Fall 2011

Alarm-Calling And Response Behaviors Of The Black-Tailed Prairie Dog In Kansas

Lloyd W. Towers III
Fort Hays State University

Recommended Citation

Towers, Lloyd W. III, "Alarm-Calling And Response Behaviors Of The Black-Tailed Prairie Dog In Kansas" (2011). *Master's Theses*. 158.
DOI: 10.58809/DMIP3110
Available at: https://scholars.fhsu.edu/theses/158

ALARM-CALLING AND RESPONSE BEHAVIORS
OF THE BLACK-TAILED PRAIRIE DOG
IN KANSAS

being

A Thesis Presented to the Graduate Faculty
of the Fort Hays State University in
Partial Fulfillment of the Requirements for
the Degree of Master of Science

by

Lloyd Winston Towers III
B.S., Texas A&M University

Date______________________ Approved___________________________________
Major Professor

Approved___________________________________
Chair, Graduate Council

This Thesis for

The Master of Science Degree

By

Lloyd Winston Towers III

Has Been Approved

Chair, Supervisory Committee

Supervisory Committee

Supervisory Committee

Supervisory Committee

Chair, Department of Biological Sciences

This thesis is written in the style appropriate for publication in the *Journal of Mammalogy*.

ABSTRACT

Prairie dogs (*Cynomys* spp.) use alarm calls to warn offspring and other kin of predatory threats. Dialects occur when vocalizations contain consistent differences among populations not isolated by geographic barriers. The Gunnison's prairie dog (*C. gunnisoni*) has dialects in its alarm calls. The objectives of my study were to: (1) assess if the black-tailed prairie dog (*C. ludovicianus*) responded differently to alarm calls from other colonies than it did to alarm calls from its own colony, and (2) detect dialects, if they existed, in the alarm calls of the black-tailed prairie dog. The study included 8 black-tailed prairie dog colonies in western and central Kansas. I obtained alarm calls by using a human (*Homo sapiens*) predator model. Playback experiments were conducted at each study colony by using alarm calls recorded at all 8 colonies. I also compared alarm calls within and among different colonies. The geographic origin of an alarm call did not appear to have an effect on how the black-tailed prairie dog responded to the call. The black-tailed prairie dog might respond to an alarm call regardless of the colony of its origin because: (1) the alarm call encodes information about the predator and (2) my sites might have all been part of a larger historic colony. My data suggested the black-tailed prairie dog did not appear to have dialects in its alarm call. Dialects in the alarm call might not exist because they might not have any adaptive value.

ACKNOWLEDGMENTS

I thank the following individuals, for without them I could not have accomplished this thesis. I thank my advisor, Dr. Elmer J. Finck, and the rest of my graduate committee, Dr. Jack F. Cully, Dr. Greg H. Farley, and Dr. Brian R. Maricle, for their patience, guidance, suggestions, and support. I thank the following organizations and landowners for allowing me onto their property and providing advice for recording locations: The Nature Conservancy (Randy Martin), The U.S. National Park Service, Larry and Betty Haverfield, Norman Johanning, Dolores Rusco, and Richard Schroder.

I am very grateful to Dr. John L. Hoogland and Dr. Con N. Slobodchikoff for their suggestions and feedback on prairie dog behavior. I thank the following individuals for informing me of black-tailed prairie dog town locations: Zachary Eddy, Chasen Gann, Stephanie Kane, Pamela Martin, and Curtis Wolf. I am especially grateful to Jessica Casey for helping me characterize my study sites from a floral perspective. Although I was unable to use the following materials in my research, I thank Dr. Jack F. Cully for the badgermobile, Curtis Schmidt for providing the badger (*Taxidea taxus*) specimen, Zachary Schwenke for helping me prepare the badger skin, and Chasen Gann for helping me make platforms. I am particularly grateful to Dr. Robert B. Channell for his help with my statistical analyses. The following people also provided statistical assistance: Alex Galt, Darren Gemoets, and Ryan Pinkall. I am especially grateful to Anthony Dalisio for helping me understand the Raven Pro software and introducing me to the Spectrographic Cross-Correlation analysis. I thank Brandon Calderon, Amanda

Cheeseman, and Victoria Cikanek for their help with GIS. I truly appreciate Dr. Jordge LaFantasie, Justin Anderson, Elita Baldridge, and Curtis Wolf for taking time to help edit sections of my thesis. I thank Casey Brown, Phillip Sechtem, and Andrew Tincknell for their explanations about sounds and sound software. I also appreciate the assistance of the Raven support team at the Cornell Lab of Ornithology for their quick and helpful responses, especially Tim Krein and Laura Strickhart. I am very grateful to Sheran Powers and the student helpers at Forsyth Library of Fort Hays State University for their prompt responses to my many interlibrary loan requests. I also thank the Department of Biological Sciences at Fort Hays State University and the Kansas Wetlands Education Center for providing me with the assistantships that helped support me through graduate school.

Finally, I would be nowhere without the constant patience, loving guidance, and never-diminishing support of my parents Lloyd W. Towers II and Kathy Towers; my sisters Emily Breclaw and Hillary Shenkle; my brothers-in-law Derrick Breclaw and Bob Shenkle; my nephews Andrew Breclaw and Wyatt Shenkle; and my nieces Molly, Sarah, and Rose Breclaw and Madelyn Shenkle. Thank you all for being the unfaltering foundation of my life.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (CONTINUED)

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

LIST OF APPENDICES

INTRODUCTION

Alarm calls are used in threatening situations; some animals rely on alarm calls to minimize the risk of predation. Individuals give alarm calls to warn conspecifics about a perceived threat. Some animals have specific alarm calls for different predators, eliciting predator-specific escape behaviors (Kiriazis and Slobodchikoff 2006; Seyfarth et al. 1980; Zuberbühler et al. 1997). While an alarm call typically warns the caller's relatives of predatory threats (Hoogland 1995; Sherman 1977), heterospecifics sometimes respond to the alarm calls as well (Hauser 1988; Lea et al. 2008; Shriner 1998; Zuberbühler 2000).

Many species of ground squirrel (e.g., yellow-bellied marmot—*Marmota flaviventris*, Richardson's ground squirrel—*Urocitellus richardsonii,* and prairie dogs—*Cynomys* spp.) use alarm calls. For example, the Belding's ground squirrel (*Urocitellus beldingi*) uses alarm calls to warn relatives of predatory threats (Sherman 1977). Some ground squirrels are able to identify individual conspecifics based on their calls (Blumstein and Munos 2005; Hare 1998; Hare and Atkins 2001; McCowan and Hooper 2002). Repeated calls can lead to more vigilance from colony members (Hoogland 1995; Loughry and McDonough 1988; Sloan and Hare 2008), although too much calling can lead to habituation to the alarm call, meaning the alarm-calling individuals will be ignored (Hare 1998; Hare and Atkins 2001; Loughry and McDonough 1988; Smith 1958).

Some ground squirrels even respond to heterospecific alarm calls. The yellow-bellied marmot and the golden-mantled ground squirrel (*Callospermophilus lateralis*) are sympatric, but they rarely interact. Despite the lack of interaction, both species respond to the other's alarm calls (Shriner 1998). Woodchucks (*Marmota monax*) will respond to alarm calls of eastern chipmunks (*Tamias striatus*), but will spend less time vigilant after hearing the chipmunk alarm call than it will to hearing the call of a conspecific (Aschemeier and Maher 2011).

The black-tailed prairie dog (*Cynomys ludovicianus*) uses alarm calls to warn relatives of predatory threats (Hoogland 1995). When a predator approaches a prairie dog colony, individuals with offspring and other kin in close proximity will call while the rest of the prairie dogs remain silent (Hoogland 1995). Upon hearing an alarm call, the black-tailed prairie dog will scan for predators. If it does not detect any threats, it will continue with the activity it was engaged in prior to the call (e.g., foraging). However, if the black-tailed prairie dog detects a predator, it will retreat to a burrow without necessarily entering it and might even contribute to the alarm-calling (Hoogland 1995). The black-tailed prairie dog does not have a defined calling bout; an individual can alarm call for up to an hour with minimal pauses between the calls, although the duration of the calling is normally less than 30 minutes (Waring 1970). During this time, the intensity of each call and the time between each call can vary (Waring 1970). Although other alarm-calling animals have different alarm calls for different predators (Kiriazis and Slobodchikoff 2006; Seyfarth et al. 1980; Zuberbühler et al. 1997), the black-tailed prairie dog only has one distinct alarm call (Hoogland 1995). However, variations of this call might convey information about the type of predator or the level of predation risk (Frederiksen and Slobodchikoff 2007; Hoogland 1995).

Slobodchikoff et al. (1991) suggest the Gunnison's prairie dog (*Cynomys gunnisoni*) is able to provide semantic information about the attacking predator in its alarm calls. The Gunnison's prairie dog has different escape tactics when confronted with a human (*Homo sapiens*), red-tailed hawk (*Buteo jamaicensis*), coyote (*Canis latrans*), or domestic dog (*Canis lupus familiaris*—Kiriazis and Slobodchikoff 2006). The Gunnison's prairie dog is able to encode information about predator color in its alarm call (Slobodchikoff et al. 2009a). Frederiksen and Slobodchikoff (2007) verified the black-tailed prairie dog conveys predator information similarly to the Gunnison's prairie dog.

