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Contributed Paper

Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks

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Abstract: *Increasing evidence suggests that chronic noise from human activities negatively affects wild animals, but most studies have failed to separate the effects of chronic noise from confounding factors, such as habitat fragmentation. We played back recorded continuous and intermittent anthropogenic sounds associated with natural gas drilling and roads at leks of Greater Sage-Grouse (*Centrocercus urophasianus*). For 3 breeding seasons, we monitored sage grouse abundance at leks with and without noise. Peak male attendance (i.e., abundance) at leks experimentally treated with noise from natural gas drilling and roads decreased 29% and 73%, respectively, relative to paired controls. Decreases in abundance at leks treated with noise occurred in the first year of the study and continued throughout the experiment. Noise playback did not have a cumulative effect over time on peak male attendance. There was limited evidence for an effect of noise playback on peak female attendance at leks or male attendance the year after the experiment ended. Our results suggest that sage-grouse avoid leks with anthropogenic noise and that intermittent noise has a greater effect on attendance than continuous noise. Our results highlight the threat of anthropogenic noise to population viability for this and other sensitive species.*

Keywords: chronic noise, energy development, *Centrocercus urophasianus*, roads

Evidencia Experimental de los Efectos de Ruido Antropogénico Crónico sobre la Abundancia de *Centrocercus urophasianus* en Leks

Resumen: *El incremento de evidencias sugiere que el ruido crónico de actividades humanas afecta negativamente a los animales silvestres, pero la mayoría de los estudios no separan los efectos del ruido crónico de los factores de confusión, como la fragmentación del hábitat. Reprodujimos sonidos antropogénicos intermitentes y continuos asociados con la perforación de pozos de gas natural y caminos en leks de* Centrocercus urophasianus. *Durante 3 épocas reproductivas, monitoreamos la abundancia de* C. urophasianus e *leks con y sin ruido. La abundancia máxima de machos (i.e., abundancia) en leks tratados con ruido de la perforación de pozos de gas natural y caminos decreció 29% y 73% respectivamente en relación con los controles pareados. La disminución en abundancia en leks tratados con ruido ocurrió en el primer año del estudio y continuó a lo largo del experimento. La reproducción de ruido no tuvo efecto acumulativo en el tiempo sobre la abundancia máxima de machos. Hubo evidencia limitada para un efecto de la reproducción de ruido sobre la abundancia máxima de hembras en los leks o sobre la asistencia de machos el año después de que concluyó el experimento. Nuestros resultados sugieren que* C. urophasianus *evita leks con ruido anropogénico y que el ruido intermitente tiene un mayor efecto sobre la asistencia que el ruido continuo. Nuestros*

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resultados resaltan amenaza del ruido antropogénico para la viabilidad poblacional de esta y otras especies sensibles.

Palabras Clave: *Centrocercus urophasianus*, desarrollo energético, ruido crónico, caminos

Introduction

Noise associated with human activity is widespread and expanding rapidly in aquatic and terrestrial environments, even across areas that are otherwise relatively unaffected by humans, but there is still much to learn about its effects on animals (Barber et al. 2009). Effects of noise on behavior of some marine organisms are well-documented (Richardson 1995). In terrestrial systems, the effects of noise have been studied less, but include behavioral change, physiological stress, and the masking of communication signals and predator sounds (Slabbekoorn & Ripmeester 2008; Barber et al. 2009). These effects of noise on individual animals may lead to population decreases if survival and reproduction of individuals in noisy habitats are lower than survival and reproduction of individuals in similar but quiet habitats (Patricelli & Blickley 2006; Warren et al. 2006; Slabbekoorn & Ripmeester 2008). Population declines may also result if animals avoid noisy areas, which may cause a decrease in the area available for foraging and reproduction.

There is evidence of variation among species in their sensitivity to noise. Noise sensitivity may also differ with the type of noise, which varies in amplitude, frequency, temporal pattern, and duration (Barber et al. 2009). Duration may be particularly critical; most anthropogenic noise is chronic and the effects of chronic noise may differ substantially from those of short-term noise in both severity and response type. For example, brief noise exposure may cause elevated heart rate and a startle response, whereas chronic noise may induce physiological stress and alter social interactions. Therefore, when assessing habitat quality for a given species, it is critical to understand the potential effects of the full spectrum of anthropogenic noise present in the species' range.

The effects of noise on wild animals are difficult to study because noise is typically accompanied by other environmental changes. Infrastructure that produces noise may be associated with fragmentation of land cover, visual disturbance, discharge of chemicals, or increased human activity. Each of these factors may affect the physiology, behavior, and spatial distribution of animals, which increases the difficulty of isolating the effects of the noise.

Controlled studies of noise effects on wild animals in terrestrial systems thus far have focused largely on birds. Recent studies have compared avian species richness, occupancy, and nesting success near natural gas wells operating with and without noise-producing compressors. In these studies, spatial variation in noise was used to control for confounding visual changes due to infrastructure (Habib et al. 2007; Bayne et al. 2008; Francis et al. 2009). Results of these studies show that continuous noise affects density and occupancy of a range of bird species and leads to decreases or increases in abundance of some species and has no effect on other species (Bayne et al. 2008; Francis et al. 2009; Francis et al. 2011). Results of these studies also show that noise affects demographic processes, such as reproduction, by reducing the pairing or nesting success of individuals (Habib et al. 2007; Francis et al. 2009).

