with playbacks every 30 min, designed to mimic high- and low-use trails by recreationists (Fig. 1). At the nature-sound control sites, we broadcast nature sounds at the high rate in every deployment area. For our second field season in 2025, we randomized treatment types and sites without replacement so that no sites had the same treatment as the previous year. This arrangement allowed us to control for environmental variation across the landscape (deployment areas) while standardizing site types. We relocated four sites with low detection rates or high human interference (e.g., popular with off-trail recreationists or hunters) within their deployment area before the 2025 field season.

The 12 sites played their assigned sounds starting in either late May or early June for the 2024 and 2025 field seasons, respectively, and ending in early September. We programmed the APDs to broadcast each day for a 12-h playback period from 0700 to 1900 and then be silent from 1900 to 0700. All sites followed the same daily schedule with playback from 0700 to 1900 (ON) and complete silence from 1900 to 0700 (OFF). Each site also included four motion-triggered cameras (Reconyx Hyperfire 2 Professional Covert Infrared) spanning a 50–100 m length along the game trail to capture any medium- or large-bodied mammals. We programmed the outer two cameras to record 90-s

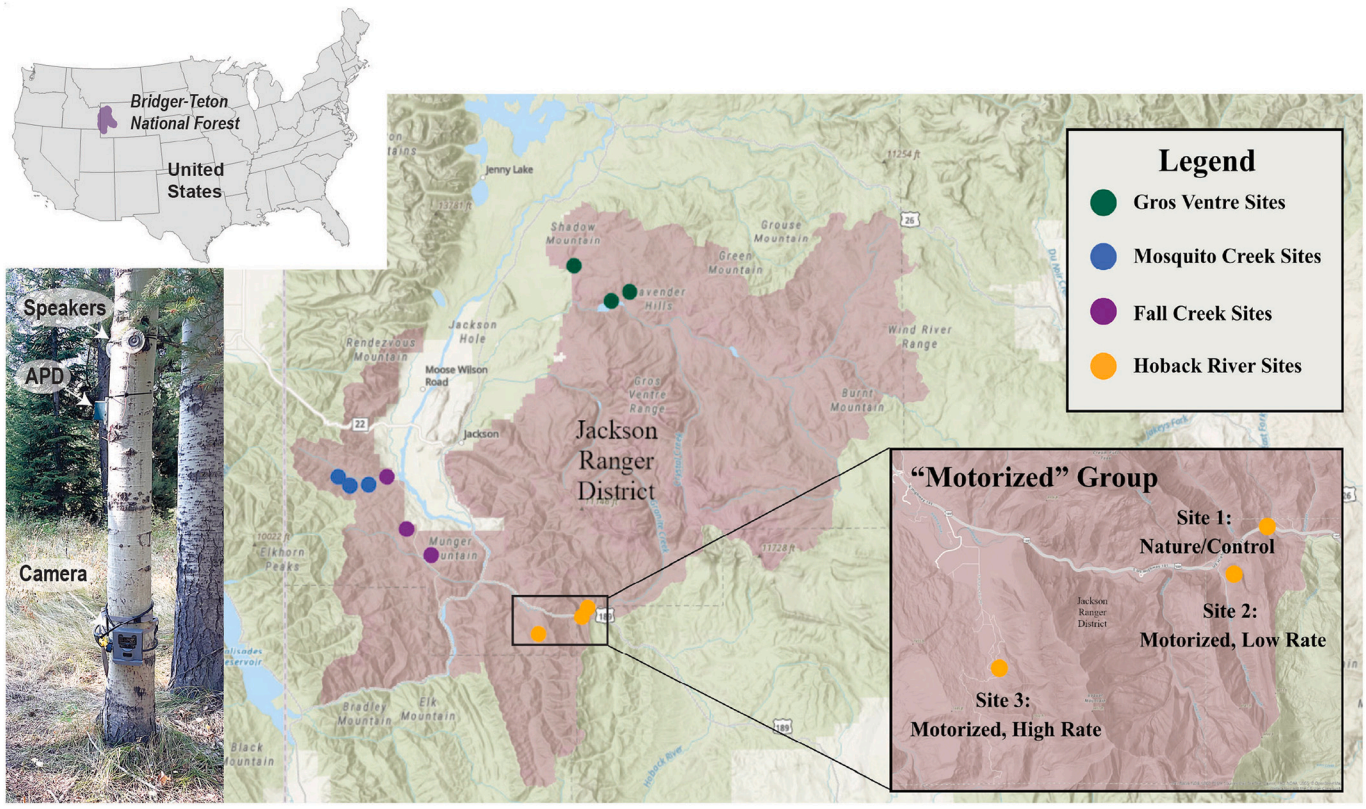

Fig. 1. Study area showing 4 deployment areas with three sites each. Recreation type was randomly assigned to each deployment area, then recreation frequency and nature-control sites were randomly assigned to each site within a deployment area. An example of a motorized deployment area is shown in the map inset along with a portion of the field setup including one (out of four per site) camera trap, audio playback unit (APD), and the associated speakers.

video clips per trigger, and the central two cameras to record 10-s video clips following Zeller et al. (2024). The cameras used no-flash infrared technology to minimize visible-light disturbance and were positioned to maximize the field of view around the APD while reducing false triggers from vegetation or topography. We checked equipment every two weeks to replace batteries, collect and replace SD cards, and verify APD function, ensuring consistent operation while minimizing disturbance to the sites. All procedures were reviewed and approved by the USDA Forest Service's Institutional Animal Care and Use Committee (IACUC).

2.3. Data preparation and analysis

After removing videos generated by false triggers (i.e., with no animals present), we retained videos showing species the size of a red fox or larger. We grouped individual videos into events by merging detections across all cameras within a site of the same species occurring within 20 min using the *lubridate* package in R (Grolemund and Wickham, 2011). We then assigned each event to a numeric week, with Week 1 starting the day the treatment and control sounds were first deployed at each site. We summed weekly detections for each site-year and classified events as occurring during the 0700–1900 period when treatment sounds were broadcast or outside that period. We conducted all data handling and modeling in R version 4.5.2 (R Core Team, 2024).