The Gunnison's prairie dog also has dialects in its alarm call (Slobodchikoff and Coast 1980). A dialect exists if a vocalization exhibits consistent differences among different populations of the same species (Le Boeuf and Peterson 1969). Eiler and Banack (2004) suggest dialects exist between populations with no restriction of gene flow due to long distance or geographic barriers. Dialects in songbirds can arise from learning, improvisation, errors in learning, and transmission of errors to future generations (Lemon 1975; Slater 1986). However, the alarm calls of Gunnison's prairie dogs appear to be influenced by habitat structure (Perla and Slobodchikoff 2002;

Slobodchikoff and Coast 1980). No current literature indicates whether the black-tailed prairie dog has dialects in its alarm calls.

Slobodchikoff et al. (2009b) suggest alarm calls from one colony need to be played back to colonies locally and throughout the geographic range to see if response behaviors differ. I investigated responses to playback experiments throughout the range of the black-tailed prairie dog in Kansas. Because black-tailed prairie dog and Gunnison's prairie dog share similarities in alarm-calling behavior, I also investigated whether the black-tailed prairie dog had dialects in its alarm call.

The objectives of my study were to: (1) assess if the black-tailed prairie dog responded differently to alarm calls from other colonies than it did to alarm calls from its own colony, and (2) detect dialects, if they existed, in alarm calls of the black-tailed prairie dog. I hypothesized the black-tailed prairie dog would show little or no response to alarm calls that were not from its own colony. I also hypothesized there would be significant differences in alarm calls from different colonies.

MATERIALS AND METHODS

Study sites.—I collected recordings from 8 black-tailed prairie dog (hereafter prairie dog) colonies in Barton, Logan, Pawnee, and Scott counties of Kansas (Fig. 1). Three colonies at the Smoky Valley Ranch (SVR1-3) and 1 colony at the Haverfield Ranch (HR) were in Logan County. Colonies SVR1-3 were at the Smoky Valley Ranch approximately 28.3 km south and 11.3 km west of Oakley, KS. Colony SVR1 (38^o86’N, -100^o98’W) was approximately 90.8 ha and 852-875 m above sea level; SVR2 (38^o85’N, -100^o96’W) was approximately 142 ha and 837-887 m above sea level; SVR3 (38^o83’N, -100^o94’W) was approximately 165 ha and 834-861 m above sea level. Slope of these colonies was approximately 0-5%. The pasture containing a portion of SVR2 and all of SVR3 had a grazing intensity of 0.3 animal unit months per hectare (AUM/ha), assuming conventional animal units. Colonies were in mixed prairie typically characterized by big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), and blue grama (*B. gracilis*—Küchler 1974; Appendix I). Colony HR (38^o79’N, -101^o16’W) was approximately 13.7 km south of Russell Springs, KS and was approximately 115 ha. Colony HR had an elevation of 906-935 m and had 0-3% slope. The grazing intensity on this colony was 1.4 AUM/ha. Colony HR was located in short grass prairie typically characterized by blue grama and buffalograss (*Buchloe dactyloides*—Küchler 1974; Appendix I).

The colony at the Palmer Ranch (PR; 38^o58’N, -100^o94’W) was in Scott County approximately 7.9 km north and 3.2 km west of Scott City. The colony was approximately 66.3 ha and 886-916 m above sea level. Colony PR had 0-2% slope and was in short grass prairie typically characterized by blue grama and buffalograss (Küchler 1974; Appendix I). The northwestern end of PR had a grazing intensity of 1.1 AUM/ha, assuming conventional animal units.

Two of my smallest colonies were on the Rusco (RR) and Johanning (JR) ranches in Barton County. Both were in mixed prairie typically characterized by big bluestem, little bluestem, sideoats grama, and blue grama (Küchler 1974; Appendix I). Colony RR (38°40’N, -98°66’N) was approximately 8.8 ha, was 4.7 km north and 6.4 km west of Ellinwood, KS, and had an elevation of 560-567 m and 0-2% slope. The pasture had a small pond at one end and a grazing intensity of 5.9 AUM/ha, assuming conventional animal units. Colony JR (38°43’N, -98°57’W) was approximately 9.7 ha, was 7.4 km north of Ellinwood, KS, and had an elevation of 553-558 m and a 0-1% slope. Half of the colony had patches of eastern redcedar (*Juniperus virginiana*) while the other half was cultivated with alfalfa (*Medicago sativa*). Most of the prairie dogs did not have burrows directly under the eastern redcedar (Appendix I).

One colony was at the Fort Larned National Historic Site (FLR; 38°12’N, -99°24’W) in Pawnee County, approximately 7.6 km south and 11.3 km west of Larned, KS. Colony FLR was approximately 4.6 ha and 631-640 m above sea level with 0-4% slope. Vegetation of the colony was mixed prairie typically characterized by big bluestem, little bluestem, sideoats grama, and blue grama (Küchler 1974; Appendix I).

Alarm call recording.—All recordings were made from 22 May to 10 July 2010 by using the guidelines of the Animal Use and Care Committee of the American Society of Mammalogists (Gannon et al. 2007). I acted as a human predator model. Because prairie dogs are able to provide semantic information in their alarm calls (Frederiksen and Slobodchikoff 2007), I maintained the same physical appearance throughout the sampling period. Recordings were made with a Marantz PMD660 Portable Solid State Recorder (D&M Professional, Itasca, Illinois) and Sennheiser K6 omnidirectional microphone (Sennheiser Electronic Corporation, Old Lyme, Connecticut) set in a universal parabola (Telinga Microphones, Tobo, Sweden).

Alarm-calling prairie dogs were approached at approximately 0.30 m/s and recorded until they entered their burrows. I recorded a waypoint of the burrow on a Garmin GPSMAP 60CSx (Garmin International, Inc., Olathe, Kansas) and physically marked the burrow with a surveyor's flag. Each waypoint was averaged to 2 m estimated accuracy. I also recorded the date, time, ranch, pasture, recording file, predator model, number of prairie dogs on the mound, Beaufort scale of the wind, and elevation.

After recording a prairie dog alarm call (Figs. 2 and 3), I selected a direction to travel by looking at the second hand on my watch and walking approximately 100 m before recording again. I did not mark animals so I reduced the possibility of getting multiple recordings from any individual by keeping each recording a minimum of 100 m apart.

All alarm calls used in the dialect analysis were recorded as .mp3 files with 44.1 kHz sampling and a bit rate of 128 kbps. Because the .mp3 format is a compression format, a few .wav format recordings were made for comparison. The .wav files had a 48 kHz sampling rate and a bit rate of 768 kbps and were compared to .mp3 recordings from the same pasture. The .wav recordings were not 100 m from other recordings, but otherwise the same recording protocol was used. The .wav recordings were only used for the comparison of the .mp3 and .wav formats.

Analyses of .mp3 and .wav formats.—Alarm calls were selected randomly from .wav and .mp3 recordings and the following variables were measured: call length, number of harmonics, maximum harmonic frequency, dominant harmonic frequency, and fundamental frequency (Fig. 2). I ran a MANOVA (Tabachnick and Fidell 2007) by using format of the recording (.mp3 or .wav) as the independent variable and call length, number of harmonics, maximum frequency, dominant harmonic frequency, and fundamental frequency as the dependent variables. I ran Mann-Whitney U tests when the assumptions of post hoc ANOVA were violated (Zar 1996).

Playback observation.—I conducted playback experiments from 12 July to 5 September 2010. Each experiment had a unique playlist composed of 8 randomly selected recordings, with one from each colony. I made 85 playlists and stored them on an iPod Nano (Apple, Cupertino, California). Approximately half of the marked burrows of each study colony were used for the playback experiments.

I used my vehicle as a blind (Frederiksen and Slobodchikoff 2007; Smith 1958). A Cass Creek Big Horn Remote Speaker 80 (Altus Brands, Traverse City, Michigan) was placed approximately 30 cm above the ground, the average height of an adult black-tailed prairie dog sitting up (Hoogland 1995). Most of the prairie dogs were ≥ 50 m from the vehicle. I waited at least 30 minutes for the prairie dogs to habituate to the vehicle before proceeding with the experiment. The order of the recordings in the playlist was shuffled and behaviors of each visible prairie dog were recorded. There was a 15 minute waiting period after each playback. If prairie dogs were alarm-calling during the 15 minute interval, I waited until calling ceased or until other prairie dogs appeared to ignore the alarm caller. Behaviors were characterized into two broad categories: response and no response. I considered the following behaviors as responses: alarm call, running, sitting alert, submerging, and tail-flicking. The following behaviors were considered as no responses: emerging from burrow, excavation, foraging, grooming, and jump-yip. If a prairie dog displayed multiple behaviors (e.g., sat alert and then ran to its burrow), I scored each behavior. Each playback experiment lasted approximately 2.5 hrs, with approximately 11 minutes of this time occupied by recordings.

