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C. N. Slobodchikoff
Northern Arizona University

S. H. Ackers
Northern Arizona University

M. Van Ert
Northern Arizona University

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GEOGRAPHIC VARIATION IN ALARM CALLS OF GUNNISON'S PRAIRIE DOGS

C. N. SLOBODCHIKOFF, S. H. ACKERS, AND M. VAN ERT

Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640

Geographic variation in alarm calls of Gunnison's prairie dogs (*Cynomys gunnisoni*) was analyzed at regional and local scales. Alarm calls in response to a common stimulus (the same human) were recorded at four colonies near Flagstaff, Arizona, and at six sites throughout the southwestern United States. The acoustic structure of calls was analyzed for seven call variables. Regional differences fit the prediction of greater differences with increased geographical separation. Differences between colonies at a local scale were not related to geographical distance, suggesting that local dialects exist within a region. Differences in the level of predation by humans between colonies or habitat effects on sound propagation may explain variation in calls at the local level.

Key words: *Cynomys*, alarm calls, dialects

Dialects can be considered phenotypic variation in vocalizations between populations of a given species. Dialectic differences in vocalizations related to courtship and territorial defense (Asquith et al., 1988; Balaban, 1988; Marler and Pickert, 1984; Marler and Tamura, 1962; Somers, 1973; Tubaro and Segura, 1995) and in alarm calls (Gannon and Lawlor, 1989; Slobodchikoff and Coast, 1980; Somers, 1973) have been reported in a variety of species. Although dialects in vocalizations related to mating could contribute to reproductive isolation among subpopulations, the origin and function of dialects in alarm calls is less apparent. Slobodchikoff and Coast (1980) identified local dialects in alarm calls of Gunnison's prairie dogs (*Cynomys gunnisoni*) on the basis of three call characteristics: syllable length, number of syllables, and length of calls.

Gunnison's prairie dogs live in colonies of up to several hundred individuals. Each colony is subdivided into smaller territories occupied by social groups or solitary individuals (Rayor, 1988; Slobodchikoff, 1984). Upon detecting a predator, several individuals within a colony run to a burrow mound, stand bipedally, and emit an alarm

vocalization that functions to warn genetic relatives (Dunford, 1977; Maynard Smith, 1965; Sherman, 1977). The acoustic structure of these calls varies according to predator species and characteristics of individuals predators (Slobodchikoff et al., 1986, 1991). Dialects among alarm calls of prairie dogs have been identified and differences between colonies may be related to effects of habitat on sound propagation and differences in the complement of predators attacking different colonies (Slobodchikoff and Coast, 1980). Differences in alarm calls related to different selection pressures, such as differences in habitat structure between areas, might show a pattern similar to differences in morphological traits. However, because the complement of predators at a given colony might change unpredictably through time, dimensions of alarm-call dialects due to differences in predation risk should vary independently of morphological traits.

We expanded the analysis of prairie-dog dialects to consider the acoustic structure of alarm calls on a regional and local scale. We analyzed geographic variation at a regional level to identify acoustic components of the calls that may differentiate through