2.4. Establishing an expected baseline from nature-control sites

To establish a baseline of animal detections of all present species or specific species, we modeled weekly detections from the nature-control sites only. The purpose was to establish a model of expected detection that captures the seasonal shift of animal activity from lower elevations, where our sites were located, to higher elevations. We modeled detections of animal activity using generalized linear mixed models (GLMMs), fit using the *glmmTMB* (Brooks et al., 2017) and the *splines* packages with a negative binomial distribution using the formulation,

$$\text{event\_count} \sim \text{ns}(\text{week\_bin}, \text{df} = \text{best\_df}) + (1 \mid \text{site\_year})$$

where event_count is the count of events at a site for each week, week_bin is the week of the study, best_df is the degree(s) of freedom for the spline that resulted in the lowest AIC value (we tested 1–3 degrees of freedom), and site_year is a random intercept for the combination of the specific site and year. We used natural cubic splines due to the nonlinear variation in detections throughout the season during both years of data collection (Chuang et al., 2011) and identified the optimal df based on AIC for each baseline model. We assumed a negative binomial distribution to accommodate potential overdispersion (Stoklosa et al., 2022). We generated separate models for data during the sound-on (diurnal) and sound-off (nocturnal) periods at the nature-control sites. We generated weekly predictions from the nature-control site models using the *ggeffects* package (Lüdecke, 2018) for all mammals in our study (Fig. 2), mule deer only (the only species where we had enough data at the sites to adequately fit species-specific models), and all mammals except for mule deer. Because mule deer had the largest sample size of all species in our study, we ran the latter two models to determine how much mule deer were driving the overall patterns we observed and to further understand species differences.

2.5. Calculating time-to-return for noise treatments

We subset species detections within the treatment sites into eight categories based on sound-on/sound-off period, recreation type (Motorized/Non-motorized), and recreation frequency (High/Low). We calculated the residuals for each category based on the deviation between observed weekly detections at each treatment site and predicted baseline detections from the corresponding nature-control models for the same week of the year (e.g., Figs. **S5 & S6**). The difference (residual) quantified weekly departures from the nature-sound baseline expectation (estimated from the pooled control-site model) for the same week of the season.

Next, we evaluated habituation through time by fitting GLMMs with the residual deviations from the nature-sound control weekly number of detections as the response variable. We used a similar approach to the nature-control baseline models but assuming a Gaussian distribution. We fit separate models for each of the eight treatment subsets using natural cubic splines for week (best_df = 1–3) and a random intercept for site-year, following the same formulation as the models of the expected baseline from nature-control sites, except with the residual value as the response variable.

$$\text{Residual} \sim \text{ns}(\text{week\_bin}, \text{df} = \text{best\_df}) + (1 \mid \text{site\_year})$$

We then used the resulting top models of the residuals to create weekly predictions for each of the eight subsets using the *ggpredict* function. We classified weekly local use as greater than the predicted control baseline when the lower bound of the 95% CI for the predicted residual was ≥ 0 and as lower than the baseline when the upper bound was ≤ 0. We operationally defined time-to-return as the first week after treatment initiation in which the predicted 95% CI for the residual

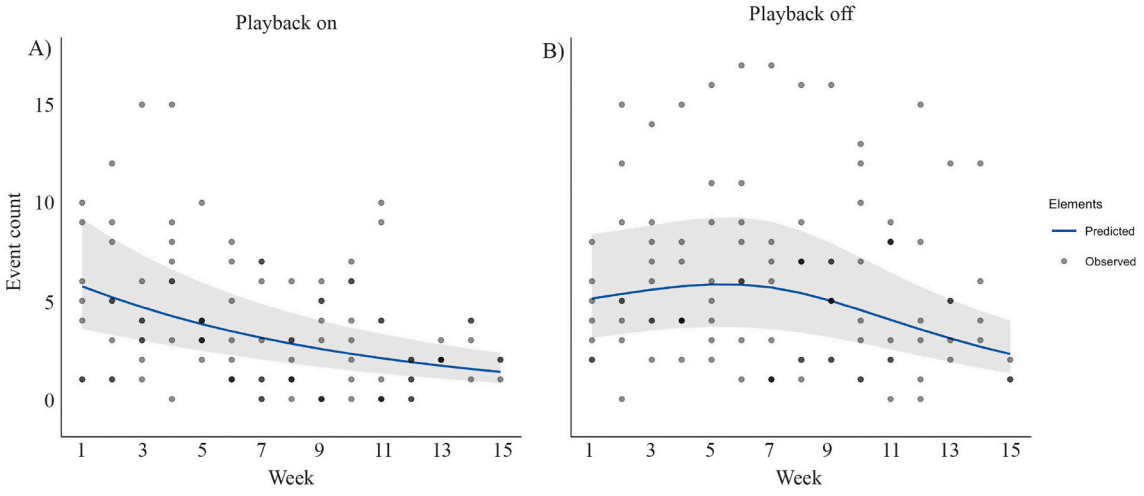

Fig. 2. Baseline species detections for all mammals show a decline across our sampling period. Modeled detections of all mammal species (blue line), with 95% confidence intervals (grey shading), at the nature-control playback sites during (A) daytime playback-on periods and (B) nighttime playback-off periods. Raw counts of detections are shown as points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

overlapped zero, indicating no detectable deviation from the nature-sound baseline expectation. For longer time-to-return intervals, we calculated the number of detections above or below either the mean or the relevant 95% CI estimate across the time-to-return interval to produce liberal and conservative estimates of species detection gains or losses. Because confidence intervals overlapping zero do not demonstrate the absence of treatment effects, this metric should be interpreted as an operational estimate of recovery rather than definitive evidence that recreation effects ceased. None of the models in which detections were suppressed deviated from baseline detections once the confidence intervals overlapped 0.

For all species except mule deer, we did not fit a model to the residuals for each individual species due to limited sample sizes. The models for these species were susceptible to the influence of outlier sites, and so, in addition to running models that included all species except mule deer, we plotted the residuals for each individual species by week and reported the percentages of residual values that were either positive (more detections than expected based on the pooled nature-control baseline model) or negative (fewer detections than expected based on the pooled nature-control baseline model).

3. Results

During 2235 trap nights across both years, camera traps recorded a total of 3678 events comprised of mule deer (*Odocoileus hemionus*, 2293 events), elk (*Cervus canadensis*, 359), red fox (*Vulpes vulpes*, 353), moose (*Alces americanus*, 306), black bear (*Ursus americanus*, 141), coyote (*Canis latrans*, 94), wolf (*Canis lupus*, 32), pronghorn (*Antilocapra americana*, 29), cougar (*Puma concolor*, 28), grizzly bear (*Ursus arctos horribilis*, 26), white-tailed deer (*Odocoileus virginianus*, 16), and a single detection of bighorn sheep (*Ovis canadensis*). These species and associated detections comprised the all-species analysis.

Detections for all mammals at nature-control sites declined seasonally in both periods as expected, due to animal movement to higher elevations. During daytime nature playbacks (0700–1900), predicted number of detections declined from 5.73 events [95% CI: 3.58–9.17] in Week 1 to 1.39 (95% CI [0.82–2.35]) in Week 15 (Fig. 2A). During nighttime silence (1900–0700), predicted detections declined from 5.12 events (95% CI: 3.12–8.40) in Week 1 to 2.30 events (95% CI: 1.32–4.00) in Week 15 (Fig. 2B). Mule deer at nature-control sites showed similar seasonal patterns (**Fig. S1**).

