



PRIFYSGOL
BANGOR
UNIVERSITY

Alarm call modification by prairie dogs in the presence of juveniles

Wilson-Henjum, Grete; Job, Jacob; McKenna, Megan F.; Shannon, Graeme; Wittemyer, George

Ethology

DOI:

[10.1007/s10164-018-0582-8](https://doi.org/10.1007/s10164-018-0582-8)

Published: 01/05/2019

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Wilson-Henjum, G., Job, J., McKenna, M. F., Shannon, G., & Wittemyer, G. (2019). Alarm call modification by prairie dogs in the presence of juveniles. *Ethology*, 37(2), 167-174. <https://doi.org/10.1007/s10164-018-0582-8>

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 Alarm-call Modification by Prairie Dogs in the
2 Presence of Juveniles

3

4 Grete Wilson-Henjum¹, Jacob Job¹, Megan McKenna², Graeme Shannon³, George
5 Wittemyer¹

6

7 Author Affiliates:

8

1. Department of Fish, Wildlife, and Conservation Biology, Colorado State
9 University, Fort Collins, Colorado, USA

10

2. National Park Service Natural Sounds and Night Skies Division, 1201 Oakridge
11 Dr., Suite 100, Fort Collins, CO 80525, USA

12

3. School of Biological Science, Bangor University, Bangor, UK

13

14 Author Contact Information:

15

Grete Wilson-Henjum: gretewh5@gmail.com, 301-821-5495; No Orchid ID

16

Jacob Job: jrjob@rams.colostate.edu; 970-491-0637; No Orchid ID

17

Megan McKenna: megan_f_mckenna@nps.gov; 970-267-2123; Orchid ID: 0000-0003-
18 3475-0785

19

Graeme Shannon: g.shannon@bangor.ac.uk; 01248 382318; No Orchid ID

20

George Wittemyer: G.Wittemyer@colostate.edu; 970 491-6598; Orchid ID: 0000-0003-
21 1640-5355

22

23

24 Total text pages, including abstract: 12

25

3 figures, 3 tables, 1 supplementary recording

26

27

Key words: alarm call, call modification, *Cynomys ludovicianus*, vocal plasticity, signal
28 receiver, audience affect, acoustic ecology, black-tailed prairie dog

29

30

1 **Abstract**

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

While several drivers of wildlife alarm calls have been identified, recent work on the impact of the audience in the plasticity of alarm calling indicates that intraspecific communication can drive the 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 who 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 the calling and potentially the audience receiving the message. Furthermore, this may support that alarm calling is intended to reach conspecifics, rather than to send a message to the predator itself.

1 Introduction

2 Alarm calling in wildlife is a seemingly counterintuitive behavior that appears to
3 increase the risk of predation to the signaler (Taylor et al 1990). The evolutionary
4 maintenance of this behavior has been explained through applications of theories such as
5 Maynard Smith's (1965) kin selection (e.g. Griesser and Ekman 2004) and Robert
6 Triver's (1971) reciprocal altruism (e.g. Krams et al 2006). Under these contexts, alarm
7 calls are considered altruistic since the signaler is put at risk and others gain a fitness
8 benefit (Smith 1965). However, other hypotheses posit that alarm calls do not increase
9 the risk of predation to the signaler (Sherman 1985), suggesting other functions of alarm
10 calling outside of altruism. For instance, alarm calls in some rodents are directed at
11 predators, with conspecifics secondarily benefitting (Shelley and Blumstein 2004).
12 Additionally, some alarm calls used to elicit mobbing behavior are debatably delivered
13 with selfish intent, as the signaler summons conspecifics to protect itself from potentially
14 being predated upon (Wheeler 2008). Finally, some individuals alter alarm calls based on
15 the audience present, suggesting multiple motivations for alarm calling, as well as
16 conscious control of the message to be delivered (Marler et al 1986; Townsend et al
17 2012; reviewed in Zuberbühler 2009).

