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Anthropogenic noise alters bat activity levels and echolocation calls



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ABSTRACT

Negative impacts from anthropogenic noise are well documented for many wildlife taxa. Investigations of the effects of noise on bats however, have not been conducted outside of the laboratory. Bats that hunt arthropods rely on auditory information to forage. Part of this acoustic information can fall within the spectrum of anthropogenic noise, which can potentially interfere with signal reception and processing. Compressor stations associated with natural gas extraction produce broadband noise 24 hours a day, 365 days a year. With over half a million producing gas wells in the U.S. this infrastructure is a major source of noise pollution across the landscape. We conducted a 'natural experiment' in the second largest gas extraction field in the U.S. to investigate the potential effects of gas compressor station noise on the activity levels of the local bat assemblage. We used acoustic monitoring to compare the activity level (number of minutes in a night with a bat call) of the bat assemblage at sites with compressor stations to sites lacking this infrastructure. We found that activity levels for the Brazilian free-tailed bat (*Tadarida brasiliensis*) were 40% lower at loud compressor sites compared to quieter well pads, whereas the activity levels of four other species (*Myotis californicus*, *M. cillolabrum*, *M. lucifugus*, *Parastrellus hesperus*) were not affected by noise. Furthermore, our results reveal that the assemblage of bat species emitting low frequency (<35 kHz) echolocation calls also showed a response, with a 70% reduction in activity levels at loud sites compared to quieter well pad sites whereas the assemblage using high frequency (>35 kHz) echolocation did not exhibit altered activity levels in noise. Lower activity levels of Brazilian free-tailed bats at loud sites indicate a potential reduction in habitat for this species. Additionally, a comparison of echolocation search calls produced by free-tailed bats at sites with and without compressor stations reveal that this species modifies its echolocation search calls in noise—producing longer calls with a narrower bandwidth. Call alterations might affect prey detection. These preliminary findings highlight the important need for further research of how anthropogenic noise affects bats on a landscape scale.

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1. Introduction

Human infrastructure removes wildlife habitat, alters connectivity, causes mortality, and introduces ecological pollutants (Sih et al., 2011). A meta-analytical study found that bird densities decline within 1 km of infrastructure and non-volant mammal densities are reduced within 5 km (Benítez-Lopez et al., 2010). Less is known about bats' response to human alteration of habitat but recent work has shown that bat diversity and activity decline with increasing human development (Jung and Kalko, 2011). For instance, roads cause direct mortality (Medinas et al., 2013) and appear to function as barriers and filters to bat assemblages by restricting movement (Abbott et al., 2012; Bennett and Zurcher, 2012) and changing space use (Bennett et al., 2013). Because the disturbance created by roads and other human infrastructure is comprised of multiple components it is difficult to estimate the strength of any single influence (Forman et al., 2003).

Anthropogenic noise associated with infrastructure is an overlooked stimulus that could affect bat habitat use (Barber et al., 2010; Francis and Barber, 2013). Laboratory experiments have shown that gleaning bats exposed to traffic and gas compressor station noise exhibit reduced foraging efficiency (Siemers and Schaub, 2011; Bunkley and Barber, in preparation) and, when presented with the option, avoid hunting in noise (Schaub et al., 2008). Gleaning bats hunt using prey-generated sounds, which could be masked by anthropogenic noise. The potential effects of noise on these bats as well as on bats that utilize echolocation for prey detection are poorly understood at the landscape scale.

Two approaches have been used to tease apart the independent role of noise from other stimuli associated with anthropogenic disturbance of wildlife. Large-scale playback experiments have shown that traffic noise caused over a one-quarter decline in migrating songbird abundance (McClure et al., 2013) and gas drilling and truck noise reduced male Greater Sage-Grouse (*Centrocercus urophasianus*) lek attendance (Blickley et al., 2012). Other investigators have taken advantage of 'natural experiments' in natural gas extraction fields, comparing quiet sites to loud sites with compressor stations. These studies have found that breeding bird densities decrease by one-third at loud sites (Bayne et al., 2008) and avian communities are substantially altered (Francis et al., 2009), resulting in the disruption of key ecological services such as seed dispersal (Francis et al., 2012). Despite strong evidence illustrating habitat degradation and loss for birds, no study has attempted to identify the effects of noise on habitat use by bats.

Here we present data from our investigation of bat activity levels in the second largest gas extraction field in the U.S., in northwest New Mexico. Compressor stations used for the extraction and transportation of natural gas produce spectrally broadband noise 24 h a day, 365 days a year. We compared bat activity levels and sonar call structure at control well pad sites to nearby sites with compressor stations and predicted that this noise source would influence bat activity levels and shape echolocation characteristics. In this 'natural experiment', control sites lacked a compressor station with its characteristic broadband, high intensity noise, but were otherwise similar to treatment sites with compressors. We quantified the background sound level of sites using continuously deployed Acoustic Recording Units while simultaneously acoustically monitoring bat activity. We hypothesized two potential responses of bat activity level to noise: (1) a continuous response with activity decreasing as background dB levels increased, indicating that bats respond to noise exposure in a dose-response fashion, or (2) a binary response to compressor noise with more activity at well pads than compressor sites and with equal activity between treatment sites, regardless of differences in background dB level, indicating a step-function response to noise exposure.