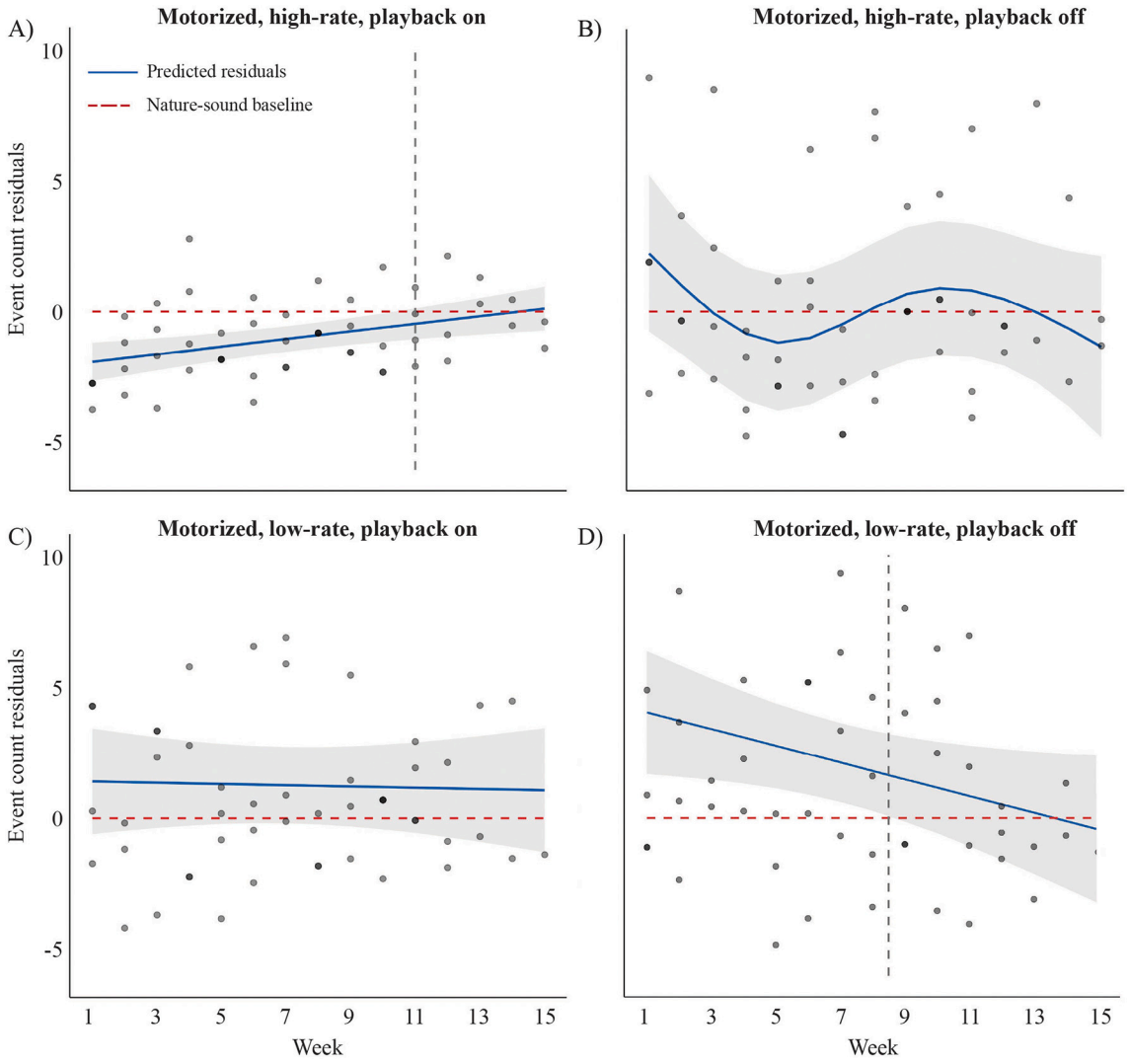

Fig. 3. Differences in species detections (predicted residuals) at the motorized treatment sites compared to the baseline control sites (red dashed line). Values above the baseline indicate more detections than predicted by the baseline models; values below the zero baseline indicate fewer detections than predicted by the baseline models. Mean residuals (blue line) are shown with 95% confidence intervals (grey shading). Raw residual data are shown as points. Motorized treatments where detections were initially different from the baseline have a vertical grey dashed line indicating the first week when detections returned to baseline levels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.1. Return to baseline interval: All mammals

Low-rate motorized sites showed no evidence of a daytime treatment effect: predicted deviations in detections during motorized broadcasts remained near zero, and 95% CIs overlapped zero throughout the season (Fig. 3C). In contrast, during nighttime silence at these same sites, deviations in detections declined through time from above-baseline use early in the season (Week 1: +4.03 [95% CI: 1.69–6.38]) toward baseline by Week 9 (Fig. 3D**; Fig. S4**), with an estimated 9.00–37.67 additional events during Weeks 1–9 (Table 1).

High-rate motorized broadcasts produced strong early suppression of detections (Week 1: −1.91 (95% CI: −2.64 to −1.19) followed by gradual return toward baseline, with CIs overlapping zero by Week 11 (see vertical dashed line in Fig. 3A) and an estimated 7–18 events below baseline over that interval (Table 1). During nighttime silence at the same sites, deviations in detections generally overlapped zero throughout the season (Fig. 3B**; Fig. S4;** Table 1), suggesting avoidance was largely constrained to daytime broadcast periods.

We had considerably fewer mammal detections at sites where the non-motorized recreation noises were broadcast at a low rate, with a mean predicted detection rate that was −2.58 (95% CI: −3.60 to −1.55) below the nature-sound baseline (Fig. 4C**; Fig. S5**). The associated return-to-baseline time interval was 9 weeks, with a predicted loss in detections ranging from 7 to 20 (Table 1). During nighttime silence at the same sites, deviations fluctuated through time, but 95% CIs overlapped zero throughout (Fig. 4D), indicating no consistent departure from baseline during non-broadcast periods. At sites receiving high-rate non-motorized recreation playback, predicted deviations from the nature-sound baseline were minor (−1.17 to +1.18). Mean deviations were modest, and weekly 95% CIs overlapped zero throughout the season (Fig. 4A**; Fig. S5;** Table 1). Similarly, during the periods when the non-motorized recreation noises were not broadcast, we found no consistent departure from the nature-sound baseline (control-model prediction; all weekly 95% CIs overlapped zero, no strong temporal trend; Fig. 4B**;** Table 1**),** indicating similar detection patterns at these sites even during periods of high-intensity non-motorized noises.

