CHAPTER 3
POTENTIAL ACOUSTIC MASKING OF GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) DISPLAY COMPONENTS BY CHRONIC INDUSTRIAL NOISE

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Abstract.—Anthropogenic noise can limit the ability of birds to communicate by masking their acoustic signals. Masking, which reduces the distance over which the signal can be perceived by a receiver, is frequency dependent, so the different notes of a single song may be masked to different degrees. We analyzed the individual notes of mating vocalizations produced by Greater Sage-Grouse (*Centrocercus urophasianus*) and noise from natural gas infrastructure to quantify the potential for such noise to mask Greater Sage-Grouse vocalizations over both long and short distances. We found that noise produced by natural gas infrastructure was dominated by low frequencies, with substantial overlap in frequency with Greater Sage-Grouse acoustic displays. Such overlap predicted substantial masking, reducing the active space of detection and discrimination of all vocalization components, and particularly affecting low-frequency and low-amplitude notes. Such masking could increase the difficulty of mate assessment for lekking Greater Sage-Grouse. We discuss these results in relation to current stipulations that limit the proximity of natural gas infrastructure to leks of this species on some federal lands in the United States. Significant impacts to Greater Sage-Grouse populations have been measured at noise levels that predict little or no masking. Thus, masking is not likely to be the only mechanism of noise impact on this species, and masking analyses should therefore be used in combination with other methods to evaluate stipulations and predict the effects of noise exposure.

Key words: acoustic masking, *Centrocercus urophasianus*, Greater Sage-Grouse, industrial noise.

Enmascaramiento Acústico Potencial de Mayor Sage-Grouse (*Centrocercus urophasianus*) Mostrar Componentes por Ruido Industrial Crónica

Resumen.— Antropógena ruido puede limitar la capacidad de las aves para comunicarse por enmascarar sus señales acústicas. Enmascaramiento, que reduce la distancia sobre la que se puede percibir la señal por un receptor, es frecuencia dependiente, por lo que las diferentes notas de una canción pueden enmascararse en diferentes grados. Analizamos las notas individuales de apareamiento vocalizaciones producidas por mayor Sage-Grouse (Centrocercus urophasianus) y el ruido de infraestructura de gas natural para cuantificar el potencial de tal ruido a vocalizaciones de mayor Sage-urogallo de máscara en distancias cortas y largas. Hemos encontrado que ruido producido por la infraestructura de gas natural fue dominado por las frecuencias bajas, con considerable superposición en frecuencia con pantallas acústicas de mayor Sage-urogallo. Tal superposición predijo enmascaramiento sustancial, reduciendo el espacio activo de detección y discriminación de todos los componentes de vocalización y que afectan particularmente a notas de baja frecuencia y baja amplitud. Estas máscaras podrían aumentar la dificultad de evaluación de mate para lekking mayor Sage-urogallo. Analizaremos estos resultados en relación con las actuales disposiciones que limitan la proximidad de la infraestructura de gas natural a leks de esta especie en algunas tierras federales en los Estados Unidos. Impactos

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significativos a las poblaciones de mayor Sage-urogallo han sido medidos en los niveles de ruido que predicen el enmascaramiento de poca o ninguna. Así, enmascaramiento no es probable que sea el único mecanismo de impacto de ruido en esta especie, y enmascaramiento análisis debe por lo tanto, utilizarse en combinación con otros métodos para evaluar las estipulaciones y predecir los efectos de la exposición al ruido. Así, enmascaramiento no es probable que sea el único mecanismo de impacto de ruido en esta especie, y enmascaramiento análisis debe por lo tanto, utilizarse en combinación con otros métodos para evaluar las estipulaciones y predecir los efectos de la exposición al ruido.

Birds use acoustic signals to communicate with conspecifics for a host of biologically important functions, including mate attraction, territory defense, parent–offspring communication, and predator avoidance. In order for this communication to be successful, the signal must travel from the signaler to the receiver through the local environment. The local physical and acoustic environment, therefore, plays an important role in determining the active space of a signal, the area in which a receiver can successfully perceive it (Brenowitz 1982, Dooling et al. 2009). Background noise, a conspicuous feature of most natural environments, can result in acoustic masking if this noise is loud in relation to the signal of interest. Animals have numerous acoustic and behavioral adaptations to maximize the active space of their signals in the presence of natural background noise. For example, the structural and temporal properties of many acoustic signals appear to be adapted to maximize the propagation distance and minimize masking from abiotic and biotic noise sources in the environment (Marten and Marler 1977, Wiley and Richards 1982, Ryan and Brenowitz 1985, Brumm 2006). However, the spread of humans into natural landscapes has resulted in the proliferation of anthropogenic noise sources, with the potential to affect many of the animal species that live and communicate in these environments (Barber et al. 2010). Acoustic signals that are adapted to deal with natural noise sources may still be susceptible to masking from anthropogenic noise sources if the anthropogenic noise differs enough from natural noise sources in frequency, duration, or daily or seasonal pattern.