Analyses of playback experiments.—I used logistic regressions to determine whether the prairie dog responds to alarm calls from other colonies (Tabachnick and Fidell 2007). I also investigated the effect of age class (juvenile and adult) on response. I ran binomial logistic regressions for each colony to determine if the individuals of those colonies responded or not. I also ran multinomial logistic regressions on each colony to see if any specific behavior in the response or no response categories was more prevalent than the others. I excluded data on emergence, excavation, grooming, and jump-yip behaviors because they represented 12 of the 3737 total cases in my data set and were not recorded at all of the colonies.

Each colony's data were resampled randomly because of unbalanced samples between response and no response behaviors at each colony. The logistic regression in SPSS ver. 12.0 (IBM, Chicago, Illinois) automatically predicts the dominant category

(Tabachnick and Fidell 2007). For the program to predict the behaviors accurately, the response and no response behaviors needed to be similar in number. Due to multiple comparisons, my Bonferroni corrected significance value was set to 0.00625.

The dependent variable of the binomial logistic regressions was the general behavior (response or no response) and independent variables included colony and age class (adult or juvenile). The dependent variable of the multinomial logistic regressions was the specific behavior (alarm call, foraging, running, sitting alert, submerging, or tail-flicking) and the independent variables were colony and age class.

Preparation of sound files for analysis.—Each spectrograph in the analysis was produced with the default spectrograph parameters in Raven Pro ver. 1.3 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, New York). These parameters produced spectrographs that clearly resembled previously published prairie dog alarm spectrographs (Smith et al. 1977; Waring 1970). My window type was Hann and window size was 256 samples with a 3 dB filter bandwidth of 248 Hz. I used a 50% overlap with a hop size of 128 samples. The discrete Fourier transform (DFT) size was 256 samples with a grid spacing of 172 Hz. I did not use clipping and the averaging was 1 spectrum. I randomly selected a representative alarm call from the sound file and filtered out any background noises (e.g., insects) from the call.

Analyses of dialects.—I used a Spectrographic Cross-Correlation (SPCC) (Clark et al.1987) to calculate a similarity matrix for the prairie dog alarm calls. Rows and columns of the matrix represented alarm calls and cells contained the similarity values. Each pairing of sounds (Fig. 4B, C) was compared and the peak similarity value (Fig.

4A) was calculated from this comparison. Background noise has little effect on the similarity value produced by the SPCC because the procedure enhances common components of the two sounds it is comparing (Clark et al. 1987). A bandpass filter of 0.539 kHz - 16 kHz was applied to each recording, and I used a normalized and biased batch correlation with linear power.

I ran a Principal Coordinates Analysis (PCO) on the results of the SPCC (Cortopassi and Bradbury 2000). I converted the similarity matrix into a distance matrix by using:

$$\text{Distance} = 1 - \text{Similarity}$$

The distance matrix was entered into NTSYSpc ver. 2.11X (Applied Biostatistics Inc., Port Jefferson, New York) for the PCO.

I ran a Multivariate Analysis of Variance (MANOVA) in SPSS to determine whether colony of origin for calls had significant effect on the extracted PCO axes. Cortopassi and Bradbury (2000) recommended this set of analyses because time-frequency patterns of spectrographs determine the placement of sounds in PCO space; the technique is robust to changes in signal-to-noise ratio, duration, and number of harmonics.

The SPCC and PCO reveal if the alarm calls cluster into groups but do not reveal the variables grouping alarm calls (Baker and Louge 2003; Cortopassi and Bradbury 2000; Rice and Bass 2009). I therefore measured multiple variables (Figs. 2 and 3) from the alarm calls in an attempt to characterize alarm calls if they separated into distinct groups: call length (s), number of syllables, number of peaks, number of harmonics, maximum harmonic frequency (kHz), dominant harmonic frequency (kHz), super-dominant harmonic frequency (kHz), interharmonic interval (kHz), fundamental frequency (kHz), and maximum frequency (kHz). Call length was the duration of the individual alarm call measured from the sound's waveform graph. Number of syllables was defined as the number of acoustically distinct parts in a single alarm call. Number of peaks was determined as the number of peaks found in each full harmonic. Number of harmonics equaled the number of complete harmonics. Maximum harmonic frequency was measured from the top of the highest complete harmonic of the alarm call. Dominant harmonic frequency was measured from the top of the harmonic with the most acoustic energy (Frederiksen and Slobodchikoff 2007; Perla and Slobodchikoff 2002). Super-dominant harmonic frequency was measured from the top of the harmonic located above the harmonic with the most acoustic energy. Interharmonic interval was the difference in frequency between the super-dominant harmonic frequency and dominant harmonic frequency. Fundamental frequency was measured from the top of the lowest harmonic in the alarm call. Maximum frequency was the highest partial or full harmonic frequency associated with the alarm call. I also located each alarm call from the original recording and measured the average rate of calling over 4 seconds and the average interval length (s) between alarm calls before and after the call of interest.

RESULTS

Comparison of .mp3 and .wav files.—I excluded one .mp3 recording from the analysis due to poor recording quality. There was a significant difference between alarm calls recorded with .mp3 and .wav formats (MANOVA Hotelling's Trace: $F_{5, 15} = 3.277$, $p = 0.034$, observed power = 0.748, effect size = 0.522; Box's M: $F_{15, 584.825} = 1.365$, $p = 0.159$). The following variables had equal variance: call length, number of harmonics, dominant harmonic frequency, and fundamental frequency (Levene's Test of Equality of Error Variances: $F_{1, 19} \geq 0.087$, $p \geq 0.394$). However, there was a significant difference in the equality of variance of maximum harmonic frequency (Levene's Test of Equality of Error Variances: $F_{1, 19} = 4.488$, $p = 0.048$). Format type had no significant effect on call length, dominant harmonic frequency, and fundamental frequency (ANOVA: $F_1 \geq 0.018$, $p \geq 0.086$, observed power ≤ 0.405, effect sizes ≤ 0.147). Format type had a significant influence on the number of harmonics (ANOVA: $F_1 = 6.439$, $p = 0.020$, observed power = 0.673, effect size = 0.253). Format type had a significant influence on maximum harmonic frequency (Mann-Whitney U: $U_{14, 7} = 14.0$, $p = 0.007$).

Playback experiments.—With the exception of colony PR, adult and juvenile prairie dogs did not respond differently to alarm calls from other colonies (Binomial logistic regression: $X^2_{7\text{-}8} \geq 9.110$, $p \geq 0.010$; Multinomial logistic regression: $X^2_{8\text{-}40} \geq 16.239$, $p \geq 0.010$). At colony PR, either age class or colony of origin influenced the prairie dogs' behaviors (Binomial logistic regression: $X^2_8 = 21.604$, $p = 0.006$, Naglekerke $R^2 = 0.046$). Adults were more likely to respond to alarm calls than juveniles at colony PR ($B_1 = 1.006$, Wald = 9.363, Exp (B) = 2.734, $p = 0.002$), but the colony of the recording had no significant effect on the behavior of the prairie dogs ($p > 0.00625$ for all comparisons).

Dialect experiments.—I excluded 12 recordings because they had too much background noise to isolate individual alarm calls, 1 recording had too many prairie dogs calling in the background to isolate a single individual, 3 recordings had weak call signals, 1 had poor recording quality, and 5 because they were recorded within 100 m of other calls. The PCO produced 11 axes with an eigenvalue > 1. These axes cumulatively accounted for approximately 93.45% of the total variation in the data set (Table 1). I extracted the first 4 axes, which accounted for approximately 64.65% of the total variation in the data set (Table 1).

The first two PCO axes were graphed to see if the recordings clustered into their respective colonies (Fig. 5a). I did not detect any noticeable clustering among the different colonies from the graph. I also graphed axes 2 and 3 to see if the recordings clustered into their respective colonies (Fig. 5b) and did not detect any noticeable clustering. Because colonies SVR1-3 were possibly part of the same colony, I combined them to form colony SVR and graphed the first axes (Fig. 5c). I did not detect any noticeable clustering based on colony. I graphed axes 2 and 3 with colony SVR and again did not detect any noticeable clustering (Fig. 5d).

There were no dialects in black-tailed prairie dog alarm calls because colony of the recording had no significant effect on how the alarm calls were distributed in the graphs (MANOVA Pillai's Trace: $F_{28, 600} = 1.333$, $p = 0.119$, observed power = 0.959, effect size = 0.059; Box's M: $F_{60, 3039.325} = 1.168$, p = 0.178). Even after combining SVR1-3 into the single colony SVR, there were still no dialects in the alarm calls of the black-tailed prairie dog (MANOVA Pillai's Trace: $F_{20, 608} = 1.449$, p = 0.093, observed power = 0.927, effect size = 0.046; Box's M: $F_{40, 1520.408} = 1.240$, p = 0.146). Variables measured from the alarm calls showed similar means among colonies and large standard deviations within each colony (Table 2).

