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Active space of grasshopper mouse vocalizations (*Onychomys*) in relation to woody plant encroachment

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Abstract

The efficacy of animal acoustic communication depends on signal transmission through an oft-cluttered environment. Anthropogenic-induced changes in vegetation may affect sound propagation and thus habitat quality, but few studies have explored this hypothesis. In the southwestern United States, fire suppression and cattle grazing have facilitated displacement of grasslands by pinyon-juniper woodlands. Northern grasshopper mice (*Onychomys leucogaster*) inhabit regions impacted by juniper encroachment and produce long-distance vocalizations to advertise their presence to conspecifics. In this study, we coupled acoustic recordings and electrophysiological measurements of hearing sensitivity from wild mice in the laboratory with sound transmission experiments of synthesized calls in the field to estimate the active space (maximum distance that stimuli are detected) of grasshopper mouse vocalizations. We found that mice can detect loud (85 dB SPL at 1 m) 11.6 kHz vocalizations at 28 dB SPL. Sound transmission experiments revealed that signal active space is approximately 50 m. However, we found no effect of woody plant encroachment on call propagation because juniper and woody plant density were inversely associated and both present barriers to a 9 cm mouse advertising at ground level. Our data indicate that woody plant encroachment does not directly impact the efficacy of grasshopper mouse communication, but vegetation shifts may negatively impact mice via alternative mechanisms. Identifying the maximum distance that vocalizations function provides an important metric to understand the ecological context of species-specific signalling and potential responses to environmental change.

Keywords

active space, anthropogenic, *Onychomys*, vocalization.

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1. Introduction

Active space, or the maximum distance that signals can be detected by receivers (Marten & Marler, 1977; Brenowitz, 1982), is the product of signal properties, receiver sensory systems, and environmental constraints on signal transmission, including ambient noise (Marten & Marler, 1977; Wiley & Richards, 1982; Ryan & Brenowitz, 1985; Bradbury & Vehrencamp, 2011). In the acoustic domain, the structural complexity of an environment is an important factor influencing sound degradation (Morton, 1975; Brenowitz, 1986). Acoustic scattering resulting from reflection, refraction, and/or diffraction of sound energy by physical objects such as vegetation contributes to attenuation and may cause selection on signal form to optimize transmission (Morton, 1975; Seddon, 2005; Wilkins et al., 2013; but see Boncoraglio & Saino, 2007).

Anthropogenic-induced changes to the environment can have diverse impacts on animal behaviour (Berger-Tal et al., 2011; Blumstein & Fernandez-Juricic, 2010). In the context of acoustic communication, most studies have focused on the effects of noise (Shannon et al., 2016; Rosa & Koper, 2018). For example, anthropogenic noise is associated with changes in song properties that impact signal propagation (Slabbekorn & Peet, 2003; Parris & McCarthy, 2013) and acoustic masking of receivers that decreases active space (Clark et al., 2009; Grade & Sieving, 2016). In contrast, relatively little is known about alternative mechanisms underlying anthropogenic-induced changes of the acoustic signalling environment. Rising temperatures associated with atmospheric warming may decrease the echolocation distance of foraging bats (Luo et al., 2014) and alter perch height of advertising birds to maximize sound propagation (Möller, 2011). Concomitant changes in vegetation associated with climate change (Allen & Breshears, 1998) or other anthropogenic causes may also impact the efficacy of acoustic communication, but few studies have investigated this phenomenon.

In the southwestern United States, woody plant encroachment caused by fire suppression and cattle grazing has converted grassland and shrubland into pinyon-juniper woodlands (Miller et al., 2000; Sankey & Germino, 2008). Increased vegetation density is predicted to change the signaling environment by increasing sound attenuation via interference with plants (Marten & Marler, 1977; Wiley & Richards, 1978; Richards & Wiley, 1980). Northern grasshopper mice (*Onychomys leucogaster*) are nocturnal, predatory rodents that inhabit deserts and prairies throughout the western United States

(Stapp, 1999), including grasslands affected by woody plant encroachment. Grasshopper mice feed primarily on arthropods but also include small mammals and reptiles in their diet (Flake, 1973; Stapp, 1997). As a consequence of their predatory lifestyle, grasshopper mice maintain large home ranges through scent marking and long-distance advertisement vocalizations (Ruffer, 1966; Hafner & Hafner, 1979; Frank, 1989; Pasch et al., 2016). The loud, tonal vocalizations (range: 9.5–13.5 kHz; Hafner & Hafner, 1979; Miller & Engstrom, 2012; Pasch et al., 2016; Campbell et al., 2019) facilitate localization of mates and rivals during the mating season (Frank, 1989).

