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## Original Research Article

## Varying behavioral responses of wildlife to motorcycle traffic

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## ABSTRACT

Roads are a pervasive feature across the U.S., and traffic and its associated noise has significant impacts on wildlife. However, we know little about the effect of motorcycle traffic and the potential for prolonged response of animals to loud and periodic traffic disturbances. We studied the behavioral response of multiple species in Devils Tower National Monument to the Sturgis Motorcycle Rally, which raised median A-weighted sound levels by more than 20 dB for 7 days. Different taxa demonstrated different responses to the event, which we categorized into three different patterns of behavioral shifts: weak evidence of a response, temporary response during the rally, and a sustained response that lasted after the rally. We found little evidence that western wood-pewee (*Contopus sordidulus*) vocal activity, our behavioral metric, was affected by the rally. Activity patterns of white-tailed deer (*Odocoileus virginianus*) and black-tailed prairie dogs (*Cynomys ludovicianus*) shifted during the rally, and deer reverted to pre-rally activity patterns when motorcycle activity declined. The diversity of bat species active was also lower during the rally, and the diversity of species active remained low several weeks after the rally. Our observations suggest that most species shifted their behavior to avoid motorcycle traffic but the ability to return to pre-disturbance behavioral patterns varied. Examining responses to traffic activity and noise across a broad array of species can identify relative sensitivity to such disturbances and infer community-level impacts, helping to inform strategies to reduce effects or plan for recovery.

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## 1. Introduction

Road networks are prevalent across vast stretches of the globe, including protected areas (Garriga et al., 2012; Riitters and Wickham, 2003). Road encroachment affects wildlife by fragmenting habitat and extending the reach of human activity and traffic into rural landscapes (Fahrig and Rytwinski, 2009). Roads are also one of the leading sources of noise in protected areas (Buxton et al., 2017), and noise from traffic alone can have negative effects on wildlife (McClure et al., 2013). Exploring the

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responses of animals to intense and unpredictable traffic activity, as well as recovery following the disturbance, can provide critical information for understanding the potential ecological consequences of traffic noise.

Traffic and its associated noise affect animals in myriad ways, including significant alterations in animal behavior (Barber et al., 2010). Documented behavioral shifts in response to traffic and associated noise include avoidance (McClure et al., 2013; Ware et al., 2015), changes in activity patterns (Baker et al., 2007), vocal adjustment (Patricelli and Blickley, 2006; Sun and Narins, 2005), and alteration of behavioral time budgets (Shannon et al., 2014). These behavioral changes can lead to decreased body condition (Ware et al., 2015), and, ultimately, lower reproductive success and fitness (Halfwerk et al., 2011). Chronic noise, such as noise from sustained traffic, interferes with an animal's abilities to detect important sounds, while high intensity, intermittent noise events are often perceived as a threat (Francis and Barber, 2013). Finally, alteration of the distribution and behavior of key species can have indirect effects on other species through disruption of interspecific interactions (Francis et al., 2012).

Typically, studies examining the impact of traffic compare behavior of animals exposed to roadways with varying levels of traffic volume or periods with and without experimental application of traffic noise (Fahrig and Rytwinski, 2009; McClure et al., 2013; Shannon et al., 2014). Little research has examined prolonged effects of traffic noise on animals; thus, it is unclear whether animals return to previous behavioral patterns after disturbance ceases. Behavioral shifts can be short- or long-term adjustments, and animals likely reverse costly avoidance behavior after a disturbance ends (Frid and Dill, 2002). However, behavioral adjustments are constrained by numerous ecological and life-history related factors (Sih et al., 2011; Wong and Candolin, 2015). Moreover, sensitivity to traffic varies widely across taxa and context (Francis and Barber, 2013). With increasing interest in strategies aimed at mitigating the effects of traffic (National Research Council, 2010), consideration of the prolonged effects of traffic disturbance on behavior across species would be valuable.

Motorcycles are a major source of noise in the United States (EPA, 1980) and a prevalent means of touring national parks (Miller, 2008). Each August hundreds of thousands of motorcyclists participate in the Sturgis Motorcycle Rally, a motorcycle festival in South Dakota, USA. Devils Tower National Monument (DETO) is a popular destination for riders during the week of the rally, where thousands of motorcyclists generate sound pressure levels 20–50 dB above natural ambient levels for much of the day (National Park Service, 2010). The park generally receives high levels of traffic in the summer, with over 100,000 visitors per month from June–August (National Park Service, 2015). Thus, the Sturgis Motorcycle Rally represents a unique opportunity to understand the effects of an acute, abrupt, and extreme traffic noise disturbance event embedded within the park's chronic background noise. Considering DETO contains important habitat for numerous species (Griscom and Keinath, 2011; Panjabi, 2005), examining the impact of the motorcycle event on multiple species in the community is particularly important.

We used the 75th anniversary of the Sturgis Motorcycle Rally as a natural experiment to examine behavioral responses across various taxa to an intense traffic event and the ability to revert to pre-disturbance behavior after the event. Moreover, we assessed whether animals respond to daily fluctuations in traffic noise levels throughout the study period. We could not separate the effects of noise from other aspects of the disturbance (e.g., visual disturbance, chemical pollution), thus we examined the general effects of increased motorcycle traffic and its associated noise levels. We observed vocal activity of bats and western wood-pewee (*Contopus sordidulus*), and behavior and daily site use of white-tailed deer (*Odocoileus virginianus*), at sites near and far from the road from one month before the rally to one month after the rally. We also assessed behavior of black-tailed prairie dogs (*Cynomys ludovicianus*) during and after the rally. We predicted that behavior would differ before, during, and after the week of the rally, the busiest day of the rally, with the proximity to the main road, and with varying daily noise levels.