Effective communication requires that a receiver be able to detect a given signal, discriminate that signal from other possible signals, and recognize features that may convey information about the specific signaler. The active space of a signal may be different for each of these receiver tasks (Lohr et al. 2003). Detection provides the receiver with the lowest level of information—simply that a signal is present—and requires the lowest contrast between the signal and background noise. For a signal to be successfully detected in a noisy environment requires that the ratio of the signal to the background noise (i.e., signal-to-noise ratio [SNR], the difference between signal and noise amplitudes measured in decibels) within a frequency band exceed a critical detection threshold (Klump 1996). The critical detection threshold for a "typical bird" ranges from 18 dB to 37 dB across frequency bands. Discrimination of the signal from other signals, as would be required to identify the species of the sender or the functional category of the signal, requires a higher SNR than detection. In a laboratory study of two bird species, Lohr et al. (2003) found that discrimination of conspecific song required an SNR approximately 3 dB higher than the levels required for detection. An even more challenging task for a receiver is signal recognition, discerning variation among signals within a category, such as information about individual identity or reproductive quality. For example, receivers may use the acoustic features of the signal such as frequency structure, relative amplitude of notes, and note duration to recognize the identity of the signaling individual. Signal recognition may require an even higher SNR (Dooling and Popper 2007); however, we do not yet know how much higher the signal must be for recognition to occur.

The fitness consequences of being able to detect a signal versus discriminate or recognize a signal is likely to be signal specific. For example, a predator alert call, which functions to alert a conspecific to danger, may be effective so long as it exceeds the critical ratio for detection. However, a mate-attraction call that is used by females to assess the quality of a potential mate may need to exceed the critical recognition threshold in order to be effective. For example, the ability to recognize individual signals is critical to mate choice in the Swamp Sparrow (*Melospiza georgiana*): females use song features such as trill rate and frequency bandwidth to assess the quality of potential mates (Ballentine et al. 2004). Introduced

noise has been demonstrated to weaken pair bonds in captive Zebra Finches (*Taeniopygia guttata*; Swaddle and Page 2007), which suggests that reduced recognition can have fitness consequences.

Active space can vary within a given signal as well as among signals. Many bird vocalizations are highly complex and are composed of multiple acoustic components (bouts, phrases, syllables, or notes). Some multicomponent signals may encode either distinct ("multiple messages hypothesis") or redundant ("redundancy hypothesis") information about the signaler (Møller and Pomiankowski 1993, Hebets and Papaj 2005). For example, the trill note and note complex of White-crowned Sparrow (*Zonotrichia leucophrys*) song each convey distinct information about dialect and individual identity, respectively (Nelson and Poesel 2007). Each component can vary in frequency structure, duration, and relative amplitude; these factors interact with the local physical and acoustic environment to determine the active space of the signal component (Patricelli et al. 2008). The result of this variation is that each component of a complex vocalization may have a different active space and be uniquely susceptible to masking by a given noise source.

Anthropogenic noise is typically dominated by low frequencies, so low-frequency signal components and features are most susceptible to masking (Brumm and Slabbekoorn 2005, Slabbekoorn and Ripmeester 2008). Even if a signal is not completely masked, low-frequency background noise could distort a signal, resulting in a higher-frequency note being perceived as having higher relative amplitude than a masked lower-frequency note. Such distortion could result in increased difficulty in assessment or identification.

Our focal species, the Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-gouse"), is a medium-bodied gallinaceous bird that has long been used as a model system for studies of sexual selection and communication (Wiley 1973; Gibson 1989, 1996). During the breeding season, males gather on strutting grounds (leks) where they establish small display territories that are visited by females for courtship. Males produce a complex visual and acoustic display. Sound is critical to the breeding system on both large and small spatial scales because females use the acoustic component of the display to locate strutting males and, once on a lek, to select a male (Gibson 1989, 1996; Patricelli and Krakauer 2010).

The sage-grouse vocal display is composed of three major note types: a series of low-frequency "coo" notes, two broadband "pops," and a frequency-modulated "whistle" (Fig. 1). The rate of display (strut rate) is positively correlated with male success in mating (Gibson and Bradbury 1985, Gibson 1996, Patricelli and Krakauer 2010). In addition, the time interval between the two pop notes during which the whistle note occurs, the inter-pop interval (IPI), is positively correlated with mating success (Gibson et al. 1991, Gibson 1996). This suggests that assessment of the two pop notes might be particularly critical in female mating decisions. Whistles may also be important in female choice. Gibson and Bradbury (1985) found that the time interval from the first pop to the whistle peak as well as the maximum frequency of the whistle at the apex are related to male mating success. Female sage-grouse also may assess amplitude of the whistle; unpublished results suggest that whistle amplitude may be positively correlated with mating success (J. W. Bradbury pers. comm.), and males orient during courtship so that the highly directional whistle is beamed toward females (Dantzker et al. 1999). This female preference for male-display quantity
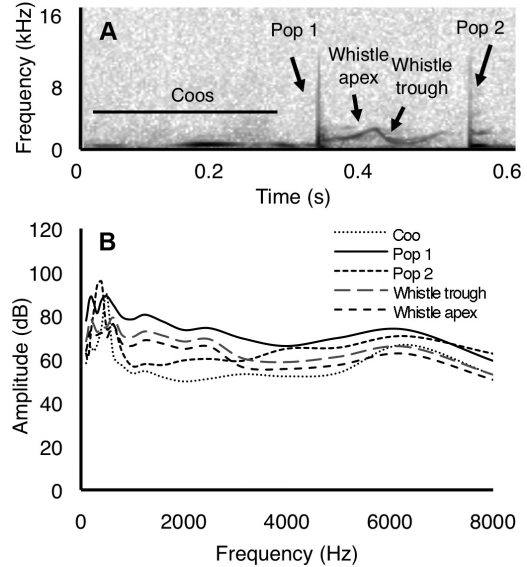

Fig. 1. Spectrogram and (B) power spectra of a male Greater Sage-Grouse strut display with distinct display components labeled. Low-frequency coos are followed by a broadband pop (pop 1), a frequency-modulated whistle with an apex of ~2,500 Hz (whistle apex) and a minimum of ~630 Hz (whistle trough), and another broadband pop (pop 2).

and quality suggests that masking of one or all of these notes by background noise may negatively affect a female's ability to assess males on the lek.

