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Referential specificity in the alarm calls of the black-tailed prairie dog

J.K. Frederiksen [1] and C.N. Slobodchikoff [1,2]

[1] *Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86001, USA*

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In this study, we show that black-tailed prairie dogs (*Cynomys ludovicianus*) have a referential system of communication, i.e., their alarm calls have specificity for different characteristics of humans. In a series of experiments, we tested the ability of black-tailed prairie dogs to encode information into their alarm calls about the color of clothes and general shape of humans who were potential predators. We also assessed the information encoded into the alarm calls elicited after a human fed the prairie dogs, and after a human shot a weapon within the colony. The results show that black-tailed prairie dogs have a referential communication system similar to that described for Gunnison's prairie dogs, with qualitatively and quantitatively different alarm calls for different predator characteristics.

KEY WORDS: referential communication, prairie dogs, acoustics, alarm calls, vocalizations, cognition, predation.

[2] Address correspondence to: Dr C.N. Slobodchikoff, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA (E-mail: Con.Slobodchikoff@nau.edu).

INTRODUCTION

Studies of several animal species have provided evidence of qualitatively and quantitatively different alarm calls in response to different predators (e.g., domestic fowl, *Gallus gallus* (Gyger et al. 1987, Evans et al. 1993, Evans & Evans 1999), vervet monkeys, *Cercopithcus aethiops* (Cheney & Seyfarth 1990; Seyfarth et al. 1980a, 1980b), suricates, *Suricata suricata* (Manser 2001, Manser et al. 2001), California ground squirrels, *Spermophilus beecheyi* (Leger & Owings 1978, Leger et al. 1980, Owings & Leger 1980, Owings & Virginia 1978), black-tailed prairie dogs, *Cynomys ludovicianus* (Owings & Loughry 1985) and Gunnison's prairie dogs, *Cynomys gunnisoni* (Slobodchikoff et al. 1986, 1991; Placer & Slobodchikoff 2000, 2004; Kiriazis & Slobodchikoff 2006; Slobodchikoff & Placer 2006). Such differences have been called referential specificity, in that the calls refer to something external to the animal in its environment (Marler et al. 1992, Evans 1997). For example, Evans et al. (1993) and Evans & Evans (1999) found that chickens emit different alarm calls in response to terrestrial and aerial predators. Seyfarth et al. (1980a, 1980b) and Cheney & Seyfarth (1990) showed that vervet monkeys have several distinct vocalizations, each of which is restricted to a class of predators, such as snakes, birds of prey and quadruped terrestrial predators. Owings & Leger (1980) and Leger et al. (1980) found differential alarm calling by California ground squirrels in response to predator-specific encounters, and Owings & Loughry (1985) showed that black-tailed prairie dogs vary their jump-yip call structure according to the species of intruding snake.

Although a number of examples of referential communication are known from species that incorporate information about predator classes (e.g., aerial vs terrestrial) or predator species, there has been little information suggesting that animals can incorporate descriptive information about their predators. Slobodchikoff et al. (1991) showed that Gunnison's prairie dogs produce distinctly different calls in response to differences in the color of clothes and general shape of individual humans. Templeton et al. (2005) showed that Black-capped chickadees (*Poecile atricapilla*) can incorporate information into their alarm calls about the size of their predators.

This paper assesses whether black-tailed prairie dogs, like Gunnison's prairie dogs, produce differential alarm calls in response to the color of clothes of individual humans. Slobodchikoff et al. (1991) have suggested the importance of addressing the possibility that prairie dogs may assess the level of danger associated with each individual predator within a predator category. Therefore, in addition to a partial replication of Slobodchikoff et al.'s (1991) study with another species of prairie dog, we tested the hypothesis that black-tailed prairie dogs will produce distinctly different alarm calls to different levels of danger associated with different individual humans acting as potential predators.

The general alarm-calling behavior of black-tailed prairie dogs is summarized by Hoogland (1995). When a predator approaches, the adult and yearling prairie dogs of both sexes sometimes give an alarm call, which alerts other individuals in a colony about the predator's proximity. Such differences in calling response appear to be related to the distance between any given animal and the predator, the size of the animal's social group, and the presence of other prairie dogs nearby. The calls of black-tailed prairie dogs are varied in acoustic structure (Waring 1970, Smith et al. 1977), primarily the continuous barks are used as alarm calls for different predators (WARING 1970, SMITH et al. 1977) and the jump-yip calls are used for snakes and non-predator contexts (OINWGS & LOUGHRY 1985).