## 2. Methods

### 2.1. Study sites and design

DETO is a small park (545.1 ha) characterized by a prominent rock formation with a mosaic of habitat types that provide habitat for many species (Fig. 1; Griscom and Keinath, 2011; Panjabi, 2005). The 75th anniversary of the Sturgis Motorcycle Rally occurred in Sturgis, South Dakota, from August 3–7, 2015, where motorcycle traffic was over 40% higher than levels recorded during the rally in the previous decade (SDOT, 2017). DETO, about 129 km east of Sturgis, was a popular destination throughout the week of the rally, but on August 5th motorcyclists participated in the “Devils Tower Run”, and motorcycle activity in DETO reached its peak.

To assess the impact of the motorcycle rally, we observed animal behavior at sites near and far from the main paved road, except for prairie dogs as there was only one colony within the park located adjacent to the main road near the park entrance. We note that due to the small size of DETO, we were unable to sample broadly (>1 km from the main road), meaning that motorcycle noise was likely audible at each sample site and we were unable to establish a true control. However, the sites far from the main road were much quieter than sites near the road (Fig. S1.1), and thus we expected the effect of traffic to differ between these sites. For locations near and far from a road, behavior was measured in both pine forest and prairie grassland habitat, based on Geological Survey Land Cover 4 Dataset in ArcGIS (<https://landcover.usgs.gov/>; Fig. 1).

### 2.2. Data collection

To measure changes in bird and bat vocal activity, and ambient sound levels, four acoustic recorders (SM3BAT, Wildlife Acoustics Inc., Concord, MA, details in Appendix 1) were placed at two sites ~100 m from the main road and two sites >500 m

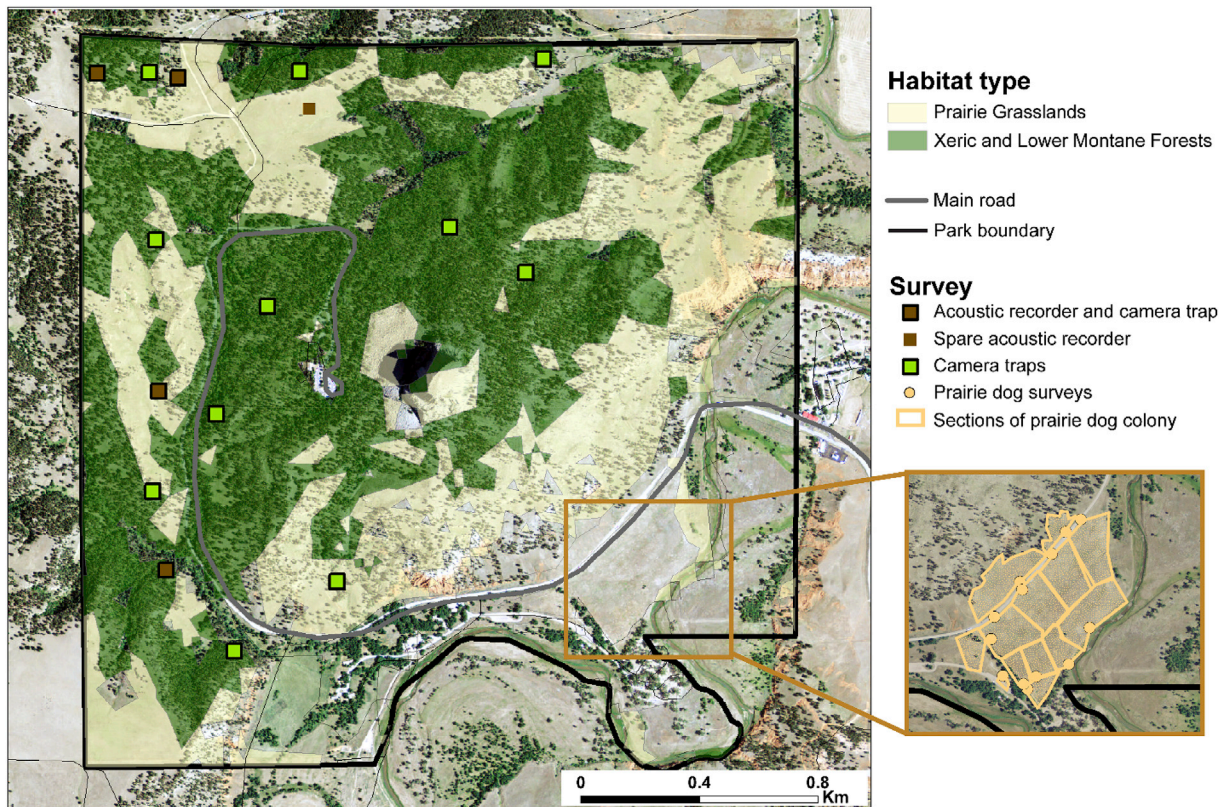


Fig. 1. Locations of the different survey methods in Devils Tower National Monument.

from the main road but within 100 m of a gravel road, where motorcycles were unable to travel (Fig. 1). Automated software extracted the number of vocalizations from the acoustic recordings, including bat calls to measure bat activity and bird song to measure singing activity. At one site (far from road, grassland) the microphone for detecting bat calls failed during the week of the rally; instead we included acoustic data from a recorder with an identical setup less than 400 m from the site, in the same habitat type, and at a similar distance from the gravel road (Fig. 1).

A measure of motorcycle noise was calculated from the acoustic recordings. First we converted audio data from all four sites to end-to-end calibrated 1 sec  $1/3$  octave band SPLs measured as  $Leq_{1s}$  in dB. We then calculated median daily sound levels ( $L_{50}$  dB) in the 100 Hz octave band. This metric had the highest probability of changing during the days surrounding the rally and peaked during the rally at sites near the road only (Figure S2.2); thus, we use these values to represent noise exposure from motorcycles (hereafter “motorcycle noise”). Because motorcycle noise was highest between August 1 and August 7 and peaked on August 5 at sites near the road, we structured our analysis to investigate the week of the rally (August 1–7) and the peak day of the rally (August 5; Fig. S2.2). To account for different sampling period lengths, daily or nightly acoustic metrics were extracted for one month before (July 1st, 2015) and after (September 1st, 2015) the start of the rally.