Sage-grouse populations are declining across their range (Connelly et al. 2004, Garton et al. 2011), leading sage-grouse to be listed as endangered under Canada's Species at Risk Act and designated as a candidate species for listing in the United States under the federal Endangered Species Act. Natural gas development has expanded rapidly over the past decade and has been implicated in contributing to population declines (Holloran 2005, Walker et al. 2007, Copeland et al. 2009, Holloran et al. 2010). In particular, noise associated with energy development has been demonstrated to result in reduced attendance on leks (Blickley et al. 2012) and is associated with increased stress hormones in males on noisy leks (J. L. Blickley and G. L. Patricelli unpubl. data). Masked communication has been suggested as a mechanism of this impact, so understanding the potential for introduced noise sources to mask signals used in mating could lead to improved management of vulnerable sage-grouse populations.

The present study addresses the potential for noise pollution from natural gas development to mask or distort acoustic signals that are used in breeding by sage-grouse. We analyzed the individual acoustic components of sage-grouse vocalizations (Fig. 1) and noise from natural gas infrastructure (a compressor station, generator, and drilling rig; Fig. 2) to quantify the potential for such noise to mask sage-grouse vocalizations over both long and short distances. We compared the effect of such noise on the level of both detection and discrimination and discuss the utility of this approach for predicting the impacts of noise on this and other species. For the masking analysis, we focused primarily on noise measurements at 75 m and 400 m (~1/4 mile), which represent a typical distance to the edge of surface disturbance (the pad) from a compressor station or drilling rig and the distance stipulated as the minimum surface-disturbance buffer around leks in our study region, respectively (Bureau of Land Management 2008).

Methods

Field recordings and measurements.—Between 1 and 5 May 2010, we collected field recordings and vocal amplitude measurements from adult male sage-grouse on Preacher Reservoir lek
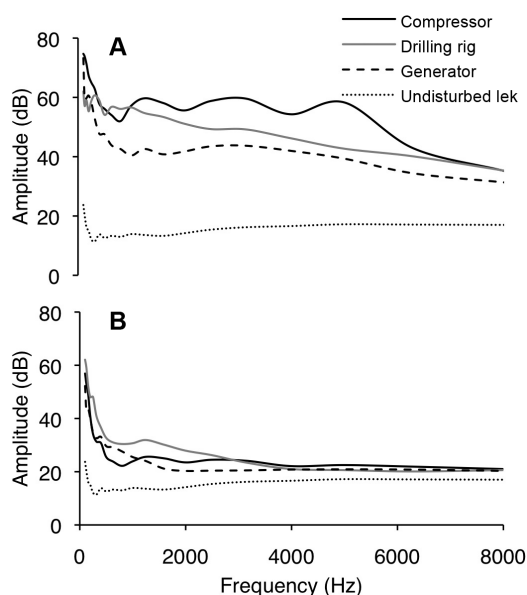

Fig. 2. Power spectra of ambient noise levels at (A) 75 m and (B) 400 m from a natural gas compressor station, natural gas drilling rig, and generator in Sublette County, Wyoming, and on an undisturbed lek (quiet) in Fremont County, Wyoming. Values were interpolated if a measurement for that distance was not available. Noise was dominated by low frequencies at both short and medium distances from the source.

(42°53.597′N, 108°28.417′W) in Fremont County, Wyoming. Recordings and amplitude measurements were collected simultaneously from a blind on the lek using a handheld Larson Davis 824 sound level meter (software version 3.12) using the logging function with a time-history resolution of 1/32 s and an amplitude resolution of 0.1 dB. A Marantz PMD670 portable solid-state recorder continuously recorded the audio stream from the SPL meter (through the AC/DC output) at 16-bit linear PCM format at 44.1 kHz. Each sound level measurement started prior to the initiation of a display by an individual male. The SPL meter measured and logged the average and peak amplitude in unweighted decibels (dB) at each time interval (0.03 s). Immediately after the vocalization was recorded, the distance between the vocalizing bird and the microphone was measured with a range finder (Leupold RX750). Sage-grouse strut displays are highly directional (Dantzker et al. 1999), so the orientation of the bird and distance to the microphone were also noted for each display measured. We used only high-quality and comparable measurements

in the analysis, including only vocalizations that we recorded from individuals in a small range of orientations and at similar distances in relation to the microphone. All vocalizations included in the analysis were from individuals with side-facing orientations ranging from 30 to 90 degrees (if zero degrees reflects an orientation with the bird directly facing the observer). We did not use recordings if there was temporal overlap with other strutting males or background noises, such as songbirds. Because of the difficulty of obtaining such recordings, a total of only 6 vocalizations, collected from 2 individuals (2 from one male, 4 from the other), were used in the final analysis.

Ambient noise levels were measured on Chugwater Reservoir lek (42°47.192′N, 108°26.292′W), a lek with little human disturbance in Fremont County, Wyoming. Noise was quantified as a 2-min L_{eq} (equivalent sound pressure level); this is a type of average, defined as the equivalent steady sound level that would produce the energetic equivalent of the actual fluctuating sound levels over the defined 2-min period. The sound level meter calculated an overall L_{eq} for the noise level as well as the 2-min L_{eq} for each 1/3-octave band frequency, which was used for SNR analysis (see below). Ambient measurements were made after lekking in the morning. Ambient noise levels tend to be slightly higher during this time than during the lekking hours (J. L. Blickley and G. L. Patricelli unpubl. data), so this measure is a slight overestimate of ambient levels on an undisturbed lek, leading to a slight underestimate of masking on disturbed leks.