METHODS

Study site

The study site was a black-tailed prairie dog colony located 12 km southwest of Amarillo, Texas. The colony covered an area of 15 ha at an elevation of 1062 m. The colony was very large and included a population of at least 246 prairie dogs. Daily counts done at randomized times for 2 weeks showed that between 123 (the low) and 246 (the high) prairie dogs were counted and could be observed to be above ground at any time. The average of the counts was 170 prairie dogs. Predators observed at the site were coyotes (*Canis latrans*), red-tailed hawks (*Buteo jamaicensis*), prairie rattlesnakes (*Crotalus viridis viridis*), and humans (*Homo sapiens*).

Equipment

Equipment used at the site to record the vocalizations of the prairie dogs was an RCA camcorder (cc507, 64×) interfaced with a Sennheiser unidirectional microphone (ME88). The recording equipment was concealed in a blind (2 m × 1.1 m) mounted on a Nissan pickup. The blind, which was constructed of PVC pipe and shadecloth, also served as a disembarkment area for humans acting as potential predators.

Procedures

The humans in these experiments all differed in size and shape. TF was a 47 year-old male who weighed 97 kg, had a height of 175 cm, and was balding with dark blond hair. BR was a male in his early 20s who weighed 77 kg, had a height of 188 cm, and was balding with blond hair. TD was a female in her early 20s who had a height of 163 cm, weighed 50 kg, and had long, past-the-shoulders dark hair. KF was a 44 year-old female who weighed 75 kg, had a height of 168 cm, and had long past-the-shoulders blond hair. Each person used the same slow speed in approaching the prairie dogs.

All experimental conditions involved a human approaching a targeted adult prairie dog in order to elicit alarm barks. In this investigation there were three experimental conditions. The first two experimental conditions were replications of the SLOBODCHIKOFF et al. (1991) study, and tested whether black-tailed prairie dogs could discriminate among persons wearing different colored clothing better than when these same persons dressed identically.

For the first experiment, the White Coat Condition (WCC), two human males (TF and BR) and one human female (TD) were dressed identically in jeans, a white lab coat and sunglasses. In the second experiment, the Four Person Four Color Condition (4p4c), the same individuals from the WCC participated, along with an additional female (KF). Each individual wore a specifically-colored shirt and blue jeans. The individual color conditions involved each of the humans wearing a specific color of shirt. The physical attributes and characteristics of each human along with the color worn by that person made up the particular condition. The humans and their color conditions were: TF-gray, KF-green, TD-orange, and BR-blue.

The third experiment examined two levels of interactions between the animals and humans. One level involved a person who fed the prairie dogs (Feeding Condition or FC), and the other level involved a person who fired a weapon in their colony (Weapon Condition or WC). These latter experiments tested whether the black-tailed prairie dogs would give different alarm calls to the identically-dressed persons from the 4p4c condition after those individuals had either fed them or fired the weapon. For the Feeding Condition (FC), KF wore jeans and alternated wearing one of two different colored shirts, either the green shirt from the 4p4c Condition or a yellow shirt. In the Weapon Condition (WC), BR wore the same blue shirt he wore in the 4p4c Condition. The third experiment was conducted after the other two experiments were completed, and the two different conditions were interspersed randomly, as was the wearing of the yellow and the green shirts, so that the prairie dogs were equally likely to encounter a person feeding and wearing a yellow or green shirt, or a person who had fired a weapon.

The prairie dogs were habituated to the blind and its movement around the colony for a 3-week period. For each of the experimental conditions/test situations, a minimum of 10 trials was set as the field criterion for each person. In reality, however, many more trials per person proved to be possible. The general procedure for each trial consisted of an individual human leaving the blind and walking slowly toward a targeted prairie dog. The human wore the designated shirt color for the experimental condition. When the focal animal began to alarm call, the calls were recorded. A calling bout was defined as onset of barking by the particular animal and continued until the animal ceased barking or submerged in a burrow. Recordings for the prairie dog's vocalizations were made at varying distances from the animals (3-22 m).

