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

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Abstract

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 behavioural 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 behavioural 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).

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

Introduction

Human-induced rapid environmental change is having far-reaching impacts on natural ecosystems across the globe, affecting animal behaviour, 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 behaviour and demography, with particular focus on how anthropogenic noise affects acoustic communication (Shannon, McKenna, et al. 2016).

Songbirds in particular have been the focus of numerous studies on the effects of anthropogenic noise on behaviour and communication in urban environments, due to their relative abundance, the important role of vocal communication in many aspects of their behaviour (e.g., territoriality, mate attraction and agonistic social interactions) and the established methodology for studying changes in song structure and singing behaviour (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 communication have demonstrated a range of responses to mitigate the effects of noise exposure, which include adjusting the time of vocalising (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

70   2008). These behavioural adjustments are believed to be adaptive responses that reduce

71   the masking of key signals by low frequency anthropogenic noise, which is

72   predominantly concentrated at <2KHz (Brumm et al. 2017). Furthermore, evidence

73   indicates that anthropogenic noise exposure may structure animal communities (Francis

74   et al. 2009; Proppe et al. 2013), as species that vocalise at lower frequencies with limited

75   behavioural flexibility are forced to adjust their distribution (Francis 2015). This suggests

76   responses to noise are likely conditioned on the degree of plasticity in communication

77   modalities.

78   Although the effects of anthropogenic noise on acoustic communication have

79   been studied extensively across a range of taxa, including birds, marine mammals,

80   amphibians and even invertebrates, there has been limited exploration of these effects in

81   terrestrial mammals (Shannon, McKenna, et al. 2016). Terrestrial mammals display

82   flexibility in call structures relative to social and geophysical conditions (Ey and Fischer

83   2009; Townsend and Manser 2013), and recent work has demonstrated that mongooses

84   exhibit reduced responsiveness to conspecific and heterospecific vocalisations in road

85   noise (Kern and Radford 2016; Morris-drake et al. 2017). However, studies explicitly

86   exploring the effects of noise on vocalisations have largely been limited to research on

87   bats. For example, Brazilian free-tailed bats (*Tadarida brasiliensis*) reduced the

88   bandwidth of their echolocation search calls when exposed to noise (Bunkley and Barber

89   2015), fringe-lipped bats (*Trachops cirrhosus*) shifted from targeting prey-generated

90   sources of sound to using echolocation when hunting in noise (Gomes et al. 2016), and

91   Asian particolored bats (*Vespertilio sinensis*) simplified the complexity and raised the

92   amplitude of their social calls when exposed to traffic noise (Jiang et al. 2019) but did not

93   adjust the vocal rate or duration of these vocalisations (Song et al. 2019). Other studies

94   have also explored shifts in frequency and amplitude of echolocating bats, but the

95   researchers exposed the animals to noise with a specific frequency (bandpass filtered),

96   compared with the broadband frequencies that are typical of anthropogenic noise (Hage

97   et al. 2013; Hage et al. 2014). The paucity of research on a wider range of mammal

98   species risks overlooking the impacts of a key anthropogenic stressor on terrestrial

99   systems.

100   In this paper, we explore whether a gradient of increasing urban traffic and

101 associated environmental noise affects the alarm call characteristics of black-tailed prairie

102 dogs (*Cynomys ludovicianus*) - hereafter referred to as prairie dogs. Prairie dogs are prey

103 species for a wide range of grassland predators including badgers (*Taxidea taxus*),

104 coyotes (*Canis latrans*), hawks and snakes (Hoogland 1995). Alarm calls – a series of

105 rapid high-pitched barks – provide one of the key anti-predator strategies employed by

106 this group-living species (Hoogland 1995), but the production of these calls appears to be

107 influenced by social context. For example, prairie dogs have been shown to give alarm

108 calls more readily when in the presence of kin compared to unrelated conspecifics

109 (Hoogland 1983; Hoogland 1995). This provides evidence that the seemingly costly

110 behaviour of an individual alerting a predator to their presence may have indirect fitness

111 benefits (Shelley and Blumstein 2005). Moreover, we recently demonstrated that the

112 presence of young influenced the alarm call characteristics of adult prairie dogs –

113 whereby they lowered the central concentration of energy in their calls (Wilson-Henjum

114 et al. 2019). The social context and function of alarm call production provides an

115 interesting avenue for exploring the effects of exposure to anthropogenic noise on animal

116 vocalisation, particularly when contrasted with findings from the significant body of

117 work focussing on advertisement calls and songs (reviewed by Shannon, McKenna, et al.