Sound level measurements were made on a large compressor station (Falcon Compressor, which consisted of two Ariel JGC-4 compressors driven by 3,500-HP engines; 42°31.319′N, 109°40.271′W) and a deep natural-gas drilling rig (Questar Drilling Rig no. 232; 42°43.501′N, 109°50.876′W) on the Pinedale Anticline Project Area in Sublette County, Wyoming, and at a generator (East Litton Generator, a 300-kW MQ Power diesel generator powered by a Volvo engine; 43°31.501′N, 105°25.573′W) in the Powder River Basin, Campbell County, Wyoming. These noise sources are all commonly found in areas of natural gas development and typically operate 24 h day–1, year round. Noise was measured along one transect extending from each noise source. Noise measurements were taken at points 75, 200, 300, and 400 m from the Falcon Compressor; at points 8, 16, 32, 64, 128, 256, and 512 m

from the East Litton Generator; and at points 75 and 400 m from the Questar Drilling Rig. At each point, distance from the source was measured with a laser range finder (Bushnell Yardage Pro). Noise levels were measured using a Larson Davis 824 sound level meter. During measurements, the sound level meter was held 25 cm from the ground, similar to the height of a grouse. The sound level meter calculated an overall L_{eq} for the noise level as well as the 2-min L_{eq} for each 1/3-octave band frequency. Noise levels are reported in unweighted decibels (reported as dB) re 20 µPa because an unweighted measure of amplitude is required for the estimation of masking potential; A-weighted values (dB[A]) are also presented for comparison. All noise measurements were made in the early morning, before the wind rose to detectable levels. Because of the similarity of noise from each of these sources (see Fig. 2), only noise measurements from the Falcon Compressor were used in the masking analysis; results from other noise sources should be very similar. Noise levels were estimated at distances >400 m from Falcon Compressor using NMSIM software (Wyle Laboratories, Arlington, Virginia). NMSIM generates spatially explicit estimates of noise propagation utilizing input topography, ground impedance, and source spectra. We developed a custom source spectrum for Falcon Compressor using noise measurements from transect data and modeled propagation from the source across flat and open ground using a topographic layer from a location at similar elevation to our study site at 200 rayls ground impedance and –1.1°C air temperature. We used NMSim to estimate the noise spectra at receiver points placed along a transect extending from the source.

Sound analysis.—Individual vocalizations were identified from a spectrogram of the field recording using RAVEN, version 1.3 beta (Cornell Lab of Ornithology, Ithaca, New York; Hann window function, FFT = 512 with 50% overlap). Audio recordings were synchronized with SPL measurements by identifying distinctive high-frequency device noise produced by the SPL meter with the initiation of the measurement; this allowed us to identify the 1/32-s sample(s) in the SPL-meter output that corresponds to each note on the spectrogram and measure the overall amplitude of that note. Each vocalization was then extracted and low-pass filtered at 8.0 KHz to exclude this device noise. For each vocalization, the amplitude of the 1/3-octave band frequencies was

measured at intervals of 0.004 s using SPECTRA-PLUS (Pioneer Hill Software, Poulsbo, Washington). Call components were identified in the audio recordings in RAVEN and matched with the corresponding overall amplitude measurement from synchronized SPL measurement data. The absolute amplitude of each component was calibrated using the equation

$$\text{Peak dB} = \sum 10^{(aX/10)}$$

where a represents a scaling factor and X represents the average amplitude for each 1/3-octave band frequency. By adjusting the value of the scaling factor, we could adjust the overall average amplitude (dB) of the vocalization while maintaining the same relative power at each frequency band. The scaling factor was adjusted to yield different overall average amplitudes (dB) for each vocalization for analysis of masking potential at different source levels. Frequency-specific amplitudes for each call component were averaged across vocalizations.

In order to determine the masking potential of the noise sources at different distances from the vocalizing bird and the noise source, SNRs were calculated for each vocalization by subtracting the average amplitude (dB) for 1/3-octave band frequencies of noise sources (taken from 2-min L_{eq} measurements; see above) from the average amplitude (dB) for 1/3-octave band frequencies of vocalizations as measured in SPECTRAPLUS. Each note of the sage-grouse vocalizations was calibrated to absolute amplitude measures made using the SPL meter (see above). We calculated the expected amplitude of the vocalization at distances 2, 4, 8, 16, 32, 64, and 128 m from the vocalizing bird, based on a 6-dB decrease in amplitude for every doubling of distance due to spherical spreading and frequency-specific rate of excess attenuation. Excess attenuation is attenuation caused by propagation of sound through the environment and is determined by habitat characteristics (e.g., groundcover, temperature) and distance of the vocalizing bird from the ground. To model propagation of vocalizations, we estimated frequency-specific rates of excess attenuation by comparing the overall rate of sound attenuation measured along noise transects with predicted amplitude loss due to spherical spreading alone. These estimated amplitudes were used to scale the vocalizations (see scaling equation above), in order to calculate the SNR for the

maximum SNR frequency at different distances from the bird and from the noise source. Vocalizations were defined as "masked" if the SNR of the peak SNR frequency did not exceed the minimum threshold (critical ratio) for detection or discrimination (Dooling 2002, Lohr et al. 2003). Minimum masked distance was used to estimate the maximum detection or discrimination distance (active space). Estimates of sage-grouse critical ratios for detection were drawn from the average critical ratios for detection of 15 bird species, the only ones that have been measured to date (Dooling 2002), and ranged from 22 dB at 400–630 Hz to 27 dB at 2,500 Hz. The critical ratios for discrimination at each frequency band were estimated to be 3 dB higher than the critical ratio for detection in that band (Lohr et al. 2003). The critical ratios for detection and discrimination have not been measured specifically for sage-grouse, but there is relatively little variation in hearing abilities among bird species tested thus far, so estimates of the critical ratio are likely to be accurate to within 5 dB (Dooling 2002). All results are presented ± SE unless otherwise noted.