3.2. Return to baseline interval: Mule deer

Overall, mule deer tended to be more tolerant of recreation noise treatments relative to results obtained for all mammals. For instance, mule deer exhibited more rapid habituation when exposed to the high-rate motorized recreation noises (**Fig. S2)**. Their return to baseline occurred five weeks earlier than in the all-mammal model (week 6 vs. week 11), and the predicted loss in detections was 0.59–6.63 over those 6 weeks (Table 1). Mule deer exhibited greater than expected mean detections at the low-rate motorized recreation noises (note: the 95% CIs for Weeks 1–2 slightly overlapped zero; **Fig. S2**), and when the broadcast was turned off, mule deer displayed a return-to-baseline of 9 weeks (**Fig. S2**) with an estimated 13.74–51.83 additional detections during this period (Table 1**)**. Mule deer matched the all-mammal pattern: strong suppression under low-rate non-motorized broadcasts, but near-baseline deviations during several sound-off conditions (**Fig. S3**). Mule deer were also detected less frequently than expected at sites with low-rate non-motorized playbacks (week 1: - 2.22 [95%CI: −2.96 to −1.48]), with a return-to-baseline interval that matched the overall mammal model (week 9; $p < 0.0001$; **Fig. S3**), and an estimated reduction of 6.91–16.87 mule deer detections during these weeks (Table 1).

3.3. Return to baseline interval: All species except mule deer

For high-rate motorized treatments during the playback on period, the other species in our study did not return to the baseline number of detections within the duration of our sampling period (15 weeks; **Fig. S5**). The predicted loss of detections over the study was 6.09–19.46 (Table 1). Although the first weeks at the high-rate motorized playback

Table 1
Number of wildlife detections for each experimental treatment compared to the baseline nature-control sites. Negative residuals indicate fewer detections than the baseline sites; positive residuals indicate more detections than the baseline sites. When there was no difference between the treatment sites and the control sites, there was no return to baseline interval or gains/losses in detections from baseline. Therefore, these treatments have an NA in the last two columns.

Experimental treatment	Mean residual at week 1	First week when treatment matches control	Sum of mean residuals prior to matching control	Detection gain/loss estimate [CI range]
	All species			
Motorized, high rate, sound on	−1.91	11	−12.60	−18.20 to −7.04
Motorized, high rate, sound off	2.22	0	NA	NA
Motorized, low rate, sound on	1.40	0	NA	NA
Motorized, low rate, sound off	4.03	9	23.33	9.0–37.67
Non-motorized, high rate, sound on	−1.17	0	NA	NA
Non-motorized, high rate, sound off	3.10	0	NA	NA
Non-motorized, low rate, sound on	−2.58	9	−13.71	−20.02 to −7.36
Non-motorized, low rate, sound off	1.05	0	NA	NA
	Mule deer			
Motorized, high rate, sound on	−0.91	6	−3.6	−6.63 to −0.59
Motorized, high rate, sound off	−0.31	0	NA	NA
Motorized, low rate, sound on	1.21	11	12.72	−0.19–25.65
Motorized, low rate, sound off	2.38	9	32.78	13.74–51.83
Non-motorized, high rate, sound on	−0.21	0	NA	NA
Non-motorized, high rate, sound off	3.47	0	NA	NA
Non-motorized, low rate, sound on	−2.22	9	−11.88	−16.87 to −6.91
Non-motorized, low rate, sound off	−0.59	0	NA	NA
	All species except mule deer			
Motorized, high rate, sound on	−1.71	>15	−16.01	−19.46 to −6.09

(*continued on next page*)

Table 1 (*continued*)

Experimental treatment	Mean residual at week 1	First week when treatment matches control	Sum of mean residuals prior to matching control	Detection gain/ loss estimate [CI range]
Motorized, high rate, sound off	1.86	4, 11	−10.45	−17.65 to −3.22
Motorized, low rate, sound on	−0.72	0	NA	NA
Motorized, low rate, sound off	−1.23	13	−12.53	−21.43 to −3.62
Non-motorized, high rate, sound on	−1.75	7	−7.03	−11.01 to −3.04
Non-motorized, high rate, sound off	−0.68	0	NA	NA
Non-motorized, low rate, sound on	−1.10	7	−5.26	−9.41 to −1.13
Non-motorized, low rate, sound off	0.51	0	NA	NA

off periods had higher counts than baseline, by week four, the counts were lower than baseline and remained lower for the next seven weeks (**Fig. S5**) with an associated loss of detections of 3.2–17.65 (Table 1), indicating site avoidance persisted during sound-off periods. Unlike mule deer, in response to high-rate non-motorized treatments during the playback on period, these species showed a decrease in detections with a return to baseline observed at seven weeks (**Fig. S6**) and a loss in detections from 3.04 to 11.01 (Table 1). For low-rate non-motorized treatments, the return to baseline was also at seven weeks – two weeks earlier than observed for mule deer (**Fig. S6**) and with predicted losses of detections from 1.13 to 9.41 (Table 1).

3.4. Moose and Elk detections

Elk and moose were detected far less frequently at sites with high-rate recreation noise broadcasts. The percentages of site-weeks where residuals were less than 0 (fewer detections than the baseline) were 80% and 93% during exposure to high-rate motorized during playback periods, for moose and elk respectively (**Figs. S9 & S11, Tables S1 & S2**). The proportion of negative weekly residuals was similar or larger when considering the non-motorized high-frequency treatments (100% of values for moose and 93% for elk had fewer detections than the baseline). The influence of the low-rate motorized (73% of weeks for moose, 80% for elk) and non-motorized (80% moose, 80% elk) broadcast periods also indicated some avoidance of sites (**Figs. S10 & S12**). Both species used the study sites more frequently when playback sounds were absent, but residuals during these sound-off periods were still predominantly negative across all recreation types and playback rates (Tables S1 and S2), indicating that some individuals likely avoided these sites entirely.

3.5. Large carnivore detections

Black bears exhibited some signs of avoidance of treatment sites, especially where motorized recreation noises were broadcast. Detections were almost always lower than expected in both the low-rate (93% of weeks) and high-rate (93% of weeks) of motorized sites when the sound was on, while detections when the sound was off also were less than expected (93% low-rate and 93% high-rate; **Fig. S13, Table S3**). Black bears also had lower detections than baseline at non-motorized sites, both at the low-rate (93%) and high-rate (73%) sites. Nocturnal detections were similarly affected, with 87% of weeks showing lower than expected detections at high frequency sites and 93% at low frequency sites (**Fig. S14, Table S3).**

The other large-bodied carnivores (cougar, wolf, grizzly bear, coyote) were typically detected less than expected at recreation-noise sites in both the playback on and off periods, consistent with broad avoidance (**Figs. S15 & S16, Table S4).** Avoidance was especially acute after the first 3–4 weeks of broadcast at a site. The primary exception was during playback off periods at non-motorized, high-rate sites, but we still observed that during 73% of the weeks, detections were lower than the nature-sound baseline.