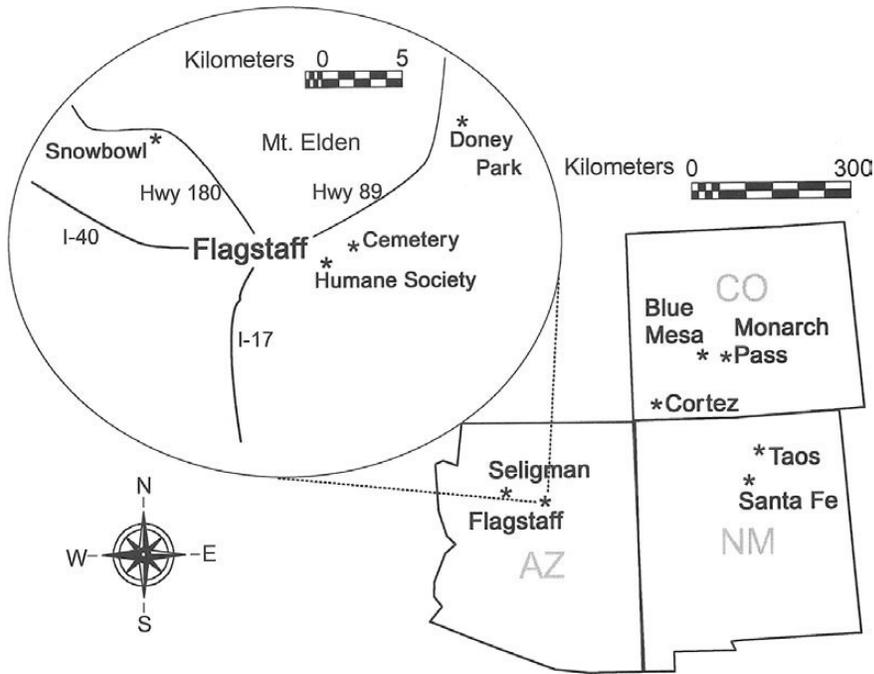


FIG. 1.—Locations of colonies of Gunnison's prairie dogs where recordings of alarm calls were obtained. State maps indicate regional sites where alarm calls were recorded from several colonies. The expanded portion indicates the locations of individual colonies in the Flagstaff region.

geographic isolation. We also assessed local variation among incompletely isolated colonies to identify acoustic components that may differentiate in the presence of gene flow.

MATERIALS AND METHODS

Study sites.—We recorded alarm calls of Gunnison's prairie dogs at four colonies within 15 km of Flagstaff, Coconino Co., Arizona: Cemetery (35°11'N, 111°34'W); Doney Park (35°14'N, 111°28'W); Humane Society (35°11'N, 111°36'W); and Snow Bowl (35°16'N, 111°43'W; Fig. 1). We also sampled six additional sites throughout the southwestern region of the United States: Seligman, Coconino Co., Arizona (35°25'N, 112°50'W); Santa Fe, Santa Fe Co., New Mexico (35°40'N, 105°55'W); Taos, Taos Co., New Mexico (36°25'N, 105°35'W); Monarch Pass, Gunnison Co., Colorado (38°25'N, 106°35'W); Blue Mesa Reservoir, Gunnison Co., Colorado (38°30'N, 107°5'W); and Cortez, Montezuma Co., Colorado (37°15'N, 108°35'W; Fig. 1). All colonies around Flagstaff were connected by

habitat suitable for prairie dogs, and several colonies were present between colonies chosen for study. Among the regional sites, Santa Fe and Taos, New Mexico, were not separated by any barriers to dispersal nor were Monarch Pass and Blue Mesa, Colorado. When these two pairs of sites were considered as units, all other pairs of regional sites were separated by geologic and associated vegetative barriers (Küchler, 1964) or distances of >100 km.

Procedure.—The same human wearing a white shirt and black shorts was used as a common stimulus to elicit alarm calls at all colonies. Alarm calls were recorded on audio tape using a Sennheiser ME-88 directional microphone connected to a Sony TC-D5PRO II cassette recorder. The first bout of alarm calling from each caller was used in the analysis. Although prairie dogs were not individually marked, bouts from different individuals could be recognized on the spectrograph. Different portions of each colony were sampled to assure that each bout came from a different animal. Spectrographs of the bouts of alarm calling were produced using a

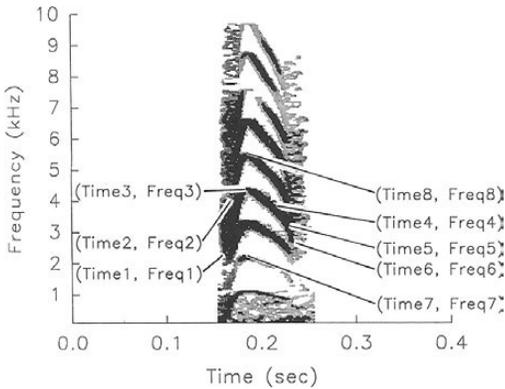


FIG. 2.—A spectrograph of a typical prairie dog alarm call produced in response to a human wearing a white shirt and black shorts. These calls occurred in bouts of 5–60 calls with 0.15–0.3 s between calls. The points labelled on the call are the coordinates that were digitized from the screen and used to calculate variables used in the discriminant function analyses. Variables used in the discriminant function analyses were calculated as follows: dominant harmonic frequency (DHF) = freq3; fundamental frequency (FF) = freq7; supradominant frequency (SHF) = freq8; inter-harmonic interval (IHI) = freq8 – freq3; duration (DUR) = time6 – time1; ascending slope (SLOPEA) = (freq3 – freq1)/(time3 – time1); descending slope (SLOPED) = (freq5 – freq3)/(time5 – time3).

RTS Real-Time Spectrogram computer package (version 1.2; Engineering Design, Belmont, MA). Sample rate was set at 25 KHz with a frequency resolution of 48.8 Hz.

