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ARTICLE

Alarm call modification by prairie dogs in the presence of juveniles

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Abstract

While several drivers of wildlife alarm calls have been identified, recent work on the impact of the audience on the plasticity of alarm calling indicates that intraspecific communication can drive this behavior. We build on this literature by assessing changes in call characteristics in black-tailed prairie dogs (*Cynomys ludovicianus*) in the presence of recently emerged juveniles. Alarm calls were elicited by approaching individuals, and then recorded using a shotgun microphone. Presence and distance of pups were noted prior to recording. Alarm calls were analyzed for changes in spectral and temporal characteristics relative to those of adults that were not in the immediate presence of pups. Our analyses indicated that adult prairie dogs lowered the central concentration of energy in their alarm calls when calling in the presence of pups. This may show that prairie dogs are conscious of the type of alarm call produced based on the behavioral context of calling and potentially the audience receiving the message. Furthermore, this may support the hypothesis that alarm calling is intended to reach conspecifics, rather than to send a message to the predator itself.

Keywords *Cynomys ludovicianus* · Vocal plasticity · Signal receiver · Audience affect · Acoustic ecology · Black-tailed prairie dog · Altruism · Call characteristics

Introduction

Alarm calling in wildlife is a seemingly counterintuitive behavior that appears to increase the risk of predation to the signaler (Taylor et al. 1990). The evolutionary maintenance of this behavior has been explained through applications of theories such as Smith's (1965) kin selection (e.g., Griesser and Ekman 2004) and Trivers' (1971) reciprocal altruism (e.g., Krams et al. 2006). Under these contexts, alarm calls are considered altruistic since the signaler is put at risk and others gain a fitness benefit (Smith 1965). However, other hypotheses posit that alarm calls do not increase the risk of predation to the signaler (Sherman 1985), suggesting other functions of alarm calling than altruism. For instance, alarm calls in some rodents are directed at predators, with conspecifics secondarily benefitting (Shelley and Blumstein 2004). Additionally, some alarm calls used to elicit mobbing behavior are debatably delivered with selfish intent, as the signaler summons conspecifics to protect itself from potentially being predated upon (Wheeler 2008). Finally, some individuals alter alarm calls based on the audience present, suggesting multiple motivations for alarm calling, as well as conscious

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control of the message to be delivered (Marler et al. 1986; Townsend et al. 2012; reviewed in Zuberbühler 2009).

Black-tailed prairie dogs (*Cynomys ludovicianus*) are known for their high degree of sociality, manifesting in tight-knit colonies, called "coteries" (Hoogland 1995). Vocalizations are part of prairie dog sociality, often used to manipulate an interaction between two individuals, such as one coterie member rejecting another coterie member's attempt to allogroom, or defending territory from a member of a different coterie (Smith et al. 1977). Prairie dogs also exhibit a more functionally complex "jump-yip" signal, named for the high-pitched squeak and associated front limb extension, which is used to communicate various circumstances, such as the end of a predatory threat (King 1955; Smith et al. 1977; Hoogland 1995) or as a general contact call (Waring 1970). Coterie members altruistically alert others to the presence of potential predators using alarm calls, significantly reducing predation compared to that of other species within the same genus that do not share this behavior, ultimately increasing overall survival and reproductive rates (Hoogland 1981). Black-tailed prairie dogs code specific information within their alarm calls pertaining to the specific nature of the threat (e.g., aerial versus terrestrial predator) (Frederiksen and Slobodchikoff 2007), allowing coterie members to respond appropriately. Additionally, prairie dogs add another layer of complexity to their signaling by calling more frequently in the presence of their offspring (Hoogland 1983), suggesting an element of kin selection (Hamilton 1964). Thus far, other call properties (e.g., frequency spectra and acoustic energy allocation) in relation to offspring presence have not been investigated.