Although these studies in areas near natural gas wells controlled for the effects of most types of disturbance besides noise, they could not address the effect of noise on naïve individuals in areas without natural gas wells and compressors. Furthermore, there have been no controlled experiments that address the effects of chronic but intermittent noise, such as traffic, which may be more difficult for species to habituate. Road noise may have large negative effects because it is widespread (affecting an estimated 20% of the United States) (Forman 2000) and observational studies indicate that noise may contribute to decreases in abundance of many species near roads (e.g., Forman & Deblinger 2000).

Noise playback experiments offer a way to isolate noise effects on populations from effects of other disturbances and to compare directly the effects of noise from different sources. Playback experiments have been used to study short-term behavioral responses to noise, such as effects of noise on calling rate of amphibians (Sun & Narins 2005; Lengagne 2008), heart rate of ungulates (Weisenberger et al. 1996), diving and foraging behavior of cetaceans (Tyack et al. 2011), and song structure of birds (Leonard & Horn 2008), but have not been used to study effects of chronic noise on wild animals because producing long-term noise over extensive areas is challenging. We conducted a playback experiment intended to isolate and quantify the effects of chronic noise on wild animals. We focused on the effects of noise from natural gas drilling on Greater Sage-Grouse (*Centrocercus urophasianus*).

Greater Sage-Grouse occur in the western United States and Canada and have long been a focus of sexual selection studies (Wiley 1973; Gibson 1989; Gibson 1996). Greater Sage-Grouse populations are decreasing in density and number across the species' range, largely due to extensive habitat loss (Connelly et al. 2004; Garton et al. 2010). The species is listed as endangered under Canada's

Species at Risk Act and is a candidate species for listing under the U.S. Endangered Species Act. Deep natural gas and coal-bed methane development have been expanded rapidly across the species' range since 2000 and substantial evidence suggests that these processes may contribute to observed decreases in the number of Greater Sage-Grouse (Holloran 2005; Walker et al. 2007; Holloran et al. 2010). Many factors associated with deep natural gas and coal-bed methane development are thought to lead to these decreases, including habitat loss, increased occurrence of West Nile Virus, and altered fire regimes due to the expansion of nonnative invasive species (Naugle et al. 2004; Walker et al. 2007; Copeland et al. 2009).

The noise created by energy development may also affect sage grouse by disrupting behavior, causing physiological stress, or masking biologically important sounds. During the breeding season (February–May), male sage grouse gather on communal breeding grounds called leks. Male attendance (number of male birds on the lek) at sage grouse leks downwind of deep natural gas development decreases up to 50% per year compared with attendance at other leks, which suggests noise or aerial spread of chemical pollution as factors contributing to these decreases (Holloran 2005).

We sought to test the hypothesis that lek attendance by male and female sage grouse is negatively affected by both chronic intermittent and continuous noise from energy development. To do so, we conducted a noise playback experiment in a population that is relatively unaffected by human activity. Over 3 breeding seasons (late February to early May), we played noise recorded from natural gas drilling rigs and traffic on gas-field access roads at sage grouse leks and compared attendance patterns on these leks to those on nearby control leks.

We conducted our experiment at leks because lekking sage grouse are highly concentrated in a predictable area, which makes them good subjects for a playback experiment. More importantly, sage grouse may be particularly responsive to noise during the breeding season, when energetic demands and predation risk are high (Vehrencamp et al. 1989; Boyko et al. 2004). Additionally, noise may mask sexual communication on the lek. Lekking males produce a complex visual and acoustic display (Supporting Information) and females use the acoustic component of the display to find lekking males and select a mate (Gibson 1989; Gibson 1996; Patricelli & Krakauer 2010). Furthermore, lek attendance is commonly used as a metric of relative abundance of sage grouse at the local and population level (Connelly et al. 2003; Holloran 2005; Walker et al. 2007). We used counts of lek attendance (lek counts) to assess local abundance relative to noise versus control treatments.

Methods

Study Site and Lek Monitoring

Our study area included 16 leks (Table 1 & Supporting Information) on public land in Fremont County, Wyoming, U.S.A. (42° 50′, 108° 29′). Dominant vegetation in this region is big sagebrush (*Artemisia tridentata wyomingensis*) with a grass and forb understory. The primary land use is cattle ranching, and there are low levels of recreation and natural gas development.

We paired leks on the basis of similarity in previous male attendance and geographic location (Table 2 & Supporting Information). Within a pair, one lek was

Table 1. Pairing, treatment type, location, and baseline attendance for leks used in noise playback experiment.