Each bout was partitioned into 1-s intervals prior to obtaining measurements from the spectrograph screen. Time and frequency coordinates were digitized from eight points on each call and used to calculate seven dependent variables used in the statistical analyses. Acoustic variables that were measured were: dominant harmonic frequency, supra-dominant harmonic frequency, fundamental frequency, inter-harmonic interval, slope of the ascending portion of the call, slope of the descending portion of the call, and duration of the call (Fig. 2). The mean-standardized measurements for the first bout of calls were calculated for each individual. Two stepwise-discriminant-function analyses (Norusis, 1985) were used to determine if calls differed with respect to regional variation (i.e., between the six

sites throughout Arizona, Colorado and New Mexico) and local variation (i.e., between the four sites near Flagstaff, Arizona). Discriminant function analysis involves calculating new variables (i.e., canonical variables) based on linear combinations of the original variables that maximize variance between groups. The three discriminant functions that explained the largest proportion of the between-group variance were used to determine the pattern of differences between sites (regional analysis) and colonies (local analysis). The relative contribution of each of the original variables to call variance between sites was determined by calculating pooled within-groups correlations between discriminating variables and canonical variables. The method of minimizing Wilks' λ was used as the stepping criterion and prior probabilities were calculated based on the sample sizes for each treatment (Norusis, 1985). Mean call variables for each site were calculated and entered into a cluster analysis to produce a dendrogram of the variation between all 10 sites; only variables included in the stepwise-discriminant-function procedure were included in the cluster analysis. Squared Euclidean distances were calculated between centroids to determine the pattern of clustering (Norusis, 1985).

RESULTS

Regional level analysis.—Alarm-call structure differed between sites at the regional level (Wilks' $\lambda = 0.117$; $d.f. = 5, 6, 117$; $P < 0.001$; Fig. 3a). Pairwise comparisons showed that sites that were nearest each other did not differ while sites separated by geographical barriers or distances of >100 km were significantly different (Table 1). Cluster analysis showed a similar pattern of differences although Cortez was grouped with Blue Mesa and Monarch Pass rather than with Taos and Santa Fe as in the discriminant function analysis (Fig. 3a and 4).

Local level analysis.—Alarm-call structure differed between colonies at the local level (Wilks' $\lambda = 0.054$; $d.f. = 5, 3, 28$; $P < 0.001$; Fig. 3b). Pairwise comparisons showed that all colonies differed ($P < 0.05$), except the two most geographically

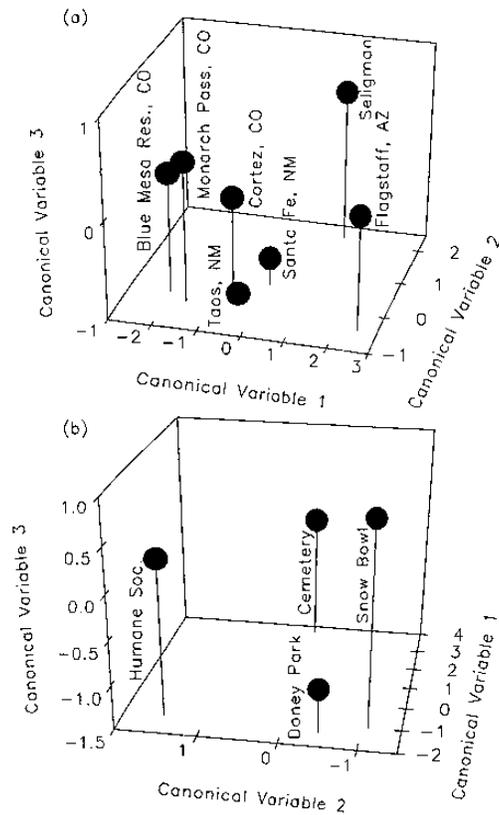


FIG. 3.—Positions in discriminant space of alarm calls of Gunnison's prairie dogs recorded at two different scales of geographic variation: a) seven regions throughout the southwestern United States and b) four colonies within the Flagstaff region. Both graphs have been rotated to show the greatest amount of separation.

separated colonies (Doney Park and Snow Bowl) that differed at $P = 0.06$ (Table 1).

Regional versus local variation.—Different combinations of variables were important in producing differences at regional and local levels. The supra-dominant harmonic frequency (SHF), duration (DURATION), and slope of the descending portion of the dominant harmonic frequency (SLOPED) loaded strongly in both the regional and local discriminant function analyses. The fundamental harmonic frequency (FF) and the inter-harmonic interval (IHI) were correlated with differences between sites at the regional level but were not included by the stepwise discriminant function procedure at the local level. The dominant harmonic frequency (DHF) and the slope of the ascending portion of the dominant harmonic frequency (SLOPEA) were associated with differences between colonies at the local level but not at the regional level (Table 2). A greater proportion of the variance was explained by a single discriminant function in the regional analysis, but the proportion of variance explained by the second and third function was greater in the local analysis (Table 3).