In this study, we quantified the active space of northern grasshopper mice vocalizations by measuring properties of senders, receivers, and the environment. Specifically, we measured the call amplitude and hearing sensitivity of wild-captured *O. leucogaster* in the laboratory and conducted sound propagation experiments of synthesized calls in the field to measure acoustic attenuation. We predicted that long-distance calls would exhibit greater attenuation in areas of high juniper density due to increased attenuation imposed by greater vegetation density.

2. Methods

2.1. Animals

We live-captured mice in the San Simon and Animas Valleys, New Mexico using Sherman traps (Model LFATDG) baited with dry cat food. Mice were transported to animal facilities at Northern Arizona University, Flagstaff, AZ, USA and singly housed in standard mouse cages (Ancare N40HT; 48 × 27 × 16 cm). We maintained the animal facility on a 14: 10 light/dark cycle at 20 ± 3°C and provided rodent chow and water ad libitum.

2.2. Acoustic recording

At the animal facilities, we recorded spontaneous vocalizations of 36 adult *O. leucogaster* ($N = 18$ males and 18 females). Animals were placed within a semi-anechoic sound cubicle maintained on the same 14: 10 light cycle as the colony room for overnight (10 h) acoustic recording for 3 nights. We used 0.64-cm microphones (Type 40BE, GRAS Sound & Vibration, Twinsburg, OH, USA) connected to preamplifiers (Type 26 CB, GRAS Sound & Vibration) to obtain acoustic pressure recordings 33.3 cm above focal animals. Microphone response was flat within ±1.5 dB from 10 Hz to 50 kHz, and pre-amplifier response was flat within ±0.2 dB from 2 Hz to 200 kHz. Microphones were connected to a National Instruments DAQ (National Instruments USB 4431) sampling at 102.4 kHz to a laptop computer running MATLAB (Version 2018a). The average fundamental frequency (11.6 kHz) was reported in Green et al. (2019). In this study, we calculated the average sound pressure levels (dB SPL re: 20 μPa at 1 m) from the total number of calls recorded ($\bar{x} = 38.3$, range $=$ 1–250) over the three nights of recording. Values are reported as ± standard deviation.

2.3. ABR thresholds

We measured auditory brainstem responses of wild *O. leucogaster* in the laboratory to estimate physiological hearing sensitivity. The data presented herein represent a subset of the larger dataset published in Green et al., 2019. Following methods described therein, we administered sodium pentobarbital (25 mg/kg; 0.1 ml/40 g) intraperitoneally to anesthetize mice and occasionally injected an additional dose ($<$0.05 ml) 10 min after the initial dose to maintain an anaesthetic plane. Mice were positioned on a gel heating pad (32 ± 5°C) to maintain body temperature within in a shielded semi-anechoic chamber (ETS Lindgren SD-1; internal dimensions 91.4 × 91.4 × 91.4 cm) lined with acoustic foam. We placed three needle electrodes (27 gauge, 12 mm; Rochester Electro Medical, Lutz, FL, USA) subdermally behind (1) the left ipsilateral ear receiving the stimulus (reference), (2) at the vertex of the skull (active channel), and (3) behind the contralateral right ear (ground) to obtain monaural ABR signals. Electrodes were connected to a head stage (RA4LI, Tucker Davis Technologies (TDT), Alachua, FL, USA) and preamplifier (RA4RA, TDT) attached to a processor (RZ6, TDT) via a fibre optic cable. We used SigGenRZ software (version 5.7.0, TDT) to create auditory stimuli (2.5 ms tone bursts with a 0.4 ms gate, 512 averages). Stimuli were presented through a speaker (MF1, TDT) positioned 10 cm away from the left ear of the mouse using BioSigRZ software (version 5.7.0, TDT). Stimulus frequencies ranged from 4–32 kHz in 2–4 kHz increments, with each frequency stimulus beginning at 80 dB and decreasing to 10 dB, in 10 dB increments. Auditory-evoked responses were filtered (high-pass at 100 Hz, low-pass at 3 kHz, and notch-filtered at 60 Hz) and digitized at a sampling rate of 24.4 kHz. After each trial, animals were monitored until fully recovered from anaesthesia.