1.1. Methods

We conducted this work in May and June of 2013 in and near Rattlesnake Canyon Habitat Management Area in the San Juan Basin in northwestern New Mexico (Figs. 1 and 2). The San Juan Basin is the second largest natural gas basin in the United States and the largest coal-bed methane reservoir in the world, producing about one trillion cubic feet of gas per year from more than 150 gas fields (Fassett, 2010).

Piñon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*) trees are the dominant plants in this arid region (Francis et al., 2012). Rock outcroppings and a nearby canyon and reservoir are also prominent features on the landscape. The San Juan Basin is within the range of 17 bat species (Nowak, 1994), 14 of which were detected during this study. All identified species are in the family Vespertilionidae except for *T. brasiliensis*, which is in the Molossidae family (Nowak, 1994). Piñon-juniper woodlands in New Mexico support an abundant and diverse bat community (Jones, 1965; Chung-MacCoubrey, 1996, 2005). In part this is because piñon-juniper forest is a transition zone between the arid grass/shrubland community at lower elevations and mesic forests at higher elevations, thus, providing habitat for species from both regions (Jones, 1965).

Piñon-juniper habitat in general is considered suitable in terms of food availability, water, and roosts for *E. fuscus*, *M. ciliolabrum*, *M. evotis*, *M. thysanodes*, and *M. volans* (Chung-MacCoubrey, 2005). Large bodies of water, such as the Navajo reservoir, are also important resources for *T. brasiliensis* (Chung-MacCoubrey, 2005). Thus, we consider the piñon-juniper habitat to be generally suitable to the range of bats we sampled at our sites. Treatment and control sites can be considered similar in terms of roost habitat and potential foraging opportunities. We sampled during a time of high bat activity, which coincides closely with pregnancy and parturition of many bat species and thus represents a time of higher energy requirements for females (Altringham, 2011; Fenton, 1997; Kunz et al., 1982). Reproductive females appear to prefer piñon-juniper habitat to the grass/shrubland and mesic forest communities, both for maternity roosts and for rearing young (Chung-MacCoubrey, 2005).

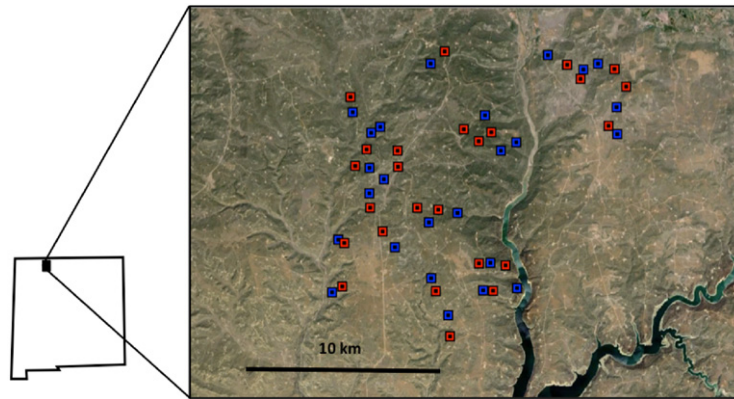


Fig. 1. Study area in the San Juan Basin New Mexico. Red/gray markers indicate sites with a compressor station (treatment) and blue/white markers identify well pads that lack a compressor station (control). Sites were matched by proximity and sampled simultaneously. Bare spaces on the aerial photos illustrate the physical footprints of the gas extraction sites. The Navajo reservoir is visible in the Southeast corner of the map.

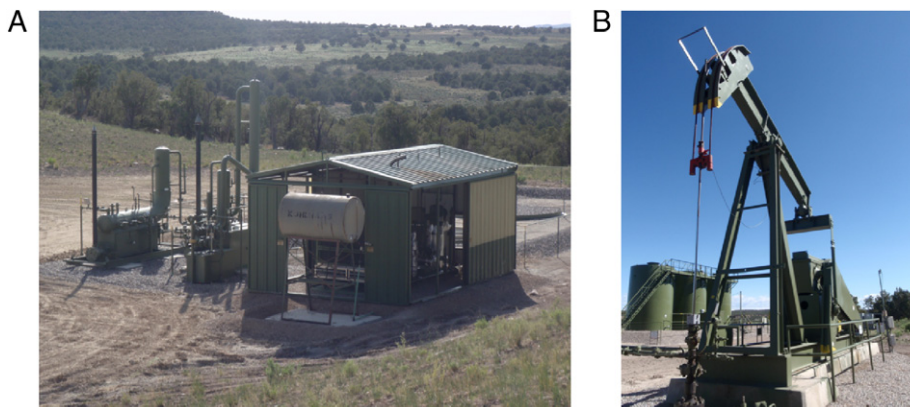


Fig. 2. A. A typical compressor station associated with a well pad. B. A derrick present on a site without a compressor station.