DISCUSSION

Phenotypic characters commonly are used to make inferences about genetic dif-

TABLE 1.—F-matrix for pairwise comparisons between colonies of Gunnison's prairie dogs over regional (d.f. = 5, 133) and local (d.f. = 5, 24) geographic areas. All F statistics were significant at $P < 0.05$ except where indicated (n.s.). Regional colony abbreviations are: Flag. (Flagstaff, AZ), Selig. (Seligman, AZ), S.F. (Santa Fe, NM), Taos (Taos, NM), Mon. (Monarch Pass, CO), B.M. (Blue Mesa Reservoir, CO), Cort. (Cortez, CO). Local colony abbreviations are: H.S. (Humane Society), Cem. (Cemetery), S.B. (Snow Bowl), D.P. (Doney Park). All local colonies are included in the Flagstaff, AZ region.

Colonies	Regional variation						Local variation			
	Flag.	Selig.	S.F.	Taos	Mon.	B.M.	Colonies	H.S.	Cem.	S.B.
Selig.	10.65						Cem.	17.88		
S.F.	13.56	5.38					S.B.	4.83	16.34	
Taos	23.51	10.24	1.24 (n.s.)				D.P.	3.76	18.18	2.55 (n.s.)
Mon.	50.77	16.23	7.54	6.87						
B.M.	37.93	14.68	6.75	5.87	1.14 (n.s.)					
Cort.	18.86	8.72	4.11	3.21	5.41	4.20				

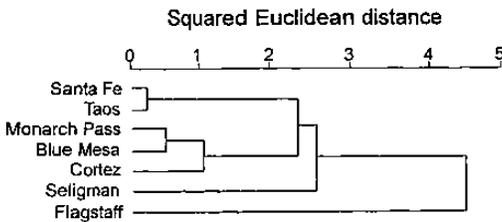


FIG. 4.—Cluster analysis of regional dialects of Gunnison's prairie dog alarm calls. Clustering was determined using the centroid method on the standardized means for each region. Only the call variables included in the stepwise-discriminant function were used in calculating centroids.

ferentiation among populations. Small populations that are geographically separated such that gene flow is restricted are expected to diverge genetically through natural selection and genetic drift (Hartl and Clark, 1989). Geographic barriers to dispersal are important for maintaining genetic heterogeneity although such barriers can vary with respect to how effectively they isolate populations. Geologic features, large bodies of water, or bands of unsuitable habitat may or may not isolate populations completely. Distance between populations within continuous suitable habitat provides a variable degree of isolation that is dependent upon the vagility of the species. Greater distances decrease the probability of suc-

cessful migration; therefore, differentiation between populations should increase with increasing distance.

The grouping of prairie-dog alarm calls across regions fits the prediction of greater differentiation of a phenotypic character with increased geographical distance. At the regional level, calls from sites that were not separated by a barrier to dispersal did not differ significantly while sites separated by high elevation habitats, deserts, or distances >100 km were significantly different. Significant differences in alarm calls of prairie dogs between geographical regions follows a similar pattern as variation in morphological characters (Pizzimenti, 1975; Pizzimenti and Hoffmann, 1973). This suggests that the acoustic structure of alarm calls of prairie dogs is associated with genetic differentiation between populations in a manner similar to morphological characters.

Among colonies of prairie dogs in the Flagstaff region, the pattern of differences in alarm calls is independent of geographical barriers or the distance between colonies. The two colonies that were not significantly different were the most widely separated and were on opposite sides of mountainous habitat unsuitable for prairie dogs. Given the low margin of acceptance

TABLE 2.—Pooled within-group correlations between discriminating variables and canonical discriminant functions from alarm calls of Gunnison's prairie dogs. Discriminating variables are listed in the order that they were entered by stepwise discriminant function analyses based on the method of minimizing the overall Wilks' λ .

Variation	Variables entered ^a	Correlation with function 1	Correlation with function 2	Correlation with function 3
Regional	FF	0.123	-0.280	0.881
	SHF	-0.171	-0.022	0.911
	DURATION	-0.253	0.751	0.153
	SLOPED	0.791	0.533	-0.079
	IHI	-0.515	0.423	0.413
Local	DHF	0.207	0.380	0.834
	SHF	0.191	0.566	0.738
	DURATION	-0.582	0.175	0.254
	SLOPEA	0.536	0.459	0.076
	SLOPED	0.172	0.701	0.578

^a Acronyms identified in Materials and Methods.