4. Discussion

Using a field-based acoustic playback experiment, we showed that recreation noise altered mammal site use in ways that depended on recreation type and trail-use frequency (playback rate). Our experimental design allowed us to quantify time-to-return intervals under repeated exposure, information that is critical in understanding the role of habituation to recreation noise. Detections were most strongly suppressed under high-rate motorized and low-rate non-motorized treatments, with slow return to baseline that resulted in temporal habitat loss over that period (Rivera et al., 2022). In contrast, detections did not deviate detectably from controls during low-rate motorized or high-rate non-motorized broadcasts. However, these all-species patterns should be interpreted in light of strong species differences: mule deer comprised a larger percentage of detections and showed comparatively rapid habituation (e.g., week six for high-rate motorized), which can make displacement appear concentrated during broadcast periods even when other species respond differently. Indeed, for our high-rate motorized broadcast model that included all species except for mule deer, detections did not return to baseline for the 15-week span of our study. We also observed a reduction in detections at those sites during playback off periods, indicating the treatment resulted in avoidance of the sites altogether instead of a compensatory shift to nighttime use. The all-species model showed no decline under high-frequency non-motorized broadcasts; however, once mule deer were removed, the remaining species declined and returned to baseline at seven weeks. Together, our results provide both empirical findings and an approach to quantify return-to-baseline dynamics under repeated disturbance but also suggest that apparent “recovery” across all species can mask heterogeneous responses, where more abundant, tolerant species do not avoid sites or resume use sooner while more sensitive species may have shown avoidance for longer periods.

Predictability and timing of recreation use may mediate the negative effects of recreation by influencing how animals respond to repeated exposure (Westekemper et al., 2018; Smith et al., 2021). Trails with more regular and concentrated use can provide more predictable cues, but predictability is distinct from intensity, and high-intensity sounds may still trigger strong avoidance. This may allow wildlife to better anticipate repeated disturbance and adjust their responses through time (Parlin et al., 2026; Wilson et al., 2020), and when the disturbance is not associated with direct threats to wildlife, habituation can result. Conversely, intermittent disturbance (like that occurring on more sparsely used recreation trails) can function as pulses of risk that elicit stronger avoidance and slower attenuation than more continuous exposure (Sih and McCarthy, 2002). In our experimental design, playback rate primarily manipulated temporal frequency. Higher-frequency playbacks created more regular exposure and likely increased the temporal predictability of disturbance relative to low-frequency playbacks, which were more intermittent. A predictability framework is one possible explanation for the non-motorized pattern in the all-species model, where low-rate playbacks produced stronger suppression and

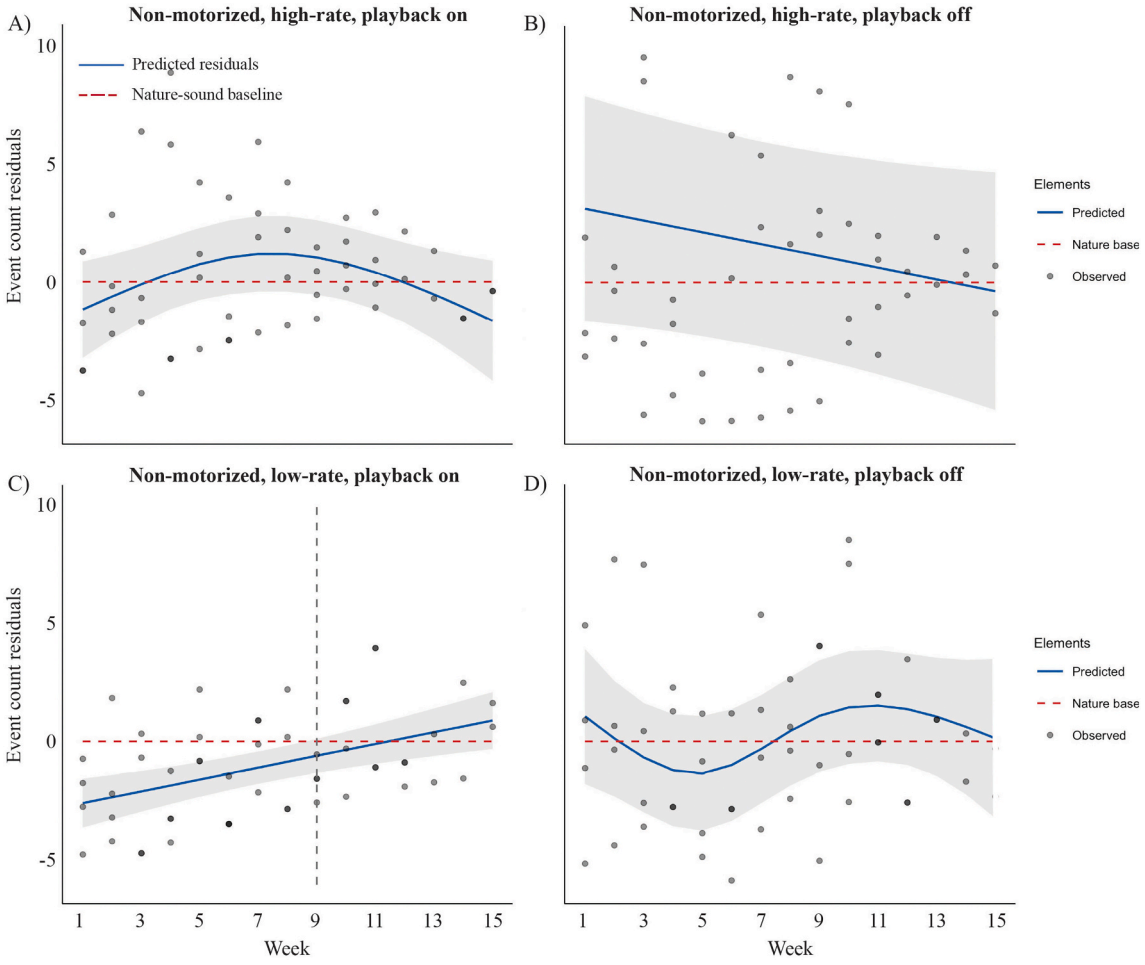

Fig. 4. Differences in species detections (predicted residuals) at the non-motorized treatment sites compared to the baseline control sites (red dashed line). Values above the baseline indicate more detections than predicted by the baseline models; values below the zero baseline indicate fewer detections than predicted by the baseline models. Mean residuals (blue line) are shown with 95% confidence intervals (grey shading). Raw residual data are shown as points. Non-motorized treatments where detections were initially different from the baseline have a vertical grey dashed line indicating the first week when detections returned to baseline levels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

slower return than high-rate playbacks. This pattern, however, was driven largely by mule deer; once mule deer were removed, the remaining species were suppressed under high-rate non-motorized broadcasts as well, indicating that any discounting of more regular, lower-threat cues was not general across species. Because playbacks followed a fixed schedule, animals could encounter both broadcast and silent windows while moving through sites, which likely makes our estimates conservative relative to real-world trails where use occurs in clustered groups or prolonged events. However, playback frequency simultaneously altered temporal regularity and cumulative acoustic exposure. Consequently, our experiment cannot fully distinguish whether observed differences reflect predictability, total exposure, or both.