DISCUSSION

The .mp3 format recordings were significantly different from the .wav format recordings regarding the number of harmonics and the maximum harmonic frequency. However, this is not much of a concern for this study because Cortopassi and Bradbury (2000) reveal the SPCC followed by a PCO and MANOVA is robust to variable numbers of harmonics. The .mp3 format is has a smaller file size than the .wav format but includes the major harmonics of a prairie dog's call. The human hearing range is between 20-20,000 Hz (Slobodchikoff et al. 2009b). While the black-tailed prairie dog has a hearing range at 29-26,000 Hz, its ability to hear high frequencies is poor (Heffner et al. 1994). In regards to the high frequency range of the prairie dog, Heffner et al. (1994) were only able to get consistent responses to frequencies up to 22,400 Hz. Possibly, the .mp3 format is excluding frequencies a prairie dog can hear, but this is unlikely.

The prairie dog in western and central Kansas did not behave differently in response to alarm calls from a different colony than it would behave in response to alarm calls from its own colony. Also, with the exception of colony PR, the age of a prairie dog did not affect how the individual responds to alarm calls. At colony PR, adults were more likely than juveniles to respond to alarm calls. However, the regression model explained less than 5% of the total variation. The discrepancy between the two types of regression could have been due to the behaviors being broadly defined in the binomial logistic regression.

Colony PR did not appear different from the other colonies. However, every day I spent recording calls at this colony I witnessed shooting of the prairie dogs. I did not notice any shooting when I returned to colony PR in July for the playback experiments. The Smoky Valley Ranch uses shooting as a management technique in some pastures (Randy Martin, personal communication). Prairie dogs might be shot without landowner consent on my other study colonies as well. However, this was the only colony where I witnessed the shooting. My hypothesis for why adults were more likely to respond at this colony is the prairie dogs are more aware of the shooting. It is possible older, more experienced adults respond to the alarm calls more readily than juveniles. However, with the marginal significance of these results and the low Naglekerke R Square value, it is difficult to assess whether this is the reason for the difference in age class response. Regardless, significant differences in behavior to the alarm calls were only found in the age class of the prairie dogs at one colony, not the colony of origin of the alarm call.

I propose several hypotheses on why the prairie dog responded the same way to alarm calls regardless of the alarm call's colony of origin. First, it was beneficial for an individual to respond to any alarm call because this vocalization was given to warn of predatory threats. Therefore, a prairie dog would be selected to take advantage of this information, regardless of the source of the alarm call. If it did not recognize and respond to this information, then the individual potentially would have reduced fitness.

The black-tailed prairie dog has a historic range from southern Saskatchewan, Canada to New Mexico and central Texas (Hoogland 1996). Prior to the 1800s, black-tailed prairie dog colonies could sometimes occupy more than 20,000 hectares

(Slobodchikoff et al. 2009b). Because of eradication starting in the mid-1800s, the black-tailed prairie dog now only occupies an estimated 1-2% of its former range (Hoogland 1995, 1996; Slobodchikoff et al. 2009b). This decline is recent. Colonies near each other might be fragments of a single historic colony. Therefore, it is possible members of those colonies might still recognize alarm calls from the other colonies. Dialects did not appear to exist in black-tailed prairie dog alarm calls in Kansas. If there were no consistent differences in alarm calls among different populations of the black-tailed prairie dog, then the origin of the alarm call should not affect the associated response behaviors.

The results of my playback experiment might reflect the relatively small scale of my study. As an example, colonies HR and FLR represent my most distant colonies; the distance between these colonies was approximately 229 km. Slobodchikoff et al. (2009b) suggested an experiment needs to be conducted where alarm calls of one colony are played back to nearby colonies as well as colonies throughout the geographic range to determine where, if at all, the animals stop recognizing the alarm calls. My results address a small-scale portion of Slobodchikoff et al.'s (2009b) call for research by indicating the black-tailed prairie dog does not respond any differently to alarm calls from other colonies than it does to alarm calls from its own colony.

Colony had no significant effect on the axes extracted from the PCO, which indicated there were no dialects in the alarm calls of the black-tailed prairie dog. One possible hypothesis for a lack of dialects is dispersal of individuals from different colonies homogenizes the alarm calls. It is not known whether the prairie dog learns its calls from other members of the colony or whether it inherits the alarm calls from its parents. However, research on the Cascade golden-mantled ground squirrel (*Callospermophilus saturatus*) and the congeneric golden-mantled ground squirrel indicate their alarm calls are at least partially learned (Eiler and Banack 2004). If prairie dog alarm calls are learned, then juveniles in a colony might learn alarm calls from adults who have dispersed into the colony. However, the average distance of intercolonial dispersal is 2.4 km and the mortality rate for intercolonial dispersers is significantly greater than the mortality rate for residents of a colony (Garrett and Franklin 1988). Therefore, dispersal does not seem to be a likely hypothesis for the lack of dialects.

Alarm calls might not be an appropriate vocalization to study dialects in the prairie dog. Few studies have indicated dialects in animal alarm calls of other species (Eiler and Banack 2004; Slobodchikoff and Coast 1980; Slobodchikoff et al. 1998). Somers (1973) revealed dialects in the short calls of the American pika (*Ochotona princeps*). Short calls are used in alarm and territorial disputes. However, another study on pika short calls indicates differences in the calls are due to geographic isolation rather than dialects (Conner 1982). Because prairie dog alarm calls alert conspecifics of predatory threats, one would not expect any evolutionary advantage to dialects in the alarm call. An alerted prairie dog should not need to differentiate the alarm caller from a different population to take advantage of the predator information in a call. Prairie dogs did not respond any differently to alarm calls from their colonies or other colonies. If any prairie dog alarm call will alert the prairie dog to a predatory threat, then no specific alarm call should be selected over any other.

Other studies investigating animal dialects focused on vocalizations such as contact calls between conspecifics, territorial calls, and song (Ford 1989; Harbison et al. 1999; Le Boeuf and Peterson 1969; Lemon 1975; Mitani et al. 1992; Slater 1986). The prairie dog has multiple vocalizations used in situations ranging from being chased by conspecifics to territorial disputes (Smith et al. 1977; Waring 1970). Perhaps it would be more appropriate to record one of these vocalizations to investigate potential dialects. For instance, the jump-yip is a behavior where the black-tailed prairie dog will stand on its hind legs, stretch its front legs up, and emit a two-syllable vocalization (Waring 1970). This contagious behavior is often used after a predatory threat has left, but it is also used in territorial disputes (Hoogland 1995; Waring 1970). A territorial call might be an appropriate vocalization to study for dialects because natural selection will select prairie dogs with threatening and effective territorial calls. Prairie dogs that effectively defend resources will have greater probability of survivorship and will be more likely to pass genes controlling these behaviors to the next generation.

Because Gunnison's and black-tailed prairie dogs can encode predator information in their alarm calls (Frederiksen and Slobodchikoff 2007; Slobodchikoff et al. 1991, 2009a) it is intriguing the Gunnison's prairie dog has dialects in its alarm calls (Slobodchikoff and Coast 1980; Slobodchikoff et al. 1998) while the black-tailed prairie dog does not appear to have dialects. This might be because the Gunnison's prairie dog has smaller colonies and is less social than the black-tailed prairie dog (Hoogland 1996; Pizzimenti and Hoffmann 1973; Slobodchikoff et al. 2009b). Gunnison's prairie dog has limited gene flow between populations and low levels of genetic diversity (Travis et al.

1997) ; when combined with the small colony sizes and low sociality of the species, this could account for dialects in its alarm calls. Dobson et al. (1997) indicate while there is inbreeding at the population level of the black-tailed prairie dog, there was little inbreeding in coteries. They suggest this is because females tend to stay in their natal coteries, males disperse out of their natal coteries, and males recognize their female offspring. Hoogland (1992) also mentions a female black-tailed prairie dog will avoid mating with close relatives, such as fathers or brothers, but will breed with relatives as close as full and half first cousins. The large colony sizes, increased sociality, and moderate (as opposed to high) inbreeding levels might explain the lack of dialects in the alarm calls of the black-tailed prairie dog.

In conclusion, it appears the black-tailed prairie dog does not respond differently to alarm calls from another colony than it would to recordings from its own colony. It also appears dialects do not exist in the alarm calls of the black-tailed prairie dog. Future research should focus on a larger geographic scale. Also, interested scientists could compare colonies where prairie dogs are shot to colonies where they are not shot to examine whether adults and juveniles respond differently to alarm calls. Finally, other vocalizations would probably be more appropriate for those interested in investigating dialects in the black-tailed prairie dog.

LITERATURE CITED

ASCHEMEIER, L.M., AND C.R. MAHER. 2011. Eavesdropping of woodchucks (*Marmota monax*) and eastern chipmunks (*Tamias striatus*) on heterospecific alarm calls. Journal of Mammalogy 92:493–499.

BAKER, M.C., AND D.M. LOGUE. 2003. Population differentiation in a complex bird sound: a comparison of three bioacoustical analysis procedures. Ethology 109:223–242.

BLUMSTEIN, D.T., AND O. MUNOS. 2005. Individual, age, and sex-specific information is contained in yellow-bellied marmot alarm calls. Animal Behaviour 69:353–361.

CLARK, C.W., P. MARLER, AND K. BEEMAN. 1987. Quantitative analysis of animal vocal phonology: an application to swamp sparrow song. Ethology 76:101–115.

