



Original Article

Vocal characteristics of prairie dog alarm calls across an urban noise gradient

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Increasing anthropogenic noise is having a global impact on wildlife, particularly due to the masking of crucial acoustical communication. However, there have been few studies examining the impacts of noise exposure on communication in free-ranging terrestrial mammals. We studied alarm calls of black-tailed prairie dogs (*Cynomys ludovicianus*) across an urban gradient to explore vocal adjustment relative to different levels of noise exposure. There was no change in the frequency 5%, peak frequency, or duration of the alarm calls across the noise gradient. However, the minimum frequency—a commonly used, yet potentially compromised metric—did indeed show a positive relationship with noise exposure. We suspect this is a result of masking of observable call properties by noise, rather than behavioral adjustment. In addition, the proximity of conspecifics and the distance to the perceived threat (observer) did affect the frequency 5% of alarm calls. These results reveal that prairie dogs do not appear to be adjusting their alarm calls in noisy environments but likely do in relation to their social context and the proximity of a predatory threat. Anthropogenic noise can elicit a range of behavioral and physiological responses across taxa, but elucidating the specific mechanisms driving these responses can be challenging, particularly as these are not necessarily mutually exclusive. Our research sheds light on how prairie dogs appear to respond to noise as a source of increased risk, rather than as a distraction or through acoustical masking as shown in other commonly studied species (e.g., fish, songbirds, marine mammals).

Lay Summary: Songbirds, amphibians, and marine mammals have been shown to alter their vocalizations in noisy environments. We conducted one of the first studies on the effects of noise on communication in a terrestrial mammal—the prairie dog. Interestingly, prairie dogs did not appear to adjust their alarm call frequency or duration with increasing noise exposure, while our previous research demonstrated that their behavioral response to noise is similar to elevated predation risk—reduced foraging and increased vigilance.

Key words: acoustics, anthropogenic disturbance, communication, mammal, masking, predation.

INTRODUCTION

Human-induced rapid environmental change is having far-reaching impacts on natural ecosystems across the globe, affecting animal behavior, demographic processes, and community composition (Sih et al. 2011). The pervasive nature of rising anthropogenic noise levels across terrestrial and aquatic habitats provides a prime example of how human activities can dramatically alter the environment over a comparatively short time frame (Barber et al. 2010). During the past two decades, increasing research effort has explored the effects of noise on animal behavior and demography,

with particular focus on how anthropogenic noise affects acoustic communication (Shannon et al. 2016b).

Songbirds in particular have been the focus of numerous studies on the effects of anthropogenic noise on behavior and communication in urban environments, due to their relative abundance, the important role of vocal communication in many aspects of their behavior (e.g., territoriality, mate attraction, and agonistic social interactions) and the established methodology for studying changes in song structure and singing behavior (Slabbekoorn 2013). The seminal paper by Slabbekoorn and Peet (2003), which demonstrated that elevated noise levels in urban environments significantly altered vocal communication in great tits (*Parus major*), was a key catalyst for research effort on this topic. Scientists exploring avian acoustic

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communication have demonstrated a range of responses to mitigate the effects of noise exposure, which include adjusting the time of vocalizing (Fuller et al. 2007), increasing the amplitude of the call (Lowry et al. 2012), lengthening the duration of the call (Díaz et al. 2011), reducing syllable rate (Potvin et al. 2011), and shifting the minimum call frequency upwards (Slabbekoorn and Ripmeester 2008). These behavioral adjustments are believed to be adaptive responses that reduce the masking of key signals by low frequency anthropogenic noise, which is predominantly concentrated at <2 KHz (Brumm et al. 2017). Furthermore, evidence indicates that anthropogenic noise exposure may structure animal communities (Francis et al. 2009; Proppe et al. 2013), as species that vocalize at lower frequencies with limited behavioral flexibility are forced to adjust their distribution (Francis 2015). This suggests responses to noise are likely conditioned on the degree of plasticity in communication modalities.