2.4. GIS modelling and juniper density classes

We processed Landsat 8 imagery from the United States Geological Survey (USGS), Earth Explorer (USGS, 2015) taken in August 2014 (Path 37, Row 35) in ArcMap (Version 10.5.1, ESRI, Redlands, CA, USA) GIS software to create three juniper density classes based on the density of woody plants. The Landsat image was clipped to a subset of the CO Bar Ranch, consisting of 21 742 ha of the Babbitt Ranches, approximately 73 km NW of Flagstaff, Arizona, USA. Dominant vegetation on the study site were blue grama (*Bouteloua gracilis*), rabbitbrush (*Ericameria* spp.), broom snakeweed (*Gutierrezia sarothrae*), Utah juniper (*Juniperus osteosperma*), and pinyon pine (*Pinus edulis*; Colorado Natural Heritage Program, 2005; Comer et al., 2012). The Landsat image was converted into five juniper density classes as described for the CO Bar Ranch survey design (SWCA Environmental Consulting, 2016). The five classes described were (1) bare soil, (2) dense pinyon-juniper woodlands (over 40 % cover), (3) less dense pinyon-juniper woodlands (under 40% cover), (4) semi-desert shrub-steppe with scattered pinyon-juniper and (5) semi-desert shrub-steppe. We grouped the dense and less dense pinyon-juniper woodlands into a single category and re-classified the layer to create our ‘High’ class, semi-desert shrub-steppe with scattered pinyon-juniper as ‘Medium’, and semi-desert shrub-steppe as ‘Low’. Following digital classification, we visited sites to verify appropriate class designation by estimating the number and ratio of trees and shrubs visible from the road. Following verification, we randomly placed ten points within 100 m of remote, unmaintained two-track dirt access roads within each vegetation class, resulting in 30 sites. Visual surveys of our sites indicated that proximity to the road did not influence vegetation composition or density. In addition, sites were within the range of *O. leucogaster* as verified through audible and visual detection of mice near our transects.

2.5. Sound propagation experiment and vegetation measurements

We conducted all sound propagation experiments in July–August 2017 at dusk (1800–2200 h) coincident with times that mice typically call following emergence from burrows (Frank, 1989). We used a local national weather station (35°39′00.0″N 112°04′12.0″W, $<$10 km from our field sites) to record wind speed and temperature and did not conduct experiments if wind speed was $>$16 kph. At each site, we set a 60 m transect line in a random direction. At each site, we recorded the number of shrubs ($\leqslant$1 m in height) and pinyon and juniper trees ($\geqslant$1 m in height) within 1 m of each side of the acoustic transect, covering a total of 120 m^2. Counts were converted to density estimates for statistical analyses. Along the transect, we placed flagging at 1, 5, 10, 20, 30, 40, 50 and 60 m for eventual speaker placement (below). The maximum distance was selected based on preliminary studies indicating that stimuli were indistinguishable from background noise after 60 m. At 0 m, we placed a 0.64-cm pre-polarized freefield microphone (Type 40BE, G.R.A.S.) connected to a constant current power preamplifier (Type 26 CB, G.R.A.S.) 9 cm above the ground to mimic the height of a hypothetical mouse receiver. Microphone response was flat within ±1.5 dB from 10 Hz to 50 kHz, and preamplifier response was flat within ±0.2 dB from 2 Hz to 200 kHz. The microphone was attached to a data acquisition unit (DAQ; National Instruments USB-4431) connected to a laptop computer (Lenovo ThinkPad X230; Windows 10). To broadcast stimuli, we attached the DAQ to a speaker (Ultrasonic Dynamic Speaker, ScanSpeak, Avisoft Bioacoustics, flat frequency response within ±1.5 dB from 10–45 kHz) via a 60 m BNC cord to mimic a hypothetical vocalizing mouse. The amplifier was powered by a 12V lithium iron phosphate portable battery (PowerStream Technology Model PST-BP75-LFP7.5).