CONNER, D.A. 1982. Geographic variation in short calls of pikas (*Ochotona princeps*). Journal of Mammalogy 63:48–52.

CORTOPASSI, K.A., AND J.W. BRADBURY. 2000. The comparison of harmonically rich sounds using spectrographic cross-correlation and principal coordinates analysis. Bioacoustics 11:89–127.

DOBSON, F.S., R.K. CHESSER, J.L. HOOGLAND, D.W. SUGG, AND D.W. FOLTZ. 1997. Do black-tailed prairie dogs minimize inbreeding? Evolution 51:970–978.

EILER, K.C., AND S.A. BANACK. 2004. Variability in the alarm call of golden-mantled ground squirrels (*Spermophilus lateralis* and *S. saturatus*). Journal of Mammalogy 85:43-50.

FORD, J.K.B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology 67:727–745.

FREDERIKSEN, J.K., AND C.N. SLOBODCHIKOFF. 2007. Referential specificity in the alarm calls of the black-tailed prairie dog. Ethology Ecology and Evolution 19:87–99.

GANNON, W.L., R.S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809-823.

GARRETT, M.G., AND W.L. FRANKLIN. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. Journal of Mammalogy 69:236–250.

HARBISON, H., D.A. NELSON, AND T.P. HAHN. 1999. Long-term persistence of song dialects in the mountain white-crowned sparrow. The Condor 101:133–148.

HARE, J.F. 1998. Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. Animal Behaviour 55:451–460.

HARE, J.F., AND B.A. ATKINS. 2001. The squirrel that cried wolf: reliability and detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). Behavioral Ecology and Sociobiology 51:108–112.

HAUSER, M. D. 1988. How infant vervet monkeys learn to recognize starling alarm calls: the role of experience. Behaviour 105:187–201.

HEFFNER, R.S., H.E. HEFFNER, C. CONTOS, AND D. KEARNS. 1994. Hearing in prairie dogs: transition between surface and subterranean rodents. Hearing Research 73:185–189.

HOOGLAND, J.L. 1992. Levels of inbreeding among prairie dogs. The American Naturalist 139:591–602.

HOOGLAND, J.L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. The University of Chicago Press, Chicago, IL.

HOOGLAND, J.L. 1996. *Cynomys ludovicianus*. Mammalian Species 535:1–10.

KIRIAZIS, J., AND C.N. SLOBODCHIKOFF. 2006. Perceptual specificity in the alarm calls of Gunnison's prairie dogs. Behavioural Processes 73:29–35.

KÜCHLER, A.W. 1974. A new vegetation map of Kansas. Ecology 55:586–604.

LEA, A. J., J.P. BARRERA, L.M. TOM, AND D.T. BLUMSTEIN. 2008. Heterospecific eavesdropping in a nonsocial species. Behavioral Ecology 19:1041–1046.

LE BOEUF, B.J., AND R.S. PETERSON. 1969. Dialects in elephant seals. Science 166:1654–1656.

LEMON, R.E. 1975. How birds develop song dialects. The Condor 77:386–406.

LOUGHRY, W.J., AND C.M. MCDONOUGH. 1988. Calling and vigilance in California ground squirrels: a test of the tonic communication hypothesis. Animal Behaviour 36:1533–1540.

MCCOWAN, B., AND S.L. HOOPER. 2002. Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada. Journal of the Acoustical Society of America 111:1157–1160.

MITANI, J.C., T. HASEGAWA, J. GROS-LOUIS, P. MARLER, AND R. BYRNE. 1992. Dialects in wild chimpanzees? American Journal of Primatology 27:233–243.

PERLA, B.S., AND C.N. SLOBODCHIKOFF. 2002. Habitat structure and alarm call dialects in Gunnison's prairie dog (*Cynomys gunnisoni*). Behavioral Ecology 13:844–850.

PIZZIMENTI, J.J., AND R.S. HOFFMANN. 1973. *Cynomys gunnisoni*. Mammalian Species 25:1–4.

RICE, A.N., AND A.H. BASS. 2009. Novel vocal repertoire and paired swimbladders of the three-spined toadfish, *Batrachomoeus trispinosus*: insights into the diversity of the Batrachoididae. The Journal of Experimental Biology 212:1377-1391.

SEYFARTH, R.M., D.L. CHENEY, AND P. MARLER. 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210:801–803.

SHERMAN, P.W. 1977. Nepotism and the evolution of alarm calls: alarm calls of Belding's ground squirrels warn relatives, and thus are expressions of nepotism. Science 197:1246–1253.

SHRINER, W.M. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Animal Behaviour 55:529-536.

SLATER, P.J.B. 1986. The cultural transmission of bird song. Trends in Ecology and Evolution 1:94–97.

SLOAN, J.L., AND J.F. HARE. 2008. The more the scarier: adult Richardson's ground squirrels (*Spermophilus richardsonii*) assess response urgency via the number of alarm signallers. Ethology 114:436–443.

SLOBODCHIKOFF, C.N., S.H. ACKERS, AND M. VAN ERT. 1998. Geographic variation in alarm calls of Gunnison's prairie dogs. Journal of Mammalogy 79:1265–1272.

SLOBODCHIKOFF, C.N., AND R. COAST. 1980. Dialects in the alarm calls of prairie dogs. Behavioral Ecology and Sociobiology 7:49–53.

SLOBODCHIKOFF, C.N, J. KIRIAZIS, C. FISCHER, AND E. CREEF. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. Animal Behaviour 42:713–719.

SLOBODCHIKOFF, C.N., A. PASEKA, AND J.L. VERDOLIN. 2009a. Prairie dog alarm calls encode labels about predator colors. Animal Cognition 12:435–439.

SLOBODCHIKOFF, C.N., B.S. PERLA, AND J.L. VERDOLIN. 2009b. Prairie dogs: communication and community in an animal society. Harvard University Press, Cambridge, MA and London, England.

SMITH, R.E. 1958. Natural history of the prairie dog in Kansas. Miscellaneous Publication 16. Museum of Natural History and State Biological Survey, University of Kansas 36p.

SMITH, W.J., S.L. SMITH, E.C. OPPENHEIMER, AND J.G. DEVILLA. 1977. Vocalizations of the black-tailed prairie dog, *Cynomys ludovicianus*. Animal Behaviour 25:152–164.

SOMERS, P. 1973. Dialects in southern rocky mountain pikas, *Ochotona princeps* (Lagomorpha). Animal Behaviour 21:124–137.

TABACHNICK, B.G., AND L.S. FIDELL. 2007. Using multivariate statistics. 5th ed. Pearson Education, Inc., Boston, Massachusetts.

TRAVIS, S.E., C.N. SLOBODCHIKOFF, AND P. KEIM. 1997. DNA fingerprinting reveals low genetic diversity in Gunnison's prairie dog (*Cynomys gunnisoni*). Journal of Mammalogy 78:725–732.

WARING, G.H. 1970. Sound communications of black-tailed, white-tailed, and Gunnison’s prairie dogs. American Midland Naturalist. 83:167–185.

ZAR, J.H. 1996. Biostatistical analysis. 3rd ed. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

ZUBERBÜHLER, K. 2000. Causal knowledge of predators’ behavior in wild Diana monkeys. Animal Behaviour 59:209–220.

ZUBERBÜHLER, K., R. NOË, AND R. M. SEYFARTH. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. Animal Behavior 53:589–604.

TABLE 1.—The first 11 Principal Coordinate Analysis (PCO) axes and their corresponding eigenvalues produced by the Principal Coordinates Analysis for black-tailed prairie dog (*Cynomys ludovicianus*) alarm calls.

PCO Axis	Eigenvalue	Percent of Variation	Cumulative Percent of Variation
1	10.9	23.5	23.5
2	9.2	19.7	43.2
3	5.9	12.6	55.8
4	4.1	8.9	64.7
5	3.0	6.4	71.1
6	2.6	5.5	76.6
7	2.1	4.6	81.2
8	2.0	4.3	85.5
9	1.4	3.0	88.5
10	1.2	2.6	91.1
11	1.1	2.4	93.5

TABLE 2.—Measurements recorded from black-tailed prairie dog (*Cynomys ludovicianus*) alarm calls after the Spectrographic Cross-Correlation. Values presented include duration of the call and number of syllables in the call. The number of peaks was the number of peaks in the harmonics, number of harmonics was the number of harmonics in the call, maximum harmonic frequency was the frequency of the highest full harmonic, dominant harmonic frequency was the frequency of the harmonic with the most energy, super-dominant harmonic frequency was the harmonic frequency above the dominant harmonic frequency, interharmonic interval was the frequency difference between the super-dominant and dominant harmonic frequencies, fundamental frequency was the lowest frequency in the alarm call, maximum frequency was the highest frequency in the call, average rate of calling was the average number of calls recorded 2 seconds before and 2 seconds after the alarm call of interest, and average interval length was the average time between the call of interest and the calls just prior and post. FLR: Fort Larned National Historic Site; HR: Haverfield Ranch; JR: Johanning Ranch; PR: Palmer Ranch; RR: Rusco Ranch; SVR: Smoky Valley Ranch.