Although the effects of anthropogenic noise on acoustic communication have been studied extensively across a range of taxa, including birds, marine mammals, amphibians, and even invertebrates, there has been limited exploration of these effects in terrestrial mammals (Shannon et al. 2016b). Terrestrial mammals display flexibility in call structures relative to social and geophysical conditions (Ey and Fischer 2009; Townsend and Manser 2013), and recent work has demonstrated that mongooses exhibit reduced responsiveness to conspecific and heterospecific vocalizations in road noise (Kern and Radford 2016; Morris-drake et al. 2017). However, studies explicitly exploring the effects of noise on vocalizations have largely been limited to research on bats. For example, Brazilian free-tailed bats (*Tadarida brasiliensis*) reduced the bandwidth of their echolocation search calls when exposed to noise (Bunkley and Barber 2015), fringe-lipped bats (*Trachops cirrhosus*) shifted from targeting prey-generated sources of sound to using echolocation when hunting in noise (Gomes et al. 2016), and Asian particolored bats (*Vespertilio sinensis*) simplified the complexity and raised the amplitude of their social calls when exposed to traffic noise (Jiang et al. 2019) but did not adjust the vocal rate or duration of these vocalizations (Song et al. 2019). Other studies have also explored shifts in frequency and amplitude of echolocating bats, but the researchers exposed the animals to noise with a specific frequency (bandpass filtered), compared with the broadband frequencies that are typical of anthropogenic noise (Hage et al. 2013; Hage et al. 2014). The paucity of research on a wider range of mammal species risks overlooking the impacts of this key anthropogenic stressor on terrestrial systems.

In this article, we explore whether a gradient of increasing urban traffic and associated environmental noise affects the alarm call characteristics of black-tailed prairie dogs (*Cynomys ludovicianus*)—hereafter referred to as prairie dogs. Prairie dogs are prey species for a wide range of grassland predators including badgers (*Taxidea taxus*), coyotes (*Canis latrans*), hawks, and snakes (Hoogland 1995). Alarm calls—a series of rapid high-pitched barks—provide one of the key antipredator strategies employed by this group-living species (Hoogland 1995), but the production of these calls appears to be influenced by social context. For example, prairie dogs have been shown to give alarm calls more readily when in the presence of kin compared to unrelated conspecifics (Hoogland 1983; Hoogland 1995). This provides evidence that the seemingly costly behavior of an individual alerting a predator to their presence may have indirect fitness benefits (Shelley and Blumstein 2005). Moreover, we recently demonstrated that the presence of young influenced the alarm call characteristics of adult prairie dogs—whereby they lowered the central concentration of energy in their calls (Wilson-Henjum et al. 2019). The social context and function of alarm call production provides an interesting avenue

for exploring the effects of exposure to anthropogenic noise on animal vocalization, particularly when contrasted with findings from the significant body of work focusing on advertisement calls and songs (reviewed by Shannon et al. 2016b).

Although prairie dog populations across the United States have been dramatically reduced as a result of land-use changes and disease (Miller, Ceballos, & Reading, 1994; Miller et al., 2007), they have shown the ability to inhabit urban environments (Magle et al. 2010; Magle and Fidino 2018). In common with other wildlife species that can survive in human-dominated landscapes, this persistence is likely to be a function of their behavioral flexibility, which allows them to adjust to the environmental conditions of their surroundings (Lowry et al. 2013). Prairie dogs therefore provide an interesting study species for furthering our understanding of behavioral and demographic responses to anthropogenic disturbance in a social mammal. In addition to exploring vocal plasticity relative to noise exposure in a free-ranging terrestrial mammal, this study also focuses on a form of vocal communication that has received less attention in this field of research—alarm calling to signal the presence of a perceived threat (Potvin et al. 2014; Templeton et al. 2016). While calls and songs aimed at attracting mates and defending territories play a crucial role in the reproductive success of an animal, alarm calls arguably have an even more immediate and profound effect on fitness through the mediation of survival.

Our previous research found that prairie dogs exposed to noise adjusted their vigilance and foraging behavior, consistent with the risk disturbance hypothesis, which predicts anthropogenic disturbance will elicit increased antipredator behavior (Shannon et al. 2014). Because of their enhanced vigilance, prairie dogs detected and responded to an approaching predator quicker in noise than during the ambient control—contrary to the distracted prey hypothesis (Shannon et al., 2016a). Here, we explore whether prairie dogs exhibit vocal plasticity in noise—a potential mechanism to overcome acoustical masking—to further illustrate how prairie dogs perceive and respond to this novel pollutant. This will not only broaden the types of communication studied in the context of increasing anthropogenic noise, but has implications for conserving animals in evolutionarily novel environments, such as urban areas that are dramatically expanding with human population growth. We predicted that prairie dogs would elevate the lower frequency limit of their alarm calls when exposed to increasing road traffic noise—so as to minimize acoustical masking.