In this study, we explored whether adult black-tailed prairie dogs (herein "prairie dogs") adjust anti-predatory alarm calls in the presence of pups. We recorded anti-predator alarm calls from multiple adults elicited by human approaches to prairie dogs at two coteries in Fort Collins, Colorado. We tested whether differences exist in the peak and 5th percentile frequency (spectral call traits), as well as whether the duration of call notes and duration between call notes (temporal call traits) were related to social context. Given previous research suggesting that alarm calling in this species provides benefits to conspecifics, we use these data to test if call properties change relative to the presence of pups in the vicinity of the caller. We hypothesize that properties of alarm calls in response to human approaches will change relative to the social context in which the call is elicited, indicating that calls are directed at conspecifics rather than predators. In contrast, alarm call properties that do not change across different social circumstance suggest that social context does not affect calls, and indicate that calls are directed at predators. We derive several predictions about the manner in which the temporal and spectral characteristics of prairie dog calls could be altered so as not to attract predators directly to kin.

Materials and methods

Study sites

We recorded anti-predator alarm calls from prairie dogs in coteries in Pineridge Natural Area (herein "Pineridge"; 40°33′04.0″N, 105°08′33.7″W) and Coterie Natural Area (herein "Coterie"; 40°33′59.5″N, 105°02′29.3″W) in Fort Collins, Colorado. Pineridge is a 250-ha natural area that transitions from a short-grass steppe to foothill shrub ecosystem. Recreational users such as mountain bikers, joggers, and walkers largely dominate human usage at this site. The area east of this site is well developed with housing, but otherwise adjacent land remains largely undeveloped. Pineridge's prairie dog colony spans approximately 40 ha. Coterie is a 1.6-ha natural area located at the intersection of two roads with heavy traffic. The site also has human usage on paved walking and biking trails. The prairie dog colony living within Coterie extends beyond the natural area's boundaries, and covers a total area of 1 ha. Both sites are short-grass prairie habitat with a similar vegetation structure of grasses close cropped by prairie dog grazing.

Data collection

Recordings of prairie dogs delivering anti-predator calls were collected beginning in early May 2015 when pups first emerged from their burrows and continued through mid-June of the same year. During this time, pups were able to leave the burrows on their own, but stayed nearby since they still rely on maternal care at this age (Hoogland 1995).

To elicit an anti-predator call response, the researcher (G. W. H.) approached all prairie dogs to within 20 m. Once an individual began alarm calling, a 30-s sample of their alarm call was recorded, while keeping the shotgun microphone pointed < 45° away from the focal individual to maintain the highest signal-to-noise ratio possible. Recordings were collected on days with no precipitation and wind speeds < 5 m/s using a standard focal recording set up that included a handheld Rode NTG-2 shotgun microphone attached to a Roland Moore R-05 digital audio recorder [16-bit, 48-kHz sampling rate, Waveform audio file format (WAV)]. Prairie dogs maintain short vegetation structure within coteries to maximize predator detection (King 1955; Hoogland 1995). All recordings took place internally with regards to the coterie, where prairie dogs maintain the vegetative structure, and thus there was minimal acoustical interference by vegetation or heterogeneity in vegetation structure. Since none of the prairie dogs were uniquely marked, preventing us from confidently identifying individuals, we took measures to reduce the likelihood of recording any single individual more than once per day. To do this, we only gathered recordings from individuals that were separated by at least 50 m, as the average burrow length is 30 m (Sheets et al. 1971). In turn, only a few individuals (between one and six individuals) were recorded per day at a site. Furthermore, to reduce the chance of recording the same individual twice, notes were taken about where in the coteries a recording was taken, in order not to record at the same burrow outlet twice.

Alarm calls are characterized by repetitive call notes (Fig. 1), typically with 0.15–1.5 s between call notes (Waring 1970) and, based on this patterned structure, are completely distinguishable from call notes delivered for other non-anti-predatory reasons. A minimum recording of 30 s was established based on observed approximate average alarm-calling bout length prior to a fleeing response. The 30-s recordings yielded an average of 68 ± 1.78 individual call notes. After recordings were collected, a Laser Tech TruPulse 360B digital range finder was used to determine the distance between the recording location and focal prairie dog, as well as the distance between the nearest pup and the focal prairie dog.