Twenty-five sites with gas compressor stations (treatment) were spatially matched with 25 well pad sites without compressors (control) that were within 500–1000 m (Figs. 1 and 2). Importantly, we sampled control and treatment sites matched by proximity simultaneously, controlling for the effects of moon phase, time, weather, and other factors that can influence bat activity. None of the sites were artificially illuminated during the night, excluding potential affects of anthropogenic light pollution. Using Wildlife Acoustics SM2 or SM2BAT+ Bat Detectors with SMX-US omni-directional, ultrasonic microphones, we conducted passive, acoustic surveys of bat activity levels (the number of minutes in a sampling night with an identified bat call; [Kuenzi and Morrison, 1998](#)).

We rotated 12 detectors through the 50 sites for one to seven nights per site using our simultaneous sampling regime of matched control and treatment pairs throughout. Sampling two to five nights typically detects 40%–60% of species richness at a site ([Skalak et al., 2012](#)). Five sites were sampled for only a single night as a result of battery failure; however, these data still proved to be useful and were included in analyses. Although it is unlikely that 100% of species were detected for every site, by having detectors deployed simultaneously at both the matched treatment and control sites, the detection rate should be comparable between site types.

Acoustic sampling of bats is regarded as an effective tool of assessing bat species and activity level and is a widely used method ([Kunz and Brock, 1975](#); [Kuenzi and Morrison, 1998](#); [O'Farrell and Gannon, 1999](#)). As with all data collection techniques, there are limitations to acoustic monitoring. The detection area of bat detectors varies with the temperature, humidity, wind, and the frequency and directionality of bat sonar, with an estimated 30–90 m detection distance (Wildlife Acoustics). Fortunately, with our spatially matched sampling design, monitors at control and treatment sites likely varied similarly in their detection range due to comparable microclimates.

Acoustic Recording Units (ARUs; Roland R05 or R09; MP3 128 kbps) were simultaneously deployed with bat detectors to measure the sound level at each site ([Mennitt and Fristrup, 2012](#); Figs. 3 and 4). We used custom programs (Damon Joyce, NPS, AUDIO2NVSPL) to convert the MP3 recordings into hourly sound pressure levels and then to hourly LEQ (equivalent continuous sound level) values in dB(A) (Damon Joyce, NPS, Acoustic Monitoring Toolbox). These hourly sound levels were averaged over the duration of the bat detector deployment, which allowed us to use the continuous variable of decibel level (dB(A)) or the discrete variable of treatment (control vs. treatment) for the noise condition of a site in statistical analyses.

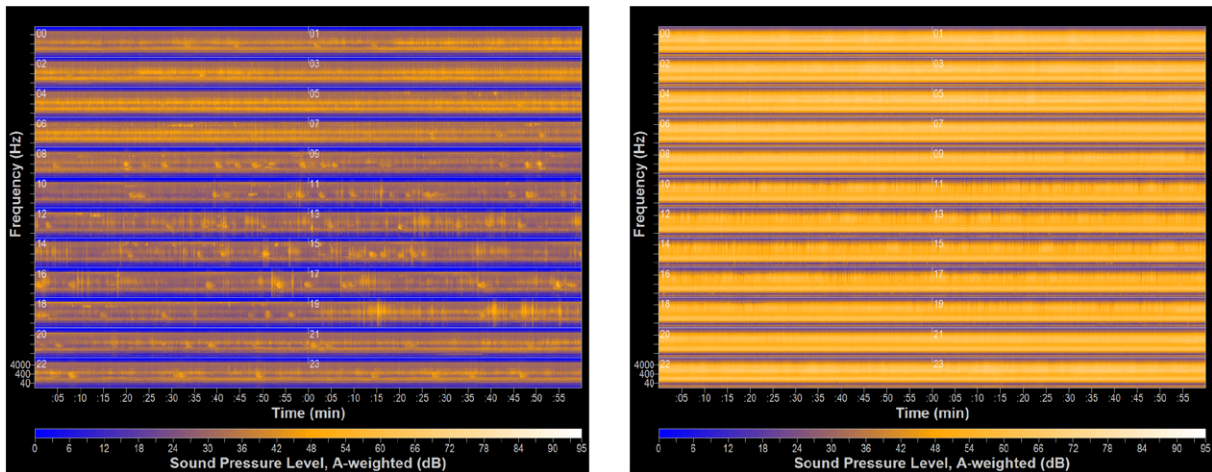


Fig. 3. Twenty-four hour spectrograms of control site 7 (left) and treatment site 7 (right) made using Roland R05 recording units, MP3 128 kbps. Frequency (kHz) is on the y-axis and time (minutes) is on the x-axis. Each line represents a two-hour block of time. The intensity of the color ramp illustrates amplitude or volume.