METHODS

Study sites

The study was conducted across three prairie dog colonies in predominantly shortgrass prairie habitat located within or adjacent to the city of Fort Collins, Colorado, USA. The sites were selected to provide a gradient of exposure to urban traffic and associated noise. Pineridge Natural Area (250 ha), located on the western edge of the city with a small country road on the northwest boundary (~750 m from the center of the colony), experiences the least anthropogenic noise of the three colonies and is a site that we have used for previous research on prairie dog responses to road traffic noise (Shannon et al. 2016a). Coyote Ridge Natural Area, situated close to the southwest boundary of the city, is 840 ha in extent and adjacent to a larger open space to the south and west; the center of the prairie dog colony is located ~350 m from the relatively busy County Road 19. The Coterie Natural Area is a small (1.6 ha) site

located within the city at the intersection of two main roads (~50 m to the center of the colony), resulting in considerable levels of urban noise. All three of the sites can be accessed by trails that are used by walkers, runners, and cyclists. The prairie dogs are therefore regularly exposed to human activity.

Alarm call measurements

Prairie dog alarm calls were recorded from 28 August to 6 December 2014 using a Rode NTG-2 shotgun microphone, which was connected to a Roland Moore R-05 digital recorder. Data collection was carried out during daylight hours (0700–1900) by the same single observer (G.W.H.). Alarm calls were elicited by the observer approaching a randomly selected prairie dog—with a systematic approach employed to ensure that different areas of the colony (and animals) were sampled from one study site visit to the next. Once the prairie dog began alarm calling the observer remained stationary and recorded 30 s of vocalization while the animal was in situ. Distance to the target animal and the distance from this individual to their nearest neighbor was measured using a laser range finder. All calls were recorded within a distance of 18 m from the animal (mean \pm SD = 9 m \pm 3) with small differences between sites (Pineridge = 10 m \pm 2, Coyote Ridge = 11 m \pm 3, The Coterie = 8 m \pm 2). In order to reduce the possibility that the same prairie dog was selected more than once during the same recording session, the observer ensured that there was a minimum of 30 m (the average size of a burrow system; Sheets et al. 1971) between the individuals targeted for inclusion in the study. Wind speed and the prevailing weather conditions were all documented at the time of recording. A total of 137 alarm call recording periods were collected across the three sites (Pineridge = 46, Coyote Ridge = 44, The Coterie = 47).

A band-limited automated detector was used in Raven Pro v1.5 to select each of the individual barks in the 30-s calling bouts and to optimize extraction of call parameters. The following settings were used in the detector: minimum frequency of 2000 Hz, maximum frequency of 15,000 Hz, minimum signal duration of 0.008 s, maximum signal duration of 0.2 s, minimum separation of 0.2 s, minimum occupancy of 30%, and a signal-to-noise threshold of 15 dB. Before measurements were extracted on the individual barks, all detections were examined manually for accuracy and adjusted to maximize the detection of all barks within a recording period and to ensure the entire bandwidth and duration of calls were selected. Because prairie dogs produce short duration, broadband barks, a standardized maximum frequency (15,000 Hz) was used for each detection box. Random selections of half of the barks in a calling bout ($n = 4516$) were then measured.

Four acoustic metrics were calculated for each bark: 1) minimum frequency (Hz)—the lower frequency limit of the call, a commonly used metric in previous studies; 2) frequency 5% (Hz)—the frequency where the summed energy equals 5% of the total, a measure of lower frequency properties; 3) peak frequency (Hz)—the frequency with the highest concentration of energy; and 4) bark duration (milliseconds) (Figure 1).

Ambient sound level measurements

Ambient sound levels were measured using a calibrated Larson-Davis 831 sound level meter (frequency weighting = A) over a 2-min period as soon as the vocalization recording was completed. Sound pressure levels were measured as 1-s frequency weighted (12.5Hz–20kHz) equivalent continuous levels ($L_{Aeq, 1s}$). Although ambient sound levels may fluctuate slightly from the time that the