Alarm call measurements

Spectrograms of all recordings were visualized in the audio analysis program Raven Pro version 1.5 (1024 fast Fourier transformation, Hann window, 50% overlap, 43-Hz frequency resolution, 11-ms temporal resolution). A total of fifty-one, 30-s alarm call recordings were collected at each site. For ten recordings (Coterie, $n = 9$; Pineridge, $n = 1$), the gain level setting on the audio recorder was different from that for the rest of the recordings, so these recordings were not used for frequency analyses, but were retained for temporal measures. We employed the band-limited energy detector function in Raven to automatically highlight all call notes within a recording. The detector settings were set as such to search for potential call notes within a frequency range of 2000–6000 Hz, a signal duration range of 0.008-0.2 s, a minimum separation between successive call notes of 0.2 s, a signal-to-noise minimum occupancy of 30%, and a signal-to-noise threshold of 15 dB. All automatic detections were then manually examined for accuracy with some adjustments made to fully capture all call notes within a recording. To maintain objective standardization for the impulsive call notes even when manually adjusting the automatic detections, a standardized maximum frequency (15,000 Hz) was used for each detection box.

We randomly subsampled half of the call notes in each recording to be used during analyses of acoustic parameters. Subsampled detections were adjusted in the Raven software to ensure the entire bandwidth and duration of call notes were measured accurately. The same spectrogram parameters were used when making adjustments. Call notes were analyzed for the spectral traits peak frequency (frequency with the highest concentration of energy; Hertz) and the 5th percentile frequency (frequency with the lowest 5% concentration of energy; Hertz). We selected peak frequency because it represents the section of call notes where prairie dogs place the most energy, and the 5th percentile frequency because it is a robust measurement of the lowest frequency of the call note [for bias in "by-eye practice" minimum frequency measurements, see Ríos-Chelén et al. (2017)]. The temporal call traits analyzed included call note duration (length of each call note; seconds) and inter-call note

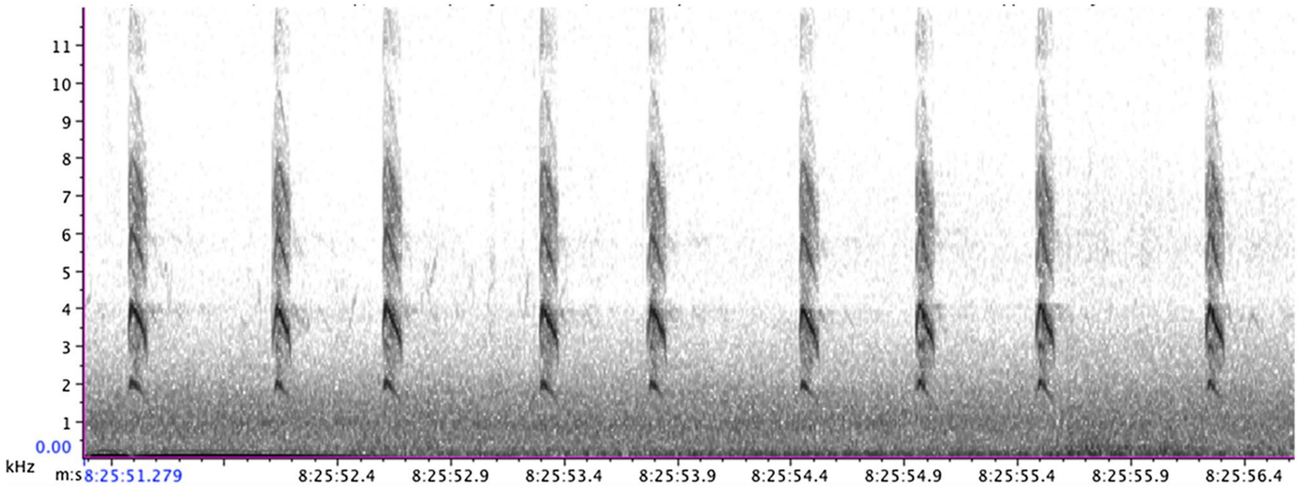

Fig. 1 Spectrogram of a typical black-tailed prairie dog's alarm call generated in Raven Pro version 1.5. Spectrogram settings include: 1024 fast Fourier transformation, Hann window, 50% overlap, 43-Hz frequency resolution, 11-ms temporal resolution. Waveform audio file format file available in Supplementary Material

interval (time between each call note; seconds). The inter-call note interval was analyzed for changes in the variance, as it was observed during recordings that adults produced less rhythmic alarm calls in the presence of pups.