Lek	*Pair*	*Pair noise type*	*Noise or control*	*Years of playback*	*Baseline attendance*[*]
Gustin	A	drilling	control	3	26
Preacher Reservoir	A	drilling	noise	3	49
North Sand Gulch	B	road	control	3	32
Lander Valley	B	road	noise	3	67
East Twin Creek	C	drilling	control	3	44
Coal Mine Gulch	C	drilling	noise	3	83
East Carr Springs	D	road	control	3	67
Carr Springs	D	road	noise	3	92
Powerline	E	drilling	control	2	49
Conant Creek North	E	drilling	noise	2	44
Monument	F	road	control	2	53
Government Slide Draw	F	road	noise	2	55
Nebo	G	drilling	control	2	18
Arrowhead West	G	drilling	noise	2	24
Onion Flats 1	H	road	control	2	41
Ballenger Draw	H	road	noise	2	38

[*] *Baseline attendance is the average peak male attendance value (annual maximum number of males observed averaged across years) for that lek from 2002 to 2005.*

Table 2. Mixed-effect candidate models used to assess change in peak attendance of male Greater Sage-Grouse at leks from pre-experiment baseline attendance during the natural gas drilling noise playback (2006–2008) and after the experiment (2009).

Model (year)[a]	K[b]	ΔAIC_c[c]	w_i[d]
Male experiment (2006–2008)			
treatment × type+season[e]	9	0	0.64
treatment × type[e]	7	1.8	0.26
treatment+experiment year	6	6.1	0.03
treatment+season	7	6.8	0.02
treatment	5	7.3	0.02
treatment × experiment year	7	8.0	0.01
treatment × type+treatment × season+experiment year	12	8.6	<0.01
treatment × type+treatment × season	11	9.9	<0.01
treatment × type+treatment × season+treatment × experiment year	13	10.0	<0.01
treatment+type	6	10.4	<0.01
treatment × season	9	16.2	<0.01
null- random effects only	4	57.0	<0.01
Male after experiment (2009)			
null, random effects only[e]	3	0.0	0.84
treatment	4	3.3	0.16

[a] *All models contain pair as a random effect, and experiment (2006–2008) models also include year as a random effect. Covariates: treatment, lek treatment (noise or control) assigned to individual leks within a pair; type, pair noise treatment type (road or drilling assigned to pair); season, time of year (early [late February to 1 week prior to peak female attendance for that lek; female peak ranged from 15 March to 6 April], mid [1 week before and after female peak], and late [starting 1 week after female peak]); experiment year, years of experimental noise exposure.*

[b] *Number of parameters in the model.*

[c] *Difference in AIC_c (Akaike's information criterion for small sample size) values from the model with lowest AIC_c.*

[d] *Akaike weight.*

[e] *Model with substantial support ($\Delta AIC_c < 2$).*

randomly assigned to receive experimental noise treatment and the other lek was designated a control. We randomly assigned the experimental leks to receive playback of either drilling or road noise. In 2006, we counted attendance at 8 leks (2 treated with drilling noise, 2 treated with road noise, and 4 control). In both 2007 and 2008, we included an additional 8 leks for a total of 16 leks (4 treated with drilling noise, 4 treated with road noise, and 8 controls).

Throughout the breeding season, we counted males and females on leks with a spotting scope from a nearby point selected to maximize our visibility of the lek. We visited paired leks sequentially on the same days between 05:00 and 09:00, alternating the order in which each member of the pair was visited. We visited lek pairs every day during the breeding season in 2006 and, after expanding our sample size in 2007, every 2–4 days in 2007 and 2008. Peak estimates of male attendance from >4 visits are a highly repeatable measure of abundance at individual leks (Garton et al. 2010), so the lower frequency of visits in 2007 and 2008 was unlikely to have a substantial effect on estimates of peak male attendance. At a minimum, we conducted 2 counts per visit at 10- to 15-min intervals. The annual peak attendance was the highest daily attendance value at each lek for the season for males or females. For males we also calculated the peak attendance in 3 nonoverlapping date ranges: early (late February to 1 week prior to peak female attendance for that lek; female peak ranged from 15 March to 6 April), mid (1 week before and after female peak), and late (starting 1 week after female peak).

Noise Introduction

We recorded noise used for playback near natural gas drilling sites and gas-field access roads in a region of extensive deep natural gas development in Sublette County, Wyoming (Pinedale Anticline Gas Field and Jonah Gas Field). We recorded drilling noise in 2006 within 50 m of the source on a digital recorder (model PMD670, 44.1 kHz/16 bit; Marantz, Mahwah, New Jersey) with a shotgun microphone (model K6 with an ME60 capsule; Sennheiser, Old Lyme, Connecticut). We recorded road noise in 2005 with a handheld computer (iPAQ h5550 Pocket PC, 44.1 KHz/16 bit; Hewlett Packard, Palo Alto, California) and omnidirectional microphone (model K6 with an ME62 capsule; Sennheiser). Drilling noise is relatively continuous and road noise is intermittent (Supporting Information). Both types of noise are predominantly low frequency (<2 kHz).