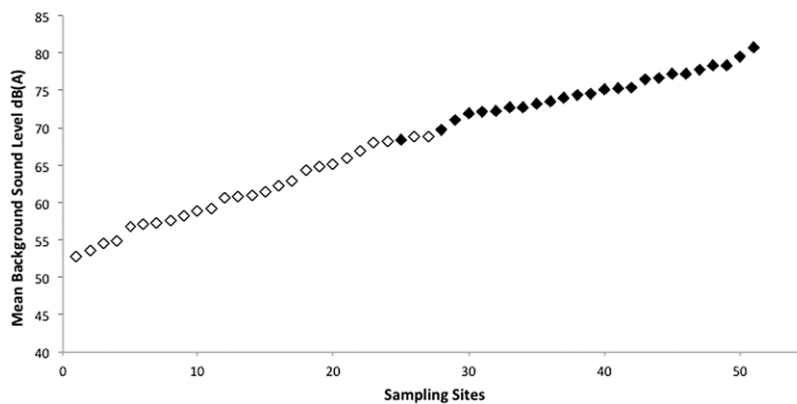


Fig. 4. Mean background sound level dB(A), which includes compressor station noise for treatment sites, varies as a continuous variable by site. White diamonds are sites that did not have compressor stations (control) and black diamonds represent sites that did have operating compressor stations (treatment).

We placed the bat detectors and ARUs approximately 1.5 m above the ground and positioned them along a woodland well pad edge approximately 50 m away from the center of the site. The triggering program for all bat detectors was designed to exclude any background noise below 24 kHz (the frequency band of compressor noise) to ensure that compressor noise did not bias triggering for the treatment sites. The triggering programs were identical for control and compressor sites, which avoided any triggering bias based on treatment. This was confirmed in a laboratory test by playing bat calls in quiet and compressor noise played back at the same sound level as field recordings. Some species produce calls below the 24 kHz triggering threshold such as *Lasiurus cinereus*. Therefore, calls used in analysis are only those calls that were produced by these species above the 24 kHz triggering threshold.

To assess and classify bat echolocation calls, we used the analysis program, Sonobat 3.2.0. This software identifies bat calls and their frequency range (high: > 35 kHz; low: < 35 kHz) among other call variables. Sonobat uses call classification algorithms of acoustic features to determine species identification by referencing a known call library. For analyses that required species level classification we only used calls that had a 90% or greater discrimination probability of falling within a multivariate parameter space of species call traits (Szewczak, 2013). Additionally, calls used for analysis also had a majority of individual calls in a recording sequence identified as the same species (Szewczak, 2013). We used the high (> 35 kHz) and low (< 35 kHz) acoustic groupings established by Sonobat in our analysis because of the natural clustering of bat calls above and below the 35 kHz delineating point (Szewczak, 2013). Other researchers have used these same frequency groups due to the functional differentiation of most migratory bats producing low frequency (< 35 kHz) echolocation calls (Weller and Baldwin, 2012).

We also examined if bats change the structure of their calls in response to compressor noise. We focused on *T. brasiliensis* because it was the only individual species documented to avoid compressor sites in our models (see Section 1.2). Seventy-two *T. brasiliensis* calls from separate recordings taken at control sites and 48 calls from unique recordings taken at treatment sites were hand-analyzed to extract the call parameters of peak frequency (F_{peak}), maximum frequency (F_{max}), minimum

frequency ($F_{\min}$) taken from -15 dB of F_{peak} (Surlykke and Moss, 2000), overall bandwidth (Band), maximum frequency of harmonic one ($H1_{\max}$), minimum frequency of harmonic one ($H1_{\min}$), harmonic one bandwidth ($H1_{\text{band}}$), and lowest apparent frequency (measured from the spectrogram). The frequency response curves of our microphones were ± 3 dB across the relevant spectrum.

Only calls visually identified from spectral and temporal characteristics as search phase calls (Griffin et al., 1960; Surlykke and Moss, 2000) were compared to control for behavioral variation in calls. Calls used for analysis were taken from separate recordings and are not part of the same call sequence. In limited instances calls from multiple recordings from the same site and night were used in analysis. Thus, it is possible that some of these calls could be from the same individual. However, because we did not analyze multiple calls from a single recording our results are likely conservative. We used Avisoft SASLab Pro Version 5.2.07 (Specht, Avisoft Bioacoustics) for sound analyses. We created spectrograms of the call using a Hanning window Fast Fourier Transformation (FFT) of 1024 to increase resolution of spectral features. Call duration was measured from the oscillogram and guided by the spectrogram.