By moving to another quadrant of the colony and different burrow systems for each trial, we tried to avoid using a particular prairie dog's response more than once to a particular test situation. Although the escape responses of prairie dogs in avoiding predators may sometimes include the burrows of other coteries, we estimated that we moved farther for each trial than an escaping animal would run. Additionally, a spotter kept either the previously recorded animal or the burrow that the animal ran to in sight while we moved to a new area and started recording again. Although we would have preferred to have trapped and marked each individual animal, the time frame of these experiments coincided with an outbreak of Hanta

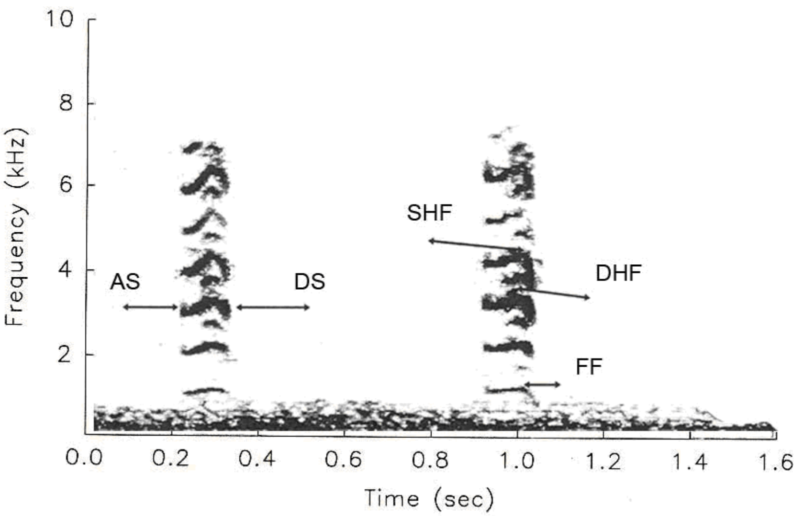

Fig. 1. — Alarm calls elicited for a human from black-tailed prairie dogs, showing the variables that were measured. AS refers to ascending slope, measured as two variables, AS1, the first half of the ascending slope, and AS2, the second half of the ascending slope. DS refers to descending slope, measured as two variables, DS1, the first half of the descending slope, and DS2, the second half of the descending slope. FF refers to fundamental frequency, DHF refers to dominant harmonic frequency, SHF refers to super-dominant harmonic frequency. Although two call elements are shown here for illustrative purposes, all measurements were done on single call elements (single barks). See methods for further explanation.

virus, and we were not permitted by university and county health regulations to handle the animals, for fear of possible contagion.

The trials for the WC condition were conducted and recorded during a 5-day period, while those for the 4p4c Condition were recorded over a 4-day period. All of the trials for these two experiments were conducted in the month of July, 1993.

In preparation for the Feeding Condition trials, KF fed the prairie dogs twice daily, late morning and late afternoon. During a 3-week period, a total of one hundred pounds of whole oats was distributed to the animals, near burrow openings.

A week prior to recording trials for the Weapon Condition, BR fired a 12-gauge shotgun into the ground, once daily, for 5 days. On each occasion, BR was visible to the prairie dogs for 1-5 min before the weapon was fired. Large spaces in the colony where no burrow systems occurred were used for discharge of the weapon. When firing the weapon, BR was never any closer to an individual burrow system or animal than 10 m and in such cases he fired the weapon away from burrow systems/animals and toward uninhabited areas. Large spaces in the colony where no burrow systems occurred were used for discharge of the weapon. Sites for the weapon discharge were randomly chosen throughout the colony. When BR fired the weapon, no other human was present at the colony. Subsequent to these firings, the gun was never brought into the field again during the actual trials for the Weapon Condition.

Trial recording times were conducted during the month of August and the first week of September, 1993. All tests were randomized as to time of day, with the majority of the trials being conducted during late morning or late afternoon.

Camcorder use facilitated isolation of individual alarm callers, allowing identification of a calling bout made by the targeted animals. Individual bouts were broken down into individual calls, i.e., a single call within a calling bout (SLOBODCHIKOFF et al. 1991), and these calls were then analyzed using an RTS Sound Analysis System and a Gateway 4000 486 computer. Only the first call within a bout was measured for each prairie dog responding to a particular test situation, to avoid pseudoreplication by artificially inflating the sample size.