18 Black-tailed prairie dogs (*Cynomys ludovicianus*) are known for their high degree
19 of sociality, manifesting in tight-knit colonies, called coterie (Hoogland 1995).
20 Vocalizations are part of prairie dog sociality, often used to manipulate an interaction
21 between two individuals, such as one coterie member rejecting another coterie member's
22 attempt to allogroom, or defending territory from a member of a different coterie (Smith
23 et al 1977). Prairie dogs also exhibit a more functionally complex "jump-yip" signal,

1 named for the high-pitched squeak and associated front limb extension, which is used to
2 communicate various circumstances, such as the end of a predatory threat (King 1955;
3 Smith et al 1977; Hoogland 1995) or as a general contact call (Waring 1970). Coterie
4 members altruistically alert others to the presence of potential predators using alarm calls,
5 significantly reducing predation compared to that of other species within the same genus
6 that do not share this behavior, ultimately increasing overall survival and reproductive
7 rates (Hoogland 1981). Black-tailed prairie dogs code specific information within their
8 alarm calls pertaining to the specific nature of the threat (e.g. aerial versus terrestrial
9 predator) (Frederiksen and Slobodchikoff 2007), allowing coterie members to respond
10 appropriately. Additionally, prairie dogs add another layer of complexity to their
11 signaling by calling more frequently in the presence of their offspring (Hoogland 1983),
12 suggesting an element of kin-selection (Hamilton 1964). Thus far, investigation of other
13 call properties (e.g. frequency spectra and acoustic energy allocation) in relation to
14 offspring presence has not been investigated.

15 In this study, we explored whether adult black-tailed prairie dogs – herein referred
16 to as prairie dogs - adjust anti-predatory alarm calls in the presence of pups. We recorded
17 anti-predator alarm calls from multiple adults elicited by human approaches to prairie
18 dogs at two coterie in Fort Collins, CO, USA. We tested whether differences exist in the
19 peak and 5th percentile frequency (spectral call traits), as well as the duration of call notes
20 and duration between call notes (temporal call traits) were related to social context. Given
21 previous research suggesting alarm calling in this species provides benefits to
22 conspecifics, we use these data to test if call properties change relative to the presence of
23 pups in the vicinity of the caller. We hypothesize that properties of alarm calls to human

1 approaches would change relative to the social context in which the call was elicited,
2 indicating calls were directed at conspecifics rather than predators. In contrast, alarm call
3 properties not changing across different social circumstance suggests social context does
4 not affect calls, indicating calls were directed at predators. We derive several predictions
5 about the manner in which the temporal and spectral characteristics of their calls could be
6 altered so as to not attract predators directly towards kin.

7

8 **Methods**

9 **Study Sites**

10 We recorded anti-predator alarm calls from prairie dogs in coterie located at
11 Pineridge Natural Area (40°33'04.0"N, 105°08'33.7"W) and Coterie Natural Area
12 (40°33'59.5"N, 105°02'29.3"W) in Fort Collins, Colorado, USA. Pineridge Natural Area
13 is a 250 ha natural area that transitions from a short-grass steppe to foothill shrub
14 ecosystem. Recreational users such as mountain bikers, joggers, and walkers largely
15 dominate human usage at this site. East of this site is well developed with housing, but
16 otherwise adjacent land remained largely undeveloped. Pineridge's prairie dog colony
17 spans approximately 40 ha. The Coterie Natural Area is a 1.6 ha natural area located at
18 the intersection of two heavily trafficked roads. The site also sees human usage on paved
19 walking and biking trails. The prairie dog colony living within the Coterie extends
20 beyond the natural area's boundaries, and totals 1 ha. Both sites are short-grass prairie
21 habitat with similar vegetation structure of close-cropped grasses due to prairie dog
22 grazing.

23 **Data Collection**

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

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

1 Alarm calls are characterized by repetitive call notes (Figure 1), typically with
2 0.15-1.5 s between call notes (Waring 1970) and are completely distinguishable from call
3 notes delivered for other non-anti-predatory reasons based on this patterned structure. A
4 minimum recording of 30 s was established based on observed approximate average
5 alarm-calling bout length prior to a fleeing response. The 30 s recordings yielded an
6 average of 68 ± 1.78 individual call notes. After recordings were collected, a Laser Tech
7 Inc. TruPulse 360B digital range finder was used to determine the distance between the
8 recording location and focal prairie dog, as well as the distance between the nearest pup
9 and the focal prairie dog.