We played noise on experimental leks from 2 to 4 rock-shaped outdoor speakers (300 W Outdoor Rock Speakers; TIC Corporation, City of Industry, California) hooked to a car amplifier (Xtant1.1; Xtant Technologies, Phoenix, Arizona) and an MP3 player (Sansa m240; SanDisk, Milpitas, California). The playback system was powered with 12 V batteries that we changed every 1–3 days when no birds were present. We placed the speakers

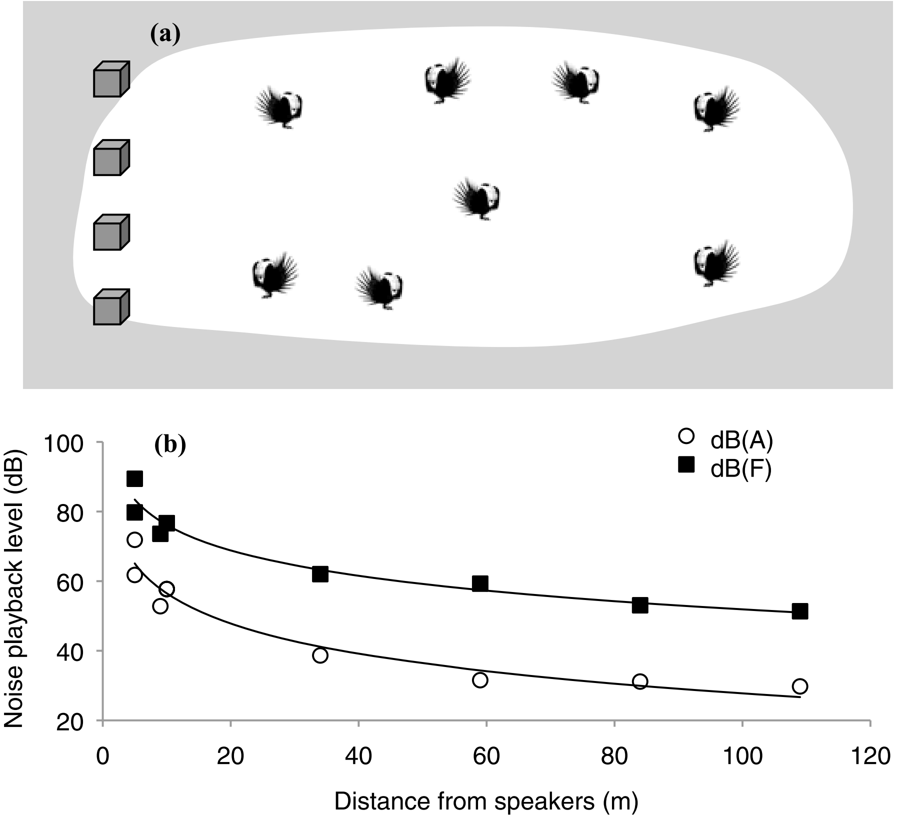

Figure 1. (a) Placement of speakers (on noise-treated leks) or dummy speakers (on control leks) (boxes) at Greater Sage-Grouse leks. (b) Mean maximum noise level (unweighted decibels, dB[F], and A-weighted decibels, dB[A], measured in Lmax [highest root-mean-square sound pressure level within the measurement period]) at Greater Sage-Grouse leks measured on transects at 25-m intervals from the line of speakers on a typical lek treated with road noise. Playback levels of natural gas drilling noise (measured in Leq) followed the same pattern. Ambient levels of noise at control leks ranged from 30 to 35 dB(A).

in a straight line across one end of the lek (Fig. 1a). In 2006 we placed 3 speakers at leks treated with drilling noise and 2 speakers at leks treated with road noise. In 2007 and 2008, we increased the number of speakers, placing 4 at each noise-treated lek to increase the area in which noise was present on the lek. At control leks, we placed dummy speakers of similar size and color to playback speakers (68-L plastic tubs). Within each lek pair, dummy and real speakers were placed in similar configurations. To control for playback-related disturbance, the leks in each pair were visited an equal number of times during the morning for counts of birds and in the afternoon for battery changes.

We played drilling noise and road noise on leks at 70 dB(F) sound pressure level (unweighted decibels) measured 16 m directly in front of the speakers (Fig. 1 & Supporting Information). This is similar to noise levels measured approximately 400 m from drilling rigs and main access roads in Pinedale (J. L. Blickley and G. L. Patricelli, unpublished data). Four hundred meters (0.25 miles) is the minimum surface disturbance buffer around leks at this location (BLM 2008). We calibrated and measured noise playback levels with a hand-held meter that provides sound-pressure levels (System 824; Larson-Davis, Depew, New York) when wind was <9.65 k/h. On drilling-noise-treated leks, where noise was continuous, we calibrated the noise playback level by measuring the average sound level (Leq [equivalent continuous sound level]) over 30 s. On leks treated with road noise, where the amplitude of the noise varied during playback to simulate the passing of vehicles, we calibrated the playback level by measuring the maximum sound level (Lmax [highest root-mean-square sound pressure level within the measurement period]).

For leks treated with drilling noise, recordings from 3 drilling sites were spliced into a 13-min mp3 file that played on continuous repeat. On leks treated with road noise, we randomly interspersed mp3 recordings of 56 semitrailers and 61 light trucks with 170 thirty-second silent files to simulate average levels of traffic on an access road (Holloran 2005). Noise playback on experimental leks continued throughout April in 2006, from mid February or early March through late April in 2007, and from late February through late April in 2008. We played back noise on leks 24 hours/day because noise from deep natural gas drilling and vehicular traffic is present at all times. This experimental protocol was reviewed and approved by the Animal Care and Use Committee at University of California, Davis (protocol 16435).