118 2016).

119   Although prairie dog populations across the United States have been dramatically

120 reduced as a result of land-use changes and disease (Miller, Ceballos, & Reading, 1994;

121 Miller et al., 2007), they have shown the ability to inhabit urban environments (Magle et

122 al. 2010; Magle and Fidino 2018). In common with other wildlife species that can survive

123 in human-dominated landscapes, this persistence is likely to be a function of their

124 behavioural flexibility, which allows them to adjust to the environmental conditions of

125 their surroundings (Lowry et al. 2013). Prairie dogs therefore provide an interesting study

126 species for furthering our understanding of behavioural and demographic responses to

127 anthropogenic disturbance in a social mammal. In addition to exploring vocal plasticity

128 relative to noise exposure in a free-ranging terrestrial mammal, this study also focuses on

129 a form of vocal communication that has received less attention in this field of research –

130 alarm calling to signal the presence of a perceived threat (Potvin et al. 2014; Templeton

131 et al. 2016). While calls and songs aimed at attracting mates and defending territories

132 play a crucial role in the reproductive success of an animal, alarm calls arguably have an

133 even more immediate and profound effect on fitness through the mediation of survival.

134   Our previous research found that prairie dogs exposed to noise adjusted their

135 vigilance and foraging behaviour, consistent with the risk disturbance hypothesis, which

136 predicts anthropogenic disturbance will elicit increased antipredator behaviour (Shannon

137 et al. 2014). Because of their enhanced vigilance, prairie dogs detected and responded to

138 an approaching predator quicker in noise than during the ambient control - contrary to the

139 distracted prey hypothesis (Shannon, et al., 2016). Here, we explore whether prairie dogs

140 exhibit vocal plasticity in noise – a potential mechanism to overcome acoustical masking

141 – to further illustrate how prairie dogs perceive and respond to this novel pollutant. This

142 will not only broaden the types of communication studied in the context of increasing

143 anthropogenic noise, but has implications for conserving animals in evolutionarily novel

144 environments, such as urban areas that are dramatically expanding with human

145 population growth. We predicted that prairie dogs would elevate the lower frequency

146 limit of their alarm calls when exposed to increasing road traffic noise – so as to

147 minimize acoustical masking.

148

149 **Methods**

150 *Study sites*

151 The study was conducted across three prairie dog colonies in predominantly shortgrass

152 prairie habitat located within or adjacent to the city of Fort Collins, Colorado, USA. The

153 sites were selected to provide a gradient of exposure to urban traffic and associated noise.

154 Pineridge Natural Area (250 ha), located on the western edge of the city with a small

155 country road on the northwest boundary (~750m from the center of the colony),

156 experiences the least anthropogenic noise of the three colonies and is a site that we have

157 used for previous research on prairie dog responses to road traffic noise (Shannon et al.

158 2016). Coyote Ridge Natural Area, situated close to the southwest boundary of the city, is

159 840 ha in extent and adjacent to a larger open space to the south and west; the center of

160 the prairie dog colony is located ~350m from the relatively busy County Road 19. The

161 Coterie Natural Area is a small (1.6 ha) site located within the city at the intersection of

162   two main roads (~50m to the center of the colony), resulting in considerable levels of

163   urban noise. All three of the sites can be accessed by trails that are used by walkers,

164   runners and cyclists. The prairie dogs are therefore regularly exposed to human activity.