To examine white-tailed deer behavior and habitat use, we placed 15 camera traps (model 119467, Bushnell Outdoor Products, Kansas City, MO) at stratified random points, where 8 cameras were placed <250 m of the main road and 7 were placed >300 m from the road (distances extracted from U.S. Census Bureau, 2015 using ArcGIS 10.3, ESRI Inc., USA); 4 cameras were placed in grassland habitat and 11 in pine forest. There was a minimum distance of 300 m between each camera (Fig. 1). Cameras were triggered based on motion and heat and once triggered captured 3 images in succession, with 1 s between images. Each camera was strapped to a tree ~1 m from the ground and aimed at a game trail. Most cameras were functioning for 60–65 days from one month before to one month after the rally, with the exception of one camera that failed for the first three weeks of July.

We assessed whether prairie dog behavior changed during and after the rally and with varying traffic levels; logistic constraints precluded prairie dog surveys before the rally. Observers visually scanned and recorded the behavior of above-ground prairie dogs from 1050 to 1250 (Mountain Daylight Time) to capture times when motorcycle traffic was high (1000–1700; Fig. S2.1) and to avoid the hottest time of day when aboveground prairie dog behavior is reduced (Shannon et al., 2014). Observations were performed for 7 consecutive days during the motorcycle rally (July 31–August 6) and 7 consecutive days three weeks after (August 29–September 4) the motorcycle rally. We divided the colony into 13 sections, using vegetation or topographic features to delineate boundaries, to facilitate behavioral scans that were conducted from the same observation

point for each section (Fig. 1). Observation points were visited sequentially with the order reversed each day. Because the observer was visible to prairie dogs, we waited for 5-mins after arrival to initiate scanning. The behavior of each aboveground prairie dog was scored as foraging, vigilant, socializing, resting, digging, aggressive, or moving (for details see Shannon et al., 2014). Two observers scanned each section from the observation point sequentially to account for observer bias. While one observer scanned prairie dog behavior, the other recorded temperature, wind speed, and wind direction using a Kestrel weather meter (3000 model; Loftopia LLC., Minneapolis, MN) and counted the number of vehicle passes per min and the number of visitors at the side of the road adjacent to the colony. We excluded observations disrupted by the presence of raptors or when visitors were walking on the path within the prairie dog colony.

### 2.3. Data analysis

We used program R version 3.4.1 for all quantitative analysis (R Core Team, 2017). To examine if behavior of bats, birds, and white-tailed deer changed during the week of the rally, on the peak day of the rally, or with daily noise levels throughout the study period, we used generalized linear mixed models (GLMM) using taxon-specific response variables in the *lme4*, *TMB*, and *nlme* packages (Bates et al., 2015; Kristensen et al., 2016; Pinheiro et al., 2017). In all global models predicting behavior metrics (detailed below, Table 1), we included the following as fixed effects: daily motorcycle noise as a linear and quadratic effect, the interaction between a categorical variable identifying the time period in relation to the peak day of the rally (three categories: before peak, peak day, and after peak) and road proximity (sites near or far from or the main road), and the interaction between a categorical variable identifying the time period in relation to the week of the rally (three categories: before rally, rally, and after the rally) and road proximity. The categories before peak day of the rally, before the week of the rally, and far from the main road were set as reference categories. Additionally, we included habitat (grassland or ponderosa pine forest) as a fixed effect and site and date as random effects. All continuous fixed effects were standardized by subtracting the mean and dividing by one standard deviation to ensure parameter estimates were comparable (Schielzeth, 2010). We computed a Spearman's correlation matrix to assess multicollinearity among fixed effects and did not include covariates with correlation coefficients >0.5 in the same model. We used a four-step process to determine the best model (details in Appendix 3).

#### 2.3.1. Bat activity

We quantified bat activity using default settings in bat call analysis software SonoBat (version 4.0.6 U.S. West Suite, Arcata, CA). Triggered recordings were first scrubbed using default settings to remove low quality bat calls and background noise. We considered the resulting files as containing a bat if the classifier was able to collect the entire suite of call measurements (11 attributes, e.g. mean duration in sec; SonoBat, 2016). Because we did not manually vet species identified, here we only analyze automated metrics of bat activity (e.g., see Bunkley et al., 2015). We calculated bat activity as the total number of bat calls per night and the diversity of bat species active per night as the Shannon diversity of bats calculated in the *vegan* package (Oksanen et al., 2013) using the species identified by SonoBat with an identification probability >0.9. In Shannon diversity calculations we removed 6 species that SonoBat identified but are unlikely to occur in DETO and combined acoustically similar species into couplets (Table S4.1, methods from; Reichert et al., 2018).

We used the nightly measures of bat activity and diversity of bat species active as response variables in two separate GLMM sets. In addition to motorcycle rally covariates, to control for the effects of moonlight and weather we included

**Table 1**

**Global model structure for each taxon-specific behavioral analysis.** Behavioral response variables, environmental fixed effects, and fixed effects relating to motorcycle traffic around the Sturgis Motorcycle Rally (August 1st – August 7th) were specific for each taxon.

Species	Response variable	Environmental fixed effects	Motorcycle fixed effects	Final model structure
Bats	Total calls <sup>a</sup> Shannon diversity of calls <sup>a</sup>	Lunar illumination, hours moon was above the horizon, temperature, wind speed, precipitation, habitat	Before, during, after rally × Near or far from road, motorcycle noise level from previous day	Negative binomial Gaussian, weighted variance structure by site
Western wood-pewee	Songs/min <sup>b</sup>	Temperature, wind speed, precipitation, habitat	Before, during, after rally × Near or far from road, daily motorcycle noise levels	Gaussian, first-order autoregressive term, weighted variance structure by site
White-tailed deer	Hours with deer present <sup>b</sup> Number of photos moving <sup>b</sup> Number of photos foraging <sup>b</sup>	Habitat	Before, during, after rally × Distance to main road, daily motorcycle noise levels	Negative binomial Zero-inflated negative binomial
Prairie dog	Total individuals above ground <sup>c</sup> Proportion vigilant <sup>c</sup> Proportion foraging <sup>c</sup> Proportion moving <sup>c</sup>	Decimal time, temperature, wind speed, binary variable indicating if the section was adjacent to the road	During vs after the rally, number of vehicle passes per min, number of vehicle passes as quadratic	Negative binomial, area offset Binomial area offset

<sup>a</sup> Nightly.