Results

Noise measurements.—Noise produced by Falcon Compressor was 48.9 dB louder than ambient levels at an undisturbed lek at a distance of 75 m from the source and 34.2 dB louder than ambient at a distance of 400 m (Table 1). Noise produced by the Questar Drilling Rig was 43.5 dB louder than ambient levels at a distance of 75 m from the source and 31.8 dB louder than ambient at a distance of 400 m. Noise produced by East Litton Generator was 24.9 dB louder than ambient levels at a distance of 75 m from the source and 18.4 dB louder than ambient at a distance of 400 m (Table 1). The noise produced by all noise sources was dominated by low frequencies (Fig. 2).

Vocalization measurements.—Individual components of the sage-grouse vocal display varied in amplitude and peak frequency (the frequency at which amplitude was the highest; Table 2). The pop 1 and pop 2 components had the highest peak amplitudes, with measures of 96 ± 2.1 and 98 ± 1.6 dB at 1 m, respectively. The coo components had an overall peak amplitude of 94 ± 1.3 dB at 1 m. The whistle component, by far the quietest component, had a peak amplitude of 84 ± 0.9 dB for the whistle trough (lowest frequency of the whistle component) and 82 ± 1.5 dB for the

TABLE 1. Overall noise levels (2-min L_{eq} measurements) measured along a transect extending from Falcon Compressor in Sublette County, Wyoming. For comparison, values from an undisturbed lek of Greater Sage-Grouse after the birds departed in late morning are also included (Chugwater Reservoir lek in Fremont County, Wyoming).

Distance	Amplitude (dB[F])	Amplitude (dB[A])
75 m	89.4	70.4
200 m	82.8	58.1
300 m	77.9	52.9
400 m	74.7	47.7
Undisturbed lek (quiet)	40.5	30.5

whistle apex (highest frequency of the whistle component) at 1 m. All vocal components had peak frequencies (400–630 Hz) overlapping with noise produced by natural gas infrastructure, except the apex of the frequency-modulated whistle, which had a peak frequency (2,500 Hz) above most of the noise.

Masking analysis.—We estimated the masking potential of compressor noise for five components of the sage-grouse vocalization: the coos, pop 1, pop 2, whistle trough, and whistle apex. Across all conditions modeled, the maximum detection and discrimination distance (i.e., the active space) for the highest-amplitude frequency band was greatest for the pop 2 component, the loudest note of the display. Overall amplitude of the note was not necessarily an indicator of greater active space—the coo component had a greater maximum detection distance than the pop 1 component (Fig. 3) despite lower overall amplitude, due to the higher amplitude of the maximum frequency. Active space of detection and discrimination for all components was substantially reduced at the noise levels found within 400 m of the compressor station in relation to the ambient conditions on an undisturbed lek (Fig. 3). At 75 m from the noise source, the maximum detection distance and maximum discrimination distance were reduced by 97% and 98%, respectively, for the coo; by 98% and 98% for pop 1; by 97% and 97% for pop 2; by 98% and 98% for the whistle trough; and by 100% and 100% for the whistle apex, in relation to the maximum distances on an undisturbed lek. At 400 m from the noise source, the maximum detection distance and maximum discrimination distance were reduced by 59% and 65%, respectively, for the coo; by 48% and 47% for pop 1; by 59% and 63% for pop 2; by 54% and 57% for the whistle trough; and by 64% and 58% for the whistle apex, in relation to the maximum distances on an undisturbed lek.

The distance from the source at which the active space for detection and discrimination were equal to that in ambient conditions (i.e., the maximum active space) varied for each component. The whistle apex reached maximum active space at 600 m from the noise source. The whistle trough reached maximum active space at 700 m from the source, whereas the coo and pop 1 required a minimum of 700 m from the source before they reached maximum active space. Pop 2 did not reach maximum active space until a minimum of 1,000 m from the noise source.

The SNR varied across frequencies for each component. Peak frequencies for coos, pops, and the whistle trough were relatively low (<1,000 Hz), leading to high overlap with the low-frequency noise produced by the Falcon Compressor and other natural gas infrastructure (Figs. 2 and 4). The SNR was substantially reduced at low frequencies at both short and medium distances to the compressor in relation to quiet lek conditions for all components (Fig. 4). For the whistle, coo, and pop 2 components, the frequency with the peak SNR remained the same under all noise conditions, indicating that no signal distortion would be expected. For the pop 1 component, the frequency with the peak SNR differed under different noise conditions, shifting from 400 Hz under quiet

TABLE 2. Amplitude and frequency characteristics of Greater Sage-Grouse vocalizations recorded in Fremont County, Wyoming. Measurements are normalized to 1 m from the source.