While the microphone remained stationary at 0 m, we moved the speaker successively from 1 m up to the maximum distance of 60 m. Stimuli were broadcast parallel to the ground 50 times per distance at each transect. To avoid pseudo-replication (McGregor et al., 1992; Kroodsma et al., 2001), we broadcast a synthesized 1 s, 11.6 kHz tone at 85 dB SPL re: 20 μPa at 1 m representing the average call fundamental frequency and amplitude reported in Green et al. (2019) and herein (Figure 1). Measurements were derived from a population of *O. leucogaster* near Animas, NM, but acoustic recordings from animals captured at CO Bar Ranch indicate that mice produce similar frequencies and amplitudes (fundamental frequency range: 11.1–11.9 kHz, dB SPL range: 83–89 dB). We used the Data Acquisition Toolbox in MATLAB (Version 2018a) to synchronize signal output and input and automate averaging of the 50 recordings to generate dB SPL estimates at each distance per site. We used MATLAB to bandpass filter the averaged recording between 11.5 and 11.7 kHz and extracted the middle 60% (0.2–0.8 s) to remove time delays and reverberation from the recorded signal. The active space was operationally defined as the distance before the site where signal amplitude became undetectable from background noise (26.3 ±

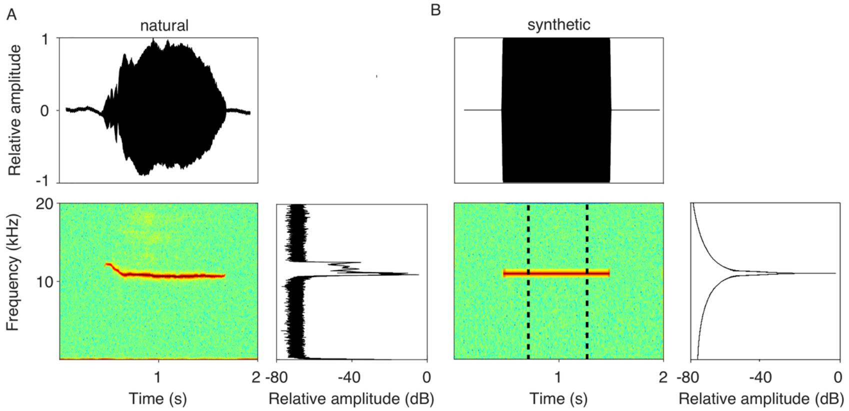

Figure 1. Long-distance vocalization of a northern grasshopper mouse. (A) Natural and (B) synthetic version of calls. Top panels depict waveforms, bottom left panels depict spectrograms, and bottom right panels depict power spectra. Synthetic calls based on the population average of fundamental (= dominant) frequency, duration and amplitude (Green et al., 2019) were used in sound transmission experiments in the field. Vertical dotted lines represent the middle 60% (0.2–0.8 s) of synthetic calls extracted for analysis.

0.7 dB) as measured from recordings at 60 m with and without signal playback. We recognize that such a definition represents energetic rather than informational masking (Watson, 1987; Clark et al., 2009; see discussion) and acknowledge that further auditory studies are required to specify mouse detection thresholds.

2.6. *Statistical analyses*

We used a two-sample t-test to compare differences in call amplitude between the sexes. To estimate auditory responsiveness, we used the visual detection method (Jacobson, 1985) whereby a researcher determined the lowest stimulus level (dB) per frequency that evoked an ABR response. The threshold was operationally defined as the dB level halfway (5 dB) between the last detectable ABR response and next lowest stimulus level. The full audiogram is reported in Green et al. (2019). Here we report only the threshold level measured at 10 kHz, the lowest threshold that was measured closest to the 11.6 kHz average fundamental frequency of *O. leucogaster* vocalizations.