<sup>b</sup> Daily.

<sup>c</sup> In each colony section.

proportion of lunar illumination (lunar package in R; Lazaridis, 2014), number of hours the moon was above the horizon from 1900–0500 (<https://www.timeanddate.com/moon/usa/casper>), temperature, wind speed, and precipitation (<https://www.ncdc.noaa.gov/cdo-web/datasets>) as fixed effects in each global model (Table 1). On some days the DETO station had no available precipitation data, in which case an average between nearby stations in Gillett, Buffalo, Midwest, and Kaycee was calculated. Lunar illumination and number of hours the moon was above the horizon were significantly correlated ( $R_s = 0.72$ ) and thus were not included in the same global model. Because bats roost during the day in DETO (Keinath and Abernethy, 2016) and noise is known to impact torpid animals (Luo et al., 2014), motorcycle noise was included from the day previous to each night's bat activity. We did not include nighttime noise levels because there was little motorcycle traffic after sunset (Fig. S2.1). The final model for bat activity had a negative binomial distribution and the final model for the diversity of bat species active had a Gaussian distribution with a weighted variance structure by site.

### 2.3.2. *Western wood-pewee*

We analyzed song rates in the most common avian species present throughout the study period, the western wood-pewee, using sound analysis software Raven Pro 1.5 (Cornell University, Ithaca, NY). We used a band-limited energy detector algorithm to identify western wood-pewee songs in recordings, removing all false positives by visually checking each detection using Raven's selection review feature. To correct for false negatives, we used predictions of song rates from a GLMM comparing manual counts of wood-pewee song to the number of wood-pewee songs identified by detectors in a subset of recordings (Appendix 4). We calculated western wood-pewee song activity as the daily average of the number of songs per minute.

We included motorcycle rally variables, temperature, wind speed, and precipitation (same source as in bat analysis, see above) as fixed effects in the global model (Table 1). The final model of song activity had a Gaussian distribution with a first-order autoregressive term and a weighted variance structure by site.

### 2.3.3. *White-tailed deer*

We used CPW Photo Warehouse to manually identify a variety of metrics for deer behavior in camera trap pictures (Ivan and Newkirk, 2016). Given the summer home range size of white-tailed deer can be double the size of the park (Lesage et al., 2000; Tierson et al., 1985) the assumption of closure among camera traps is violated. In addition, we could not individually identify all deer captured on camera. Thus, we interpreted the number of photos of white-tailed deer as an index of relative activity. To summarize daily deer activity we calculated the number of hours that photos of deer were present each day (hereafter "deer activity"; Berteaux et al., 1998; Jackson et al., 1972; Schmitz, 1991). We also counted the total number of photos in each day where deer were exhibiting specific types of behavior (i.e., moving, foraging, resting, vigilant, or unknown; Dertien et al., 2017). We observed few deer resting and vigilant (<750 photos); thus we excluded these behaviors from further analysis.

We fit three GLMM model sets with the following response variables: deer activity, the number of photos of deer foraging, and the number of photos of deer moving. Because the distance to the main paved road varied at each site, we included either distance to the main road as a continuous variable or a binary variable (sites near <250 m and far >250 m from the main road, comparable to bird and bat analyses). We included each of these covariates in a separate global model and found that including distance to the main road as a continuous variable generated the lowest Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). For daily motorcycle noise we used median levels from the two recording devices near the main paved road (acoustic recorders were not paired with cameras). The final models for deer activity had a negative binomial distribution and models examining the number of photos of deer foraging and moving were zero-inflated with a negative binomial distribution.

Finally, we used the package overlap to examine circadian activity patterns of white-tailed deer throughout the study period (Meredith and Ridout, 2017). We generated probability density functions of temporal activity patterns for the days before, during, and after the week of the rally and the peak rally day. We performed a permutation test contrasting mid-day (1200–1400) activity patterns during the rally with random days before and after the rally to assess whether circadian differed between the periods.

### 2.3.4. *Prairie dogs*

To examine if prairie dog behavior changed due to the rally, we used a similar GLMM approach as above. We ran four model sets including the total number of prairie dogs observed above ground and the proportion of prairie dogs vigilant, foraging, and moving as response variables. In the global model we included either a categorical variable for during the motorcycle rally (versus 3 weeks after the rally) or the number of vehicle passes per minute and the number of visitors at the main paved road during the observation period as both linear and quadratic fixed effects. As covariates, we included decimal time, temperature, wind speed, and a variable indicating if the section was adjacent to the road as fixed effects (Table 1). We included date, observation area, and observer as random effects. Finally, to control for the size of the observed section of the colony, we included the log area of the section as an offset term. For the total number of prairie dogs, the final global model had a negative binomial distribution and behavioral models had a binomial distribution.

**Table 2**

**Model results for western wood-pewee song rates.** Parameter estimates  $\pm$  standard error (SE), 95% confidence intervals (CI), and *P*-values for each covariate in generalized linear mixed models estimating western wood-pewee song activity in acoustic recordings from Devils Tower National Monument before the peak day (July 1st – August 4th), on the peak day (August 5th), and after the peak day (August 6th – September 1st) of the Sturgis Motorcycle Rally in 2015. Asterisks indicate significant effects.