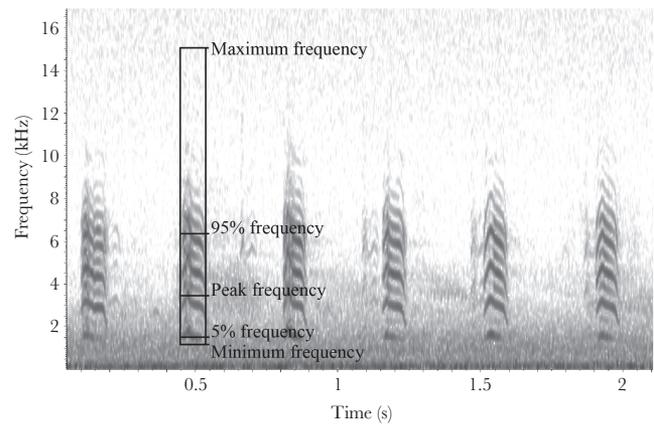


Figure 1

Spectrogram of black-tailed prairie dog alarm calls collected from the colony at The Coterie Natural Area. The extracted call parameters are shown for a single call. Spectrogram parameters: 512 fast Fourier transformation, Hann window, 50% overlap, 93-Hz frequency resolution, 3.25 ms temporal resolution. The dark band of energy below 2.5 kHz is generated by urban noise at the study site.

alarm call was recorded to the time that the sound pressure level was measured, we believe this variation was minimal relative to overall variation in ambient sound levels across sampling events and sites. Furthermore, it was not possible to conduct the measurements simultaneously, as the ambient sound level recordings would have been biased from the alarm call of the prairie dog. The sound pressure levels were downloaded with the SLM Utility-G3 and customized scripts in R were used to calculate the L_{Aeq} over 120 s associated with each recording period (see [Supplementary Material](#) for details).

Statistical analysis

To explore differences in prairie dog vocalizations across the three colonies, alarm call characteristics were initially analyzed using a one-way analysis of variance (ANOVA) with Tukey's honestly significant difference (HSD). Response variables included the four acoustic metrics described above, and the analysis calculated the mean call characteristics for each target animal, averaged across multiple barks within a bout of alarm calling. The distribution of the residuals was plotted to check that the assumptions of the model were met (e.g., normality and homogeneity). To reduce the likelihood of type 1 errors with multiple comparisons of call parameters across sites, we used an alpha level of 0.01 to assess statistical significance.

Next, a generalized linear mixed model framework using the lme4 package in R (R Core Development Team 2019) was used to understand the conditions that correlate with changes in alarm call characteristics. Response variables included the four-acoustic metrics, and characteristics of each individual bark were entered into the analyses with the individual observation number included as a random effect to account for the repeated measures (multiple barks) within a given alarm call. Akaike's Information Criterion adjusted for small sample size (AICc) was used for model selection (Burnham and Anderson 2002). A total of 29 candidate models were generated for each of the response variables using combinations of five predictor variables (Table 1). Predictor variables included the ambient sound level ($L_{Aeq, 120s}$) when the calls bouts were recorded, Julian day to establish if there was a change in response over the course of the fieldwork, distance recorded to account for variation in the distance

Table 1
Structure of candidate models assessed for the four response variables (minimum frequency, frequency 5%, peak frequency, and bark duration)

Null
Sound level
Wind speed
Julian day
Dist recorded
Dist neighbor
Sound level + Wind speed
Sound level + Julian day
Sound level + Dist recorded
Sound level + Dist neighbor
Julian day + Wind speed
Julian day + Dist recorded
Julian day + Dist neighbor
Dist recorded + Dist neighbor
Dist neighbor + Wind speed
Sound level + Julian day + Wind speed
Sound level + Julian day + Dist recorded
Sound level + Julian day + Dist neighbor
Sound level + Dist recorded + Wind speed
Julian day + Dist recorded + Wind speed
Julian day + Dist recorded + Dist neighbor
Wind speed + Dist recorded + Dist neighbor
Sound level + Windspeed + Dist recorded + Dist neighbor
Sound level + Dist neighbor + Dist recorded + Julian Day
Sound level + Windspeed + Dist recorded + Julian Day
Wind speed + Dist neighbor + Dist recorded + Julian Day
Sound level + Julian day + Wind speed + Dist recorded + Dist neighbor
Sound level × Dist recorded
Sound level × Dist Neighbor

Individual observation number was included as a random effect.

between the observer and the target animal, *wind speed* to control for the influence of fluctuating acoustic conditions, and *distance to the nearest neighbor* to determine if proximity to a conspecific influences the observed alarm call response (Table 1). Two interactions were also included to determine whether the effect of noise level exposure on acoustic parameters was modulated by distance to the observer (*ambient sound level* × *distance recorded*), and/or distance to the nearest prairie dog (*ambient sound level* × *distance to the nearest neighbor*). These predictor variables were normalized so that the relative contribution could be determined in the model-averaged output (Table 2). The AICcmoadvg package was used to extract AICc scores and model weights for candidate models of each response variable. Model averaging was conducted across models accounting for ≥0.95 of the AICc weight to extract parameter β estimates and their 95% confidence intervals (CI). The significance of the results was assessed by whether the 95% CI overlapped zero. This research was approved according to Colorado State University Animal Care and Use Committee protocol 13-4112A.