165

166   *Alarm call measurements*

167   Prairie dog alarm calls were recorded from 28 August to 6 December 2014 using a Rode

168   NTG-2 shotgun microphone, which was connected to a Roland Moore R-05 digital

169   recorder. Data collection was carried out during daylight hours (0700 – 1900) by the

170   same single observer (GWH). Alarm calls were elicited by the observer approaching a

171   randomly selected prairie dog – with a systematic approach employed to ensure that

172   different areas of the colony (and animals) were sampled from one study site visit to the

173   next. Once the prairie dog began alarm calling the observer remained stationary and

174   recorded 30 seconds of vocalization while the animal was in situ. Distance to the target

175   animal and the distance from this individual to their nearest neighbor was measured using

176   a laser range finder. All calls were recorded within a distance of 18m from the animal

177   (mean ± SD = 9m ± 3) with small differences between sites (Pineridge = 10m ± 2, Coyote

178   Ridge = 11m ± 3, The Coterie = 8m ± 2). In order to reduce the possibility that the same

179   prairie dog was selected more than once during the same recording session, the observer

180   ensured that there was a minimum of 30m (the average size of a burrow system; Sheets et

181   al. 1971) between the individuals targeted for inclusion in the study. Wind speed and the

182   prevailing weather conditions were all documented at the time of recording. A total of

183   137 alarm call recording periods were collected across the three sites (Pineridge = 46,

184   Coyote Ridge = 44, The Coterie = 47).

185   A band-limited automated detector was used in Raven Pro v1.5 to select each of

186   the individual barks in the 30-second calling bouts and to optimize extraction of call

187   parameters. The following settings were used in the detector: minimum frequency of

188   2000 Hz, maximum frequency of 15000 Hz, minimum signal duration of 0.008 seconds,

189   maximum signal duration of 0.2 seconds, minimum separation of 0.2 seconds, minimum

190   occupancy of 30 percent, and a signal-to-noise threshold of 15 dB. Before measurements

191   were extracted on the individual barks, all detections were examined manually for

192   accuracy and adjusted to maximize the detection of all barks within a recording period

193   and to ensure the entire bandwidth and duration of calls were selected. Because prairie

194   dogs produce short duration, broadband barks, a standardized maximum frequency

195   (15000 Hz) was used for each detection box. Random selections of half of the barks in a

196   calling bout (n = 4516) were then measured.

197   Four acoustic metrics were calculated for each bark: (1) minimum frequency (Hz)

198   – the lower frequency limit of the call, a commonly used metric in previous studies; (2)

199   frequency 5% (Hz) – the frequency where the summed energy equals 5% of the total, a

200   measure of lower frequency properties; (3) peak frequency (Hz) – the frequency with the

201   highest concentration of energy; and (4) bark duration (milliseconds) (Figure 1).

202

203   *Ambient sound level measurements*

204   Ambient sound levels were measured using a calibrated Larson-Davis 831 sound

205   level meter (frequency weighting = A) over a 2-minute period as soon as the vocalization

206   recording was completed. Sound pressure levels were measured as 1-second frequency

207   weighted (12.5Hz - 20kHz) equivalent continuous levels ($L_{Aeq, 1s}$). Although ambient

208 sound levels may fluctuate slightly from the time that the alarm call was recorded to the

209 time that the sound pressure level was measured, we believe this variation was minimal

210 relative to overall variation in ambient sound levels across sampling events and sites.

211 Furthermore, it was not possible to conduct the measurements simultaneously, as the

212 ambient sound level recordings would have been biased from the alarm call of the prairie

213 dog. The sound pressure levels were downloaded with the SLM Utility-G3 and

214 customized scripts in R were used to calculate the L_{Aeq} over 120 seconds associated with

215 each recording period (see Electronic Supplementary Material for details).

216

217 *Statistical analysis*

218 To explore differences in prairie dog vocalisations across the three colonies, alarm call

219 characteristics were initially analysed using a one-way ANOVA with Tukey's HSD.

220 Response variables included the four acoustic metrics described above, and the analysis

221 calculated the mean call characteristics for each target animal, averaged across multiple

222 barks within a bout of alarm calling. The distribution of the residuals was plotted to

223 check that the assumptions of the model were met (e.g., normality and homogeneity). To

224 reduce the likelihood of type 1 errors with multiple comparisons of call parameters across

225 sites, we used an alpha level of 0.01 to assess statistical significance.