To measure noise levels across experimental leks, we measured the average amplitude (15 s Leq) of white-noise played at 1–5 points along transects that extended across the lek at 25-m intervals roughly parallel to the line of speakers. We calibrated white-noise measurements by measuring the noise level of both the white noise and either a representative clip of drilling noise or a semitrailer

10 m directly in front of each speaker. To minimize disturbance, we took propagation measurements during the day. Daytime ambient noise levels are typically 5–10 dBA higher than those in the early morning (J. L. Blickley and G. L. Patricelli, unpublished data) and are likely higher than those heard by birds at a lek.

After the experiment, we counted individuals on all leks 2–6 times from 1 March through 30 April 2009. In 2009 we continued to play noise on 2 experimental leks as part of a related experiment, so we did not include these lek pairs in our analysis of postexperiment male attendance at a lek.

Response Variables and Baseline Attendance Levels

Sage grouse leks are highly variable in size and, even within pairs, our leks varied up to 50% in size. To facilitate comparison of changes in attendance on leks of different sizes, we calculated the attendance relative to attendance levels before treatment (i.e., baseline attendance levels). We obtained male baseline abundance from the Wyoming Game and Fish Department. We used the standard lek-count protocol (Connelly et al. 2003) to count birds at leks approximately 3 times/breeding season. Due to the small number of counts in pre-experiment years, we calculated male baseline attendance by averaging the annual peak male attendance at each individual lek over 4 years (2002–2005). We assessed changes in early-, mid-, and late-season peak male attendance from this 4-year baseline attendance. Female attendance was highly variable throughout the season with a short (1–3 day) peak in attendance at each lek. Due to the limited number of annual counts, female counts from 2002 to 2005 were not reliable estimates of peak female attendance and could not be used as baseline attendance levels. Because we introduced noise to experimental leks after the peak in female attendance in 2006, we used maximum female counts from 2006 as a baseline for each of the 8 leks monitored that year. We assessed changes in annual peak female attendance from this 1-year baseline attendance. The 8 leks added to the experiment in 2007 were not included in statistical analyses of female attendance due to the lack of a baseline.

Statistical Analyses

We used an information-theoretic approach to evaluate the support for alternative candidate models (Table 2). All candidate models were linear mixed-effect models that assessed the relation between covariates and the proportional difference in annual and within-season peak attendance and baseline attendance (both males and female) (Tables 2 & 3). We ranked models on the basis of differences in Akaike's information criterion for small sample sizes (ΔAIC_c) (Burnham & Anderson 2002). Akaike weights (w_i) were computed for each model on the basis of ΔAIC_c scores. We calculated model-averaged variable coefficients, unconditional 95% CI, and variable importance (weight across models) for variables contained in models that were strongly supported ($\Delta AIC_c < 2$). All statistical analyses were performed in R (version 2.12.1) (R Development Team 2010).

Table 3. Mixed-effect candidate models used to assess change in peak annual attendance of female Greater Sage-Grouse at leks from pre-experiment baseline attendance in 2006 during noise playback.

Model[a]	K[b]	ΔAIC_c[c]	w_i[d]
Null, random effects only[e]	4	0	0.71
Treatment[e]	5	1.9	0.27
Treatment+experiment year	6	8	0.01
Treatment×experiment year	7	14	<0.001

[a] *All models contained pair and year as random effects. Due to the small sample size (4 pairs), pair type variable (road versus drilling) was not included in the model set. Covariates: treatment, lek treatment (noise or control assigned to individual leks within a pair); experiment year, years of experimental noise exposure.*

[b] *Number of parameters in the model.*

[c] *Difference in AIC_c (Akaike's information criterion for small sample size) values from the most strongly supported (lowest AICc) model.*

[d] *Akaike weight.*

[e] *Model with substantial support ($\Delta AIC_c < 2$).*

The detection probability for males and females is likely to vary across a season and among leks (Walsh et al. 2004). We sought to minimize sources of error and maximize detection by conducting frequent counts from locations with a clear view of the lek and by implementing a paired treatment design (each noise lek is compared with a similar control lek, monitored by the same observer on the same days). To ensure that detection probability did not differ among noise and control leks, we corrected our data for detection probability. First, we used detection error rates, estimated as difference between the maximum count and the count immediately before or after the maximum count within a day (for both males and females), and then we applied the bounded-count method (for males only; Walsh et al. 2004). With the multiple-count estimator, estimates of detection between noise and control leks did not differ (males: $t = 1.02$, df $= 6$, $p = 0.35$; females: $t = 0.21$, df $= 3$, $p = 0.84$). We analyzed both corrected and uncorrected counts and found that neither correction qualitatively changed our results; therefore, results are presented for uncorrected counts.