10

11 **Alarm Call Measurements**

12 Spectrograms of all recordings were visualized in the audio analysis program
13 Raven Pro v1.5 (1024 Fast Fourier Transformation, Hann window, 50% overlap, 43 Hz
14 frequency resolution, 11 ms temporal resolution). A total of 51, 30 s alarm call recordings
15 were collected at each site. For ten recordings (Coterie: n=9, Pineridge: n=1), the gain
16 level setting on the audio recorder was different from the rest of the recordings, so these
17 recordings were not used for frequency analyses, but were retained for temporal
18 measures. We employed the band-limited energy detector function in Raven to
19 automatically highlight all call notes within a recording. The detector settings were set as
20 such to search for potential call notes within a frequency range of 2000-6000 Hz, a signal
21 duration range of 0.008-0.2 s, a minimum separation between successive call notes of 0.2
22 s, a signal-to-noise minimum occupancy of 30 percent, and a signal-to-noise threshold of
23 15 dB. All automatic detections were then manually examined for accuracy with some

1 adjustments made to fully capture all call notes within a recording. To maintain objective
2 standardization for the impulsive call notes even when manually adjusting the automatic
3 detections, a standardized maximum frequency (15000 Hz) was used for each detection
4 box.

5 We randomly subsampled half of the call notes in each recording to be used
6 during analyses of acoustic parameters. Subsampled detections were adjusted in the
7 Raven software to ensure the entire bandwidth and duration of call notes were measured
8 accurately. The same spectrogram parameters were used when making adjustments. Call
9 notes were analyzed for the spectral traits peak frequency (frequency with the highest
10 concentration of energy; Hz) and the 5th percentile frequency (frequency with the lowest
11 five percent concentration of energy; Hz). We selected peak frequency because it
12 represents the section of call notes where prairie dogs place the most energy, and 5th
13 percentile frequency because it is a robust measurement of the lowest frequency of the
14 call note (for bias in “by-eye practice” minimum frequency measurements, see Ríos-
15 Chelén et al 2017). The temporal call traits analyzed included call note duration (length
16 of each call note; s) and inter-call note interval (time between each call note; s). The
17 inter-call note interval was analyzed for changes in the variance, as it was observed
18 during recordings that adults elicited less rhythmic alarm calls in the presence of pups.

19

20 **Statistical Analysis**

21 We used generalized linear regression models to assess factors that relate to alarm
22 call acoustic properties. We explored four response variables in four separate models:
23 peak frequency, 5th percentile, call note duration, and inter-call note interval. The

1 influence of pup presence (a binary variable indicating if pups were observed within 30 m
2 of focal individual), site (Pineridge or the Coterie), distance from observer to focal
3 individual, wind speed (m/s), and Julian date on these spectral and temporal alarm call
4 response variables were explored.

5 Parameters were initially examined for patterns of normality and
6 heteroscedasticity, and response variables 5th percentile frequency, call note duration, and
7 inter-call note interval were transformed using a Box-Cox transformation to meet model
8 assumptions. We used information theoretic approaches to compare the performance of
9 models using different covariates for each response variable. Models were ranked
10 according to bias adjusted Akaike's information criteria (AICc) and AIC weights, where
11 initial models included all listed predictor variables. Where models were marginally
12 different (difference in AIC weight < 0.95), parameter coefficients in secondary models
13 were inspected for influence (95% confidence intervals did not overlap 0). Results from
14 the top ranked models for each response variable were used to interpret relationships as in
15 all cases the additional parameters in secondary models were weakly informative (Table
16 1). All models were run using R v 3.0.1 (R Core Team 2013), Box-Cox transformations
17 were performed using the package 'Car' (Fox and Weisberg 2011), and AIC model
18 selection was performed using the package 'AICcmodavg' (Mazerolle 2016).