We compared the density of shrubs and trees within each class using an ANOVA and post-hoc Tukey Tests using R Studio (version 3.3.3; Propagation-package: lm, anova). We used generalized linear mixed models to determine attenuation of the synthesized tones, with site ID modeled as a random effect. Distance and Distance^2 (as a non-linear model), vegetation class (High, Medium and Low), number of shrubs, number of trees (e.g., junipers and pinyons), and interactions were all included in the model. We used a Bonferroni correction with $\alpha = 0.0051$ to control for multiple comparisons. Investigation of the data indicated that sound attenuation was greatest between 1 and 20 m. To assess the effects of vegetation density on sound attenuation, we used a linear regression of the amplitude of the stimulus at 20 m with the vegetation density of shrubs and trees on the acoustic transect at 20 m (40 m^2).

2.7. *Ethical approval*

All procedures performed in studies involving animals were in accordance with the ethical standards and approval of the Institutional Animal Care and Use Committee at Northern Arizona University (Nos 15-014 and 16-001) and guidelines of the American Society of Mammalogists.

(Sikes et al., 2016). Animals were captured with a permit from the New Mexico Department of Game and Fish (No. 3562).

3. Results

3.1. *Call amplitude*

The amplitude of long-distance calls did not differ between males (85.31 ± 2.04 dB) and females (86.15 ± 1.88 dB; $t_{34} = 1.28$, $p = 0.21$) and averaged 85.73 ± 1.98 dB (range: 82.19–89.37) at 1 m (Figure 2).

3.2. *Auditory brainstem response*

Visually-detected ABR thresholds indicated that mice had an average hearing threshold of 28.33 ± 9.07 dB SPL at 10 kHz (Figure 2).

3.3. *Sound propagation and vegetation measurements*

More shrubs were present in classes designated as ‘low’ compared to ‘high’ ($F_{2,27} = 50.19$, $p < 0.001$; Figure 3a), but no differences of either from ‘medium’ ($p > 0.05$). More trees were present in the ‘high’ versus ‘low’ or ‘medium’ vegetation classes ($F_{2,27} = 14.446$, $p < 0.001$; Figure 3b). However, vegetation class did not affect sound attenuation ($p > 0.05$; Table 1). Distance was the sole predictor for stimulus amplitude ($t_1 = -24.38$,

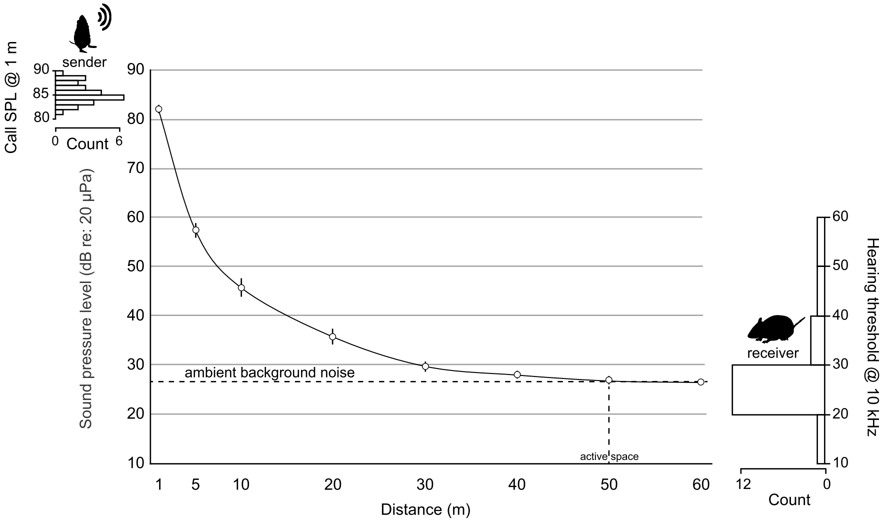

Figure 2. The active space of northern grasshopper mouse vocalizations. The upper left histogram depicts the range of amplitudes (dB SPL at 1 m) produced by senders ($n = 36$). The lower right histogram depicts the range of receiver hearing sensitivities at 10 kHz ($n = 18$). The x-axis depicts average (±SE) sound attenuation of synthesized signals broadcast at 85 dB. The horizontal dotted line represents the average background noise at 11.6 kHz.