	Colony							
	FLR	HR	JR	PR	RR	SVR1	SVR2	SVR3
Sample Size	6	28	7	30	3	29	30	24
Spectrograph Variables	$\bar{X} \pm$ SD							
Call Length (s)	0.05 ± 0.01	0.14 ± 0.32	0.07 ± 0.04	0.09 ± 0.08	0.04 ± 0.01	0.12 ± 0.09	0.09 ± 0.07	0.11 ± 0.09
Number of Syllables	1.00 ± 0.00	1.25 ± 0.44	1.29 ± 0.49	1.30 ± 0.47	1.00 ± 0.00	1.41 ± 0.50	1.20 ± 0.41	1.29 ± 0.46
Number of Peaks	1.33 ± 0.52	1.29 ± 0.46	1.29 ± 0.49	1.37 ± 0.49	1.00 ± 0.00	1.55 ± 0.51	1.43 ± 0.50	1.54 ± 0.51
Number of Harmonics	4.67 ± 1.63	4.46 ± 1.10	3.71 ± 1.25	3.87 ± 1.28	5.00 ± 3.61	5.00 ± 1.63	4.60 ± 1.67	4.92 ± 1.82
Maximum Harmonic Frequency (kHz)	7.86 ± 1.59	7.23 ± 1.91	6.79 ± 2.81	7.04 ± 2.24	8.97 ± 5.62	7.28 ± 1.66	6.97 ± 1.57	7.29 ± 2.01
Dominant Harmonic Frequency (kHz)	4.17 ± 0.80	3.55 ± 0.81	3.44 ± 0.65	3.49 ± 0.70	3.78 ± 0.76	3.68 ± 0.76	3.67 ± 0.83	3.75 ± 0.71
Super-Dominant Harmonic Frequency (kHz)	5.87 ± 1.08	5.19 ± 1.32	4.92 ± 0.78	5.16 ± 0.96	5.13 ± 0.90	5.22 ± 1.05	5.12 ± 1.14	5.01 ± 0.79
Interharmonic Interval (kHz)	1.71 ± 0.42	1.64 ± 0.74	1.48 ± 0.39	1.66 ± 0.54	1.36 ± 0.33	1.55 ± 0.66	1.45 ± 0.57	1.26 ± 0.38
Fundamental Frequency (kHz)	2.68 ± 0.88	2.02 ± 0.50	2.25 ± 0.56	2.14 ± 0.45	2.21 ± 0.74	2.06 ± 0.55	2.09 ± 0.40	2.01 ± 0.30
Maximum Frequency (kHz)	9.72 ± 3.27	8.73 ± 1.85	9.39 ± 2.93	9.52 ± 2.75	11.91 ± 2.92	9.50 ± 2.59	8.88 ± 2.51	9.94 ± 2.65
Average Rate of Calling (calls/s)	2.33 ± 0.54	2.52 ± 0.62	2.79 ± 0.78	2.83 ± 0.78	2.25 ± 1.50	2.69 ± 0.61	2.55 ± 0.64	2.52 ± 0.56
Average Interval Length (s)	0.44 ± 0.18	0.33 ± 0.19	0.31 ± 0.11	0.29 ± 0.16	1.05 ± 1.43	0.26 ± 0.14	0.33 ± 0.15	0.29 ± 0.15

FIG. 1.—The 8 black-tailed prairie dog (*Cynomys ludovicianus*) colonies in this study were in western and central Kansas. Colonies HR, SVR1, SVR2, and SVR3 were in Logan County; colony PR was in Scott County; colonies JR and RR were in Barton County; and colony FLR was in Pawnee County. Alarm call recordings and playback observations occurred at each colony. FLR: Fort Larned National Historic Site; HR: Haverfield Ranch; JR: Johanning Ranch; PR: Palmer Ranch; RR: Rusco Ranch; SVR: Smoky Valley Ranch.

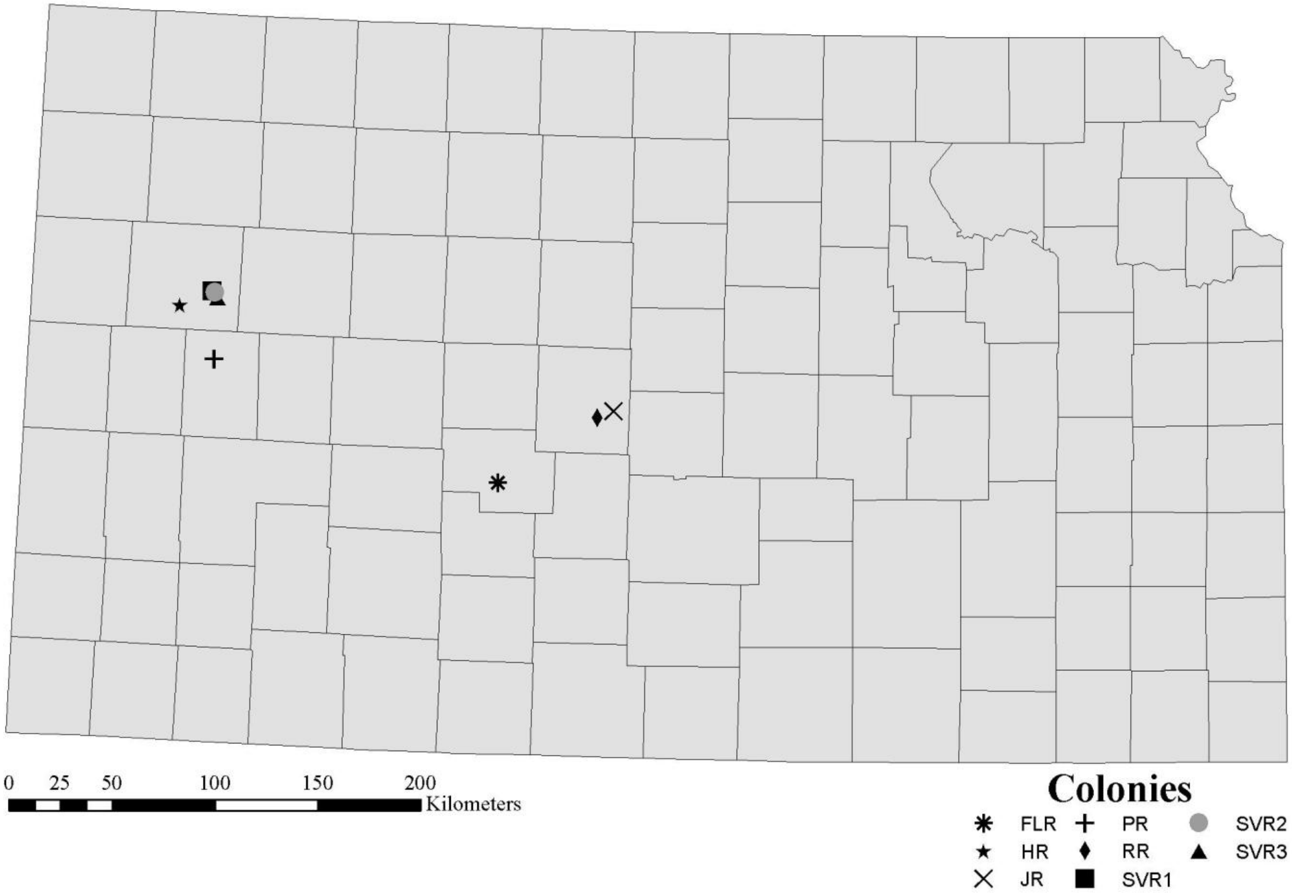


FIG. 2.— Spectrographic and waveform measurements made from black-tailed prairie dog (*Cynomys ludovicianus*) alarm calls. All measurements were made off of one randomly-selected alarm call (bordered in black) with the exception of: average rate of calling, interval before call (IBC, s), and interval after call (IAC, s). For clarity and illustrative purposes, variables in this figure were labeled on multiple alarm calls. The following measurements were made from the waveform graph (A): Call length (CL, s), IBC, and IAC. All of the following measurements were made from the spectrograph (B): number of harmonics (NH), maximum harmonic frequency (MHF, kHz), dominant harmonic frequency (DHF, kHz), super-dominant harmonic frequency (SDHF, kHz), interharmonic interval = SDHF-DHF, fundamental frequency (FF, kHz), and maximum frequency (MF, kHz).