19 20 Results

21 A total of 2820 call notes from 81 individuals were analyzed for characteristics of
22 the acoustic properties. We found wide variation in both spectral and temporal traits of
23 call notes elicited by adults (Table 2). For spectral traits, peak frequency and 5th
24 percentile frequency varied by ~2000Hz. We found that peak frequency at both recording

1 sites was significantly reduced when pups were present (Table 3). Peak frequency in the
2 presence of pups decreased ~228 Hz compared to without pups ($t_{(df=78)} = -2.246$; $P=0.03$;
3 Figure 2). Site did not have a significant impact on peak frequency (Table 3). None of our
4 predictor variables explained variation in the 5th percentile frequency (Table 3).

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

13

14 Discussion

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

22 It is known that the directionality of very low and very high frequency sounds
23 relative to hearing sensitivities are more difficult to detect. In lab experiments, this

1 phenomenon has been observed in humans (Carlile et al. 1998), as well as in smaller
2 rodent species such as the Guinea pig (*Cavia porcellus*) (Carlile and Pettigrew 1986).
3 Because attempted predation events were not part of our experiment (i.e., predator
4 elicitation was caused by an observer walking up to the subject), no predator detection of
5 prey or predator-evasion outcome could be observed. Call characteristics and associated
6 behavioral changes in relation to newborn presence have been found in other closely
7 related social sciurid species. It has been found that adult Gunnison prairie dog (*Cynomys*
8 *gunnisoni*) alarm calls have a lower dominant frequency during the pre-monsoon season
9 relative to the post-monsoon season when controlling for vegetative structure (Perla and
10 Slobodchikoff 2002). It is speculated that changes in juvenile dependency on adults from
11 the pre- to post-monsoon season drives the change in adult alarm calling; during pre-
12 monsoon season while juveniles are heavily dependent on adults call characteristics are
13 seemingly adjusted for shorter attenuation and rapid degradation in short distances, while
14 later in the season this is adjusted for longer attenuation as juveniles become more
15 independent (Perla and Slobodchikoff 2002). Our findings provide additional support that
16 changes in dominant frequency can be related to pup dependency. Furthermore,
17 Belding's ground squirrel (*Urocitellus beldingi*) mothers exhibit greater responsiveness
18 to alarm calls compared to non-maternal females (Leger and Owings 1978). Given that
19 prairie dog call notes are broadband in frequency, it is unclear whether a shift in energy
20 concentration would impact a predator's ability to detect the sources of alarm calls. The
21 possibility also remains that this relatively small shift in peak frequency does not amount
22 to a functional biological response.

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

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

18 Alternatively, it has been found in vertebrates that spatially distant populations of
19 the same species can have variation in calls and songs, known as dialects (e.g. Sperm
20 whales (*Physeter microcephalus*), Whitehead et al. 1998; Chimpanzees (*Pan*
21 *trogodytes*), Mitani et al. 1992; and many birds species, Marler and Tamura 1962;
22 Jenkins 1978; Bowman 1979). While our study sites are separated by only 10 km, they
23 are geographically isolated from one another, and it is possible that local dialects have

1 developed. Two major driving mechanisms of dialect development include young
2 learning calls from adults around them, which gradually diverge amongst isolated
3 populations (Northern cardinal (*Cardinalis cardinalis*), Lemon 1975; White-crowned
4 sparrow (*Zonotrichia leucophrys*), Marler 1970); or that physiological or morphological
5 divergences may have developed between two populations, leading to differences in call
6 structure (Atlantic canary (*Serinus canarius*), Nottebohm 1976).