Statistical analysis

We used generalized linear regression models to assess factors that relate to alarm call acoustic properties. We explored four response variables in four separate models: peak frequency, 5th percentile, call note duration, and inter-call note interval. The influence of pup presence (a binary variable indicating if pups were observed within 30 m of a focal individual), site (Pineridge or Coterie), distance from observer to focal individual, wind speed (meters/seconds), and Julian date on these spectral and temporal alarm call response variables were explored.

Parameters were initially examined for patterns of normality and heteroscedasticity, and response variables 5th percentile frequency, call note duration, and inter-call note interval were transformed using a Box–Cox transformation to meet model assumptions. We used information theoretic approaches to compare the performance of models using different covariates for each response variable. Models were ranked according to bias-adjusted Akaike's information criteria for small sample sizes (AICc) and AIC weights, where initial models included all listed predictor variables. Where models were marginally different (difference in AIC weight < 0.95), parameter coefficients in secondary models were inspected for influence (95% confidence intervals did not overlap zero). Results from the top ranked models for each response variable were used to interpret relationships as in all cases the additional parameters in secondary models were weakly informative (Table 1). All models were run using R version 3.0.1 (R Core Team 2013), Box–Cox transformations were performed using the package car (Fox and Weisberg 2011), and AIC model selection was performed using the package AICcmodavg (Mazerolle 2017).

Results

A total of 2820 call notes from 81 individuals were analyzed for characteristics of the acoustic properties. We found wide variation in both spectral and temporal traits of call notes produced by adults (Table 2). For spectral traits, peak frequency and 5th percentile frequency varied by ~ 2000 Hz. We found that peak frequency at both recording sites was significantly reduced when pups were present (Table 3). Peak frequency in the presence of pups decreased ~ 228 Hz compared to without pups [$t_{(df=78)} = -2.246$; $P = 0.03$; Fig. 2]. Site did not have a significant impact on peak frequency

Table 1 Akaike's information criteria for small sample size (*AICc*) model selection results

Model	AICc	ΔAICc	Log likelihood
Peak frequency			
Site + PupPresence[a]	2619.4	0.0	− 1305.4
Site + PupPresence + RecorderDistance	2621.6	2.2	− 1305.4
Site + Wind + PupPresence + RecorderDistance	2623.9	4.5	− 1305.4
Site + JulianDate + Wind + PupPresence + RecorderDistance	2662.0	42.5	− 1292.0
5th percentile frequency			
Site + Wind + RecorderDistance	1208.2	0.0	− 598.7
Site + Wind + PupPresence + RecorderDistance[a]	1209.6	1.4	− 598.2
Site + JulianDate + Wind + PupPresence + RecorderDistance	1238.9	30.7	− 580.5
Call note duration[b]			
Site + RecorderDistance[a]	− 666.2	0.0	− 328.8
Site + PupPresence + RecorderDistance	− 668.4	2.2	− 328.8
Site + Wind + PupPresence + RecorderDistance	− 670.8	4.6	− 328.8
Site + JulianDate + Wind + PupPresence + RecorderDistance	− 714.3	48.1	− 318.2
Inter-call note interval variance			
RecorderDistance	50.2	0.0	− 21.9
Wind + RecorderDistance[a]	51.4	1.2	− 21.5
Wind + PupPresence + RecorderDistance	53.6	3.4	− 21.4
Site + Wind + PupPresence + RecorderDistance	55.9	5.7	− 21.4
Site + JulianDate + Wind + PupPresence + RecorderDistance	105.4	55.2	− 13.7

[a] Final model

[b] Top two models for call note duration were indistinguishable from each other, but the most parsimonious model was selected as the final model

Table 2 Summary of the range and average values of alarm calls recorded during this study ($n = 2820$ call notes analyzed, from 81 individuals)

Response variables	Range	$\bar{x} \pm$ SE
Peak frequency (Hz)	2002.8–4089.2	3304.9 ± 45.1
Fifth percentile frequency (Hz)	1249.4–3294.9	2010.1 ± 45.8
Call note duration (s)	0.033–0.147	0.06 ± 0.002
Inter-call note interval variance (s)	0.0002–2.18	0.05 ± 0.03

(Table 3). None of our predictor variables explained variation in the 5th percentile frequency (Table 3).

