

Dialects in the Alarm Calls of Prairie Dogs

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Summary. 1. The alarm calls of the Gunnison's prairie dog, *Cynomys gunnisoni zuniensis*, have differentiated into local dialects.

2. Call characteristics show that, within a given dialect, the number of syllables, the length of the syllables, and the interval length between syllables are weakly correlated with one another. The number of syllables, however, is strongly correlated with the total length of the call.

3. Both the number of syllables and the total call length are strongly correlated with the complexity of the habitat: the more complex the habitat in terms of vegetation cover, rocks, and tree stumps, the more syllables there are and the longer is the call. This may be related to predation pressure, with prairie dogs in more complex habitats calling longer to warn their kin when a predator approaches.

Introduction

Dialects may be defined as consistent differences between the vocalizations of adult animals from different population of the same species (LeBeouf and Peterson 1969). Although dialects are well known in birds (Marler and Tamura 1962; Nottebohm 1969; Baker 1975; Baptista 1975), they have seldom been reported in mammals. The few mammals in which dialects have been reported include elephant seals (*Mirounga angustirostris*) (LeBeouf and Peterson 1969), pikas (*Ochotona princeps*) (Somers 1973), and Japanese monkeys (*Macaca fuscata*) (Green 1975). We report here the existence of dialects in the alarm calls of three geographically separated populations of the Gunnison's prairie dog, *Cynomys gunnisoni zuniensis*. These dialects appear to be related to the complexity of each habitat, and may be a response to different selection pressures at each site.

The alarm calls of the Gunnison's prairie dog consist of a series of repetitive barks. Sound characteristics and the alarm function of these barks have been previously described for three species of prairie dogs: the black-tailed, the white-tailed, and the Gunnison's (Waring 1970; Smith et al. 1977). Other than the alarm call, the Gunnison's prairie dog has four other calls (Waring 1970; Smith et al. 1977): (1) 'raspy chatter,' a contact call given under peaceful surroundings; (2) 'snarl' or 'rasp,' an aggressive call; (3) 'growl,' an aggressive call; and (4) 'scream,' an injury or escape call. Previous workers, however, have not reported the existence of dialects in any prairie dog call.

Material and Methods

Alarm calls of adult prairie dogs were recorded during April–September 1977 from three separate 'towns' in Arizona: Buffalo Park and Kachina Village (both near Flagstaff), and Seligman. Buffalo Park and Kachina Village are separated by 13 km; these two sites are, in turn, each separated from the Seligman site by 128 km. All three 'towns' are comparable in area and numbers of prairie dogs, and each of the three 'towns' is separated from other prairie dog 'towns' or burrow systems by at least 2 km.

During the span of this study, 384 call sequences were recorded on Sony PR-150 tape at 9.5 cm/s, using Uher Model 4000 Report IC recorders and Dan Gibson EPM P-200 parabolic microphones. A call sequence was defined as a bout of one or more calls followed by at least 3 s of silence by the individual animal. This procedure has been used by Waring (1970) in recording prairie dog alarm calls. Calls were elicited by a variety of stimuli that represented a potential threat; dogs, coyotes, hawks, and humans were the most common stimuli that elicited calling behavior at all three sites. An analysis of difference between calls elicited by different predators was performed on those calls where we could identify both the specific predator and the first animal to call in response to the specific predator. Calls of only the first-calling animals were used in the analysis of predator-identification calls. This was done so that there would not be any possibility of analyzing inappropriate calls, e.g., a call given by another animal in response to a predator or disturbing influence not seen by the observer.