Seven variables were measured from each call element (Fig. 1). These variables were the following: fundamental frequency (FF), dominant harmonic frequency (DHF), the maximum frequency associated with the harmonic that had the most acoustic energy, duration of the call element (DURATION), time and frequency were measured for the first and second half of the ascending slope (AS1, AS2), and time and frequency were again measured for the first and second half of the descending slope (DS1, DS2). For example, for ascending slope 1 (AS1), frequency (e.g., F1) and time (e.g., T1) were measured at the beginning of the rise in the chevron and at the midpoint of the rise in the chevron (e.g., F2 and T2), and then AS1 was calculated as F2-F1/T2-T1. Similar calculations were used for the other slope variables. These variables were also measured by SLOBODCHIKOFF et al. (1991) for Gunnison's prairie dogs. Discriminant function analysis (DFA) with BMDP(7M) was used to assign the most similar calls to groups (DIXON et al. 1988).

RESULTS

Alarm calls

All of the alarm calls fit the general category of continuous barks (WARING 1970, SMITH et al. 1977). Sonograms of the vocalizations are shown in Figs 2-3.

White laboratory coat condition (WCC)

For the WCC the discriminant function analysis (DFA) of the alarm calls showed that black-tailed prairie dogs appeared to be able to distinguish individu-

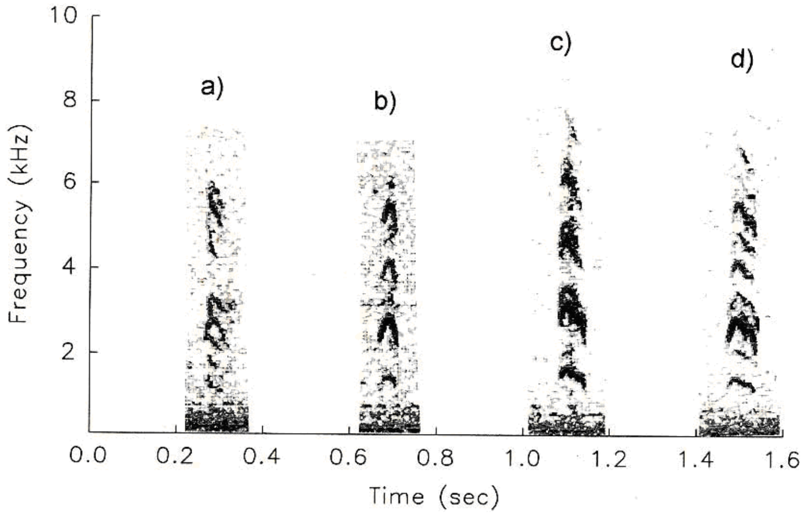

Fig. 2. — Alarm calls elicited from black-tailed prairie dogs for human referent KF under different experimental conditions: a) white coat condition (not used for experimental analyses), b) feeding, yellow t-shirt condition, c) four-person-four-color condition, green t-shirt, d) feeding, green t-shirt.

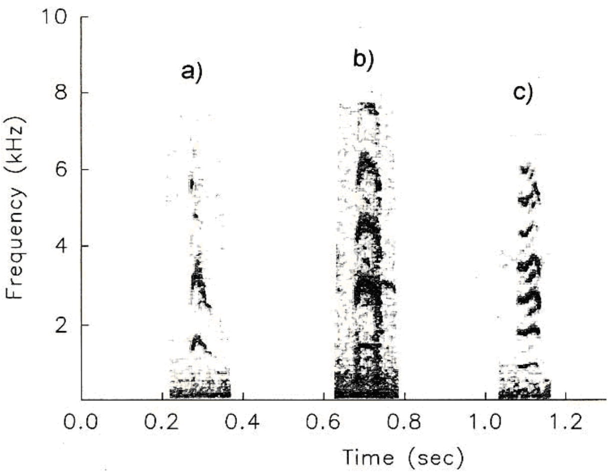

Fig. 3. — Alarm calls elicited from black-tailed prairie dogs for human referent BR under different experimental conditions: a) white coat condition, b) four-person-four-color condition, blue t-shirt, c) weapon condition, blue t-shirt.

al humans much of the time when these humans were dressed identically (Table 1). Although calls for TF were sometimes confused with those for BR and TD, and calls for BR were confused with TD and TF (Table 2), the DFA was able to correctly classify 68% of the calls to their appropriate group. The prairie dogs appeared to have less difficulty discriminating the female TD from the males TF and BR. The variable that produced that highest discrimination was DURATION, with an F = 24.43, df = 2,144.

Four person four color condition (4p4c)

In the 4p4c condition, the discrimination between the individual humans seemed to be mixed. The prairie dogs were not able to discriminate significantly between TF (wearing the grey shirt) and KF (wearing the green shirt). However, all other discriminations of the humans and their color conditions were significant (Table 3). The two females (KF and TD) had the highest correct classification at 74

Table 1.