$p < 0.001$; Table 1). The majority of acoustic attenuation occurred within the first 20 m (46.54 ± 1.53 dB; ∼79% attenuation based on estimated background noise level). However, we found only a slight trend indicating increased attenuation as tree and shrub density increased ($p = 0.404$; Figure 4). Signal amplitudes that were slightly higher than recorded background noise (26.3 ± 0.7 dB) were present at 50 m (26.6 ± 1.1 dB; Figure 2).

4. Discussion

Anecdotal reports suggest that grasshopper mouse vocalizations are audible to human observers from 50 m (Frank, 1989) to 90 m (Horner & Taylor, 1968; Hafner & Hafner, 1979).

From the perspective of intended receivers, our findings herein indicate that the lower end of this range (50 m) is a conservative estimate of signal active space. We discuss this metric in relation to experimental assumptions and variation in the three components that define active space: call properties, hearing sensitivity, and the environment.

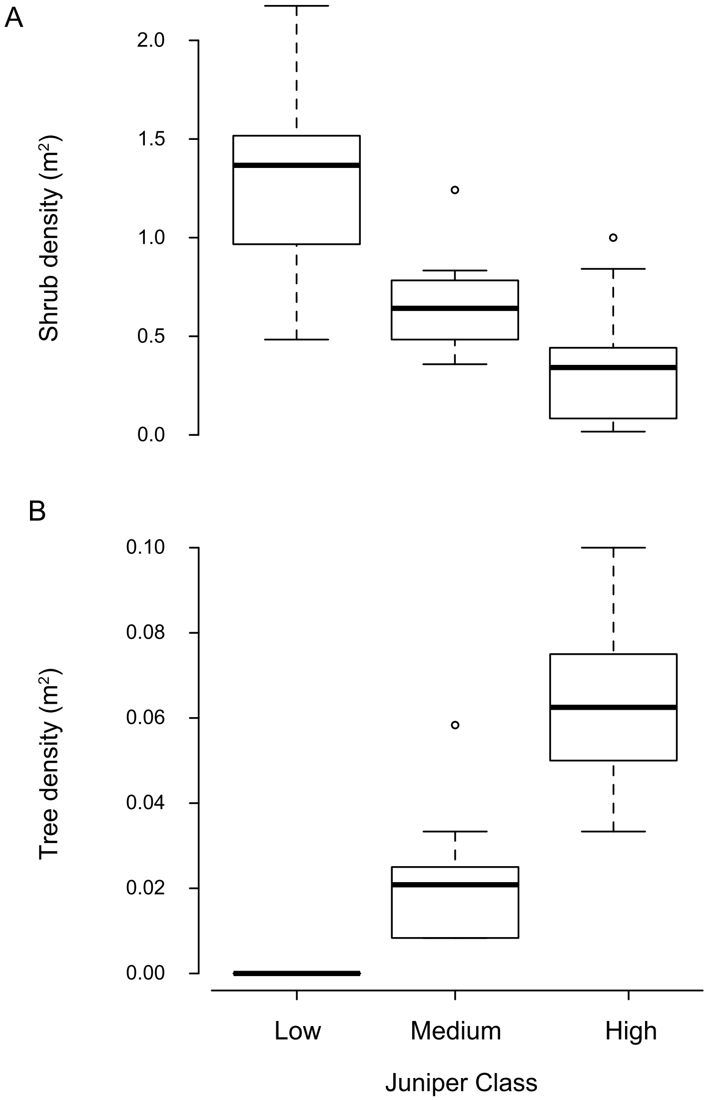

Figure 3. Vegetation characteristics along sound propagation transects (120 m^2) at the CO Bar Ranch, Flagstaff, AZ. (A) Density of shrubs and (B) density of trees in each class (designated in GIS as specified in methods; $N = 10/\text{class}$).

Call amplitudes of 85 dB SPL at 1 m concur with previous estimates of grasshopper mouse vocalizations (Pasch et al., 2016, 2017; Frank, 1989). Grasshopper mice commonly assume an upright posture with elevated head

Table 1.
Results from linear mixed models for call propagation across the landscape.