RESULTS

Pineridge Natural Area was the quietest of the three colonies with ambient sound levels of 26–50 dB $L_{Aeq,120s}$ ($N = 46$), mean = 36 dB ± 2 (95% CI), while Coyote Ridge experienced ambient sound levels of 34–54 dB $L_{Aeq,120s}$ ($N = 45$), mean = 42 dB ± 1 (95% CI) and The Coterie had the highest ambient sound levels 49–76 dB $L_{Aeq,120s}$ ($N = 47$), mean = 58 dB ± 2 (95% CI).

The minimum frequency of prairie dog alarm calls differed across the three colonies (ANOVA: $F_{2,134} = 8.703$, $P = 0.0003$); Pineridge had the lowest minimum frequency (mean = 1151 Hz ±

197 SD) followed by Coyote Ridge (1218 Hz ± 149 SD) and The Coterie (1297 Hz ± 161 SD; Figure 2a). The Tukey HSD test revealed a significant difference in minimum frequency between Pineridge and The Coterie ($P = 0.0002$), but not between Coyote Ridge and The Coterie ($P = 0.04$) and Pineridge and Coyote Ridge ($P = 0.22$). We did not detect significant differences across colonies for frequency 5% (ANOVA: $F_{2,134} = 1.694$, $P = 0.188$), peak frequency (ANOVA: $F_{2,134} = 1.442$, $P = 0.24$) or bark duration (ANOVA: $F_{2,134} = 1.648$, $P = 0.196$; Figure 2).

Minimum frequency of alarm calls was predicted by six top models, with three models contributing 63% of the AICc weight (Table 2). Ambient sound level ($L_{Aeq,120s}$) was a key parameter across these models, with increasing noise predicting elevated minimum frequency of alarm calls (Table 3). None of the other explanatory variables demonstrated a significant relationship with the minimum frequency of alarm calls (Table 3).

The frequency 5% call property was predicted by 10 top models, with three accounting for 54% of the AICc weight (Table 2). Ambient sound level ($L_{Aeq,120s}$) was not a significant predictor, with little evidence that higher noise led to a lower frequency alarm call (measured as frequency 5%) (Table 3). Frequency 5% was greater for alarm calls recorded at distances further from the observer (Dist recorded) and when calling prairie dogs were closer to the nearest neighbor (Dist Neighbor) (Table 3).

Peak frequency was predicted by 11 top models, of which three accounted for 50% of the AICc weight (Table 2). As with the analysis of frequency 5%, there was no evidence of a clear relationship between the ambient sound level and the peak frequency of the call (Table 3). Furthermore, no other variables were significant predictors of peak frequency.

Bark duration was predicted by seven top models, with three contributing 61% of the AICc weight (Table 2). No explanatory variables had a significant relationship with bark duration (Table 3).

DISCUSSION

Alarm calls provide crucial information on the presence and proximity of predatory threats—essential for prairie dogs, which are social prey species that are targeted by a number of terrestrial and aerial predators (Hoogland 1995). As such, and in line with previous research on a range of bird and marine mammal species (Shannon et al. 2016b), we predicted that prairie dogs would reduce the masking effect of urban noise by increasing the lower frequency limit of their alarm calls when exposed to elevated anthropogenic noise. The evidence for this, however, was limited. We did detect an increase in the minimum frequency of alarm calls with increasing urban noise, but there was no effect of urban noise on the frequency 5% metric, which is a more robust measure of the minimum frequency of animal vocalizations (Brumm et al. 2017). Likewise, peak frequency and bark duration of alarm calls were not related to ambient sound levels.