7 It has also been found that call duration increases in the presence of increased
8 noise (Lombard 1911; Hotchkin and Parks 2013), hypothesized as an anti-masking
9 behavior. For example, Killer whales (*Orcinus orca*) have been found to increase the
10 duration of call notes in the presence of increased anthropogenic noise (Foote et al.
11 2004). Since the Coterie sat at the intersection of two major roads, it is possible the
12 influence of louder anthropogenic sound is related to the longer call note duration.
13 However, we cannot say whether or not this was the case given we only examined two
14 small study sites and did not analyze background sound levels to evaluate the acoustic
15 environment. It is also important to note that while statistically significant, the difference
16 in duration was small enough that it may not have biological significance. Recent studies
17 have shown that anthropogenic noise can alter the dwarf mongoose's (*Helogale parvula*)
18 ability to receive and appropriately respond to heterospecific alarm signals (Morris-Drake
19 et al 2017). While our study did not take into account receiver response between the two
20 sites, future studies focused on how anthropogenic noise may impact coterie member's
21 response to alarm calls are merited.

22 It is important to note that it is unclear if the changes in peak frequency and call-
23 note duration relate to differences in sound production function, size of the animal, or

1 orientation with respect to the microphone. In addition, spectral differences above the
2 peak frequency may indicate that the measurements were not all made precisely on the
3 acoustic axis of the animal and so may include some off-axis distortion (Au 1993;
4 Dantzker et al 1999). This does not seem likely given attempts were made to implement
5 recordings in a standardized manner.

6 Understanding the plasticity of vocal communication in wildlife gives us insight
7 into the evolutionary drivers of these behaviors, which will ultimately provide guidance
8 for conservation concerns. Our findings suggest prairie dogs demonstrate vocal plasticity
9 in the face of a predatory threat when in the presence of kin. This serves to support
10 several theories surrounding alarm calling; namely that kin selection is a driver for alarm
11 calling in prairie dogs, and that flexibility in alarm calling exists based on the audience
12 receiving the alarm calls. Furthermore, our findings support the idea that behavioral
13 plasticity exists in wildlife vocalizations, rather than long-term adaptations to changing
14 environments. Finally, this study also stimulates important applied questions regarding
15 the quality and efficacy of modified signals in mammals, particularly in encroaching
16 urban environments.

Compliance with Ethical Standards

Funding: This study was funded without any grants. Recording equipment was borrowed from the National Park Service's Natural Sounds and Night Skies Division.

Conflict of Interest: The authors declare that they have no conflict of interest

Ethical approval: This research was approved by the CSU Animal Care and Use Committee protocol 13-4112A.

All authors consent to the publication of this paper.

Figure 1. Spectrogram depiction of a typical black-tailed prairie dog's alarm call generated in Raven Pro v1.5. Spectrogram settings include: 1024 Fast Fourier Transformation, Hann window, 50% overlap, 43Hz frequency resolution, 11 ms temporal resolution. Wav file available in supplementary material.