For temporal traits, call note duration varied by ~ 0.1 s between individuals, or approximately 78%, while the variance of the inter-call note interval was quite wide, ranging from 0.002 to 2.18 (Table 2). We found evidence for differences in call note duration between the two recording sites (Table 3). Prairie dogs at the Coterie had a significantly longer call note duration than those at Pineridge [$t_{(df=78)} = -2.341$; $P < 0.02$; Fig. 3], with call notes ~ 0.013 s longer. Recorder distance had no significant impact on call note duration (Table 3). Pup presence did not significantly affect any of the temporal parameters we looked at (Table 3).

Discussion

We explored the possibility of a tradeoff between prairie dogs warning conspecifics of a threat, and avoiding attracting predators to juveniles. Specifically, we tested if adults directly alter anti-predator calls in the presence of pups. Generally, we found a large variation in call note structure and pattern, including a peak frequency range of ~ 2000 Hz, and up to a 78% longer call note duration based on the site of recording. In terms of our hypothesis, we found that individuals shift the central concentration of energy of calls (peak frequency) in the presence of pups.

It is known that the directionality of very low and very high frequency sounds relative to hearing sensitivities are more difficult to detect. In lab experiments, this phenomenon has been observed in humans (Carlile et al. 1999), as well as in smaller, rodent species such as the guinea pig (*Cavia porcellus*) (Carlile and Pettigrew 1987). Because attempted predation events were not part of our experiment (i.e., predator elicitation was caused by an observer walking up to the subject), no predator detection of prey or predator-evasion outcome could be observed. Call characteristics and associated behavioral changes in relation to the presence of newborns have been found in other closely related social sciurid species. Adult Gunnison prairie dog (*Cynomys gunnisoni*) alarm calls have a lower dominant frequency during the pre-monsoon season relative to the post-monsoon season when controlling for vegetative structure (Perla and Slobodchikoff 2002). It is speculated that changes in juvenile dependency on adults from the pre- to post-monsoon season drives the change in adult alarm calling; during the pre-monsoon season while juveniles are heavily dependent on adults, call characteristics are seemingly adjusted for shorter attenuation

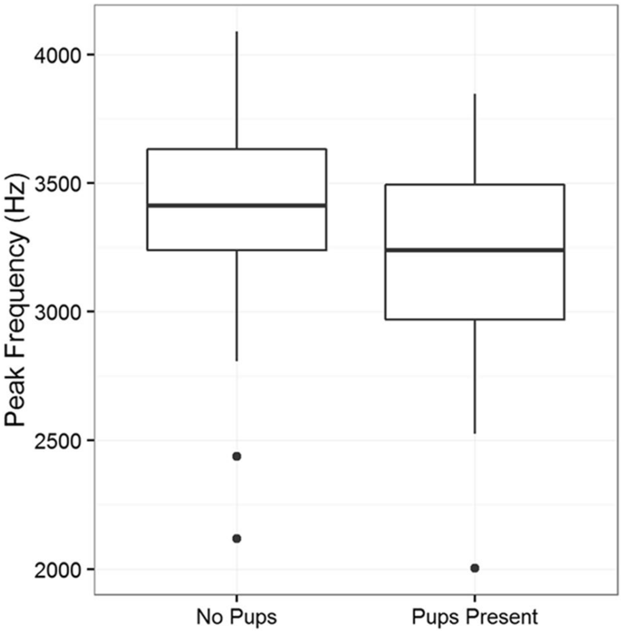

Fig. 2 Call note peak frequency (presented as raw data without transformation) decreased in the presence of pups for both study sites