Previous studies have also shown that the frequency of bird vocalizations are not consistently adjusted in urban noise across species (Hu and Cardoso 2010). And even when they are modified, they can shift in the opposite direction to that predicted, that is, with lower frequency calls in noisier conditions potentially to increase transmission distance (Potvin et al. 2014). For taxa with particularly low frequency calls, it may prove too energetically costly (or physiologically challenging) to actually shift the frequency of vocalization high enough to reduce the risk of masking, while those that use higher

Table 2
Top models for the four-acoustic metrics of prairie dog alarm calls (≥ 0.95 of the AICc weight)

	K ¹	Δ AICc	AICc weight
a) Minimum frequency			
Sound level + Dist recorded + Julian Day + Dist neighbor	7	0.00	0.29
Sound level \times Dist neighbor	6	0.84	0.19
Sound level + Dist neighbor	5	1.24	0.15
Sound level + Dist recorded + Dist neighbor + Wind speed	7	1.54	0.13
Sound level + Dist recorded + Julian Day + Dist neighbor + Wind speed	8	1.70	0.12
Sound level + Julian Day + Dist neighbor	6	1.92	0.11
b) Frequency 5%			
Dist recorded + Dist neighbor	5	0.00	0.25
Julian Day + Dist recorded + Dist neighbor	6	1.12	0.15
Wind speed + Dist recorded + Dist neighbor	6	1.12	0.14
Dist recorded + Dist neighbor + Julian Day + Wind speed	7	2.11	0.09
Dist neighbor	4	2.59	0.07
Sound level + Dist recorded + Julian Day + Dist neighbor	7	2.78	0.06
Sound level + Dist recorded + Dist neighbor + Wind speed	7	2.90	0.06
Dist neighbor + Wind speed	5	3.48	0.05
Sound level + Dist recorded + Julian Day + Dist neighbor + Wind speed	8	3.71	0.04
Julian Day + Dist neighbor	5	3.81	0.04
c) Peak frequency			
Dist neighbor	4	0.00	0.19
Dist recorded \times Sound level	6	0.27	0.16
Dist recorded + Dist neighbor	5	0.49	0.15
Dist neighbor + Wind speed	5	1.12	0.11
Sound level + Dist neighbor	5	1.71	0.08
Wind speed + Dist recorded + Dist neighbor	6	1.75	0.08
Julian day + Dist neighbor	5	2.00	0.07
Julian day + Dist recorded + Dist neighbor	6	2.50	0.05
Sound level + Julian day + Dist neighbor	6	3.70	0.03
Wind speed + Dist neighbor + Dist recorded + Julian Day	7	3.76	0.03
Sound level + Windspeed + Dist recorded + Dist neighbor	7	3.76	0.03
d) Bark duration			
Dist neighbor	4	0.00	0.28
Julian day + Dist neighbor	5	1.03	0.17
Sound level + Dist neighbor	5	1.04	0.16
Dist recorded + Dist neighbor	5	1.75	0.12
Sound level + Julian Day + Dist neighbor	6	2.27	0.09
Sound level \times Dist neighbor	6	2.32	0.09
Julian day + Dist recorded + Dist neighbor	6	2.76	0.07

All models include the individual observation number as a random effect.

frequency calls are less affected by noise and therefore might not need to adjust their calls (Hu and Cardoso 2010). Prairie dogs have short duration alarm calls that extend across a broad range of frequencies from 1 kHz to >8 kHz, with a peak frequency of approximately 3.5 kHz, while the energy in urban noise is generally focused below 2.5 kHz. It may well be the case that the relatively high frequency of their vocalizations means that prairie dogs do not experience significant masking from exposure to urban noise.

While our findings of an increase in minimum frequency with rising noise level concur with previous studies, scientists have recently questioned the methods used to measure minimum frequency because they may result in false positives (Brumm et al. 2017; Ríos-Chelén et al. 2017). Indeed, the majority of studies on this topic have relied on researchers visually inspecting the spectrogram to determine the minimum vocal frequency, a method that has been shown to potentially bias the results, particularly if the observer has a priori expectations (Brumm et al. 2017; Ríos-Chelén et al. 2017). Furthermore, the signal to noise ratio in acoustic data can result in the minimum frequency being masked under elevated noise levels, resulting in artificial inflation of the observed minimum frequency (Brumm et al. 2017). It was interesting to note the marked difference in our model results for the minimum frequency

and frequency 5% metrics, further highlighting the risk of using the absolute minimum frequency when exploring vocal adjustments by animals in anthropogenic noise.