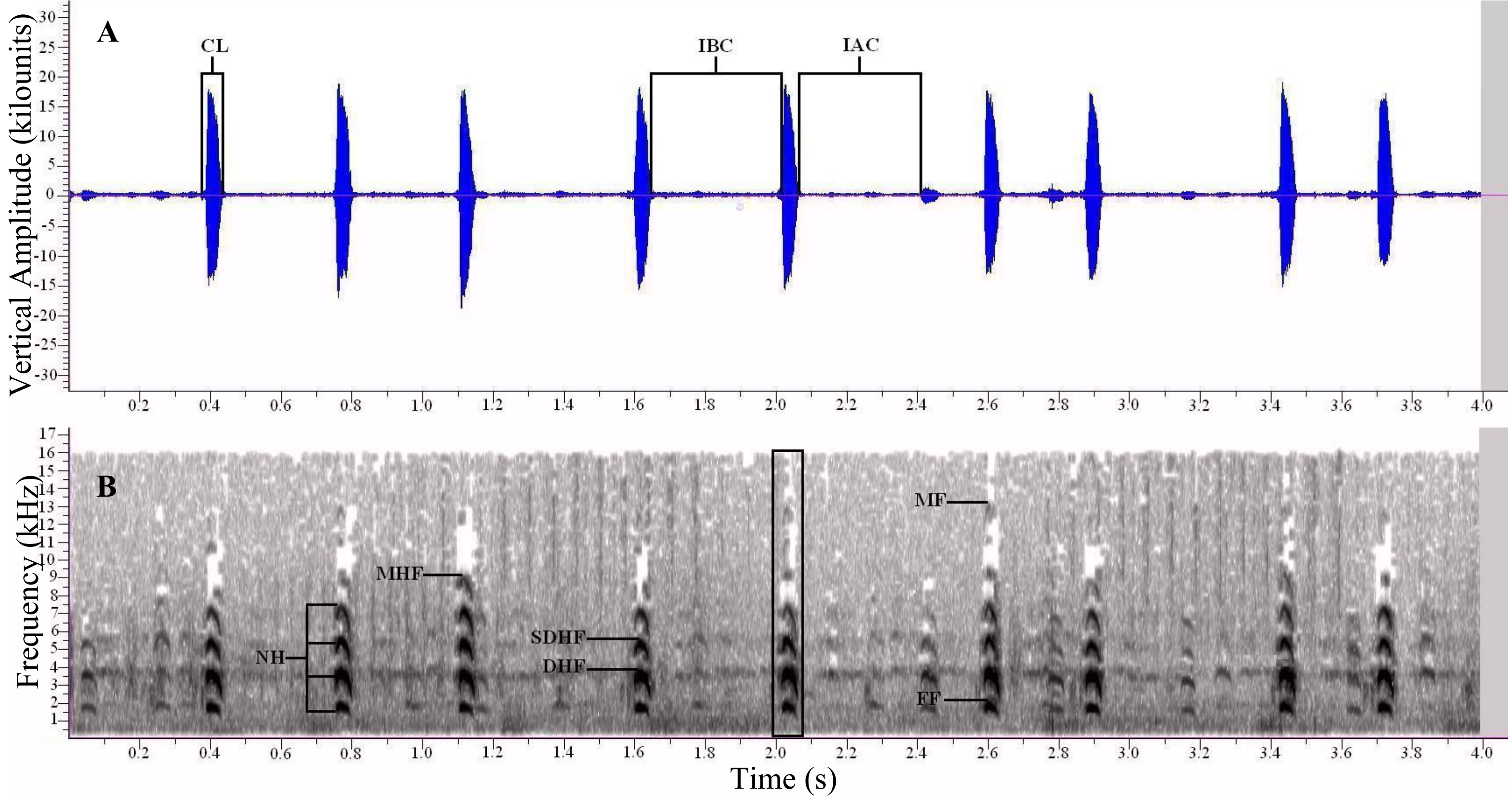


FIG. 3.—Spectrographic examples of alarm calls with: (i) one peak and one syllable, (ii) one peak and two syllables, and (iii) two peaks and one syllable.

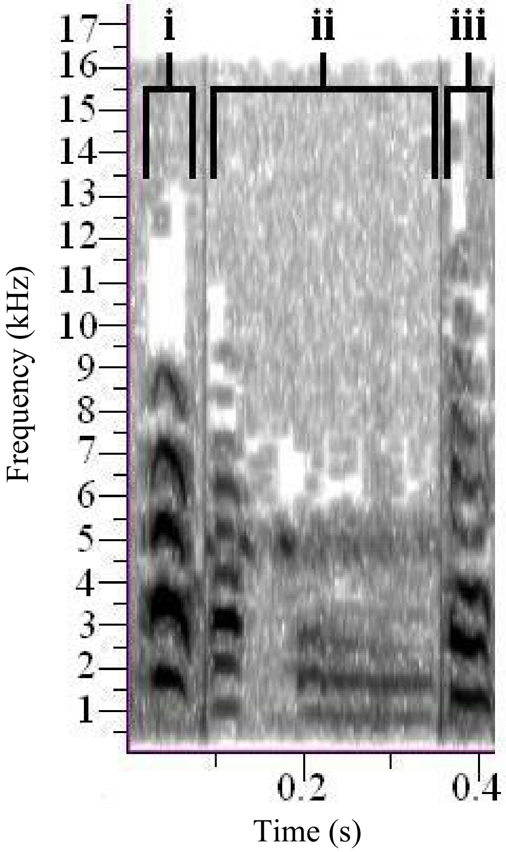


FIG. 4.—A Spectrographic Cross-Correlation (SPCC) of two black-tailed prairie dog (*Cynomys ludovicianus*) alarm calls. Panel A displays all of the similarity values calculated in the SPCC. The spectrographs in panels B and C slide past each other at timed intervals and the similarity value was calculated by comparing how the spectrographs line up. In this example, the spectrographs are lined up so the time and frequency patterns of the two spectrographs have the highest similarity. The peak similarity value, 0.93 in this figure, was recorded in a similarity matrix. The spectrographs appeared wider compared to those in Fig. 2 due to the small time scale of this figure.

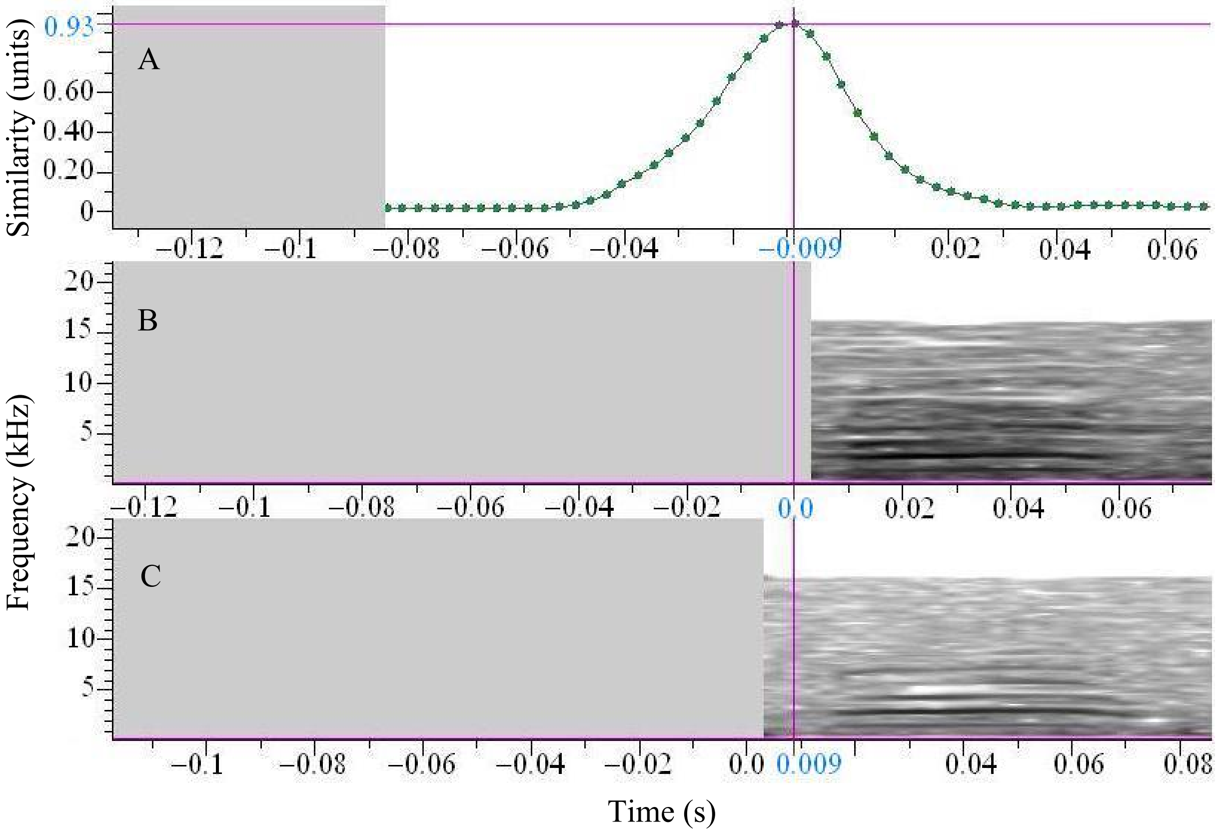
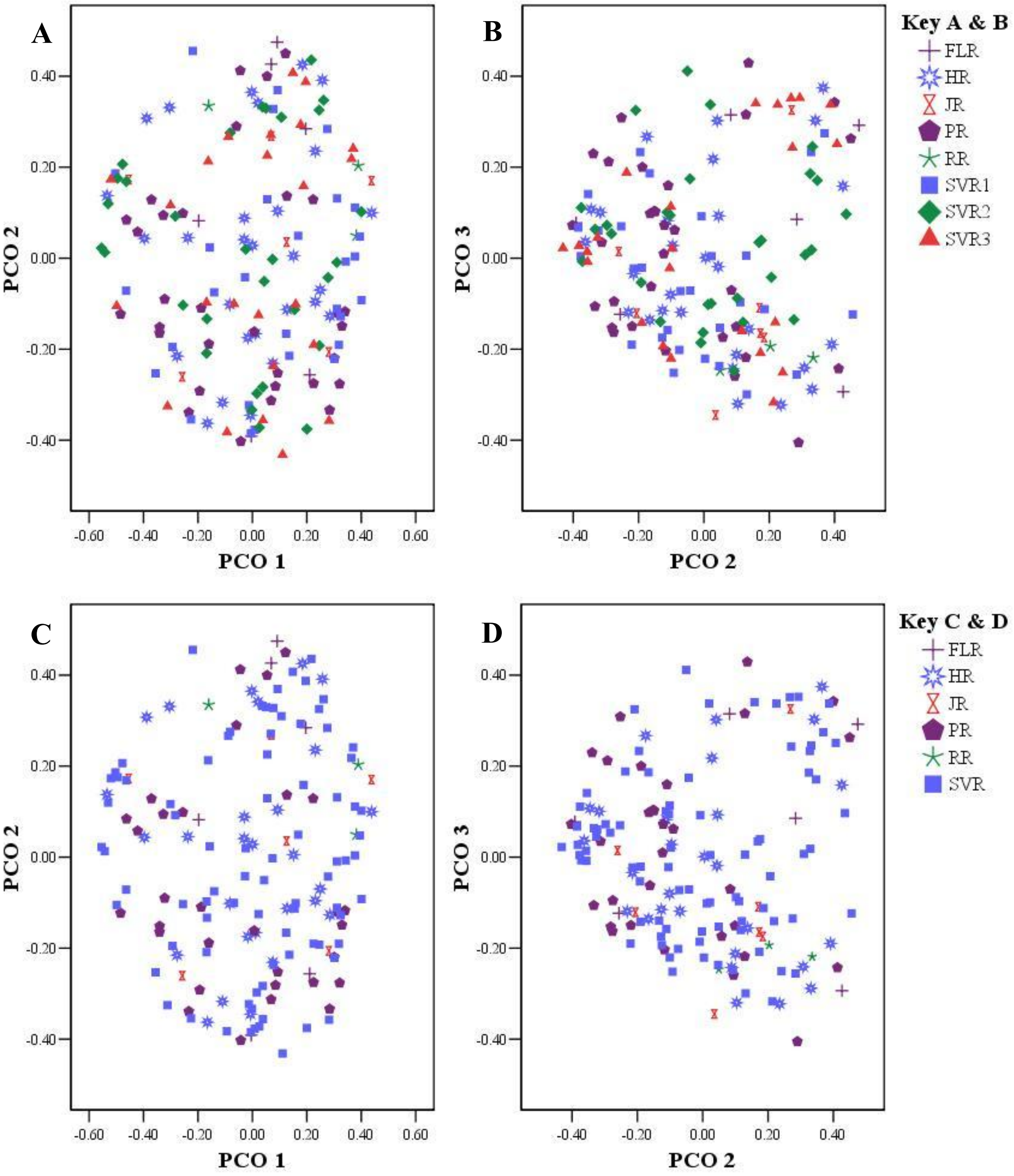