Responses to temporal regularity also differed by disturbance type, but importantly this contrast was driven largely by mule deer. Mule deer showed little suppression under regular (high-rate) non-motorized playbacks, consistent with tolerant, abundant species discounting a frequently encountered cue, whereas the remaining species continued to avoid these sites for roughly seven weeks. Regular motorized playbacks, by contrast, produced strong early suppression and delayed return even for mule deer. One interpretation consistent with this pattern is that temporal predictability governs how well an animal can anticipate a cue, while the animal's learned association between that cue and actual risk governs whether anticipation promotes tolerance or sustained avoidance. Motorized activity in this system is more closely associated with direct sources of mortality, including vehicle collision and motorized access for hunting, which may make a more regular motorized cue reinforce rather than attenuate avoidance (Smith et al., 2021). Non-motorized recreation is not free of risk here, as hunting on foot also occurs, but its acoustic cues may be less reliably linked to lethal encounters, which could allow the most tolerant species to habituate while more sensitive species continue to respond. Playback rate covaried with cumulative acoustic exposure, as noted above, so we cannot separate predictability from total exposure. The strong response of non–mule deer species to high-rate non-motorized noise also shows that any discounting of regular, lower-threat cues was not general across the community. Because most recreation studies are not experimental and cannot quantify intensity and timing simultaneously, thresholds may also exist where motorized noise becomes comparably disruptive despite prior exposure to vehicles and roads (Larson et al., 2016; Gump and Thornton, 2023). Finally, because recreation type was assigned at the deployment-area level, area-level variables such as habitat, background human activity, elevation, and predator community are confounded with recreation type; these between-type comparisons should therefore be interpreted as differences associated with, rather than caused solely by, recreation type.

Responses to disturbance may involve animals avoiding a site altogether or shifting daily activity to use an area when disturbance is lower (Westekemper et al., 2018; Gaynor et al., 2018). Across all species in our study, we did not see strong evidence of consistent temporal

redistribution into periods when playback was silenced, which likely reflects, in part, the dominance of mule deer in the all species results. In contrast, elk, moose, and large carnivores were detected less than expected during non-playback periods, suggesting carryover avoidance across diel phases rather than simple temporal switching. One exception was the low-rate motorized treatment when playback was silenced, where all-species detections were elevated relative to baseline. This elevation was also present in the mule deer model, indicating it was driven by mule deer selecting areas associated with human activity, consistent with a predator-shield mechanism (Berger, 2007). However, we did not observe the same pattern at high-rate motorized sites.

Given these differences among species, recreation has the potential to shift the composition of wildlife communities where more tolerant species habituate to the disturbance and remain, and less tolerant species avoid the area. Our time-to-return approach quantified when detections returned to baseline values, but this overall recovery (i.e., return to baseline detections relative to controls) can result from two non-exclusive processes: habituation or filtering. More tolerant species may habituate to repeated exposure, whereas less tolerant species may be filtered out of the system by avoiding areas of exposure. Overall recovery to baseline levels can arise via reduced responses within individuals over time, shifts in site use, and/or changes in which individuals or species remain in the sampled community, so apparent 'tolerance' does not necessarily imply habituation alone and can coincide with community change via filtering (Suraci et al., 2021). In our study, mule deer returned to baseline more rapidly following recreation-noise disturbance than did the other mammal species. Less tolerant species like elk and carnivores showed persistent avoidance even during nighttime when the playback was off. This could be an indication that recreation noise in our study area may result in changes in community composition of species. Indeed, in Ditmer et al. (2026), carnivores were only present at times and in places with low recreation use.

Our study implemented a novel experimental design that allowed us to directly estimate time-to-return to baseline conditions under controlled exposure. The scheduled playbacks we used imposed regularity that may increase predictability relative to some real-world trail use. Yet, we still observed months-long suppression in wildlife detectability when exposed to playback of some recreation types and trail use scenarios. Importantly, although all species and mule deer responses indicate a return-to-baseline after repeated exposure to recreation noise, this does not indicate a concurrent return to a landscape devoid of risk. When wildlife habituate to humans they may do so at the cost of increased probability of human-wildlife conflict, and reduced fear responses to threats such as vehicles or hunting (Smith et al., 2021).

To mitigate effects of recreation activity on wildlife, our results indicate that resource managers and recreation planners should consider not only how much recreation occurs, but also how predictable exposure is and whether particular disturbance types produce longer displacement. In systems where recreation can be concentrated in predictable windows or locations, doing so may reduce broader disruption for more tolerant species. For example, shuttle-based transportation can create more concentrated and predictable pulses of trail use than automobile-based access (Monz et al., 2016), and other approaches to metering use include timed-entry systems (Creany et al., 2024) and queueing at trailhead parking areas (Fuentes et al., 2017). Likewise, regulations that limit off-trail travel may help maintain more predictable conditions for wildlife (Hammitt et al., 2015), and zoning protected areas based on desired acoustic conditions could further reduce disturbance exposure (Herrera-Montes, 2018). In a National Forest setting such as ours, these considerations may be most effectively incorporated during Forest Plan Revision processes that integrate ecological and recreation data. At the same time, persistent avoidance by elk, moose, and carnivores suggests that concentrating or regularizing recreation will not eliminate impacts for all taxa, and that refugia may still be necessary, whether through seasonal trail restrictions or the placement of new trails and roads away from sensitive habitats (Ditmer et al., 2026). Education may also help reduce the spatial extent of disturbance by encouraging quieter visitor behavior; for example, signage in Muir Woods National Monument significantly lowered sound levels, producing an acoustic equivalent to an approximately 21% reduction in visitors (Levenhagen et al., 2020).

Our study was limited by the logistical constraints of deploying and maintaining experimental playback sites, which restricted sampling to 12 sites per field season. Consequently, replicates were limited, we were unable to evaluate additional treatment combinations, and smaller sample sizes for some species prevented species-specific modeling of rarer species. Although all sites were located out of sight and beyond the audible range of roads, variation in proximity to well-traveled roads may have influenced background levels of human disturbance and wildlife responses (Ditmer et al., 2026). Similarly, while sites were intentionally placed away from designated trails, incidental off-trail recreation varied among sites and may have contributed to differences in exposure to human activity. Although sites were selected to minimize direct road-noise exposure, background anthropogenic disturbance likely varied among deployment areas and may have contributed to variation in wildlife responses.