Results

Male Attendance

Peak male attendance at both types of noise leks decreased more than attendance at paired control leks, but the decreases varied by noise type. In the most strongly supported models of the candidate set ($w_i = 0.90$, all

Table 4. **Model-averaged parameter direction and effect sizes and variable importance for all variables present in strongly supported models ($\Delta AIC_c < 2$ in Table 2) of changes in peak attendance of male greater sage-grouse at leks from baseline attendance during experimental noise playback.**

Variable	*Percent effect size (SE)*	*Variable importance**
Intercept	31 (22)	1.0
Treatment, noise	−29 (7)	0.91
Type, road	33 (22)	0.91
Treatment, noise∗type, road	−40 (10)	0.91
Season, mid	18 (6)	0.66
Season, late	23 (6)	

**Variable importance is the summed weight of all models containing that variable.*

other models $\Delta AIC_c > 6.1$) (Table 2), there was an interaction of the effects of experimental treatment (control versus noise) and noise type (drilling versus road) on annual peak male attendance. At leks treated with road noise, decreases in annual peak male attendance were greater (73%), relative to paired controls, than at drilling noise leks (29%). As indicated by the effect size for the main effect of pair type, attendance at control leks paired with road noise leks was 33% greater relative to the baseline than control leks paired with drilling noise leks (Table 4). However, changes in attendance were compared within a pair to control for such differences. Male attendance increased over the course of a season, with 18% and 23% increases in peak male attendance in mid and late season from the early-season peaks, but seasonal increases were similar across noise and control leks (Table 4 & Fig. 2b).

There was no evidence that the effect of noise on attendance changed as years of exposure to noise increased. The models with substantial support did not contain a main effect of years of exposure or an interaction of years of exposure and treatment type (control versus noise) (Table 2). In spite of decreases in attendance throughout the experiment, peak male attendance exceeded baseline attendance on all leks in 2006, 13 leks in 2007, and 11 leks in 2008 (Table 4 & Fig. 2c). There was an increase in sage grouse abundance regionally in 2006 (Fig. 3).

After the experiment (2009), attendance at leks we experimentally exposed to drilling and road noise was lower relative to paired controls (Table 2). The model that included the treatment variable showed an effect size of −30% (across road and drilling noise leks) but had only moderate support ($\Delta AIC_c = 3.3$) relative to the null model.

Female Attendance

Peak female attendance at leks treated with noise in 2007 and 2008 decreased from the 2006 baseline, relative to control leks (Table 3). The most strongly supported model in the set was the null model; however, the model that included noise treatment was highly supported ($\Delta AIC_c < 2$). The effect size of noise treatment on female attendance was −48% (10% SE), which is similar to the effect of noise on male attendance averaged across both noise types (51%).

Discussion

Results of previous studies show abundance of Greater Sage-Grouse decreases when natural gas and coal-bed methane fields are developed (Holloran 2005; Walker et al. 2007; Doherty et al. 2008). Our results suggest that chronic noise may contribute to these decreases. Peak male attendance relative to the baseline was lower on noise leks than paired control leks, and the decrease was larger at road noise leks (73% decrease in abundance compared with paired controls) than drilling noise leks (29%; Fig. 3). These decreases were immediate and sustained. The effects of noise occurred in the first year of the study and were observed throughout the experiment, although patterns of male attendance within a season were similar at noise and control leks. Differences in male attendance between noise and control leks in the year after the experiment were not supported in the top models, which suggests attendance rebounded after noise ceased. However, the sample size for this analysis was small, and the effect size (30% average decreases in male attendance for both noise types) suggests a residual effect of noise.

There are 2 mechanisms by which noise may reduce male attendance. First, males on noise leks may have had higher mortality than males on control leks. Noise playback was not loud enough to cause direct injury to individuals, but mortality could be increased indirectly by noise playback if the sounds of predators (coyotes [*Canis latrans*] or Golden Eagles [*Aquila chrysaetos*]) were masked by noise. However, on-lek predation events were rare. We observed ≤1 predation event per lek per season during the experiment (observations of sage-grouse carcasses or feathers at a lek [J. L. Blickley, personal observation]). The cumulative effect of rare predation events would lead to a gradual decrease in attendance, rather than the rapid and sustained decrease we observed. Furthermore, experimental noise was likely too localized to substantially affect off-lek predation because noise levels decreased exponentially as distance to the speakers increased (Fig. 1b). To date, increased predation risk of adults due to anthropogenic noise has not been demonstrated in any species, but some species increase vigilance when exposed to noise, leaving less time for feeding, displaying, and other important behaviors (Quinn et al. 2006; Rabin et al. 2006). Noise may also affect off-lek mortality indirectly. For example, noise-stressed males may be more susceptible to disease due to a suppressed