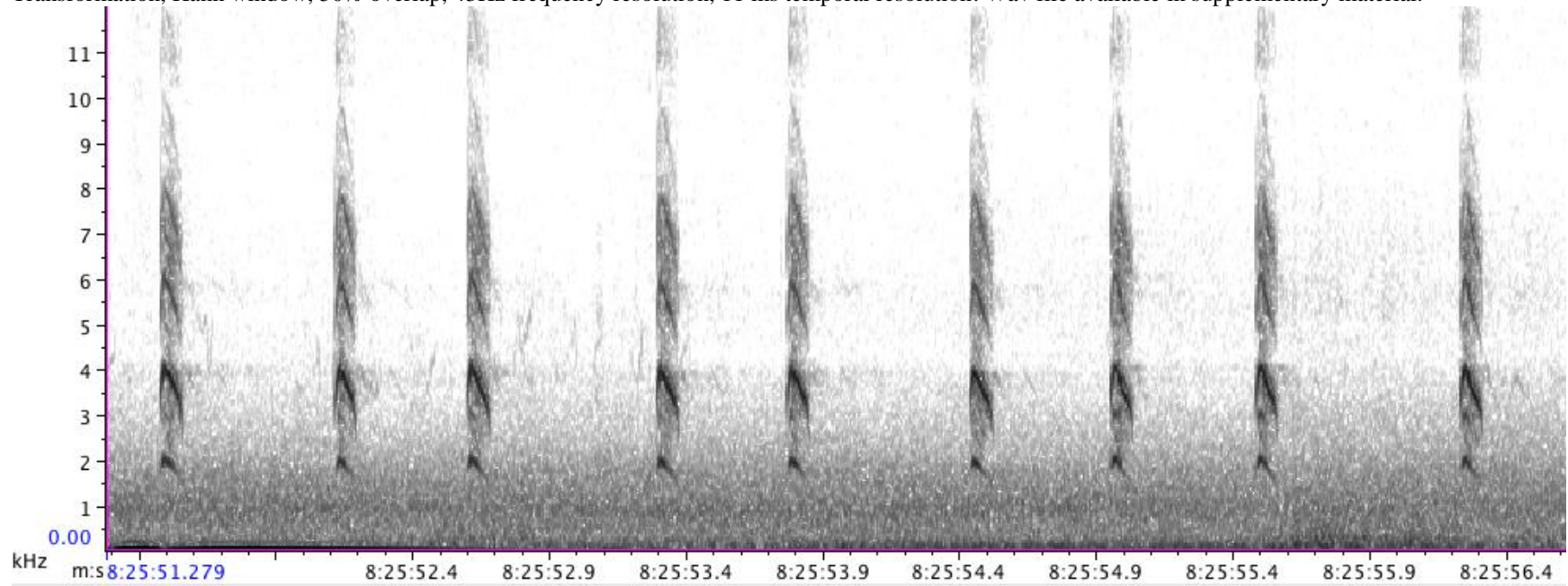


Figure 2. Call note peak frequency (presented in raw without transformation) decreased in the presence of pups for both study sites.

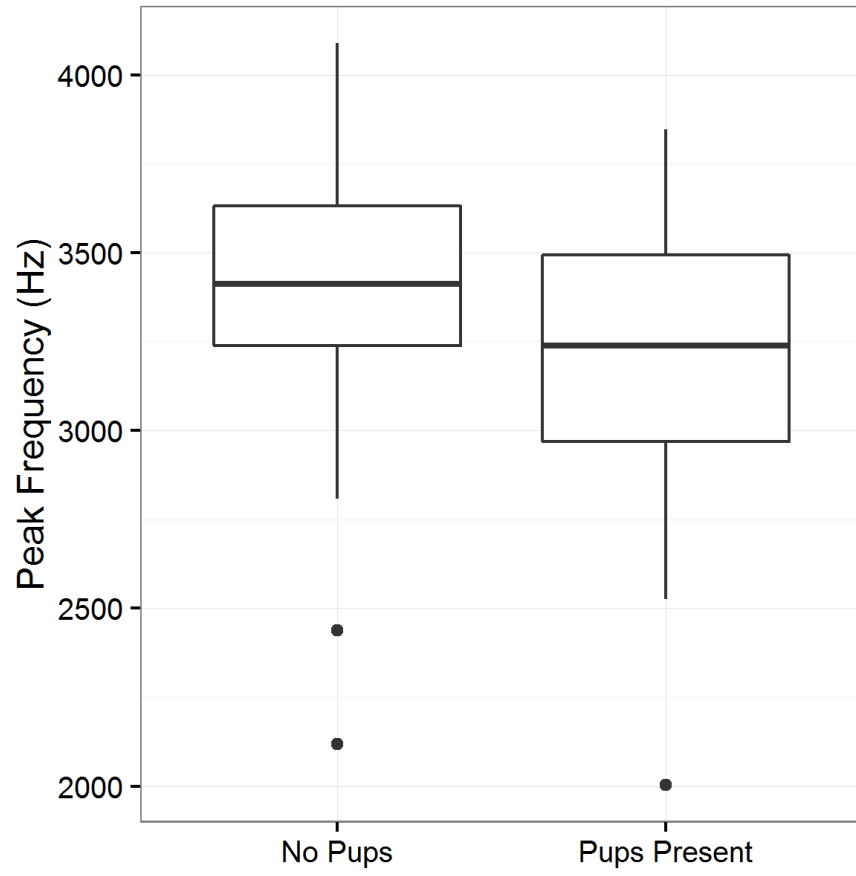


Figure 3. Call note duration was significantly greater at the Coterie, the study site with more anthropogenic disturbance.