1.2. Analysis

Using the number of echolocation calls recorded at a site, we assessed how noise affects bat activity level of species and assemblages (Weller and Baldwin, 2012). The number of minutes in a night that had an identified bat call was used as a metric of bat activity (Miller, 2001). We treated each sampling night separately and controlled for repeated sampling of sites using a random intercept. Recordings of bat calls were grouped by echolocation frequency. For these “call frequency assemblages” we used all calls identified as high and low frequency (9701 calls), not the more conservative species classification. Species with 45 or more classified calls were analyzed individually.

We analyzed data using R (R Development Core Team, 2011). We first identified and calculated habitat variables considered important to bat activity from the literature (Ciechanowski et al., 2007; Kanuch and Kristin, 2005; Korine and Pinshow, 2004). These included: percent of forest cover (the area with trees present) within 500 m of the center of each site, distance to the nearest large body of water, which was the Navajo Reservoir (the only other water present was in small, tanks set out for cattle) and a lunar metric calculated by multiplying the percent of the moon that was full by the amount of time the moon was visible. We also considered linear and quadratic effects of date in the event that there were unknown changes that might have occurred throughout the season, such as an insect hatch or seasonal movements of bat species, which might alter bat activity over time. We used a two-step procedure (Steen et al., 2013) that allowed us to test the effects of noise on bat activity level while also determining – and controlling for – other environmental factors that may drive activity levels at different sites. First, we built Poisson-distributed generalized linear mixed-effects models containing varying combinations of environmental covariates thought to affect bat activity and a random intercept for survey site. Not all combinations of environmental variables were tested because several, such as date and the moon metric, were highly correlated ($r > 0.5$) and consequently were not included in the same model. Assumptions of normality were assessed for each variable. We used Akaike's Information Criterion (AIC, Akaike, 1974) to rank models and then incorporated the covariates within the highest-ranked model into the next step.

In the second step, we tested our a priori hypothesis that noise affects activity levels of different bat assemblages. We hypothesized that noise might affect activity levels of bats in one of two ways: (1) Bats may respond to noise in a linear fashion with activity decreasing linearly with increasing background dB levels—meaning that well pad and compressor sites that are inherently noisier will experience less bat activity. Or, (2) bats may respond to noise in a binary fashion with more activity at well pads than compressor sites, but activity being equal among treatments regardless of differences in background sound levels. Each hypothesized response was represented by a model—one that added a covariate indicating the dB level of a site to the best model from step one, and another that added a binary factor indicating treatment (gas compressor = 1, well pad = 0) to the best model from step one. We ranked and compared these two models – dB and treatment – as well as the best habitat model from the first step using AIC. We considered our hypothesis of noise affecting site-use by bats as supported if either the dB or treatment models received a lower AIC value than the best model from step one, and as strong evidence if the 95% confidence interval for either the dB or treatment variable excluded zero and marginal evidence if the 85% confidence intervals excluded zero. Eight-five percent confidence intervals are more consistent with an AIC approach than are 95% confidence intervals (Arnold, 2010). All predictor variables were z-transformed before analysis to put them on the same scale and thus make them comparable during analyses.

For the analysis of the echolocation call data we used linear mixed effect models with a random intercept for point. We built three models, one containing a variable for decibel (dB) level, one with a noise treatment parameter, and a null model. Models were ranked by AIC and evaluated.

2. Results

Site activity levels were measured at the point of the detector (approximately 50 m from the center of the well pad or compressor station) with the addition of the microphone range (30–90 m). The detectors logged 9701 recordings identified as bats, of which 2278 were classified to species (Szewczak, 2013). Those calls classified to the species level met both the 90% minimum discrimination probability and the classification agreement of multiple calls in a sequence, making this a more conservative measure (Szewczak, 2013). Species identified included: low frequency (< 35 kHz) – *Antrozous pallidus*

Table 1

AIC tables of the Habitat, Habitat + Treatment, and Habitat + dB for all bats, low frequency echolocating assemblage (*Antrozous pallidus*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*, *Myotis thysanodes*, and *Tadarida brasiliensis*), the high frequency echolocating assemblage (*Lasiurus blossevillei*, *M. californicus*, *M. cillolabrum*, *M. evotis*, *M. lucifugus*, *M. volans*, *M. yumanensis*, and *Parastrellus hesperus*), and individual species for bat activity levels of 50 sites sampled in the San Juan Basin in northwest New Mexico. See Section 1.1 for call parameter information.