Further, although we were able to measure site use via detections, we were unable to directly test habituation versus filtering since our methodology did not allow for tracking individuals. Future research using marked individuals could formally test whether habituation occurs within individuals and whether it differs among behavioral types or levels of plasticity to human presence within a species, improving inference about mechanisms underlying responses to recreation. GPS collars could be paired with physiological biologgers to understand both broader impacts to space use and detect stress responses that may be otherwise unobservable (Parlin et al., 2026; Ditmer et al., 2015). Furthermore, though we were able to conduct our experiments over a relatively long period of time, we were unable to determine whether changes in recreation use across seasons affect tolerance of wildlife over even longer time periods. For example, if winter use of an area markedly declines, do wildlife that have previously habituated become less tolerant and therefore more sensitive at the beginning of each high-use season, or is habituation a response that lasts despite fluctuations in human use? For instance, black bears that habituated to drone noise in one year generally remained habituated the following spring after hibernation (Ditmer et al., 2019). Lastly, do habituation tendencies change with seasons and resources on the landscape? For example, during winter, when resources are more limited, does the risk-reward tradeoff shift so that wildlife are more tolerant of humans?

For managers, the practical message is that wildlife responses to recreation depend not only on how much use occurs, but also on how predictable that use is, the type of disturbance involved, and the sensitivity of the species exposed. Concentrating recreation into more predictable times or places may reduce disruption for some taxa, but sensitive species may still require refugia or seasonal protections. By estimating time-to-return under controlled exposure, our study provides an empirical, within-season measure of how long recreation-noise effects on mammal site use can persist. In our system, recreation-noise effects persisted for weeks to months and resulted in temporal habitat loss (Rivera et al., 2022). Differences between motorized and non-motorized disturbances underscore the need for management strategies that address multiple disturbance types (e.g., spatial zoning, temporal zoning, education, noise regulation from motorized vehicles, trail design), particularly on multi-use public lands (Larson et al., 2016; Manning and Lime, 2000; Patricelli et al., 2013). Species-level patterns, especially the muted responses of mule deer relative to more sensitive taxa, highlight that community-level metrics can be strongly shaped by abundant, disturbance-tolerant species and may not reflect the responses of less tolerant species (Beaupre et al., 2025). These results support management approaches that concentrate predictable recreation where tolerance is higher, while maintaining refugia for more sensitive species or critical life stages through spatial zoning or seasonal restrictions (Larson et al., 2016; Gaynor et al., 2018; Patricelli et al.,

2013; Abernathy et al., 2025). More broadly, time-to-return estimates can help translate acoustic disturbance exposure into measurable expectations for displacement duration, complementing existing guidance on soundscapes and strengthening how ecological change is anticipated and evaluated (Landres et al., 2020).

CRediT authorship contribution statement

Julia N.D. Daniell: Writing – review & editing, Writing – original draft, Project administration, Investigation, Formal analysis, Data curation. **Mark A. Ditmer:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **William L. Rice:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **James Wilder:** Writing – review & editing, Resources, Methodology, Conceptualization. **Brian D. Gerber:** Writing – review & editing, Supervision, Methodology. **Svea Smith:** Writing – review & editing, Investigation. **Elizabeth Reynolds:** Writing – review & editing, Investigation. **Jesse R. Barber:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Katherine A. Zeller:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was supported by the 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. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The graphical abstract was created by Shea Coons. The authors thank Dr. Martin Nie and Dr. Erin Semmens of the University of Montana for their guidance, mentorship, and valuable feedback throughout this research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.112084.

Data availability

Data will be made available on request.

References

Abernathy, H.N., Ditmer, M.A., Hibbard, S.B., Lombardi, J.V., Stephenson, T.R., Squires, J.R., Newton, J.N., Dewey, S.R., Zeller, K.A., Schwartz, M.K., Wittemyer, G., 2025. A case for human mobility data applications in wildlife management. J. Appl. Ecol. 62, 1636–1646.

Beale, C.M., Monaghan, P., 2004. Human disturbance: people as predation-free predators? J. Appl. Ecol. 41, 335–343.

Beaupre, C., Bevan, A., Young, J.R., Blecha, K.A., 2025. Recreational trail traffic counts and trail proximity as a driver of ungulate landscape utilization. Ecosphere 16, e70305.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., Allen, S., 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Mar. Ecol. Prog. Ser. 395, 177–185.

Berger, J., 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biol. Lett. 3, 620–623.

Berger, J., Cassidy, K.A., 2024. Play is a privilege in both humans and animals: how our recreation influences wildlife. J. Wildl. Manag. 88, e22664. https://doi.org/10.1002/jwmg.22664.

Blumstein, D.T., 2016. Habituation and sensitization: new thoughts about old ideas. Anim. Behav. 120, 255–262.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.A., 2017. GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.

Buxton, R.T., McKenna, M.F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L., Wittemyer, G., 2017. Noise pollution is pervasive in U.S. protected areas. Science 356, 531–533.

Cardona, L.M., Brook, B.W., Harwood, A., Buettel, J.C., 2024. Measuring the human-dimension of outdoor recreation and its impacts on terrestrial wildlife. J. Outdoor Recreat. Tour. 47, 100808.

Chuang, Y., Mazumdar, S., Park, T., Tang, G., Arena, V.C., Nicolich, M.J., 2011. Generalized linear mixed models in time series studies of air pollution. Atmos. Pollut. Res. 2, 428–435.

Creany, N., Monz, C.A., Esser, S.M., 2024. Understanding visitor attitudes towards the timed-entry reservation system in Rocky Mountain National Park: contemporary managed access as a social–ecological system. J. Outdoor Recreat. Tour. 45, 100736.

Creel, S., Fox, J.E., Hardy, A., Sands, J., Garrott, B., Peterson, R.O., 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conserv. Biol. 16, 809–814.

Ditmer, M.A., Vincent, J.B., Werden, L.K., Tanner, J.C., Laske, T.G., Iaizzo, P.A., Garshelis, D.L., Fieberg, J.R., 2015. Bears show a physiological but limited behavioural response to unmanned aerial vehicles. Curr. Biol. 25, 2278–2283.

Ditmer, M.A., Werden, L.K., Tanner, J.C., Vincent, J.B., Callahan, P., Iaizzo, P.A., Laske, T.G., Garshelis, D.L., 2019. Bears habituate to the repeated exposure of a novel stimulus, unmanned aircraft systems. Conserv. Physiol. 7, coy067.

Ditmer, M.A., Zeller, K.A., Abernathy, H.N., Wilder, J., Egan, A., Daniell, J.N.D., Barber, J.R., Rice, W.L., Schwartz, M.K., Wittemyer, G., 2026. The landscape of no worries? Increased recreation exposure decreases the landscape of human fear in wildlife. Biol. Conserv. 315, 111718.