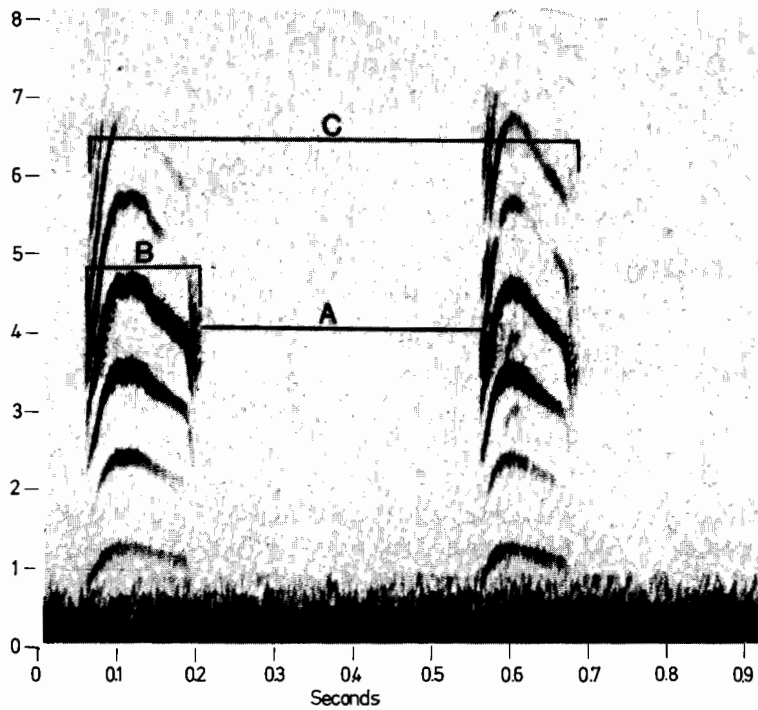


Fig. 1. Sonogram of a typical alarm bark of the Gunnison's prairie dog from Buffalo Park. A, interval length; B, syllable length; C, total call length

The parabolic microphone enabled the recording of the call sequences of individual prairie dogs. Calls were recorded from 5:30 AM to 12:00 noon. No blind was used, but an attempt was made to stay behind rocks or tree stumps to minimize the influence of the recording on the behavior of the prairie dogs. Recording was started 30 min after arrival at a site, so that the prairie dogs had time to adjust to the presence of an observer.

The call sequences were analyzed on a Kay Elemetrics Model 6061B sonograph from 80 to 8,000 Hz using a filter bandwidth of 150 Hz. Calls were analyzed to find within a call sequence: (1) the total length of the call, (2) the number of syllables per call, (3) the duration of each syllable, and (4) the time interval between syllables. Time measurements had an accuracy of 0.01 s.

Habitat diversity was measured by ten 50-m transects laid out at each site. Each transect was scored for the number of annual plants, perennial forbs, shrubs, tree stumps, large rocks, stream beds, cacti, and prairie dog mounds on the transect. Procedure for the transects at each site was as follows. The first transect was started in the approximate middle of the colony, and was laid out to the north from the starting point. Observations of ground cover were taken at 1-m intervals. From the end of the first transect, a new one was laid out, using a random number table for establishing the next direction. This procedure was repeated until data were collected from ten transects at each site. These data were analyzed using the Shannon-Weaver information index, which provided a measure of the physical complexity of each habitat.

Sound attenuation was tested by using a Hewlett-Packard 3311A Frequency Generator to produce a tone of 4 kHz, the dominant frequency of the prairie dog alarm calls. The tone was recorded on tape, using the same recording system as for the calls. The tone was played back at each site under the same temperature and humidity conditions, with the tape recorder positioned at a height of 25 cm, the mean height of a prairie dog standing on its hind legs. Another recorder was positioned at a height of 10 cm, the mean height of a prairie dog standing on all four feet. Sound

played by the first recorder was taped by the second recorder at 5-m intervals for distances of 5–30 m between the two recorders. Recordings from each site were analyzed for sound attenuation on the sonograph. Sound intensity level at 1 m was used as the reference standard for attenuation calculations.