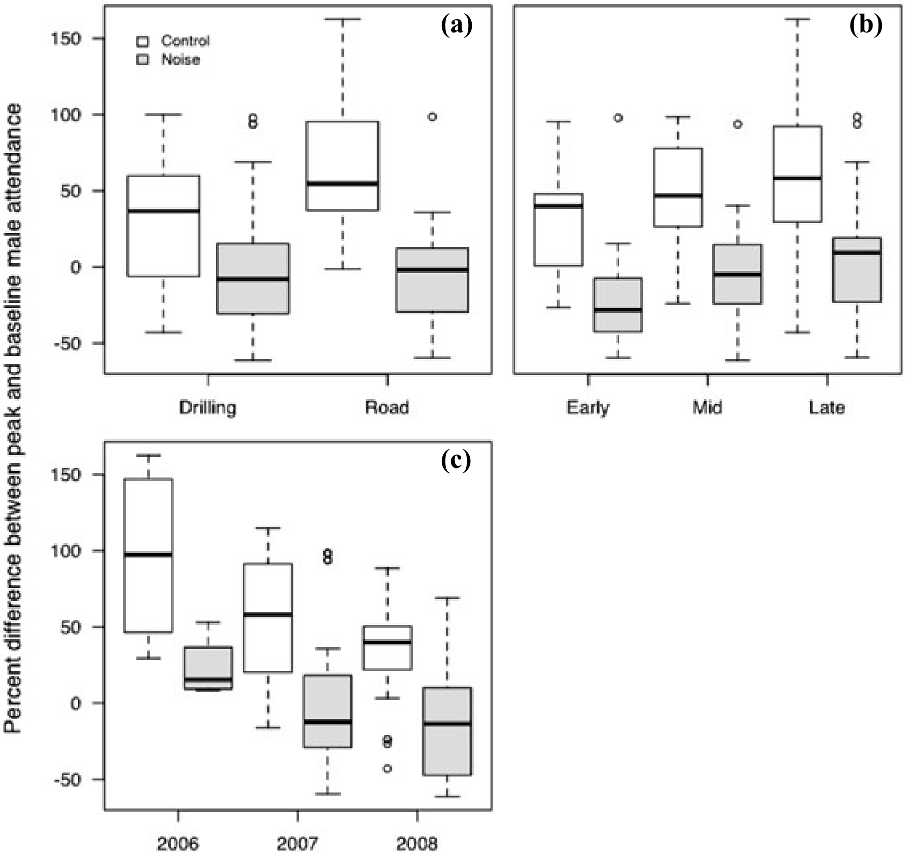

Figure 2. Percent difference between baseline attendance (i.e., abundance before experiments) of male Greater Sage-Grouse and (a) peak male attendance on control leks and leks treated with noise from natural gas drilling and road noise, (b) peak male attendance in the early (late February to 1 week prior to peak female attendance for that lek), mid (1 week before and after female peak [female peak ranged from 15 March to 6 April]), and late (starting 1 week after female peak) breeding season; on control leks and leks treated with noise, and (c) peak male attendance at control leks and leks treated with noise in experimental years 2006, 2007, and 2008 in Fremont County, Wyoming (U.S.A.) (horizontal lines, median value; box ends, upper and lower quartiles, whiskers, maximum and minimum values). Data are observed values, not model output.

immune response (Jankowski et al. 2010). Although long-term stress from noise is unlikely to be the primary cause of the rapid decreases in attendance we observed here, it may have been a contributing factor over the course of the experiment. Furthermore, in areas of dense industrial development, where noise is widespread, noise effects on mortality may be more likely.

Alternatively, noise may lower male attendance through displacement, which would occur if adult or juvenile males avoid leks with anthropogenic noise. Such behavioral shifts are consistent with the rapid decreases in attendance we observed. Adult male sage grouse typically exhibit high lek fidelity (Schroeder & Robb 2003) and visit leks regularly throughout the season, whereas juvenile males visit multiple leks and their attendance peaks late in the season (Kaiser 2006). If juveniles or adults avoid noise by visiting noisy leks less frequently or moving to quieter leks, overall attendance on noisy leks could be reduced. We could not reliably differentiate between juveniles and adults, so we do not know the relative proportion of adults and juveniles observed. Consistent with displacement due to noise avoidance, radio-collared juvenile males avoid leks near deep natural gas developments in Pinedale, Wyoming, which has resulted in decreases in attendance at leks in close proximity to development and increased attendance at nearby leks with less human activity (Kaiser 2006; Holloran et al. 2010). Reduced recruitment of juvenile males is unlikely to be the only driver of the patterns we observed because we did not observe larger decreases in lek attendance on noise-treated leks later in the season, when juvenile attendance peaks. Rather, we found immediate decreases in attendance early in the season when playback began (Fig. 2b), at which time there are few juveniles on the lek. This

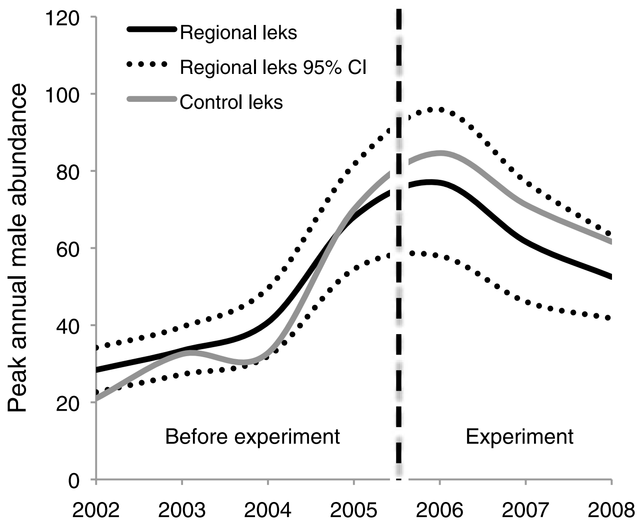

*Figure 3. Maximum abundance of male Greater Sage-Grouse from 2002 to 2008 at control leks (*n = 8*) (no anthropogenic sound played) and other leks in the region that were not part of the experiment (regional leks) (*n = 38*).*

is consistent with both adult and juvenile noise avoidance. We did not find evidence for a cumulative negative effect of noise on lek attendance, although cumulative effects may have been masked by regional population declines after 2006, a year of unusually high abundance (Fig. 3).