Variable	Estimate	SE	2.5%	97.5%	T	Est. p
Call Propagation						
Class						
High	74.40	1.53	71.46	77.33	48.64	–
Medium	−0.16	1.66	−3.34	3.03	0.09	>0.05
Low	−0.63	1.66	−3.82	2.56	0.38	>0.05
Distance	−2.35	0.096	−2.54	−2.17	24.38	<0.001*
Distance^2	0.03	0.002	0.024	0.03	17.12	<0.001*

Low and medium class coefficients compared to high class coefficient. Estimate coefficient, SE, and a 95% confidence interval (2.5% and 97.5%) for posterior distribution are reported with estimated p-values derived from the t-statistic.

and flared mouth ‘in perfect wolf form’ (Ruffer, 1966) during vocal production that increases call amplitude by 30 dB (Pasch et al., 2017). Although the directivity profile of the speaker does not likely match sound radiation patterns of actual mice, preliminary studies indicate that source levels are loudest in the direction of intended receivers (Pasch, unpublished data). Such

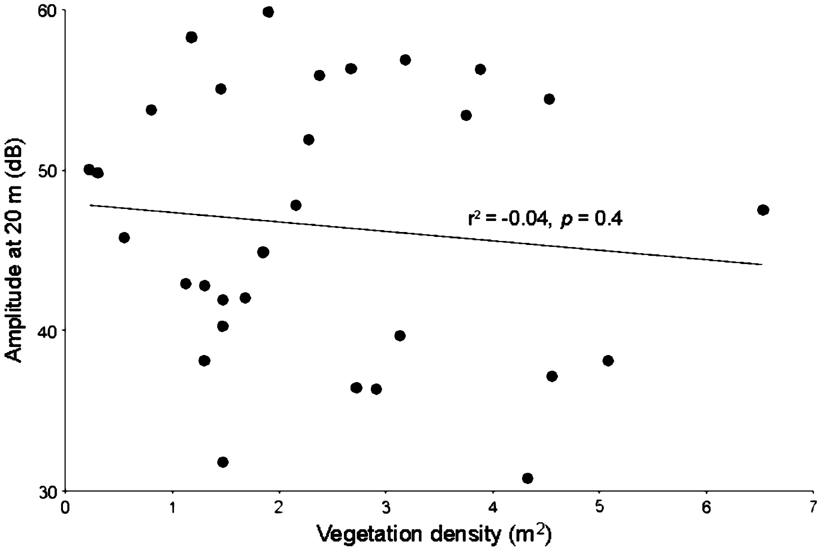

Figure 4. The relationship between vegetation density and sound attenuation within the first 20 m (40 m^2) of the transect. Vegetation density represents the presence of both trees and shrubs.

loud calls are associated with a predatory lifestyle whereby mice occupy large, exclusive home ranges (minimum convex polygon = 1.72–3.84 ha; Stapp, 1999; Kraft & Stapp, 2013) and occur at low population densities (0.89–1.88 mice/ha; Brown & Zeng, 1989; Stapp, 1997). Observations of mice in nature suggest that males and females call antiphonally to facilitate contact prior to close-distance assessment during the mating season (Frank, 1989). Assuming an idealized 1.72 ha circular home range that is 148 m in diameter, vocalizations detected at 50 m would travel less than the radius of a home range. However, grasshopper mice often travel long distances in a single night (Stapp, 1997; Kraft & Stapp, 2013) and core areas are typically 20% of home range size (Frank & Heske, 1992). In an idealized 0.34 ha circular core area that is 66 m in diameter, vocalizations detected at 50 m would travel approximately three quarters of the diameter of a core area. Thus, we infer that vocalizations are audible to at most 2–3 conspecifics, even during the mating season when males increase home range size to overlap with more females (Frank & Heske, 1992; Stapp, 1999). Such an estimate corresponds with the high repeatability but low individuality of grasshopper mouse vocalizations (Pasch et al., 2016; Campbell et al., 2019; Pasch, unpublished data), whereby their relative social simplicity reduces the need for individual signatures to facilitate discrimination (Beecher, 1989; Freeberg, 2006; Pollard & Blumstein, 2012).