Covariate	PE $\pm$ SE	2.5CI	97.5CI	P
Intercept	3.86 $\pm$ 0.64	2.59	5.13	<0.001
Precipitation*	0.11 $\pm$ 0.03	0.05	0.17	<0.001
Wind speed*	-0.16 $\pm$ 0.04	-0.23	-0.09	<0.001
Before the rally <sup>a</sup>				
Peak day of the rally*	1.92 $\pm$ 0.26	1.4	2.43	<0.001
After the rally	-0.1 $\pm$ 0.24	-0.56	0.37	0.68
Far from main road <sup>a</sup>				
Near main road	-0.71 $\pm$ 1.41	-6.78	5.37	0.67
Before rally $\times$ Distance to main road <sup>a</sup>				
Busiest day of the rally $\times$ Distance to main road	0.76 $\pm$ 0.57	-0.35	1.88	0.18
After rally $\times$ Distance to main road	0.74 $\pm$ 0.48	-0.21	1.7	0.12

<sup>a</sup> Reference category.

### 3. Results

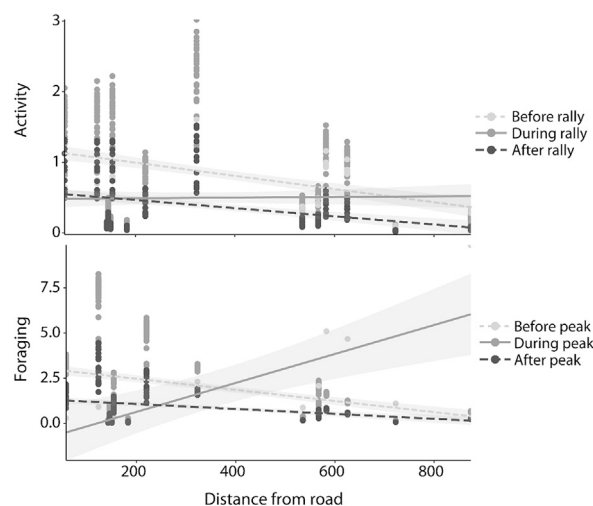
#### 3.1. Little evidence of response to the motorcycle rally

The only species showing little evidence of response to the motorcycle rally were western wood-pewees, for which song activity was highest on the peak day of the motorcycle rally (August 5). In the final model predicting song activity (Table S5.1), the interaction between day (before, during, and after the peak day of the rally) and road treatment had confidence intervals overlapping zero, suggesting this effect could be due to factors unrelated to motorcycle traffic (Table 2).

#### 3.2. Temporary avoidance during the motorcycle rally

The final models explaining different measures of deer behavior included the interaction between the categorical variable for rally week and distance to the main road (Table S5.2). In the days before and after the week of the rally, white-tailed deer activity was higher at sites closer to the main paved road, but during the week of the rally, there was no relationship between white-tailed deer activity and distance to the road (Fig. 2, Table 3). Similarly, there were more photos of foraging deer at sites closer to the main paved road on the days before and after the peak day of the rally, but fewer photos of foraging deer near the main road on the peak day of the rally (Fig. 2, Table 3). Finally, deer activity was negatively related to the daily amount of motorcycle noise (Table 3).

Circadian activity of white-tailed deer tended to differ during the rally compared to before and after the rally (Fig. S5.1,  $P = 0.05$ ). Specifically, diurnal activity was minimal and crepuscular activity (0600–0900; 1800–2000) was greater on the



**Fig. 2. Temporary responses to the motorcycle event.** Predicted daily activity of white-tailed deer (hours with pictures day<sup>-1</sup> – top panel) and the number of photographs of deer foraging (bottom panel) using generalized linear mixed models (shaded lines = standard error) at Devils Tower National Monument before (July 1st – July 31st), the week during (August 1st – August 7th), and after (August 8th – September 1st) the Sturgis Motorcycle Rally and before (July 1st – August 4th), on the day (August 5th), and after (August 6th – September 1st) the peak day of the rally.

**Table 3**

**Model results for white-tailed deer behavior.** Parameter estimates  $\pm$  standard error (SE), 95% confidence intervals (CI), and *P*-values for each covariate in mixed models estimating deer activity (the total number of hours with white-tailed deer photos per day) and for the count process in zero-inflated negative binomial models estimating the number of photos of white-tailed deer foraging and moving at Devils Tower National Monument around the Sturgis Motorcycle Rally in 2015. Asterisks indicate significant effects.

Covariate	Total				Foraging				Moving			
	PE $\pm$ SE	2.5CI	97.5CI	<i>P</i>	PE $\pm$ SE	2.5CI	97.5CI	<i>P</i>	PE $\pm$ SE	2.5CI	97.5CI	<i>P</i>
Intercept	-2.04 $\pm$ 0.49	-3	-1.09	<0.01	0.9 $\pm$ 0.3	0.31	1.49	<0.01	0.53 $\pm$ 0.39	-0.23	1.29	0.17
Distance to road **	-0.42 $\pm$ 0.24	-0.88	0.05	0.08	-0.92 $\pm$ 0.3	-1.51	-0.34	<0.01	-0.9 $\pm$ 0.39	-1.67	-0.13	0.02
Motorcycle noise <sup>b*</sup>	-0.48 $\pm$ 0.10	-0.68	-0.29	<0.01	Not included in final model				-0.13 $\pm$ 0.08	-0.29	0.03	0.12
Motorcycle noise <sup>2*</sup>	0.16 $\pm$ 0.07	0.02	0.31	0.03	Not included in final model							
Grassland habitat <sup>a</sup>												
Forest habitat*	1.43 $\pm$ 0.55	0.36	2.50	0.01								
Before rally <sup>a</sup>												
During rally *	0.13 $\pm$ 0.39 <sup>b</sup>	-0.63	0.90	0.73	0.1 $\pm$ 0.94 <sup>c</sup>	-1.73	1.94	0.91	0.95 $\pm$ 0.45 <sup>c</sup>	0.07	1.84	0.04
After rally*	-0.81 $\pm$ 0.14 <sup>b</sup>	-1.10	-0.53	<0.01	-0.52 $\pm$ 0.3 <sup>c</sup>	-1.10	0.06	0.08	-0.14 $\pm$ 0.19 <sup>c</sup>	-0.52	0.24	0.48
Before rally $\times$ Distance to road <sup>a</sup>												
During rally $\times$ Distance to road**	0.35 $\pm$ 0.18 <sup>b</sup>	0.01	0.70	0.05	1.4 $\pm$ 0.68 <sup>c</sup>	0.06	2.74	0.04	-0.31 $\pm$ 0.41 <sup>c</sup>	-1.10	0.49	0.45
After rally $\times$ Distance to road	-0.24 $\pm$ 0.16 <sup>b</sup>	-0.56	0.08	0.15	-0.17 $\pm$ 0.29 <sup>c</sup>	-0.73	0.39	0.55	0.11 $\pm$ 0.22 <sup>c</sup>	-0.33	0.55	0.63