FIG. 5.—Scatterplots from a Principal Coordinate Analysis of a Spectrographic Cross-Correlation of 158 black-tailed prairie dog (*Cynomys ludovicianus*) alarm calls. Graphs A and C plot principal coordinate 1 (PCO1) with principal coordinate 2 (PCO2). Graphs B and D plot PCO2 with principal coordinate 3 (PCO3). Graphs A and B display 8 colonies while graphs C and D display 6 colonies by combing colonies SVR1-3 into a single colony (SVR). FLR: Fort Larned National Historic Site; HR: Haverfield Ranch; JR: Johanning Ranch; PR: Palmer Ranch; RR: Rusco Ranch; SVR: Smoky Valley Ranch.



APPENDIX I

A list of plants found at each colony (FLR, HR, JR, PR, RR, SVR1, SVR2, SVR3). Presence of the plant species at a colony is indicated by ―X”. FLR: Fort Larned National Historic Site; HR: Haverfield Ranch; JR: Johanning Ranch; PR: Palmer Ranch; RR: Rusco Ranch; SVR: Smoky Valley Ranch.

Scientific Name	Common Name	FLR	HR	JR	PR	RR	SVR1	SVR2	SVR3
Achillea millefolium	Western Yarrow			X		X			
Allium sp.	Wild Onion							X	
Amaranthus sp.	Pigweed						X		
Ambrosia psilostachya	Western Ragweed				X	X		X	
Andropogon gerardii	Big Bluestem							X	
Antennaria neglecta	Field Pussytoes							X	
Aristida purpurea	Purple Threeawn	X	X	X	X		X	X	X
Artemisia sp.	Unidentified Sage				X				
Asclepias amplexicaulis	Bluntleaf Milkweed			X		X			
Asclepias fascicularis	Narrowleaf Milkweed	X							
Asclepias latifolia	Broadleaf Milkweed			X		X			
Asclepias syriaca	Common Milkweed		X		X		X	X	X
Aster sp.	Unidentified Aster						X		
Astragalus mollissimus	Woolly Locoweed		X				X		X
Bouteloua curtipendula	Sideoats Grama								X
Bouteloua gracilis	Blue Grama				X			X	X
Bouteloua hirsuta	Hairy Grama						X	X	X
Bromus japonicus	Japanese Brome							X	X
Bromus tectorum	Cheatgrass		X	X	X	X	X	X	X
Buchloe dactyloides	Buffalograss		X		X	X	X	X	X
Buglossoides sp.	Buglossoides		X		X		X	X	
Callirhoe involucrata	Purple Poppy Mallow	X		X	X			X	
Carex sp.	Unidentified Sedge			X		X			

APPENDIX I.—Continued

Scientific Name	Common Name	FLR	HR	JR	PR	RR	SVR1	SVR2	SVR3
Chenopodium album	Lambsquarters	X	X		X		X	X	X
Cirsium undulatum	Wavyleaf Thistle	X	X	X	X	X	X	X	X
Cirsium vulgare	Bull Thistle			X		X			
Convolvulus arvensis	Field Bindweed	X		X	X		X		X
Conyza canadensis	Horseweed		X				X	X	X
Croton texensis	Texas Croton	X	X		X		X	X	X
Cucurbita foetidissima	Buffalo Gourd		X		X		X		
Cymopterus glomeratus	Wild Parsley		X						
Dalea purpurea	Purple Prairie Clover								X
Echinocactus sp.	Barrel Cactus				X				
Erysimum capitatum	Western Wallflower				X				
Gaura coccinea	Scarlet Guara		X	X	X	X	X	X	X
Grindelia squarrosa	Curlycup Gumweed		X				X	X	
Gutierrezia sarothrae	Broom Snakeweed		X				X	X	X
Helianthus annuus	Annual Sunflower		X				X		X
Hordeum jubatum	Foxtail barley				X		X	X	X
Hymenopappus flavescens	Yellow Wollywhite		X				X	X	X
Juniperus virginiana	Eastern Redcedar	X		X		X			
Lepidium densiflorum	Common Pepperweed	X	X		X	X	X	X	
Liatris punctata	Dotted Gayfeather							X	
Lygodesmia juncea	Rush Skeletonweed		X					X	X
Mentzelia decapetala	Tenpetal Mentzelia				X				
Monarda sp.	Beebalm				X				
Morus alba	Mulberry					X			
Muhlenbergia paniculata	Tumblegrass		X		X				
Opuntia polyacantha	Plains Pricklypear		X		X		X	X	X
Oxalis stricta	Sheep Sorrel	X							

Appendix I.—Continued

Scientific Name	Common Name	FLR	HR	JR	PR	RR	SVR1	SVR2	SVR3
Panicum virgatum	Switchgrass			X					
Pascopyrum smithii	Western Wheatgrass			X	X	X		X	X
Physalis virginiana	Virginia Groundcherry				X				
Plantago patagonica	Woolly Plantain		X				X		X
Poa pratensis	Kentucky Bluegrass			X					
Psoralidium tenuiflorum	Scurfpea		X				X		X
Quincula lobata	Purple Groundcherry				X				
Ratibida columnifera	Prairie Coneflower		X		X		X	X	X
Rumex crispus	Curly Dock	X							
Salsola kali	Russian Thistle		X		X				
Schizachyrium scoparium	Little Bluestem							X	
Smilax sp.	Greenbriar							X	
Solanum nigrum	Black Nightshade		X						
Solanum rostratum	Buffalobur		X		X		X	X	X
Sphaeralcea coccinea	Scarlet Globe Mallow	X	X		X	X	X	X	X
Sporobolus compositus	Dropseed								X
Taraxacum officinale	Dandelion			X		X			
Tragopogon dubius	Western Salsify			X	X			X	X
Verbascum thapsus	Common Mullien	X							
Verbena stricta	Hoary Verbena	X							
Vulpia octoflora	Sixweeks Fescue					X	X	X	
Yucca glauca	Yucca		X		X		X	X	X