We found evidence for changes in vocal behavior related to the social context of the alarm calls. Prairie dogs that were at a greater distance from conspecifics (i.e., more isolated), and therefore may have been at a higher risk of predation, produced calls with lower frequencies. We suggest that this could be a result of reduced call amplitude, which is typically positively correlated with call frequency (Brumm and Naguib 2009; Zollinger et al. 2012; Nemeth et al. 2013)—however it is important to note that we were unable to measure alarm call amplitude in this study. Such a strategy of producing softer low-amplitude calls, documented across a range of species, can reduce eavesdropping and detection by a third party (Reichard and Anderson 2015), in this case an approaching predator in the form of a human observer. Prairie dogs also produced alarm calls with increased lower frequencies when the observer (i.e., predator threat) was further from the calling animal. Prairie dogs may elevate call amplitude, and consequently generate higher frequency calls, when predators are at a greater distance to increase the likelihood the vocalization is received across a greater area of the colony, without unduly increasing the risk to the caller. This is

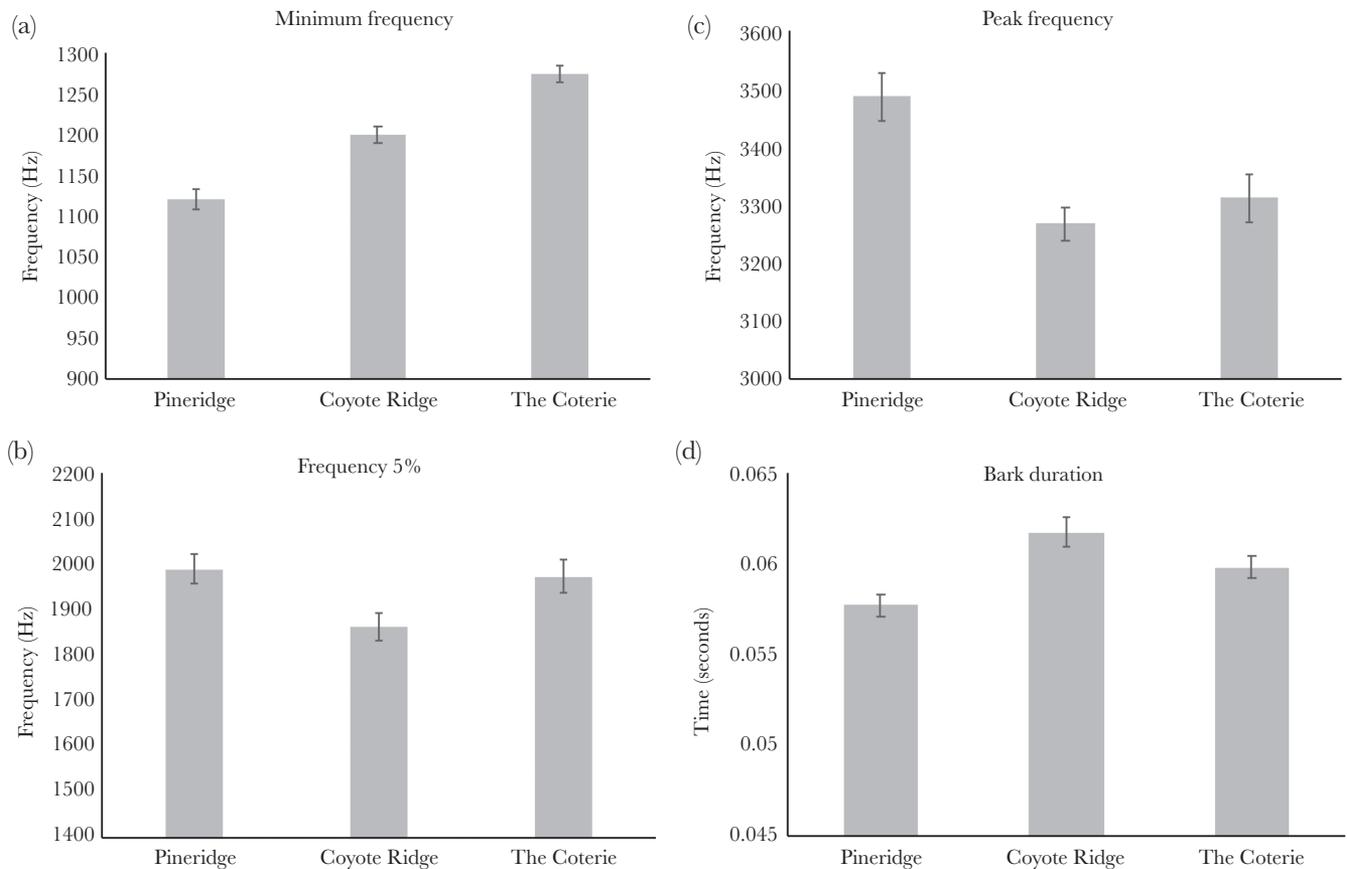


Figure 2

Mean (\pm 95% CI) values for the four acoustic metrics extracted from prairie dog calls ($n = 137$) across the three study sites with increasing noise exposure from left to right.