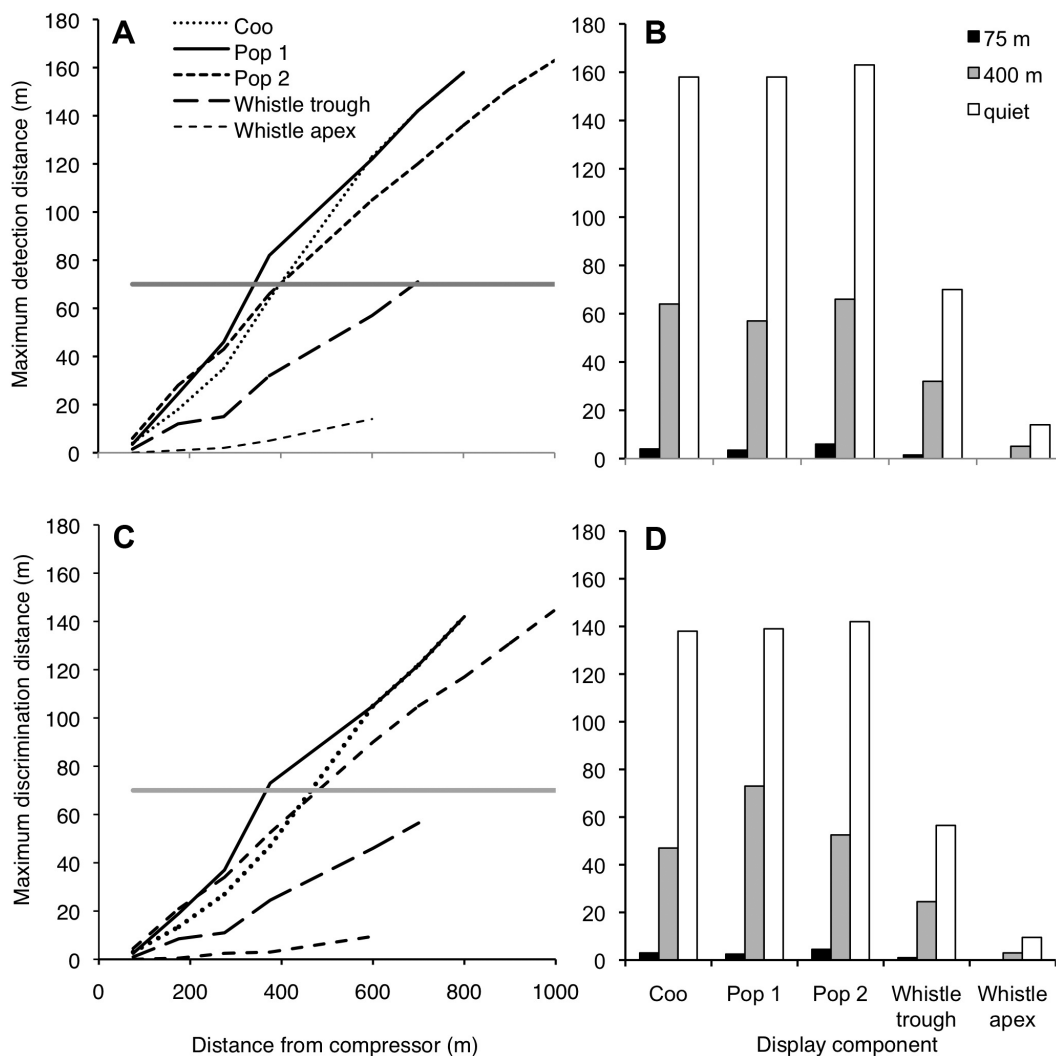| Note	Peak amplitude (dB)	Peak amplitude range (dB)	Frequency range (Hz)	Peak frequency (Hz, ⅓-octave band)
Coo	94 ± 1.3	89–98	100–800	500
Pop 1	96 ± 2.1	87–99	100–10,500	500
Pop 2	98 ± 1.6	90–100	100–11,500	400
Whistle apex	82 ± 1.3	76–87	2,200–2,600	2,500
Whistle trough	84 ± 0.9	81–87	450–800	630

Fig. 3. Maximum (A) detection and (C) discrimination distance of Greater Sage-Grouse strut display components at varying distances from a natural gas compressor station. Gray solid line represents half the length of a typical lek in Fremont County, Wyoming. Lines end at the point where the active space is equal to that under quiet ambient conditions. Maximum (B) detection and (D) discrimination distance of vocalization components at points 75 and 400 m from a natural gas compressor station and under quiet ambient conditions.

conditions to 500 Hz in noisy conditions (Fig. 4B), potentially causing distortion of the signal.

Discussion

We assessed the potential impact of anthropogenic noise on the transmission of sage-grouse vocalizations used for mate attraction (Wiley 1973; Gibson 1989, 1996; Patricelli and Krakauer 2010). Our results indicate that there are marked differences in the active space of individual notes

of the sage-grouse acoustic display, both in noisy and quiet conditions. These differences in active space are primarily determined by the frequency structure and amplitude of the different notes of the sage-grouse vocalization, and by differences in the amplitude of the background noise. These factors and their effects on the active space for detection and discrimination are discussed below.