<sup>†</sup>Daily L<sub>50</sub> in the 100 Hz band (dB).

<sup>a</sup> - Reference category.

<sup>b</sup> Before (July 1st – July 31st), the week during (August 1st – August 7th), and after (August 8th – September 1st) the motorcycle rally.

<sup>c</sup> Before (July 1st – August 4th), during (August 5th), and after (August 6th – September 1st) the peak day of the motorcycle rally.

peak day compared to before and after the peak day of the rally (Fig. S5.1). Further, during the week of the rally, white-tailed deer were 53% less active between 1200 and 1400 h compared to before the rally and 44% less active compared to after the rally, suggesting a short term response to the motorcycle event.

Although we were unable to compare to behavior before the rally, the final models explaining prairie dog behavior also suggested temporary impacts. The final models included the categorical variable for during the motorcycle rally (versus 3 weeks after the rally), temperature, time of day, wind speed, and the quadratic term for number of visitors adjacent to the road (Table S5.3). There were fewer prairie dogs above ground, a lower proportion of individuals foraging, and a greater proportion of individuals moving and vigilant during the week of the rally compared to 3 weeks after the rally (Table 4, Fig. 3). Although socializing, resting, and digging behaviors were rare, of the instances they were observed, most (>70%) were after the rally.

### 3.3. Evidence for long-term avoidance after the motorcycle rally

The final models explaining bat activity and the diversity of bat species active included the interaction between the week of the rally and road proximity (Table S5.4). During the rally, bat activity and the diversity of bat species active were lower compared to before the rally at sites near the main paved road (Fig. 4). Moreover, the diversity of bat species active remained low at sites near the main paved road 3 weeks after the rally (Table 5). The detectors identified 15 species, 6 of which were removed from further analysis (Table S4.1).

## 4. Discussion

Traffic and its associated noise has become increasingly widespread, and behavioral impacts on animals exposed to traffic noise have been reported in numerous systems (Fahrig and Rytwinski, 2009; Shannon et al., 2016). However, the degree to which animals adjust their behavior immediately or have prolonged effects after disturbance is less well understood, likely depending on plasticity and life-history characteristics (Wong and Candolin, 2015). We examined behavioral changes in a variety of species before, during, and after a motorcycle traffic event – the 75th anniversary of the Sturgis Motorcycle Rally. While noise levels during this event are elevated, traffic noise is a daily occurrence in this system, so the populations studied are not naïve to such noise sources. We found that some species had lower activity at sites near the main road both during and after the rally, while others did not change their behavior in response to the rally. We demonstrated that different species respond in varying degrees to an extreme traffic event and that some species were able to return relatively rapidly to pre-disturbance behavior after the disturbance ceased, while others were not.

### 4.1. Little evidence of response to the motorcycle rally

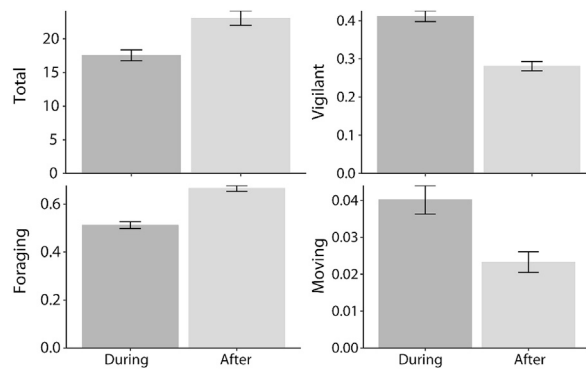
We found little evidence that the motorcycle rally affects vocal activity of western wood-pewee. Although song activity was higher on the busiest day of the rally, changes in activity on this day were observed at sites both near and far from the main road, precluding the isolation of effects of the motorcycle rally from seasonal variation in daily song activity. In other systems, there is mixed evidence for an effect of traffic noise on bird behavior. For some birds, it does not affect abundance

**Table 4**

Parameter estimates  $\pm$  standard error (SE), 95% confidence intervals (CI), and *P*-values for each covariate in generalized linear mixed models estimating the total number of prairie dogs observed above ground, and the proportion of prairie dogs foraging, vigilant, and moving at Devils Tower National Monument during (July 31st – August 6th) and three weeks after (August 29th – September 4th) the Sturgis Motorcycle Rally in 2015. Asterisks indicate significant effects.