Table 3

The observed relationship between each response variable and the model-averaged parameters from the top models (β -estimate \pm 95% CI)

	Parameter	β Estimate (95% CI)
Minimum frequency	Sound level	67.63 (20.18/115.09)
	Dist recorded	44.16 (-0.27/88.58)
	Dist neighbor	8.10 (-33.65/49.85)
	Julian day	25.29 (-13.03/63.60)
	Wind speed	-1.27 (-6.26/3.72)
Frequency 5%	Sound level \times Dist neighbor	-40.89 (-92.22/10.44)
	Sound level	17.02 (-100.00/134.04)
	Dist recorded	125.31 (11.3/239.31)
	Dist neighbor	-144.57 (-258.96/-30.18)
	Julian day	52.54 (-52.68/157.76)
Peak frequency	Wind speed	-6.93 (-20.72/6.86)
	Sound level	-50.22 (-176.87/76.43)
	Dist recorded	69.38 (-44.69/183.46)
	Dist neighbor	-45.05 (-159.71/69.61)
	Julian day	-2.74 (-109.24/103.77)
Bark duration	Wind speed	-6.38 (-20.29/7.53)
	Sound level \times Dist neighbor	-134.37 (-274.70/5.96)
	Sound level	0.91 (-1.39/3.22)
	Dist recorded	-0.55 (-3.08/1.98)
	Dist neighbor	0.12 (-2.37/2.61)
	Julian day	-1.13 (-3.44/1.18)
	Wind speed	-0.02 (-0.33/0.28)
	Sound level \times Dis neighbor	-1.34 (-4.43/1.74)

Bold text denotes β -estimates with 95% CI that do not overlap zero.

especially pertinent given that the function of the alarm call is to both warn conspecifics of approaching danger and to communicate to the predator that they have been detected (Isbell and Bidner 2016). Additional experiments conducted by our research group demonstrated that prairie dogs adjusted their alarm calls—reducing the central concentration of energy—when calling in the presence of vulnerable pups (Wilson-Henjum et al. 2019). Adjustment in prairie dog communication, therefore, appears to be structured by social context mediated by spatial proximity to an approaching threat. However, this is an area of research that warrants further detailed investigation to reveal the specific drivers of vocal modulation.

Unlike many previous studies that have explored the effects of anthropogenic noise on communication, our research focused on alarm calls rather than songs or vocalizations that animals use to advertise their quality or fitness to conspecifics (reviewed in Shannon et al. 2016b). The effective communication distance for an alarm call in a colonial species may be significantly less than that of a call or song aimed at attracting a mate or defending a territory. Therefore, even though the ambient noise levels were considerable (mean of 58 dB at the Coterie, which is comparable to normal conversation at 1m), they may not be loud enough to sufficiently mask the alarm call from being perceived by nearby conspecifics. This raises a number of interesting future research avenues regarding the function of a given vocalization and its susceptibility to masking from anthropogenic noise, as well as the plasticity in response exhibited across taxa. It is also important to note that practical limitations meant that we only had three sites in our study design, each with a different noise exposure resulting in some level of pseudoreplication. Ideally, further research on this topic will identify multiple sites at each broad level of noise exposure.

Elucidating the specific mechanisms (e.g., distraction, masking, predatory threat, social context) driving behavioral responses to anthropogenic noise can prove challenging, particularly as they are not necessarily mutually exclusive. Nevertheless, a combination of natural experiments and playback approaches can be used to identify the key mechanisms for specific taxa, which can greatly inform our understanding of the effects of noise, as well as assist in developing effective mitigation of these impacts (Francis and Barber 2013). Our work on free-ranging prairie dogs has demonstrated that they adjust critical behaviors when exposed to noise—including increased vigilance and reduced foraging—which suggests that noise is responded to as an elevated level of perceived risk (Shannon et al. 2014). Furthermore, in contrast to a number of aquatic species (Chan et al. 2010; Wale et al. 2013; Simpson et al. 2015), prairie dogs did not exhibit distraction from an approaching predator under noisy conditions—indeed, they actually became alert and took flight sooner in traffic noise than under quieter control conditions (Shannon et al. 2016a). While the findings presented here suggest that the acoustic characteristics of prairie dog alarm calls are consistent across a broad range of ambient noise levels, indicating that masking may not be a key driver shaping their vocal behavior under these conditions.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Shannon et al. (2019).

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