Model	K	AIC	Δ AIC	W_i
All bats				
Habitat	4	2500.94	0.00	0.49
Habitat + Treatment	5	2502.08	1.14	0.28
Habitat + dB	5	2502.50	1.56	0.23
Low frequency				
Habitat + dB	6	425.78	0.00	0.44
Habitat + Treatment	6	426.41	0.64	0.32
Habitat	5	426.95	1.17	0.24
High frequency				
Habitat	4	1231.62	0.00	0.52
Habitat + Treatment	5	1232.88	1.26	0.28
Habitat + dB	5	1233.45	1.83	0.21
<i>Myotis californicus</i>				
Habitat	4	217.86	0.00	0.57
Habitat + Treatment	5	219.71	1.85	0.22
Habitat + dB	5	219.83	1.97	0.21
<i>Myotis cillolabrum</i>				
Habitat	4	1142.95	0.00	0.51
Habitat + Treatment	5	1144.15	1.21	0.28
Habitat + dB	5	1144.71	1.76	0.21
<i>Myotis lucifugus</i>				
Habitat	4	226.33	0.00	0.56
Habitat + dB	5	228.17	1.84	0.22
Habitat + Treatment	5	228.28	1.95	0.21
<i>Parastrellus hesperus</i>				
Habitat	4	313.91	0.00	0.57
Habitat+Treatment	5	315.77	1.85	0.22
Habitat + dB	5	315.88	1.97	0.21
<i>Tadarida brasiliensis</i>				
Habitat + Treatment	6	368.46	0.00	0.37
Habitat	5	368.50	0.04	0.36
Habitat + dB	6	369.08	0.62	0.27

(gleaning), *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*, *Myotis thysanodes*, and *Tadarida brasiliensis* and high frequency (<35 kHz) – *Lasiurus blossevillei*, *M. californicus*, *M. cillolabrum*, *M. evotis*, *M. lucifugus*, *M. volans*, *M. yumanensis*, and *Parastrellus hesperus*. Twelve species were observed at both compressor and well sites. *M. thysanodes* was recorded only at sites with compressors and *M. volans* was detected only at well pad sites. Both species were rare and low overall levels of activity (few recordings) might be reflective of lower abundance or detectability (Table A1). Discrimination probabilities of species identification did not differ between calls recorded at treatment and control sites, indicating that background noise did not affect call classification (Linear mixed-effects model fit by maximum likelihood, All bats: $p = 0.46$; *Tadarida brasiliensis*: $p = 0.47$).

All bat species and assemblages were associated with one or more of the habitat variables (Table A2). Covariates of either noise treatment or level were then added to the best model containing habitat covariates (Table 1). Adding these noise covariates improved the fit of models for *T. brasiliensis* and the assemblage of species with low-frequency echolocation calls—supporting our hypothesis that noise affects activity levels of some bat species and assemblages. *T. brasiliensis* was negatively associated with the binary treatment factor with activity at compressor sites being 60% (85% CI = 36%–100%) that of quieter well pad sites. Species with low frequency echolocation calls were negatively associated with site dB level, with activity at the loudest sites being 33% (85% CI = 20%–55%) that of quieter sites (Fig. 5). Models with noise covariates have a lower AIC score than the habitat only models, indicating that these models overcame the 2 AIC penalty for an additional parameter and are more parsimonious. The exclusion of zero with 85% confidence intervals indicates marginal evidence that these groups are affected by noise.

The assemblage of species with high frequency echolocation calls did not have either noise variable in the top model. Additionally, the treatment and dB factors did not improve the fit of the models for *Myotis californicus*, *M. cillolabrum*, *M. lucifugus*, or *Parastrellus hesperus*, indicating that noise level is not an informative parameter for the activity levels of these species.

For the 120 *T. brasiliensis* search calls analyzed for spectral characteristics the best model for call duration included a factor for treatment indicating that calls were 0.90 ms (85% CI = 0.35–1.44, 95% CI = 0.16–1.64) longer at compressor

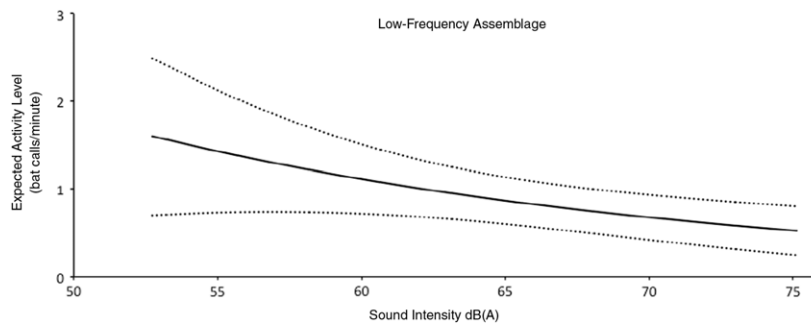


Fig. 5. Modeled activity level of the low frequency (<35 kHz) echolocating bat assemblage corresponding to background noise level (dB(A)), with standard error lines.