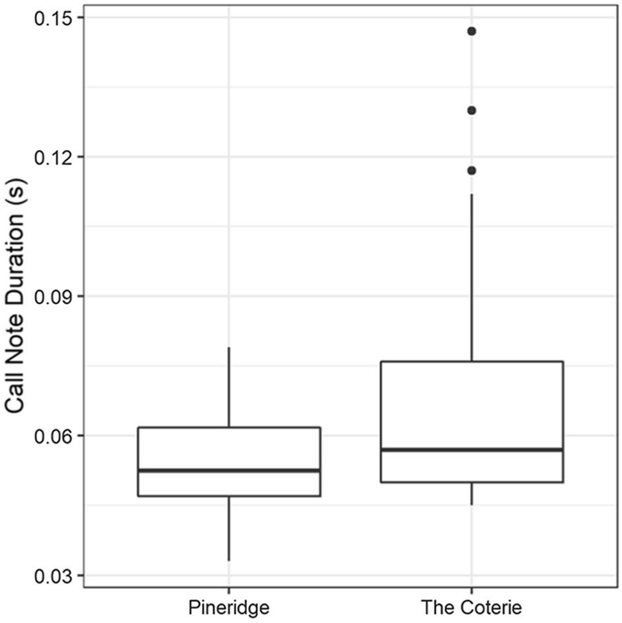

Fig. 3 Call note duration was significantly greater at Coterie Natural Area, the study site with more anthropogenic disturbance

Table 3 Results of the generalized linear regression models examining the effects that site, pup presence, wind speed, and recorder distance have on spectral and temporal measurements of alarm calls

Call characteristic	Variable	Estimate ± SE	$t_{(df)}$	P
Peak frequency (Hz)	Site	− 668,340 ± 579,031	$-1.154_{(78)}$	0.25
	Pup presence	− 1,293,168 ± 575,821	$-2.246_{(78)}$	0.03*
Fifth percentile (Hz)	Site	− 176.8 ± 110.2	$-1.604_{(76)}$	0.11
	Pup presence	− 93.0 ± 97.7	$-0.952_{(76)}$	0.34
	Wind	− 29.9 ± 25.3	$-1.179_{(76)}$	0.24
	Recorder distance	− 35.1 ± 22.3	$-1.575_{(76)}$	0.12
Call note duration (s)	Site	− 8.4 ± 3.6	$-2.341_{(78)}$	0.02*
	Recorder distance	0.4 ± 0.8	$0.496_{(78)}$	0.62
Inter-call note variance	Wind	0.02 ± 0.02	$0.979_{(78)}$	0.33
	Recorder distance	0.02 ± 0.02	$1.282_{(78)}$	0.20

* $P \leq 0.05$

and rapid degradation over short distances, while later in the season this is adjusted for longer attenuation as juveniles become more independent (Perla and Slobodchikoff 2002). Our findings provide additional support for the hypothesis that changes in dominant frequency can be related to pup dependency. Furthermore, Belding's ground squirrel (*Urocitellus beldingi*) mothers exhibit greater responsiveness to alarm calls compared to non-maternal females (Leger and Owings 1978). Given that prairie dog call notes are broadband in frequency, it is unclear whether a shift in energy concentration would impact a predator's ability to detect the source of an alarm call. The possibility also remains that this relatively small shift in peak frequency does not amount to a functional biological response.

If adjusted alarm calls are more difficult for a predator to localize, then this may imply that kin selection is the driver of alarm call evolution in prairie dogs. Additionally, the observed differences in call properties when pups are present may imply that there is an audience effect (see Introduction) that structures prairie dogs alarm calls. Irrespective of the mechanism driving the changes that we observed, our results support the hypothesis that phenotypic plasticity evolved in prairie dog vocalization behavior rather than directional selection. Our results raise questions for future studies regarding the quality of alarm calling and predator response in the presence of pups. Is alarm call efficacy for other conspecifics sacrificed in the presence of pups? With an actual predator threat, do altered alarm calls protect kin from being targeted?

In addition to our findings regarding pup presence, we also found that site influenced call note duration during alarm calls. Prairie dogs in our more urban site (Coterie) exhibited slight but significantly longer call note duration than those at our less developed site (Pineridge). The colony at Pineridge spans 40 ha, and the colony at Coterie spans 1 ha. In sciurid taxa, individual vocal complexity is driven by social group size (Pollard and Blumstein 2012). Thus, the significant difference in colony size and special confinement could be driving the differences in call note duration between Pineridge and Coterie.