Results

Alarm calls in our study have the same characteristic shape on the sonogram as those described by Waring (1970) and Smith et al. (1977) (Fig. 1). Table 1 shows the call characteristics at each site. All intersite comparisons proved to be significantly different at $P < 0.01$ (t -Test), except for the number of syllables per call at Buffalo Park and Kachina Village. The calls at each site show a strong correlation between the number of syllables in a call and the total length of the call (Buffalo Park, $r = 0.97$; Kachina Village, $r = 0.94$; Seligman, $r = 0.96$; all significant, $P < 0.01$). Correlations between the other call characteristics are considerably weaker (Table 2). Buffalo Park has no significant correlations between any of the remaining call characteristics, Kachina Village has a significant correlation between syllable length and interval length, and Seligman has low but significant correlations for all the call characteristics.

Habitat diversity is highest at Buffalo Park ($H' = 1.162$) and lowest at Seligman ($H' = 0.534$). Kachina Village has a habitat diversity value that is slightly

Table 1. Characteristics of prairie dog alarm calls from Buffalo Park, Kachina Village, and Seligman

	Buffalo Park	Kachina Village	Seligman
Syllables per call			
\bar{x}	6.85	6.53	3.37
<i>s</i>	4.75	4.03	1.83
<i>n</i>	1,157	1,453	1,177
Total call length (s)			
\bar{x}	2.95	2.32	0.97
<i>s</i>	2.04	1.24	0.66
<i>n</i>	98	93	193
Syllable duration (s)			
\bar{x}	0.13	0.11	0.12
<i>s</i>	0.02	0.02	0.02
<i>n</i>	644	616	548
Interval duration (s)			
\bar{x}	0.36	0.29	0.35
<i>s</i>	0.08	0.06	0.09
<i>n</i>	564	524	355

Table 2. Correlation matrix comparing number of syllables (N Syllables), syllable length (L Syllables), and interval length between syllables (Interval L) at Buffalo Park (BP), Kachina Village (KV) and Seligman (SL). Significance levels are indicated by NS (not significant) and * ($P < 0.01$)

	L Syllables	Interval L
N Syllables	BP: 0.11 NS KV: 0.10 NS SL: 0.25 *	BP: 0.13 NS KV: 0.10 NS SL: 0.33 *
L Syllables		BP: 0.10 NS KV: 0.44 * SL: 0.26 *

Table 3. Mean sound attenuation characteristics at three sites, and theoretical attenuation calculated according to the inverse square law. Attenuation is expressed in terms of percent of sound level recorded at 1 m

Site		Distance (m)					
		5	10	15	20	25	30
Buffalo Park	\bar{x}	82.5	58.8	53.6	35.2	23.9	36.1
	<i>s</i>	4.8	7.5	5.7	11.7	9.6	16.5
	<i>n</i>	10	10	10	9	10	10
Kachina Village	\bar{x}	84.2	47.5	34.7	22.7	15.6	15.6
	<i>s</i>	7.0	9.6	14.2	9.5	11.0	8.7
	<i>n</i>	10	10	10	9	8	9
Seligman	\bar{x}	97.0	56.9	50.8	44.7	32.1	39.1
	<i>s</i>	13.9	11.6	11.0	16.9	11.8	10.2
	<i>n</i>	10	10	10	10	9	9
Theoretical attenuation		78	62	56	51	47	44

lower ($H' = 1.029$) than that of Buffalo Park. *t*-Tests of the significance of the differences in diversity values (Poole 1974) show that the Buffalo Park–Seligman diversity values are significantly different at $P < 0.001$ ($df = 20$), the Kachina Village–Seligman diversity values are significantly different at $P < 0.01$ ($df = 20$), and the Kachina Village–Buffalo Park diversity values are not significantly different ($P = 0.38$, $df = 20$). Regression analysis shows a very strong and significant correlation ($r = 0.99$, $P < 0.05$) between the mean number of syllables at each site and the habitat diversity at the site.