Female attendance at leks treated with noise was lower than that on control leks; however, the null model and the model that included noise treatment were both highly supported, providing only moderate support for the effects on noise on attendance. For this model, the overall estimated effect of noise on female attendance (−48%) was similar to that of the effect of noise on male attendance. Due to the high variability of female daily maximum attendance throughout the season and small sample size for this analysis (female attendance data available for only 4 of the 8 lek pairs), our statistical power to detect differences in female attendance was limited and effect sizes may not be representative of actual noise effects.

Our results suggest that males and possibly females avoid leks exposed to anthropogenic noise. A potential cause of avoidance is the masking of communication. Masked communication is hypothesized to cause decreases in abundance of some animal species in urban and other noisy areas. For example, bird species with low-frequency vocalizations are more likely to have low abundance or be absent from natural gas developments, roads, and urban areas than species with high-frequency vocalizations, which suggests that masking is the mechanism associated with differences in abundance (Rheindt 2003; Francis et al. 2009; Hu & Cardoso 2010). Sage-grouse may be particularly vulnerable to masked communication because their low-frequency vocalizations are likely to be masked by most sources of anthropogenic noise, including the noises we played in our experiment (Supporting Information). This may be particularly important for females if they cannot use acoustic cues to find leks or assess displaying males in noisy areas.

Alternatively, individuals may avoid noisy sites if noise is annoying or stressful, particularly if this noise is associated with danger (Wright et al. 2007). Intermittent road noise was associated with lower relative lek attendance than continuous drilling noise, in spite of the overall higher mean noise levels and greater masking potential at leks treated with drilling noise (Supporting Information). Due to the presence of roads in our study area, sage grouse may have associated road noise with potentially dangerous vehicular traffic and thus avoided traffic-noise leks more than drilling-noise leks. Alternatively, the pattern of decrease may indicate that an irregular noise is more disturbing to sage grouse than a relatively continuous noise. Regardless, our results suggest that average noise level alone is not a good predictor of the effects of noise (Slabbekoorn & Ripmeester 2008) and that species can respond differently to different types of noise.

Our results cannot be used to estimate the quantitative contribution of noise alone to observed decreases in Greater Sage-Grouse abundance at energy development sites because our experimental design may have led us to underestimate or overestimate the magnitude of these effects. Decreases in abundance due to noise could be overestimated in our study if adults and juveniles are displaced from noise leks and move to nearby control leks, which would have increased the difference in abundance between paired leks. Similar displacement occurs in areas of energy development, but over a much larger extent than is likely to have occurred in response to localized playbacks in our experiment (Holloran et al. 2010).

In contrast, we could have underestimated noise effects if there were synergistic effects of noise and other disturbances associated with energy development. For example, birds with increased stress levels due to poor forage quality may have lower tolerance for noise-induced stress, or vice versa. Noise in our experiment was localized to the immediate lek area and only played during the breeding season, so we cannot quantify the effects of noise on wintering, nesting, or foraging birds. Noise at energy development sites is less seasonal and more widespread than noise introduced in this study and may thus affect birds at all life stages and have a potentially greater effect on lek attendance. Leks do not represent discrete populations; therefore, local decreases in lek attendance do not necessarily reflect population-level decreases in abundance. However, at large energy development sites, similar displacement of Greater Sage-Grouse away from the ubiquitous noise may result in population-level declines due to spatially extensive changes in land use or increases in dispersal-related and density-dependent sources of mortality (Aldridge & Boyce 2007). Enforcement and refinement of existing seasonal restrictions on human activity could potentially reduce these effects.

We focused on the effect of noise associated with deep natural gas and coal-bed methane development on sage grouse, but our results may increase broader understanding of the effects of noise on animals. Both intermittent and constant noise from energy development affected sage grouse. Other noise sources with similar frequency range and temporal pattern, such as wind turbines, oil-drilling rigs, and mines, may have comparable effects. Similar effects may also be associated with highways, off-road vehicles, and urbanization so that the potential for noise to have an effect is large.

We believe that noise should be investigated as one potential cause of population declines in other lekking North American grouse species that are exposed to similar anthropogenic development. Populations of many bird (van der Zande et al. 1980; Rheindt 2003; Ingelfinger & Anderson 2004) and mammal (Forman & Deblinger 2000; Sawyer et al. 2009) species have been shown to decrease in abundance in response to road, urban, and energy development, and noise produced by these activities may contribute to these decreases. Our results also demonstrate that wild animals may respond differently to chronic intermittent and continuous noise, a comparison that should be expanded to other species. Additionally, we think these results highlight that experimental noise playbacks may be useful in assessing the response of wild animals to chronic noise (Blickley & Patricelli 2010).

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Supporting Information

Spectrograms and power spectrums of drilling noise, road noise and male sage-grouse vocal display (Appendix S1), map of experimental and control leks (Appendix S2), and noise playback levels on experimental leks (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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