Alternatively, in vertebrates, spatially distant populations of the same species can have variation in calls and songs, which are known as dialects [e.g., in sperm whales (*Physeter microcephalus*) (Whitehead et al. 1998); chimpanzees (*Pan troglodytes*) (Mitani et al. 1992;) and many birds species (Marler and Tamura 1962; Jenkins 1978; Bowman 1979)]. While our study sites are separated by only 10 km, they are geographically isolated from one another, and it is possible that local dialects have developed. Two major driving mechanisms of dialect development include the young learning calls from adults around them, which gradually diverge amongst isolated populations [e.g., northern cardinal (*Cardinalis cardinalis*) (Lemon 1975); white-crowned sparrow (*Zonotrichia leucophrys*) (Marler 1970)]; or that physiological or morphological divergences may have developed between two populations, leading to differences in call structure [Atlantic canary (*Serinus canarius*) (Nottebohm et al. 1976)].

Call duration also increases in the presence of increased noise (Lombard 1911; Hotchkin and Parks 2013), hypothesized as an anti-masking behavior. For example, killer whales (*Orcinus orca*) have been found to increase the duration of call notes in the presence of increased anthropogenic noise (Foote et al. 2004). Since Coterie sits at the intersection of two major roads, it is possible that the influence of louder anthropogenic sound is related to longer call note duration here. However, we cannot say whether or not this was the case given that we only examined two small study sites and did not analyze background sound levels to evaluate the acoustic environment. It is also important to note that, although statistically significant, the difference in duration was small enough that it may not have biological significance. Recent studies have shown that anthropogenic noise can alter the dwarf mongoose's (*Helogale parvula*) ability to receive and appropriately respond to heterospecific alarm signals (Morris-Drake et al. 2017). While our study did not take into account receiver response between the two sites, future studies that focus on how anthropogenic noise may impact coterie members' responses to alarm calls are merited.

It is important to note that it is unclear if the changes in peak frequency and call note duration relate to differences in the function of produced sounds, size of the animal, or orientation with respect to the microphone. In addition, spectral differences above the peak frequency may indicate that not all the measurements were made precisely on the acoustic axis of the animal and so may include some off-axis distortion (Au 1993; Dantzker et al. 1999). However, this seems unlikely given that attempts were made to make recordings in a standardized manner.

Understanding the plasticity of vocal communication in wildlife gives us insight into the evolutionary drivers of this behavior, which will ultimately provide guidance for conservation concerns. Our findings suggest prairie dogs demonstrate vocal plasticity in the face of a predatory threat when in the presence of kin. This serves to support several theories related to alarm calling, namely that kin selection is a driver for alarm calling in prairie dogs, and that flexibility in alarm calling exists based on the audience receiving the alarm calls. Furthermore, our findings support the idea that behavioral plasticity exists in wildlife vocalizations, rather than long-term adaptions to changing environments. Finally, the findings of this study also give rise to important applied questions regarding the quality and efficacy of modified signals in mammals, particularly where their environment is encroached upon by increasing urbanization.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This research was approved according to Colorado State University Animal Care and Use Committee protocol 13-4112A. All the authors consent to the publication of this paper.

References

Au W (1993) The sonar of dolphins. Springer, New York

Bowman R (1979) Adaptive morphology of song dialects in Darwin's finches. J Ornithol 120:353–389

Carlile S, Pettigrew A (1987) Directional properties of the auditory periphery in the guinea pig. Hear Res 31:111–122

Carlile S, Delaney S, Corderoy A (1999) The localisation of spectrally restricted sounds by human listeners. Hear Res 128:175–189

Dantzker M, Deane G, Bradbury J (1999) Directional acoustic radiation in the strut display of male sage grouse *Centrocercus urophasianus*. J Exp Biol 202:2893–2909

Foote A, Osborne R, Hoelzel A (2004) Environment: whale-call response to masking boat noise. Nature 428:910

Fox J, Weisberg S (2011) An {R} companion to applied regression, second edition. Sage, Thousand Oaks, CA. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion. Accessed June 2017

Frederiksen J, Slobodchikoff C (2007) Referential specificity in the alarm calls of the black-tailed prairie dog. Ethol Ecol Evol 19:87–99

Griesser M, Ekman J (2004) Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. Anim Behav 67:933–939

Hamilton W (1964) The genetical evolution of social behavior. I and II. J Theor Biol 7:1–52