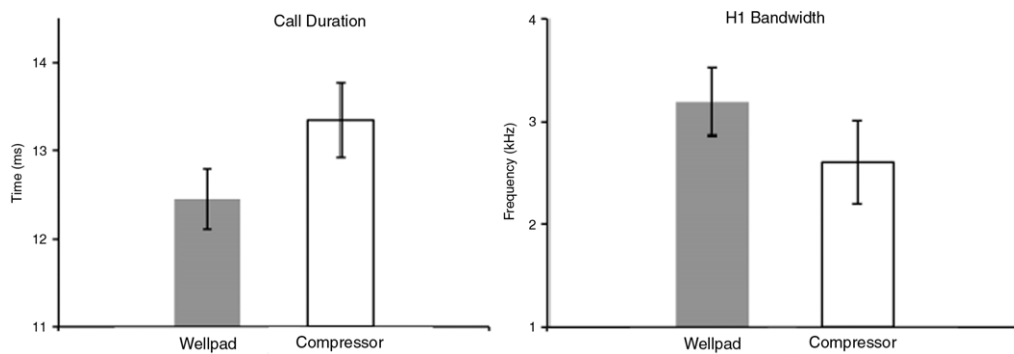


Fig. 6. *Tadarida brasiliensis* mean call duration and first harmonic bandwidth of 48 calls from sites with compressor stations (white/treatment) and 72 calls from sites without compressor noise (gray/control), with standard error bars.

Table 2

AIC tables for analyzed parameters of 120 *Tadarida brasiliensis* calls from sites with gas compressor stations (treatment) and sites lacking stations (control). See Section 1.2 for definitions of call parameters.

Model	K	AIC	Δ AIC	Wi
Call duration				
Treatment	4	497.32	0	0.674
dB	4	499.78	2.46	0.20
Null	3	500.64	3.32	0.13
H1_{band}				
Treatment	4	468.45	0	0.44
Null	3	468.56	0.11	0.41
dB	4	470.54	2.09	0.15
F_{peak}				
Null	3	432.12	0	0.55
Treatment	4	433.87	1.75	0.23
dB	4	433.98	1.87	0.22
H1_{min}				
Null	3	409.25	0	0.55
Treatment	4	410.96	1.70	0.23
dB	4	411.10	1.85	0.22
Lowest apparent frequency				
Null	3	415.53	0	0.57
Treatment	4	417.36	1.83	0.23
dB	4	417.53	2.00	0.21

sites compared to well pad sites (Fig. 6). The best model for bandwidth also included a factor for treatment (Table 2), indicating bandwidth was 600 Hz (85% CI = 70–1100) narrower at locations with compressor stations (Fig. 6). The null model (intercept only) was the best model for all other characteristics of *T. brasiliensis* search calls.

3. Discussion

Our results indicate that anthropogenic noise from natural gas compressor stations affects some bat species. Our findings offer marginal evidence that *T. brasiliensis* show lower activity levels in gas compressor noise specifically and low frequency (<35 kHz) echolocating bat species reduce activity levels in increased noise in general. Additionally, we found strong evidence that *T. brasiliensis* lengthens echolocation call duration and marginal evidence that bandwidth is narrowed in response to noise. These multiple lines of evidence reveal that some bat species are affected by noise and highlights the need for continued research in this field. Our use of spatially matched sites during data collection and modeling of habitat variables in analysis isolated noise as a primary factor driving these patterns, however, other factors such as predator abundance and prey distributions might also play a role in altered activity levels.

T. brasiliensis showed reduced activity levels at sites with compressor noise, lending support for the hypothesis that broadband, high intensity compressor noise reduces species' activity. One of the dominant species in our study site, *T. brasiliensis*, likely drove the observed effect of a negative association with dB(A) level for the assemblage of low frequency echolocating bats. However, noise had an apparently stronger effect (higher model weight (Table 1) and narrower 85% confidence intervals for the low frequency group (CI = 20%–55%) as compared to only *T. brasiliensis* (CI = 36%–100%)) indicating a general response among the low frequency group to noise. Our model shows a near linear relationship between activity levels of this assemblage and background noise level (Fig. 5). The low frequency group of bats exhibits a continuous response of decreasing activity with increasing background dB levels, lending support to the dose–response hypothesis. Interestingly, three other species that produce high frequency (>35 kHz) echolocation calls did not show a difference in activity level in loud versus quiet sites. This indicates that echolocation frequency is important to a bat species' response to noise exposure.

The effect of noise on the activity levels of low frequency echolocating bats indicates potential masking of some echolocation call frequencies (Fenton and Bell, 1981) by lower frequency anthropogenic noise (<24 kHz). Several of the species in the low frequency assemblage (*A. pallidus*, *E. fuscus*, *L. cinereus*, *L.s. noctivagans*, *M. thysanode*, *T. brasiliensis*) have echolocation calls that contain components that could be susceptible to masking by anthropogenic noise (Fenton and Bell, 1981; Szewczak, 2013). Even calls that do not directly overlap the frequency range of noise may still experience negative effects from noise. Recently, Hage et al. (2013) showed echolocation frequency shifts in the constant frequency (CF) horseshoe bat, which has a dominant resting frequency at 75 kHz (Hage et al., 2013). These bats shifted frequency upwards when presented with noise from a variety of spectra, including in the range of anthropogenic noise (10–30 kHz; Hage and Metzner, 2013), indicating that perhaps even noise that does not spectrally overlap echolocation signals can cause interference with echolocation processes.