The peripheral hearing sensitivity of grasshopper mice is broad and encompasses the dominant frequency and first harmonic of long-distance vocalizations (Heffner & Heffner, 1985; Green et al., 2019). The threshold estimate of ca. 30 dB reported herein is derived from auditory evoked potentials from the brainstem, which are typically 10–30 dB less sensitive than behavioural thresholds that estimate signal salience (Ohlemiller et al., 2010; Kobrina & Dent, 2016; Dent et al., 2018). Indeed, Heffner & Heffner (1985) estimated grasshopper mouse behavioural thresholds at 9 dB, suggesting that mice may be able to detect vocalizations at much further distances. Furthermore, the field microphone polar profile does not account for complex transfer functions associated with pinnae shape and movement (e.g., Anbuhl et al., 2017). However, background noise levels (ca. 26 dB) measured at our study site were higher than behavioural thresholds, indicating that noise may energetically mask attenuated signals to influence detection and perception (Clark et al., 2009). Formal experiments that estimate signal recognition thresholds by controlling for reproductive status (e.g., Henry & Lucas, 2009;

Miranda & Wilzynski, 2009) and motivational state (Perelmuter et al., 2019) under ecologically relevant background noise levels (e.g., Bee & Schwartz, 2009) would greatly improve active space metrics. Ideally, such experiments would occur in the field under prevailing abiotic conditions with marked animals (senders and receivers) communicating amidst the complexities of natural noise (Dent et al., 2018).

Signal amplitude decreased with transmission distance as predicted by spherical spreading, with more than half of attenuation occurring within 20 m. However, we did not detect differences in sound attenuation across juniper density classes. Vegetation analyses revealed an inverse relationship between juniper and shrub presence, with shrub density increasing as juniper density decreased. Such a pattern has been documented previously in northern Arizona, where understory vegetation more than doubled in areas of juniper removal (Clary, 1971). Thus, we infer that both vegetation types, in concert with ground level absorption, present similar acoustic barriers to a 9 cm mouse (Marten & Marler, 1977; Wiley & Richards, 1978). Similar attenuation patterns across vegetation classes may be due to equivalent mechanisms of vegetation-induced scattering or via larger contributions of wind turbulence in more open areas (Mokhtar & Marrous, 1955; Morton, 1975). Nevertheless, our data indicate that woody plant encroachment does not directly impact the efficacy of grasshopper mouse acoustic communication. However, vegetation shifts may negatively impact habitat quality via alternative mechanisms. For example, grasshopper mice exhibit preferences for open habitats associated with the presence of other small mammal burrows (Egoscue, 1960; Choate & Terry, 1973; Stapp, 1999) or areas where junipers were experimentally removed (Turkowski & Reynolds, 1970). Woody plant encroachment alters plant community composition (Clary, 1971; Miller et al., 2000; Davies et al., 2011), promotes higher predator densities (Coates & Delehanty, 2010; Gallo et al., 2016), and changes arthropod communities that grasshopper mice prey upon (Flake, 1973; Stapp, 1997; Roberts & Jones, 2000). Thus, formal trapping studies, acoustic surveys, and quantification of predator and prey abundance would help clarify the influence of woody plant encroachment on grasshopper mouse habitat use and abundance.

In summary, our findings operationally define the active space of northern grasshopper mouse vocalizations at 50 m. Our results represent a conservative estimate based in part on hypothetical estimates of sound production and perception and therefore may not entirely reflect the natural abilities of grasshopper mice. Nevertheless, estimating the maximum distance that vocalizations function in nature not only informs the ecological context of species-specific signalling but provides a metric to compare across diverse taxa (Brenowitz, 1982; Brown, 1989; Gerhardt & Huber, 2002; Alves et al., 2016; Taylor et al., 2019; Römer, 2020) to facilitate our understanding of how acoustic communication systems evolve. Due to extreme variation in rodent social systems, space use, and acoustic signalling (Janik, 2000; Wolff & Sherman, 2007; Miller & Engstrom, 2007, 2010, 2012; Pasch et al., 2011, 2017), their continued study promises to provide important insights. More broadly, our findings highlight the need to explore indirect effects of anthropogenic-induced landscape alterations in organisms whose communication systems may be more sensitive to change.

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Supplementary material

Raw auditory brainstem response data are available from the author upon request.