Frequency structure.—The active space of a vocalization is determined, in part, by the frequency structure—including peak frequency and
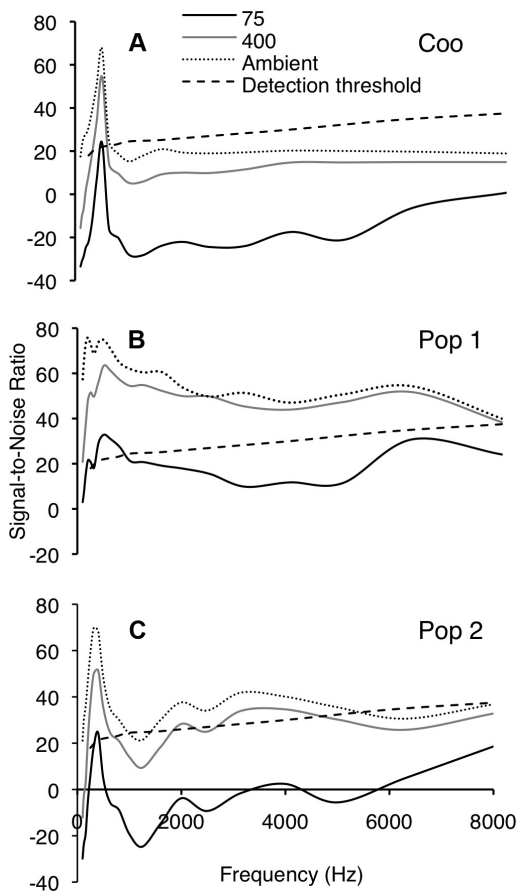
FIG. 4. Signal-to-noise ratio (SNR) of Greater Sage-Grouse acoustic display components (A) coo, (B) pop 1, and (C) pop 2 at a distance of 5 m from the vocalizing male (average close courtship distance) in ambient noise conditions measured 75 and 400 m from a natural gas compressor and on an undisturbed lek. Frequencies with an SNR that exceed the critical ratio for detection (dashed line) can be detected by a receiver. For pop 1, the frequency with the highest SNR is different in noisy and quiet environments, potentially leading to distortion of the vocalization.

frequency range—of both the acoustic signal and the background noise (Lohr et al. 2003). Both of these measures of frequency structure differed among the notes of the sage-grouse display vocalization. Notes with low peak frequencies (the coos, pops, and whistle trough) had high overlap with the noise produced by the Falcon Compressor and other natural gas infrastructure (Figs. 2 and 4), leading to predictions of a substantial reduction in active space of detection and discrimination for these notes in noisy conditions (Fig. 2).

The whistle apex had a peak frequency above most of the compressor noise energy, but was still masked because of its lower source amplitude, as discussed below.

The frequency range of a note is also important in determining the degree of overlap with background noise. The coo note of the sage-grouse display is tonal and has a very small frequency range, so the entire note is likely to be masked by low-frequency noise (Fig. 4A). For notes with a broad frequency range, like the broadband pops and the frequency-modulated whistle, some of the higher-frequency energy of the signal is likely to be detectable above background noise that is predominantly low frequency. However, higher frequencies suffer greater attenuation over distance than lower frequencies (Marten and Marler 1977), which reduces the advantage of high-frequency signals in maximizing active space. Because most anthropogenic noise is dominated by low frequencies, species that have low-frequency vocalizations, such as the sage-grouse, will disproportionately experience masking. Indeed, several studies have found that anthropogenic noise more severely affects species with lower-frequency vocalizations (Rheindt 2003; Francis et al. 2009, 2011; Goodwin and Shriver 2011).

Amplitude.—The amplitude of each note is also important in determining the active space, such that quieter notes suffer increased masking at a given distance from the noise source and vocalizing individual. Pops and coos could be detected at greater distances than the whistle apex and whistle trough, despite greater overlap with the background noise, because of greater source amplitudes. The whistle apex, which had the lowest source amplitude, had the smallest active space in noise despite the low overlap with the noise frequencies.

The acoustic directionality of a vocalization may also affect the degree to which masking reduces the overall active space. Many vocalizations radiate from the signaler in a directional pattern, such that the amplitude varies with the orientation of the vocalizing individual. Because of our small sample size, we did not include the effects of directionality on active space in our analysis, but instead assessed the impact of noise on the average active space of the signal across multiple orientations. The whistle is highly directional, with differences of up to 22 dB depending on the relative orientation of the individual (Dantzker et al. 1999). We used values from the loudest orientations of those that we measured;

therefore, masking in the quieter orientations may be much greater than described here. Given that the loudest orientation can vary for different strut components (Dantzker et al. 1999), it is possible that using this small range and averaging across vocalizations may have underestimated the maximum active space for some components. Males that adjust their orientation to beam a highly directional vocalization toward a female may gain an advantage over other males, even under quiet conditions (Brumm 2002, Brumm and Todt 2003, Patricelli and Krakauer 2010); this advantage may be even more pronounced in a noisy environment.

Potential consequences of masking.—Reductions in the active space of detection and discrimination, as predicted by our analysis, could have significant effects on the fitness of individuals in noisy landscapes. Female sage-grouse use acoustic signals to locate lekking males (Bradbury et al. 1989); thus, their ability to find leks could be compromised in noisy environments because of the reduced active space of detection. Once on the lek, females can detect males visually, making detection using acoustic signals less critical. Discrimination and recognition are likely to be more critical on this smaller spatial scale. Female sage-grouse use the acoustic components of the display to select a mate (Gibson et al. 1991, Gibson 1996). In particular, acoustic features such as the IPI, and possibly the whistle, are thought to play a role in attracting females from across the lek (Gibson 1996). Thus, noise that reduces the maximum distance of discrimination to less than half the length of leks in our study population (half average lek length = ~70 m; J. L. Blickley unpubl. data) could negatively affect a male's ability to attract females. Further, background noise could make active comparison of males difficult for females if the maximum discrimination distance is reduced to less than the average distance between males (Forrest and Raspet 1994).