Covariate	Total above ground				Proportion vigilant				Proportion foraging				Proportion moving			
	PE $\pm$ SE	2.5CI	97.5CI	P	PE $\pm$ SE	2.5CI	97.5CI	P	PE $\pm$ SE	2.5CI	97.5CI	P	PE $\pm$ SE	2.5CI	97.5CI	P
Intercept	0.33 $\pm$ 0.25	-0.15	0.81	0.18	-0.47 $\pm$ 0.25	-0.95	0.02	0.06	0.06 $\pm$ 0.52	-0.95	1.07	0.91	-3.36 $\pm$ 0.2	-3.75	-2.97	0.00
During rally <sup>a</sup>																
After rally****	0.21 $\pm$ 0.05	0.11	0.3	<0.01	-0.49 $\pm$ 0.11	-0.7	-0.28	<0.01	0.55 $\pm$ 0.08	0.4	0.7	<0.01	-0.38 $\pm$ 0.17	-0.7	-0.05	0.02
Temperature*	-0.09 $\pm$ 0.02	-0.13	-0.05	<0.01	-0.01 $\pm$ 0.03	-0.13	0.05	0.68	0.06 $\pm$ 0.04	0.01	0.13	0.1	0 $\pm$ 0.04	-0.13	0.16	0.92
Time of day***	-0.06 $\pm$ 0.02	-0.1	-0.02	<0.01	0.14 $\pm$ 0.04	0.06	0.22	<0.01	-0.17 $\pm$ 0.04	-0.24	-0.1	<0.01	0.1 $\pm$ 0.1	-0.02	0.33	0.34
Number of visitors	0.01 $\pm$ 0.02	-0.04	0.05	0.77	0.12 $\pm$ 0.07	0.02	0.25	0.1	-0.03 $\pm$ 0.05	-0.18	0.04	0.54	0.02 $\pm$ 0.07	-0.17	0.27	0.8
Number of visitors <sup>2</sup>	0 $\pm$ 0.01	-0.01	0.02	0.71	-0.05 $\pm$ 0.03	-0.09	-0.01	0.07	0.02 $\pm$ 0.02	-0.01	0.07	0.37	0.02 $\pm$ 0.03	-0.01	0.09	0.48
Wind speed	-0.02 $\pm$ 0.03	-0.07	0.03	0.37	-0.02 $\pm$ 0.04	-0.16	0.04	0.60	0.07 $\pm$ 0.04	0.02	0.15	0.09	0 $\pm$ 0.04	-0.18	0.15	0.94

<sup>a</sup> Reference category.

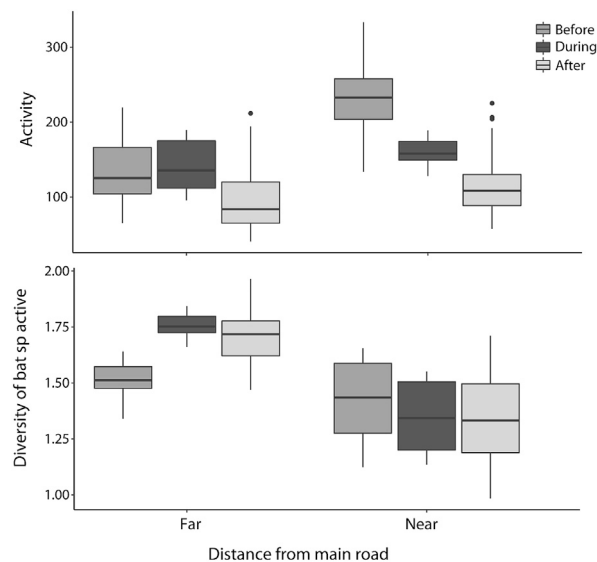


**Fig. 3.** Mean number of prairie dogs ( $\pm$ standard error) observed above ground (total) and the mean proportion of aboveground prairie dogs exhibiting behaviors during the Sturgis Motorcycle Rally at Devils Tower National Monument (July 31st – August 6th) and three weeks after the rally (August 29th – September 4th).

(Summers et al., 2011), but in other systems, it can cause an increase in song rate (Díaz et al., 2011) and the time spent singing (Sierra et al., 2017), presumably to increase the probability of signal transmission in noisy habitat. We note that in noisy environments, many avian species are known to adjust the frequency (Slabbekoorn and Peet, 2003) and amplitude (Nemeth et al., 2013) of songs. Eastern wood-pewees (*Contopus virens*) have particularly plastic song structure, adjusting the tonality of songs in immediate response to traffic noise (Gentry et al., 2018). Thus, although western wood-pewee did not adjust the number of songs, they may have altered the properties of their vocalizations, an interesting avenue for further research.

#### 4.2. Temporary avoidance due to the motorcycle rally

White-tailed deer activity was higher at sites closer to the main paved road than at sites farther from the road before and after the week of the rally. Other studies have also found greater ungulate activity and reproduction near roads, potentially in relation to vegetation changes caused by roads as well as behavioral benefits such as predator shielding from traffic-averse predators (Berger, 2007). However, during the rally, white-tailed deer activity shifted further from the main road and was lower on days with higher motorcycle noise. In addition, foraging near the road and diurnal activity were reduced during the busiest day of the rally, but returned to pre-rally conditions after the busiest day of the rally. These behavioral shifts may reflect a risk-avoidance strategy, if traffic and noise elicit anti-predator behavior in ungulates species, resulting in lower abundance near heavily travelled roadways (notably roads with motorcycle traffic; Brown et al., 2012). Regardless, white-tailed deer adjusted their behavior during the motorcycle rally, but readily returned to pre-disturbance behavior when heavy motorcycle traffic ceased.



**Fig. 4. Longer-term response to motorcycle event:** Median number of echolocation calls (activity - top panel) and Shannon diversity of bat echolocation calls (bottom panel) as predicted by generalized linear mixed models (boxes = interquartile range, whiskers = 95% confidence intervals) before (July 1st – July 31st), during (August 1st – August 7th), and after (August 8th – September 1st) the Sturgis Motorcycle Rally in 2015.

**Table 5**

**Model results for bat activity.** Parameter estimates  $\pm$  standard error (SE), 95% confidence intervals (CI), and P-values for each covariate in generalized linear mixed models estimating bat activity and the diversity of bats active in acoustic recordings from Devils Tower National Monument before (July 1st – July 31st), the week during (August 1st – August 7th), and after (August 8th – September 1st) the Sturgis Motorcycle Rally in 2015. Asterisks indicate significant effects.