Sound attenuation characteristics differ between the three sites (Table 3). Kachina Village has the most attenuation of sound with increased distance from the sound source, while Seligman has the least attenuation. *t*-Tests of significance of difference in means show that Buffalo Park and Seligman are significantly different in attenuation only at 5 m ($P < 0.01$, $df = 18$). At the remaining distances, there are no significant differences between mean attenuation at Buffalo Park and Seligman. Buffalo Park and Kachina Village have no significant differences in mean attenuation at 5 m and 25 m. The remaining distances have significantly different attenuation (10 m, $P < 0.01$, $df = 18$; 15 m, $P < 0.001$, $df = 18$; 20 m, $P < 0.05$, $df = 16$; 30 m, $P < 0.01$, $df = 17$). Kachina Village and Seligman have no significant difference in mean attenuation at 10 m. The remaining distances all have significantly different attenuation (5 m, $P < 0.05$, $df = 18$; 15 m, $P < 0.05$, $df = 18$; 20 m, $P < 0.01$, $df = 17$; 25 m, $P < 0.01$, $df = 15$; 30 m, $P < 0.001$, $df = 16$). Because of reflectance from obstructions (Wiley and Richards 1978; Morton 1975), sound is attenuated less than the theoretical expected attenuation by the inverse square law at 5 m, and is attenuated more than expected at distances of 10 m or greater at all three sites.

Within a site, there are no significant differences between calls associated with different predators. For example, at Buffalo Park the mean number of syllables for hawks ($\bar{x} = 9.0$, $s = 3.5$, $n = 7$ calls), canids ($\bar{x} = 8.5$, $s = 1.29$, $n = 4$ calls), and people ($\bar{x} = 8.9$, $s = 4.67$, $n = 29$ calls) showed no significant differences by a *t*-Test of means. Similarly, Kachina Village had no significant differences between the mean number of syllables for canids ($\bar{x} = 9.4$, $s = 3.9$, $n = 11$ calls) and hawks ($\bar{x} = 9.3$, $s = 2.2$, $n = 4$ calls), and Seligman had no significant differences between the mean number of syllables for hawks ($\bar{x} = 3.2$, $s = 1.9$, $n = 8$ calls) and people ($\bar{x} = 3.5$, $s = 0.7$, $n = 2$ calls). Significant differences were found, however, between calls announcing the same predator at different sites. For example, the mean number of syllables for the hawk call at Kachina Village and Seligman were signifi-

cantly different at $P < 0.001$ (t -Test), and the hawk calls of Buffalo Park and Seligman were significantly different at $P < 0.01$ (t -Test).

Discussion

The contrast between the high correlations of habitat diversity, number of syllables, and length of call, on the one hand, and the low correlations of the remaining call characteristics, on the other hand, suggests that selection may be strongly affecting the length and syllable number of a call, but weakly or not at all affecting the other call characteristics. In the evolution of dialects in the Gunnison's prairie dog, the syllable length and the interval length between syllables may change from site to site as a result of cultural drift imposed by isolation, while the length of the call and the number of syllables may be strongly influenced by the selection pressures imposed by the habitat.

What these selection pressures may be is difficult to determine, but the results suggest several explanations that are not necessarily mutually exclusive. The relationship of the complexity of the habitat and the number of syllables in a call suggests that sound attenuation may play a role in determining call length. By this hypothesis, sound would attenuate faster in a more complex habitat, and a longer call with more syllables would be needed in a more complex habitat to maintain the same alarm function of a shorter call in a less complex habitat. Overall, this explanation does not fit the observed results. Buffalo Park and Seligman have no significant differences in attenuation at any distance other than 5 m, yet they are at opposite ends of the complexity spectrum. In a more limited sense, however, this explanation may have some validity. At 5 m, the attenuation is related to habitat complexity, i.e., Seligman has the least complex habitat and the least attenuation, while Buffalo Park has the most complex habitat and the most attenuation. Similarly, Seligman has the shortest call, while Buffalo Park has the longest call. Distances beyond 5 m do not show this relationship between attenuation and habitat complexity.

The Gunnison's prairie dog is territorial, with the mean territory radius at 5 m (Potemkin 1976). Since residents of a prairie dog territory include several to many closely related individuals (King 1955), the warning call may be designed primarily to warn kin on a territory, and any warning given to members of another territory may be a fortuitous benefit to other prairie dogs. Within a territory, it may be important to the prairie dogs how quickly sound attenuates, and they may structure their calls accordingly. Beyond their territorial limits, it may not be impor-

tant to the prairie dogs how quickly their calls attenuate, and, for this reason, attenuation at distances beyond 5 m may have little relationship to habitat complexity from the standpoint of how the prairie dogs structure their calls.