TABLE 3.—Proportions of variance explained by the original call variables and canonical functions for the two discriminant function analyses of alarm calls of Gunnison's prairie dogs at regional and local levels. Numbers in parentheses indicate the canonical function most highly correlated with each variable.

Regional variables ^a	Percent variance explained	Local variables ^a	Percent variance explained
SLOPED (1)		DURATION (1)	
IHI (1)	87.6 (1)	SLOPEA (1)	76.9 (1)
FF (2)		SLOPED (2)	15.8 (2)
SHF (2)	6.9 (2)	DHF (3)	
DURATION (3)	4.5 (3)	SHF (3)	7.3 (3)
Total explained	99.0		100.0

^a Acronyms identified in Materials and Methods.

($P = 0.06$), it is likely that the difference between these two colonies is biologically significant. However, it is important to note that all of the Flagstaff colonies are connected through a series of smaller colonies that provide avenues for gene flow among populations. A small amount of dispersal between colonies can introduce new alleles into a population, increasing genetic homogeneity among colonies (Hartl and Clark, 1989). Several studies have confirmed that colonies of prairie dogs show low levels of genetic heterogeneity between colonies and that gene flow occurs through intermediate populations (Foltz and Hoogland, 1983; McCullough and Chesser, 1987; Travis, 1994; Travis et al., 1995). Thus, the pattern of differences within the Flagstaff region cannot be explained by genetic differentiation of populations alone.

Patterns of geographic variation in behavioral traits are difficult to assess because patterns of learned behavior can be passed between generations independently of heritable traits (Avital and Jablonka, 1994; Thompson, 1990). In highly social species, behavioral traditions may play an important role in maintaining behavioral differences among populations despite gene flow. This type of cultural inheritance could explain the pattern of differences in alarm calls

among colonies within the Flagstaff region. A few individual dispersers are more likely to learn the dialect of the new colony than influence it with the dialect from their original colony. Although low levels of dispersal can affect allelic frequencies of a population, immigrating individuals are less likely to influence existing behavioral traditions in the recipient population (Ficklen and Popp, 1995). Dispersal between colonies is therefore less likely to influence traditions of learned behavior than it is to affect allelic frequencies of a population. As a result, learned traits may show geographic variation that cannot be attributed to geographic barriers to dispersal.

In addition to different variables being correlated with differences between local colonies and regional sites, local differences also were associated with a more complex array of correlations among the original variables. Although some variables of alarm calls were associated with differences between colonies at regional and local levels, differences in variables that loaded strongly between the two levels of analysis suggested that there were differences in underlying sources of variation.

The nature of interactions with humans affects behavior of prairie dogs and can produce differences in behavior among non-isolated subpopulations (Adams et al., 1987). Similar effects also have been shown in other species (Knight, 1984; Knight et al., 1987; Marcellini and Jenssen, 1991). This suggests that experience with a given type of predator affects the way that animals perceive risk associated with that predator. Given the high degree of referent specificity in alarm calls of prairie dogs (Slobodchikoff et al., 1986, 1991), differences in behavior of humans at colonies in the Flagstaff region may have produced the observed pattern of differences in alarm calls. The colonies at Cemetery and Humane Society were located within the city limits of Flagstaff where discharging of firearms is strictly prohibited. In contrast, the colonies at Doney Park and Snow Bowl

were located in more rural areas where humans frequently kill prairie dogs for sport. The stimulus represented by a human is likely to be quite different between colonies where humans shoot prairie dogs and those where they do not. If variation in alarm calls of prairie dogs communicates information about risk of predation, the lack of a geographical pattern of variation between colonies within the Flagstaff region possibly can be explained by differences in human activity associated with different colonies.

A second possible source of variation between colonies within a region is the effect of habitat structure on the acoustic structure of calls (Morton, 1975; Wiley and Richards, 1978). Analysis of dialects in prairie dog alarm calls by Slobodchikoff and Coast (1980) showed that the duration of each call within a bout was greater with increased habitat complexity (Slobodchikoff and Coast, 1980). Although habitat structure was not measured in the present study, it is notable that call duration loaded strongly in regional and local analyses. Therefore, at least one dimension of calls may have differed with respect to variation in habitat structure between colonies in regional and local analyses.

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