Fuentes, A., Heaslip, K., D'Antonio, A., Khalilikhah, M., Soltani-Sobh, A., 2017. Evaluation of vehicle parking queueing in a national park: case study of the Laurance S. Rockefeller Preserve in Grand Teton National Park. Transp. Res. Rec. 2654, 1–10. https://doi.org/10.3141/2654-01.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science 360, 1232–1235.

Grolemund, G., Wickham, H., 2011. Dates and times made easy with lubridate. J. Stat. Softw. 40, 1–25.

Gump, K.M., Thornton, D.H., 2023. Trucks versus treks: the relative influence of motorized versus nonmotorized recreation on a mammal community. Ecol. Appl. 33, e2916.

Hammitt, W.E., Cole, D.N., Monz, C.A., 2015. Wildland Recreation: Ecology and Management, 3rd edn. John Wiley & Sons, Chichester.

Herrera-Montes, M.I., 2018. Protected area zoning as a strategy to preserve natural soundscapes, reduce anthropogenic noise intrusion, and conserve biodiversity. Trop. Conserv. Sci. 11, 1940082918804344. https://doi.org/10.1177/1940082918804344.

Landres, P., Boutcher, S., Mejicano, E., Sandeno, E. (Eds.), 2020. Wilderness character monitoring technical guide. General technical report RMRS-GTR-406. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO (tech. eds.).

Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PLoS One 11, e0167259.

Levenhagen, M.J., Miller, Z.D., Petrelli, A.R., Ferguson, L.A., Shr, Y.H. (Jimmy), Gomes, D.G.E., et al., 2020. Ecosystem services enhanced through soundscape management link people and wildlife. People Nat. 3, 176–189. https://doi.org/10.1002/pan3.10156.

Lewis, J.S., Spaulding, S., Swanson, H., Keeley, W., Gramza, A.R., VandeWoude, S., Crooks, K.R., 2021. Human activity influences wildlife populations and activity patterns: implications for spatial and temporal refuges. Ecosphere 12, e03487.

Lüdecke, D., 2018. Ggeffects: tidy data frames of marginal effects from regression models. J. Open Source Softw. 3, 772.

Maier, J., 2001. Overview of research on the effects of noise on wildlife. Effects of overflights by jet aircraft on activity, movements, habitat and terrain use of Caribou. In: Effects of Noise on Wildlife Conference. Happy Valley-Goose Bay, Labrador, pp. 60–62.

Manning, R.E., Lime, D.W., 2000. Defining and managing the quality of wilderness recreation experiences. In: Cole, D.N., McCool, S.F., Borrie, W.T., O'Loughlin, J. (Comps.) (Eds.), Wilderness science in a time of change conference – Volume 4: Wilderness visitors, experiences, and visitor management, 1999 May 23–27, Missoula, MT. Proceedings RMRS-P-15-VOL-4. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, pp. 13–52. https://research.fs.usda.gov/treesearch/22002.

Marion, S., Davies, A., Demšar, U., Irvine, R.J., Stephens, P.A., Long, J., 2020. A systematic review of methods for studying the impacts of outdoor recreation on terrestrial wildlife. Global Ecology and Conservation 22, e00917.

McClure, C.J.W., Ware, H.E., Carlisle, J., Kaltenecker, G., Barber, J.R., 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proc. R. Soc. B Biol. Sci. 280, 20132290.
McGregor, P.K., 2000. Playback experiments: design and analysis. acta ethologica 3, 3–8.
Monz, C., D'Antonio, A., Lawson, S., Barber, J., Newman, P., 2016. The ecological implications of visitor transportation in parks and protected areas: examples from research in US National Parks. J. Transp. Geogr. 51, 27–35.
Parlin, A.F., Ditmer, M.A., Laforge, M.P., Abernathy, H.N., Zeller, K.A., Stout, V., Stoner, D.C., Hersey, K.R., Larsen, R.T., McMillan, B.R., Wang, P., 2026. Roads as dynamic stressors: physiological response of mule deer to roads differs during range residency and migration. Landsc. Ecol. 41, 30.
Patricelli, G.L., Blickley, J.L., Hooper, S.L., 2013. Recommended management strategies to limit anthropogenic noise impacts on greater sage-grouse in Wyoming. Hum. Wildl. Interact. 7, 230–249.
R Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
Rivera, K., Fidino, M., Farris, Z.J., Magle, S.B., Murphy, A., Gerber, B.D., 2022. Rethinking habitat occupancy modeling and the role of diel activity in an anthropogenic world. Am. Nat. 200, 556–570.
Rogard, J., 2024. SmarterNoise (version 1.033) [computer software]. Agibili. https://smarternoise.com/.
Sih, A., McCarthy, T.M., 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Anim. Behav. 63, 437–443.
Smith, J.A., Gaynor, K.M., Suraci, J.P., 2021. Mismatch between risk and response may amplify lethal and non-lethal effects of humans on wild animal populations. Front. Ecol. Evol. 9, 604973.
Stoklosa, J., Blakey, R.V., Hui, F.K.C., 2022. An overview of modern applications of negative binomial modelling in ecology and biodiversity. Diversity 14, 320.
Suraci, J.P., Gaynor, K.M., Allen, M.L., Alexander, P., Brashares, J.S., Cendejas-Zarelli, S., et al., 2021. Disturbance type and species life history predict mammal responses to humans. Glob. Chang. Biol. 27, 3718–3731.
Tablado, Z., Jenni, L., 2017. Determinants of uncertainty in wildlife responses to human disturbance. Biol. Rev. 92, 216–233.
Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. Ecol. Appl. 13, 951–963.
U.S. Forest Service, 2021. Bridger-Teton National Forest – About the Forest. USDA Forest Service. https://www.fs.usda.gov/main/btnf/about-forest (accessed 22 April 2024).
Ware, H.E., McClure, C.J.W., Carlisle, J.D., Barber, J.R., 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proc. Natl. Acad. Sci. USA 112, 12105–12109.
Westekemper, K., Reinecke, H., Signer, J., Meißner, M., Herzog, S., Balkenhol, N., 2018. Stay on trails – effects of human recreation on the spatiotemporal behaviour of red deer *Cervus elaphus* in a German national park. Wildl. Biol. 1, 1–9 wlb.00403.
Wilson, M., Ridlon, A., Gaynor, K., Gaines, S., Stier, A., Halpern, B., 2020. Ecological impacts of human-induced animal behaviour change. Ecol. Lett. 23, 1522–1536.
Zeller, K.A., Ditmer, M.A., Squires, J.R., Rice, W.L., Wilder, J., DeLong, D., Egan, A., Pennington, N., Wang, C.A., Plucinski, J., Barber, J.R., 2024. Experimental recreationist noise alters behaviour and space use of wildlife. Curr. Biol. 34, 2997–3004.