If the interfering noise only overlaps partially with a vocalization, the frequency with the maximum active space may be different under noisy conditions than under normal ambient conditions, leading to the reception of a signal that is distorted. For example, in the pop 1 component of the sage-grouse display, we found that the frequency with the maximum active space was different in noisy compared with quiet conditions. Therefore, a receiver hearing pop 1 under noisy conditions would hear a call dominated by frequencies in the 500 Hz 1/3-octave band; but under quiet conditions, the receiver would hear a call dominated by frequencies in the 200 Hz 1/3-octave band. Depending on which characteristics of the vocalization are assessed by females or competing males, this distortion may lead to difficulty in discrimination or recognition. Previous studies have suggested that female sage-grouse do not assess natural variation among males in peak frequency during mate choice (Gibson et al. 1991), but further behavioral studies would be needed to determine what, if any, effect such distortion might have on female response to male sage-grouse vocalizations. Distortion may have more significant effects on species in which mate choice is based on the frequency of the signal. For example, in species in which females prefer males with low-frequency song (Halfwerk et al. 2011) or assess the fundamental frequency of song as an indicator of male body size, (Ryan and Brenowitz 1985), distortion may lead to increased difficulty in comparing potential mates.

Ultimately, increased difficulty in finding leks or assessing males on the leks may lead to lower female attendance on noisy leks compared with quieter locations. Males may also avoid leks with high levels of noise if they perceive that their vocalizations are masked. Blickley et al. (2012) found lower male and female attendance on leks with experimentally introduced noise from roads and drilling rigs, both of which produce primarily low-frequency sounds similar to the compressor station modeled here. These declines may be due in part to masking, which would be predicted given the substantial overlap in the frequency range of the introduced noise and the sage-grouse strut display. However, the average level of introduced noise across leks in this experiment was relatively low, especially on leks with intermittent road noise, so masking is not likely the only cause of the observed declines. As discussed below, masking is only one possible effect of noise, and other effects may have a larger impact.

Masking in the context of noise regulations.—Are current noise regulations predicted to limit the impact of masking on sage-grouse? Outside of the breeding season, energy development activities are limited within 400 m (1/4 mile) of active sage-grouse leks on federal lands at our study site (Bureau of Land Management 2008). Our analysis indicates that a compressor station, or a similar noise source such as a drilling rig, placed at

or inside this stipulated minimum surface-disturbance buffer would have a substantial effect on the ability of sage-grouse to detect a nearby lek and, potentially, to discriminate among individuals on the lek.

Regulations also institute a 2-mile (3.2-km) buffer around leks for permanent infrastructure and lekking-season drilling activities on federal lands in this region (Bureau of Land Management 2008). Our results suggest that the masking footprint of a single compressor station or drilling rig is unlikely to exceed this buffer. Within the range of the peak frequencies for sage-grouse vocalizations (400–2,500 Hz), the noise produced by the compressor station was estimated to drop to ambient levels ≤1,000 m. Even if noise travels farther during temperature inversions common in the early morning, when sage-grouse are actively lekking (Sutherland and Daigle 1998), masking on the lek is likely to be negligible for sources outside the 2-mile (3.2-km) buffer. However, off-lek communication, such as parent–offspring communication, occurs well beyond the boundaries of a lek (Lyon and Anderson 2003) and may still be susceptible to masking. Further, our analysis considered the masking impact of only a single, stationary noise source, but many developed areas contain a network of such sources connected by roads; this will lead to a much greater area of total impact.

Mechanisms to reduce masking.—Features of sound perception and flexibility in signal production may improve the ability of animals to detect signals in noise beyond the active-space predictions calculated by this method. Animals may use directional cues to separate a sound from background noise if the two sound sources are spatially separated (Schwartz and Gerhardt 1989, Dent et al. 1997). Amplitude fluctuations across the spectrum of a sound, or comodulation, may also increase the detectability of the sound against background noise, especially if the noise is relatively constant (Klump and Langemann 1995) like the noise sources investigated here. Animals in noisy areas may adjust their vocalizations to compensate for the increased background noise (Patricelli and Blickley 2006), increasing the amplitude (Brumm 2004) or redundancy (Brumm and Slater 2006) or shifting the peak or minimum frequencies to reduce overlap with background noise frequencies (e.g., Slabbekoorn and Peet 2003, Wood and Yezerinac 2006, Potvin et al. 2011). The potential for these forms of compensation is species specific; the degree to which

hearing ability and vocal adjustment affect the active space of sage-grouse vocalizations is unknown.

Noise impacts beyond masking.—Masking is one potential effect of noise on wildlife, but it is certainly not the only one (Barber et al. 2010, Blickley and Patricelli 2010, Kight and Swaddle 2011). Blickley et al. (2012) found strong evidence that sage-grouse leks with experimentally introduced intermittent road noise experienced much greater declines in male attendance than those with more continuous drilling noise, despite the lower masking potential of road noise. Even light vehicular traffic (1–12 vehicles day^{-1}) has been found to substantially reduce nest initiation rates and increase the distance of nests from lek sites in sage-grouse (Lyon and Anderson 2003), despite minimal opportunity for masking. Together, these studies suggest that masking is not the only potential effect of noise or noisy infrastructure on sage-grouse. So, although a masking analysis can be powerful in making predictions about the effects of noise on lek communication in sage-grouse, this type of analysis may not provide sufficient predictive power for estimating the overall impact of the noise on this species.

Noise pollution has been found to induce stress, disrupt physiological processes and behaviors, cause physical trauma to the auditory system, or mask other natural sounds important to survival and reproduction, such as the sound of predator approach, in a variety of species (Marler et al. 1973, Bowles 1995, Kight and Swaddle 2011). For sage-grouse, these effects may extend beyond the area in which masking of the strut display is an issue, particularly for time spent off lek. Wildlife managers that seek to reduce the overall impact of anthropogenic noise on sage-grouse and other species affected by human encroachment must address all the potential effects of noise, including masking potential.

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