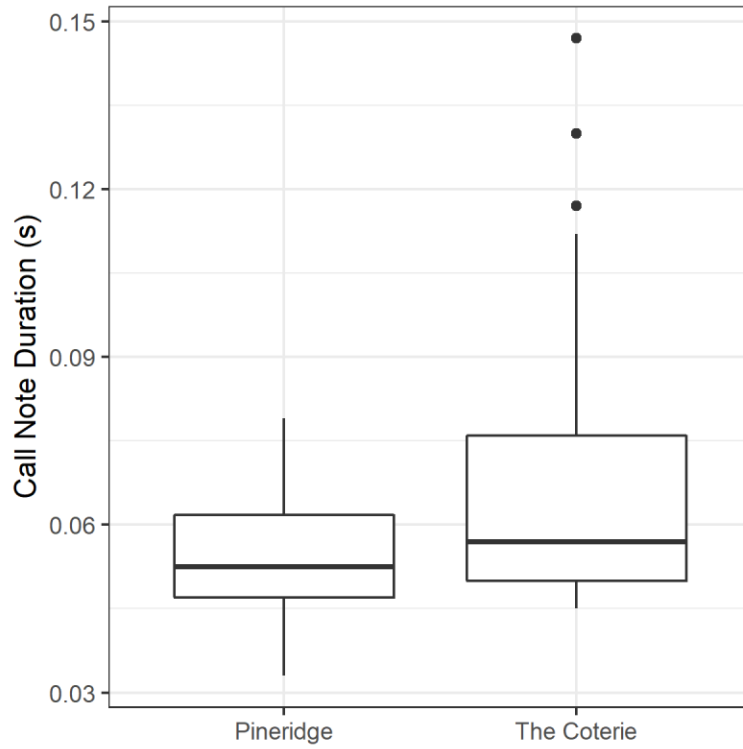


Table 1. AIC model selection results. Models with an * next to them are the final model. The top two models for Call Note Duration were indistinguishable from each other, but the most parsimonious model was selected as the final model.

Peak Frequency			
Model	AICc	ΔAICc	LogLik
Site+PupPresence*	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
5 th Percentile Frequency			
Model	AICc	ΔAICc	LogLik
Site+Wind+RecorderDistance	1208.2	0.0	-598.7
Site+Wind+PupPresence+RecorderDistance*	1209.6	1.4	-598.2
Site+JulianDate+Wind+PupPresence+RecorderDistance	1238.9	30.7	-580.5
Call Note Duration			
Model	AICc	ΔAICc	LogLik
Site+RecorderDistance*	-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			
Model	AICc	ΔAICc	LogLik
RecorderDistance	50.2	0.0	-21.9
Wind+RecorderDistance*	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

Table 2. A 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	$\bar{x} \pm \text{SE}$
Peak Frequency (Hz)	2002.8-4089.2	3304.9 \pm 45.1
Fifth Percentile Frequency (Hz)	1249.4-3294.9	2010.1 \pm 45.8
Call Note Duration (s)	0.033-0.147	0.06 \pm 0.002
Inter-Call Note Interval Variance (s)	0.0002-2.18	0.05 \pm 0.03

Table 3. Results of the generalized linear regression models examining the effect site, pup presence, wind speed, and recorder distance have on spectral and temporal measurements of alarm calls. An * denotes a significant finding.

Call Characteristic	Variable	Estimate	±	SE	<i>t</i>(<i>df</i>)	<i>P</i>
Peak Frequency (Hz)	Site	-668340	±	579031	-1.154 ₍₇₈₎	0.25
	Pup Presence	-1293168	±	575821	-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

Supplementary Material

S1. Recording sample of an alarm call used for analysis. First 30 seconds were used for analysis. Recording taken at the Coterie.