Covariate	Bat activity				Diversity of bats active			
	PE $\pm$ SE	2.5CI	97.5%CI	P	PE $\pm$ SE	2.5CI	97.5CI	P
Intercept	4.86 $\pm$ 0.15	4.563	5.15	<0.001	1.47 $\pm$ 0.13	1.203	1.733	<0.001
Temperature**	0.21 $\pm$ 0.04	0.133	0.28	<0.001	0.08 $\pm$ 0.03	0.026	0.125	0.003
Hours of moon	-0.07 $\pm$ 0.04	-0.148	0.017	0.122	Not included in final model			
Before rally <sup>a</sup>								
During rally *	0.09 $\pm$ 0.15	-0.212	0.393	0.556	0.19 $\pm$ 0.07	0.053	0.323	0.006
After rally**	-0.33 $\pm$ 0.14	-0.601	-0.063	0.016	0.20 $\pm$ 0.07	0.067	0.3427	0.003
Far from main road <sup>a</sup>								
Near main road*	0.57 $\pm$ 0.21	0.154	0.977	0.007	-0.11 $\pm$ 0.20	-0.946	0.736	0.644
Before rally $\times$ Distance to road <sup>a</sup>								
During rally $\times$ Distance to road**	-0.42 $\pm$ 0.21	-0.832	-0.013	0.043	-0.325 $\pm$ 0.11	-0.466	-0.043	0.018
After rally $\times$ Distance to main road *	-0.36 $\pm$ 0.19	-0.731	0.017	0.062	-0.23 $\pm$ 0.11	-0.459	-0.009	0.042

<sup>a</sup> Reference category.

Although we lack data on prairie dog behavior before the rally, we did detect significant differences in behavior between the week of the rally and the period three weeks later, suggesting behavioral shifts related to the motorcycle event were temporary. During the rally we observed fewer individuals above ground and proportionally less foraging, socializing, resting, and digging and more vigilance and moving than after the rally. This is consistent with previous findings that experimental traffic noise caused an increase in vigilance and a decrease in foraging and aboveground activity (Shannon et al., 2014). However, because we were limited to one prairie dog colony near the main road during and after the rally, we cannot rule out seasonal shifts in behavior.

#### 4.3. Longer term avoidance due to the motorcycle rally

For bats, activity and the number of species active were lower at sites near the main road during the rally and the number of species active declined to even lower levels three-weeks after the rally, suggesting that some bat species avoided the main road during the rally and stayed away. This implies that some species of bats may be less likely, or may take longer, to revert to pre-disturbance foraging activity levels. Our results support previous findings that bats avoid foraging in noisy settings and near roads (Berthinussen and Altringham, 2012; Schaub et al., 2008). Because we were examining the effect of daytime motorcycle traffic on night-time activity of bats, it is unlikely that these noise-induced reductions in activity were caused by disruption of foraging as in previous studies (Bunkley et al., 2015; Luo et al., 2015). Alternatively, motorcycle noise can affect nocturnal bats by disrupting sleep of individuals that roost during the day (Kight and Swaddle, 2011; Luo et al., 2014), which is the case for DETO bats (Keinath and Abernethy, 2016). Bat activity is known to increase as young emerge from maternity roosts (Nocera et al., 2019), which occurs in August in DETO (Griscom and Keinath, 2011), corresponding with the time period of the rally. Lactating females and newly-volant juveniles could be more sensitive to disturbance from traffic noise (Lacki, 2000). Finally, changes in bat activity during and after the rally near the main road may be due to shifts in the distribution of insect prey. Other studies have shown that the abundance of some arthropod families is lower at sites with higher noise; thus the decline in bat foraging activity could be reflecting altered insect abundance (Bunkley et al., 2017). To understand the mechanisms underlying these observed changes in bat activity, further research could examine corresponding changes in insect abundance and bat movement behavior in relation to increases in motorcycle traffic.

#### 4.4. Understanding the mechanisms behind behavioral responses

The four main mechanisms by which anthropogenic noise disrupts animal behavior include: masking of acoustic signals and cues, distraction and reduced attention, increased perceived risk, and indirect effects due to altered inter-specific interactions (Dominoni et al., In review). Because our study took a broader community approach rather than an assessment of specific mechanisms for a given species, we did not measure all behavior parameters for each species nor did we measure other disturbance factors associated with traffic (e.g., chemical pollution, mortality, habitat fragmentation). Thus, although we identified important differences in responses to motorcycle traffic between species, we were unable to ascertain the mechanisms by which motorcycle noise disrupts animal behavior – an essential avenue for further research.

It is important to note that traffic and associated noise can have negative impacts on fitness and population persistence in ways that are not reflected by behavioral response (Gill et al., 2001). Finally, although we found that some species return to pre-rally activity levels and behaviors, this does not indicate that the rally has no long-term impacts on fitness. Alterations in behavioral time-budgets, with less time spent foraging and more time vigilant, is costly, decreasing energy intake and in

many cases lowering fitness (Samia et al., 2013). Human activity often contributes to long-term declines in abundance within an impacted site, despite having seemingly short-term behavioral repercussions (Bejder et al., 2006).

#### 4.5. Implications of varied responses to disturbance within a community

Documenting behavioral responses of multiple species within a community to anthropogenic disturbance can provide valuable information for species management (Berger-Tal et al., 2011). For example, our results suggest that some species are flexible in their behavior, avoiding disturbance caused by the motorcycle event and returning to pre-disturbance behavior when the event ceases. Conversely, bat species may less readily (and rapidly) return to pre-disturbance activity levels as other species, or may shift their distribution in response to disturbance. Based on the prolonged response of the diversity of bat activity to the motorcycle event, particular species may be more vulnerable to major traffic events. This information is useful for park managers to make informed decisions when faced with multifaceted issues of acoustic resource use.

#### 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.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00844>.

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