Our analysis of *T. brasiliensis* echolocation search calls produced at sites with compressor noise indicates a reduction in call bandwidth at the 85% confidence level and an increase in duration at the 95% confidence level (Fig. 6). Concentrating energy spectrally likely improves signal-to-noise ratio of the call and increasing call duration increases signal redundancy and thus detectability in noisy background conditions (Schnitzler and Kalko, 2001; Brumm et al., 2004). *T. brasiliensis* is often considered an urban survivor because it commonly uses anthropogenic structures, such as bridges, for roosting (Davis et al., 1962; Allen et al., 2008). However, in a landscape where sites vary in their noise exposure, *T. brasiliensis* exhibits greater levels of nocturnal activity in quieter areas during periods when bats are likely foraging. Differences in noise tolerance at roosts versus foraging sites might be attributable to an alteration in prey detection as a result of noise induced changes in echolocation calls. Additionally, the narrower bandwidth and increased temporal variation of highway traffic noise as compared to the spectrally broad and temporally constant nature of compressor noise may also affect behavioral responses in *T. brasiliensis*.

We recognize that our data are limited in scope, due to the single sampling season, and the marginal evidence of several of our results. However, because multiple lines of evidence, lowered activity levels of low frequency echolocating bats and *T. brasiliensis*, as well as the altered echolocation signals of *T. brasiliensis*, indicate that some species of bats are likely negatively affected by noise, emphasizing the need for continued investigations into the response of bats to noise at the landscape level. The scale of anthropogenic noise across the world, including, but not limited to noise produced by energy extraction infrastructure, is immense. Given this reality in addition to the sensitive status of many bat species makes the question of bat responses to noise worthy of continued investigation.

We estimate that compressor noise affects about 356 km² of potential *T. brasiliensis* habitat in the San Juan Basin. Detectors were set approximately 50 m from the center of a compressor site and given the conservative measure of a 30 m detection rate our analysis of activity level represents a 80 m detection radius around a compressor. In 2010 there were 35,431 productive wells in the San Juan Basin (Fassett, 2010) and approximately half had compressor stations, resulting in an estimated 356 km² of habitat directly affected by noise. However, because wells are spread throughout the region, a much larger area likely experiences habitat degradation and possibly fragmentation. A map illustrating the range of *T. brasiliensis* overlaid with known compressor stations illustrates the potential scale of the problem (Fig. 7).

Bats are important indicators of ecosystem health and providers of a variety of ecosystem services (Jones et al., 2009) making them an essential group to conserve in order to maintain functioning habitats. North American bat populations are currently experiencing unprecedented declines as a result of the white nose syndrome epidemic and mortality from wind power development (Foley et al., 2011; Kunz et al., 2007). As a consequence, preventable habitat degradation should be prioritized by management agencies to reduce anthropogenic pressures on these sensitive populations. Our findings that

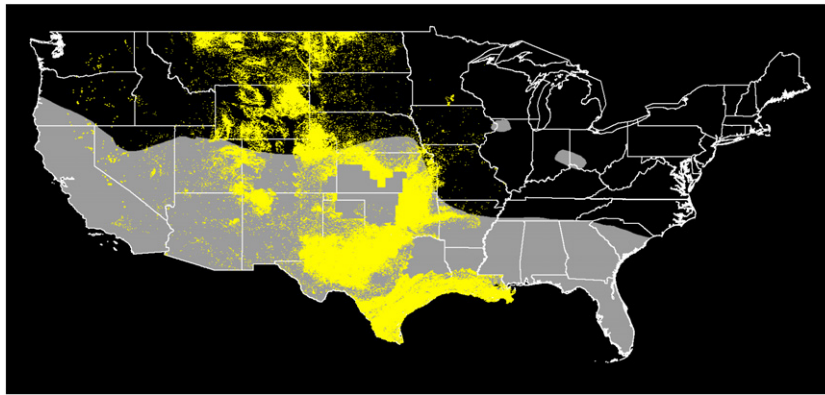


Fig. 7. The geographic overlap of *T. brasiliensis* range (gray area; Bat Conservation International, NationalAtlas.gov, 2013) with available data for compressor stations in the Western United States (yellow/white; U.S. Geological Survey, 2012).

some bat species and assemblages experience reduced activity at sites with noise suggest that anthropogenic noise is another potential threat to bat populations and should be considered when managing habitat (Francis and Barber, 2013). Fortunately, anthropogenic noise can be mitigated, for instance by building sound-damping walls around compressor stations (Francis et al., 2012). These important preliminary findings indicate that further research is promptly needed to better understand the responses of bats to anthropogenic noise on the landscape scale.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2014.11.002>.

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