226   Next, a generalized linear mixed model (GLMM) framework using the lme4

227 package in R (R Core Development Team 2019) was used to understand the conditions

228 that correlate with changes in alarm call characteristics. Response variables included the

229 four-acoustic metrics, and characteristics of each individual bark were entered into the

230 analyses with the individual observation number included as a random effect to account

10

231   for the repeated measures (multiple barks) within a given alarm call. Akaike's

232   Information Criterion adjusted for small sample size (AICc) was used for model selection

233   (Burnham and Anderson 2002). A total of 29 candidate models were generated for each

234   of the response variables using combinations of five predictor variables (Table 1).

235   Predictor variables included the *ambient sound level* ($L_{Aeq,120s}$) when the calls bouts were

236   recorded, *Julian day* to establish if there was a change in response over the course of the

237   fieldwork, *distance recorded* to account for variation in the distance between the observer

238   and the target animal, *wind speed* to control for the influence of fluctuating acoustic

239   conditions, and *distance to the nearest neighbor* to determine if proximity to a

240   conspecific influences the observed alarm call response (Table 1). Two interactions were

241   also included to determine whether the effect of noise level exposure on acoustic

242   parameters was modulated by distance to the observer (*ambient sound level * distance*

243   *recorded*), and/or distance to the nearest prairie dog (*ambient sound level * distance to*

244   *the nearest neighbor*). These predictor variables were normalized so that the relative

245   contribution could be determined in the model averaged output (Table 2). The

246   AICcmodavg package was used to extract AICc scores and model weights for candidate

247   models of each response variable. Model averaging was conducted across models

248   accounting for ≥0.95 of the AICc weight to extract parameter β estimates and their 95%

249   confidence intervals (CI). The significance of the results was assessed by whether the

250   95% CI overlapped zero. This research was approved according to Colorado State

251   University Animal Care and Use Committee protocol 13-4112A.

252

253

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

277 a significant predictor, with little evidence that higher noise led to a lower frequency

278 alarm call (measured as frequency 5%) (Table 3). Frequency 5% was greater for alarm

279 calls recorded at distances further from the observer (Dist recorded) and when calling

280 prairie dogs were closer to the nearest neighbour (Dist Neighbor) (Table 3).

281   Peak frequency was predicted by 11 top models, of which three accounted for

282 50% of the AICc weight (Table 2). As with the analysis of frequency 5%, there was no

283 evidence of a clear relationship between the ambient sound level and the peak frequency

284 of the call (Table 3). Furthermore, no other variables were significant predictors of peak

285 frequency.

286   Bark duration was predicted by 7 top models, with three contributing 61% of the

287 AICc weight (Table 2). No explanatory variables had a significant relationship with bark

288 duration (Table 3).

289

290 **Discussion**

291 Alarm calls provide crucial information on the presence and proximity of predatory

292 threats – essential for prairie dogs, which are social prey species that are targeted by a

293 number of terrestrial and aerial predators (Hoogland 1995). As such, and in line with

294 previous research on a range of bird and marine mammal species (Shannon, McKenna, et

295 al. 2016), we predicted that prairie dogs would reduce the masking effect of urban noise

296 by increasing the lower frequency limit of their alarm calls when exposed to elevated

297 anthropogenic noise. The evidence for this, however, was limited. We did detect an

298 increase in the minimum frequency of alarm calls with increasing urban noise, but there

299 was no effect of urban noise on the frequency 5% metric, which is a more robust measure

300 of the minimum frequency of animal vocalisations (Brumm et al. 2017). Likewise, peak

301 frequency and bark duration of alarm calls were not related to ambient sound levels.

302 Previous studies have also shown that the frequency of bird vocalisations are not

303 consistently adjusted in urban noise across species (Hu and Cardoso 2010), and even

304 when they are modified, they can shift in the opposite direction to that predicted, i.e. with

305 lower frequency calls in noisier conditions potentially to increase transmission distance

306 (Potvin et al. 2014). For taxa with particularly low frequency calls, it may prove too

307 energetically costly (or physiologically challenging) to actually shift the frequency of

308 vocalisation high enough to reduce the risk of masking, while those that use higher

309 frequency calls are less affected by noise and therefore might not need to adjust their calls

310 (Hu and Cardoso 2010). Prairie dogs have short duration alarm calls that extend across a

311 broad range of frequencies from 1 kHz to >8 kHz, with a peak frequency of

312 approximately 3.5 kHz, while the energy in urban noise is generally focussed below 2.5

313 kHz. It may well be the case that the relatively high frequency of their vocalisations

314 means that prairie dogs do not experience significant masking from exposure to urban

315 noise.