Hoogland J (1981) The evolution of coloniality in white-tailed prairie dogs and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). Ecol Soc Am 62:252–272

Hoogland J (1983) Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). Anim Behav 31:472–479

Hoogland J (1995) The Black-tailed Prairie Dog: social life of a burrowing mammal. University of Chicago Press, Chicago

Hotchkin C, Parks S (2013) The Lombard effect and other noise-induced vocal modifications: insight from mammalian communication systems. Biol Rev 88:809–824

Jenkins P (1978) Cultural transmission of song patterns and dialect development in a free-living bird population. Anim Behav 26:50–78

King J (1955) Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Univ Michigan Contrib Lab Vert Biol 67:1–123

Krams I, Krama T, Igaune K (2006) Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? J Avian Biol 37:131–136

Leger D, Owings D (1978) Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. Behav Ecol Sociobiol 3:177–186

Lemon R (1975) How birds develop song dialects. Condor 77:385–406

Lombard E (1911) Le signe de l'élévation de la voix. Ann Malad Oreille Larynx 37:101–119

Marler P (1970) A comparative approach to vocal learning: song development in white-crowned sparrows. J Comp Physiol Psychol 71:1–25

Marler P, Tamura M (1962) Song "dialects" in three populations of white-crowned sparrows. Condor 64:368–377

Marler P, Dufty A, Pickert R (1986) Vocal communication in the domestic chicken. II. Is a sender sensitive to the presence and nature of a receiver? Anim Behav 34:194–198

Mazerolle M (2017) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-1. https://cran.r-project.org/package=AICcmodavg. Accessed June 2017

Mitani J, Hasegawa T, Gros-Louis J, Marler P, Byrne R (1992) Dialects in wild chimpanzees? Am J Primatol 27:233–243

Morris-Drake A, Bracken A, Kern J, Radford A (2017) Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls. Environ Pollut 223:476–483

Nottebohm F, Stokes T, Leonard C (1976) Central control of song in the canary, *Serinus canaries*. J Comp Neurol 165:457–486

Perla B, Slobodchikoff C (2002) Habitat structure and alarm call dialects in Gunnison's prairie dog (*Cynomys gunnisoni*). Behav Ecol 13:844–850

Pollard KA, Blumstein DT (2012) Evolving communicative complexity: insights from rodents and beyond. Philos Trans R Soc Lond B Biol Sci 367:1869–1878

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. Accessed June 2017

Ríos-Chelén A, McDonald A, Berger A, Perry A, Krakauer A, Patricelli G (2017) Do birds vocalize at higher pitches in noise, or is it a matter of measurement? Behav Ecol Sociobiol 71:29. https://doi.org/10.1007/s00265-016-2243-7

Sheets R, Linder R, Dahlgren R (1971) Burrow systems of prairie dogs in South Dakota. J Mamm 52:451–453

Shelley E, Blumstein D (2004) The evolution of vocal alarm communication in rodents. Behav Ecol 16:169–177

Sherman P (1985) Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? Behav Ecol Sociobiol 17:313–323

Smith JM (1965) The evolution of alarm calls. Am Nat 99:59–63

Smith J, Smith S, Oppenheimer E, Devilla J (1977) Vocalizations of the black-tailed prairie dog, *Cynomys ludovicianus*. Anim Behav 25:152–164

Taylor R, Balph D, Balph B (1990) The evolution of alarm calling: a cost-benefit analysis. Anim Behav 39:860–868

Townsend S, Rasmussen M, Clutton-Brock T, Manser M (2012) Flexible alarm calling in meerkats: the role of the social environment and predation urgency. Behav Ecol 23:1360–1364

Trivers R (1971) The evolution of reciprocal altruism. Q Rev Biol 46:35–57

Waring G (1970) Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. Am Midl Nat 83:167–185

Wheeler B (2008) Selfish or altruistic? An analysis of alarm call function in wild capuchin monkeys, *Cebus apella nigritus*. Anim Behav 76:1465–1475

Whitehead H, Dillon M, Dufault S, Weilgart L, Wright J (1998) Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. J Anim Ecol 67:253–262

Zuberbühler K (2009) Survivor signals: the biology and psychology of animal alarm calling. Adv Study Behav 40:277–322