References:

- Au W (1993) *The Sonar of Dolphins*. Springer-Verlag, New York.
- Bowman R (1979) Adaptive morphology of song dialects in Darwin's finches. *Journal of Ornithology* 120:353-389.
- Carlile S, Delaney S, Corderoy A (1999) The localisation of spectrally restricted sounds by human listeners. *Hearing Research* 128:175-189.
- Carlile S, Pettigrew A (1987) Directional properties of the auditory periphery in the guinea pig. *Hearing Research* 31:111-122.
- Dantzker, M, Deane G, and Bradbury J (1999). Directional acoustic radiation in the strut display of male sage grouse *Centrocercus urophasianus*. *Journal of Experimental Biology*, 202:2893-2909.
- Foote A, Osborne R, Hoelzel A (2004) Environment: Whale-call response to masking boat noise. *Nature* 428:910.
- Fox J and Weisberg S (2011) *An {R} Companion to Applied Regression*, Second Edition. Sage, Thousand Oaks, California.
<http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- Frederiksen J and Slobodchikoff C (2007) Referential specificity in the alarm calls of the black-tailed prairie dog. *Ethology Ecology & Evolution* 19:87-99.
- Griesser M and 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.
- Hotchkin C, Parks S (2013) The Lombard effect and other noise-induced vocal modifications: insight from mammalian communication systems. *Biological Review* 88:809-824.
- Hoogland J (1981) The evolution of coloniality in white-tailed prairie dogs and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *The Ecological Society of America* 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 and London.
- 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, Contr. Lab. Vert. Biol.* 67:1-123.
- Krams I, Krama T, and Igaune K (2006) Alarm calls of wintering great tits *Parus major*: warning of mate, reciprocal altruism or a message to the predator? *Journal of Avian Biology* 37:131-136.
- Leger D, Owings D (1978) Responses to alarm calls by California ground squirrels: Effects of call structure and maternal status. *Behavioral Ecology and Sociobiology* 3:177-186.
- Lemon R (1975) How birds develop song dialects. *The Condor* 77:385-406.
- Lombard E (1911) Le signe de l'élévation de la voix. *Annales des Maladies de L'Oreille et du Larynx* 37:101-119.
- Marler P (1970) A comparative approach to vocal learning: Song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology* 71:1-25.
- Marler P, Dufty A, and 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.
- Marler P and Tamura M (1962) Song "dialects" in three populations of White-Crowned Sparrows. *The Condor*, 64:368-377.
- Maynard Smith J (1965) The Evolution of Alarm Calls. *The American Naturalist* 99:59-63.
- 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>.
- Mitani J, Hasegawa T, Gros-Louis J, Marler P, Byrne R (1992) Dialects in wild chimpanzees? *American Journal of Primatology* 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.* 223:476-83.

- Nottebohm F, Stokes T, Leonard C (1976) Central control of song in the canary, *Serinus canaries*. *The Journal of Comparative Neurology* 165:457-486.
- Perla B, Slobodchikoff C (2002) Habitat structure and alarm call dialects in Gunnison's prairie dog (*Cynomys gunnisoni*). *Behavioral Ecology* 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/>.
- 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? *Behavioral Ecology and Sociobiology* 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. *Journal of Mammalogy* 52:451-453.
- Shelley E, Blumstein D (2004) The evolution of vocal alarm communication in Rodents. *Behavioral Ecology* 16:169–177.
- Sherman, P (1985) Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behavioral Ecology and Sociobiology* 17:313-323.
- 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
- Trivers R (1971) The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology* 46:35-57.
- Townsend S, Rasmussen M, Clutton-Brock T, Manser M (2012) Flexible alarm calling in meerkats: the role of the social environment and predation urgency. *Behavioral Ecology* 23:1360–1364.
- Waring G (1970) Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. *The American Midland Naturalist* 83:167-185.
- Wheeler B (2008) Selfish or altruistic? An analysis of alarm call function in wild

capuchin monkeys, *Cebus apella nigrinus*. 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. Journal of Animal Ecology 67:253-262.

Zuberbühler K (2009) Survivor Signals: The Biology and Psychology of Animal Alarm Calling. Advances in the Study of Behavior 40:277-322.