316 While our findings of an increase in minimum frequency with rising noise level

317 concur with previous studies, scientists have recently questioned the methods used to

318 measure minimum frequency because they may result in false positives (Ríos-Chelén et

319 al. 2017; Brumm et al. 2017). Indeed, the majority of studies on this topic have relied on

320 researchers visually inspecting the spectrogram to determine the minimum vocal

321 frequency, a method that has been shown to potentially bias the results, particularly if the

322 observer has *a priori* expectations (Ríos-Chelén et al. 2017; Brumm et al. 2017).

323   Furthermore, the signal to noise ratio in acoustic data can result in the minimum

324   frequency being masked under elevated noise levels, resulting in artificial inflation of the

325   observed minimum frequency (Brumm et al. 2017). It was interesting to note the marked

326   difference in our model results for the minimum frequency and frequency 5% metrics,

327   further highlighting the risk of using the absolute minimum frequency when exploring

328   vocal adjustments by animals in anthropogenic noise.

329   We found evidence for changes in vocal behaviour related to the social context of the

330   alarm calls. Prairie dogs that were at a greater distance from conspecifics (i.e. more

331   isolated), and therefore may have been at a higher risk of predation, produced calls with

332   lower frequencies. We suggest that this could be a result of reduced call amplitude, which

333   is typically positively correlated with call frequency (Brumm and Naguib 2009; Zollinger

334   et al. 2012; Nemeth et al. 2013) – however it is important to note that we were unable to

335   measure alarm call amplitude in this study. Such a strategy of producing softer low-

336   amplitude calls, documented across a range of species, can reduce eavesdropping and

337   detection by a third-party (Reichard and Anderson 2015), in this case an approaching

338   predator in the form of a human observer. Prairie dogs also produced alarm calls with

339   increased lower frequencies when the observer (i.e., predator threat) was further from the

340   calling animal. Prairie dogs may elevate call amplitude, and consequently generate higher

341   frequency calls, when predators are at a greater distance to increase the likelihood the

342   vocalisation is received across a greater area of the colony, without unduly increasing the

343   risk to the caller. This is especially pertinent given that the function of the alarm call is to

344   both warn conspecifics of approaching danger and to communicate to the predator that

345   they have been detected (Isbell and Bidner 2016). Additional experiments conducted by

346   our research group demonstrated that prairie dogs adjusted their alarm calls – reducing

347   the central concentration of energy – when calling in the presence of vulnerable pups

348   (Wilson-Henjum et al. 2019). Adjustment in prairie dog communication, therefore,

349   appears to be structured by social context mediated by spatial proximity to an

350   approaching threat. However, this is an area of research that warrants further detailed

351   investigation to reveal the specific drivers of vocal modulation.

352   Unlike many previous studies that have explored the effects of anthropogenic

353   noise on communication, our research focussed on alarm calls rather than songs or

354   vocalisations that animals use to advertise their quality or fitness to conspecifics

355   (reviewed in Shannon, McKenna, et al. 2016). The effective communication distance for

356   an alarm call in a colonial species may be significantly less than that of a call or song

357   aimed at attracting a mate or defending a territory. Therefore, even though the ambient

358   noise levels were considerable (mean of 58 dB at the Coterie, which is comparable to

359   normal conversation at 1m), they may not be loud enough to sufficiently mask the alarm

360   call from being perceived by nearby conspecifics. This raises a number of interesting

361   future research avenues regarding the function of a given vocalisation and its

362   susceptibility to masking from anthropogenic noise, as well as the plasticity in response

363   exhibited across taxa. It is also important to note that practical limitations meant that we

364   only had three sites in our study design, each with a different noise exposure resulting in

365   some level of pseudoreplication. Ideally, further research on this topic will identify

366   multiple sites at each broad level of noise exposure.