An explanation that is related to sound attenuation is one dealing with visibility of predators. If the prairie dogs live in a more complex habitat, there are more visual obstructions that may prevent rapid localization of a predator or may make it difficult to locate the position of kin on a territory. In a more complex habitat, a prairie dog may call longer for the purpose of ensuring that all kin are aware of the approach of the predator. Even if the caller cannot see all other prairie dogs on a territory, a longer call increases the probability that all the other prairie dogs on a territory become aware of the approach of a predator. Although Sherman's (1977) work suggests that a calling animal may suffer more predation than a noncalling one, a more complex environment provides more hiding places from the predator and more visual obstacles for the predator, so that the cost of calling longer may not be significant in terms of increased predation.

Another possible explanation is that of predator identification. Owings and Virginia (1978) have shown that California ground squirrels have different calls for different predators. If prairie dogs have different calls for different predators, and the complement of predators or the frequency of occurrence of predators at the three sites were different, this might produce statistical differences suggestive of dialects but in reality being different combinations of responses that are common to all three sites. King (1955) and Smith (1958) believed that they could distinguish between a hawk call and a general predator call for the black-tailed prairie dog. However, they made no recordings of the calls, and Smith et al. (1977), analyzing black-tailed prairie dog alarm calls on a sonograph, found no indication of a hawk call different from the usual alarm call. In our study, the same predators were present in all three areas, and we could not identify on the sonograph any significant differences between calls associated with specific predators.

References

- Baker MC (1975) Song dialects and genetic differences in white-crowned sparrows (*Zonotrichia leucophrys*). *Evolution* 29: 226-41
- Baptista LF (1975) Song dialects and demes in sedentary populations of the white-crowned sparrow (*Zonotrichia leucophrys nuttali*). *Univ Calif Berkeley Publ Zool* 105: 1-52
- Green S (1975) Dialects in Japanese monkeys: vocal learning and cultural transmission of locale specific vocal behavior? *Z Tierpsychol* 38: 304-314

- King JA (1955) Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contrib Lab Vertebr Biol Univ Mich* 67:1-126
- LeBoeuf BJ, Peterson RS (1969) Dialects in elephant seals. *Science* 166:1654-1656
- Marler P, Tamura M (1962) Song 'dialects' in three populations of white-crowned sparrows. *Condor* 64:368-377
- Morton ES (1975) Ecological sources of selection on avian sounds. *Am Nat* 109:17-34
- Nottebohm F (1969) The song of the chingolo, *Zonotrichia capensis*, in Argentina: description and evaluation of a system of dialects. *Condor* 71:299-315
- Owings DH, Virginia RA (1978) Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Z Tierpsychol* 46:58-70
- Poole RW (1974) An introduction to quantitative ecology. McGraw-Hill, New York
- Potemkin JR (1976) Aggression and territoriality in the Zuni prairie dog, *Cynomys gunnisoni zuniensis*. *Am Soc Mammal 56th Annu Meet*, Lubbock, Texas
- Sherman PW (1977) Nepotism and the evolution of alarm calls. *Science* 197:1246-1253
- Smith RE (1958) Natural history of the prairie dog in Kansas. *Univ Kans Mus Nat Hist Misc Publ* 16:1-36
- Smith WJ, Smith SL, Oppenheimer EC, Devilla JG (1977) Vocalizations of the black-tailed prairie dog, *Cynomys ludovicianus*. *Anim Behav* 25:152-164
- Somers P (1973) Dialects in southern Rocky Mountain pikas, *Ochotona princeps* (Lagomorpha). *Anim Behav* 21:124-137
- Waring GH (1970) Sound communication of black-tailed, white-tailed, and Gunnison's prairie dogs. *Am Midl Nat* 83:167-185
- Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav Ecol Sociobiol* 3:69-94