367   Elucidating the specific mechanisms (e.g., distraction, masking, predatory threat,

368   social context) driving behavioural responses to anthropogenic noise can prove

369 challenging, particularly as they are not necessarily mutually exclusive. Nevertheless, a

370 combination of natural experiments and playback approaches can be used to identify the

371 key mechanisms for specific taxa, which can greatly inform our understanding of the

372 effects of noise, as well as assist in developing effective mitigation of these impacts

373 (Francis and Barber 2013). Our work on free-ranging prairie dogs has demonstrated that

374 they adjust critical behaviours when exposed to noise – including increased vigilance and

375 reduced foraging – which suggests that noise is responded to as an elevated level of

376 perceived risk (Shannon et al. 2014). Furthermore, in contrast to a number of aquatic

377 species (Chan et al. 2010; Wale et al. 2013; Simpson et al. 2015), prairie dogs did not

378 exhibit distraction from an approaching predator under noisy conditions – indeed, they

379 actually became alert and took flight sooner in traffic noise than under quieter control

380 conditions (Shannon et al. 2016). While the findings presented here suggest that the

381 acoustic characteristics of prairie dog alarm calls are consistent across a broad range of

382 ambient noise levels, indicating that masking may not be a key driver shaping their vocal

383 behaviour under these conditions.

384

Data accessibility: Analyses reported in this article can be reproduced using the data

provided by Shannon et al. (2019).

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544   **Figure legends**

545   **Figure 1.** Spectrogram of black-tailed prairie dog alarm calls collected from the colony at

546   The Coterie Natural Area. The extracted call parameters are shown for a single call.

547   Spectrogram parameters: 512 fast Fourier transformation, Hann window, 50% overlap,

548   93-Hz frequency resolution, 3.25 ms temporal resolution. The dark band of energy below

549   2.5 kHz is generated by urban noise at the study site.

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551   **Figure 2.** Mean ($\pm$ 95% CI) values for the four acoustic metrics extracted from prairie

552   dog calls (n = 137) across the three study sites with increasing noise exposure from left to

553   right.

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Table 1. Structure of candidate models assessed for the four response variables

566 (minimum frequency, frequency 5%, peak frequency and bark duration). Individual

567 observation number was included as a random effect.

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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 neighbour + Wind speed
Sound level + Julian day + Wind speed
Sound level + Julian day + Dist recorded
Sound level + Julian day + Dist neighbour
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 neighbour + Dist recorded + Julian Day
Sound level + Windspeed + Dist recorded + Julian Day
Wind speed + Dist neighbour + Dist recorded + Julian Day
Sound level + Julian day + Wind speed + Dist recorded + Dist neighbor
Sound level * Dist recorded
Sound level * Dist Neighbor

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570 **Table 2.** Top models for the four-acoustic metrics of prairie dog alarm calls (≥0.95 of the

571 AICc weight). All models include the individual observation number as a random effect.

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	K	ΔAICc	AICc weight
a) Minimum frequency			
Sound level + Dist recorded + Julian Day + Dist neighbor	7	0.00	0.29
Sound level * Dist neighbor	6	0.84	0.19
Sound level + Dist neighbor	5	1.24	0.15
Sound level + Dist recorded + Dist neighbour + 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
a) 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
b) Peak frequency			
Dist neighbour	4	0.00	0.19
Dist recorded * Dist neighbor	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

c) 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 * Dist neighbor	6	2.32	0.09
Julian day + Dist recorded + Dist neighbor	6	2.76	0.07

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589 **Table 3.** The observed relationship between each response variable and the model-

590 averaged parameters from the top models (β-estimate ±95% CI). Bold text denotes β-

591 estimates with 95% CI that do not overlap zero.

592

	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)
	Sound level * Dist neighbor	-40.89	(-92.22 / 10.44)
Frequency 5%	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)
	Wind speed	-6.93	(-20.72 / 6.86)
Peak frequency	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)
	Wind speed	-6.38	(-20.29 / 7.53)
	Sound level * Dist neighbor	-134.37	(-274.70 / 5.96)
Bark duration	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 * Dis neighbor	-1.34	(-4.43 / 1.74)

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