F statistics for pairwise comparisons of calls for each person in the White Lab Coat Condition.

Person	BR	TF
TD	48.51 ***	10.64 ***
BR	—	8.88 ***

*** $P < 0.001$, df = 1,144.

Table 2.

DFA classification of alarm calls elicited by each person in the White Lab Coat Condition.

	Predicted person			
Person	N	TD	BR	TF
TD	41	85%	7%	8%
BR	71	15%	61%	24%
TF	35	17%	20%	63%
Total	147			

Total percentage of calls correctly classified was 68%.

Table 3.

F statistics for the pairwise comparisons of calls for each person in the four person four color condition.

Person/Color:	TD/Orange	BR/Blue	TF/Grey
KF/Green	35.28 ***	17.34 ***	2.44 NS
TD/Orange	—	3.08 *	19.34 ***
BR/Blue	—	—	6.87 *

* $P < 0.05$. *** $P < 0.001$, df = 1,198.

and 65%, respectively. Overall correct classification was 53% (Table 4). The variable with the highest discrimination was DHF, with an F = 14.06, df = 3,198.

Feeding condition (FC)

Discriminatory ability for this condition was analyzed in two separate ways. The first analysis (green vs green), compared recordings for the black-tailed prairie dog alarm calls elicited by KF wearing a green shirt in the 4p4c experiment, to alarm calls elicited by KF, as the Feeding Person (FP), wearing the same green shirt in the FP experiment. The DFA was able to correctly classify 71% (Table 5) of the alarm calls elicited by KF wearing green to their appropriate contexts, either non-feeding or feeding conditions (F = 14.93, df = 2,96, $P < 0.01$, corrected with Bonferroni's procedure for multiple hypothesis DURATION (F = 29.74, df = 1,96) and DHF (F = 17.12, df = 1,96).

The second part of the Feeding Condition compared alarm calls recorded in response to KF wearing green during feeding (FP) to alarm calls in response to KF wearing yellow during feeding (FP). Comparisons (green FC versus yellow FC) were made of the alarm calls elicited by KF after feeding the animals. Results showed a significant discriminatory ability for the comparison of color in this second analysis of the Feeding Condition (F = 87.25, df = 1,101, $P < 0.01$, corrected with Bonferroni's procedure for multiple hypothesis testing (SACHS 1984). The DFA was able to correctly classify 75% of the alarm calls for the green-shirted KF and 95% of the calls for the

Table 4.

DFA classification of alarm calls elicited for each person in the four person four color condition.

		Predicted Person/Color			
Person/ Color	N	TD/ Orange	KF/ Green	BR/ Blue	TF Grey
TD	51	65%	18%	10%	7%
KF	50	8%	74%	16%	2%
BR	50	12%	18%	52%	18%
TF	51	12%	37%	29%	24%

Total percentage of calls correctly classified was 54%.

Table 5.

DFA classification of alarm calls elicited by condition KF/Green in Non-Feeding Condition (NFC) vs KF/Green in the Feeding Condition (FC).

	Predicted Person/Color		
Condition:	N	KF/FC	KF/NFC
KF/FC	49	71%	29%
KF/4P4C	50	28%	72%

Total percentage of calls correctly classified was 71%.

yellow-shirted KF (Table 6). Correct overall classification for this condition was 86 percent. The variable that had the highest discrimination was FF (F = 87.25, df = 1,101).

Weapon condition (WC)

A high level of discrimination was shown in this last condition (Table 7). Comparisons were made between alarm calls in response to BR wearing a blue shirt while not shooting a weapon, and alarm calls given in response to BR wearing the same blue shirt after shooting the weapon. The differences were very significant (F = 95.77, df = 2,97, $P < 0.001$, corrected with Bonferroni's procedure for multiple hypothesis testing (Sachs 1984). There was very little incorrect classification of the animals' alarm calls to BR for the two conditions, and the structural characteristics of the calls given for the two situations were different, producing both qualitatively and quantitatively different sonograms (Fig. 3). The correct DFA classifications of alarm calls elicited by BR wearing a blue shirt while not shooting a weapon was 90% and for BR wearing the same blue shirt after shooting the weapon was 96%. Overall accuracy was 93% (Table 7). The variables that had the highest discrimination were AS2 (F = 71.86, df = 1,97) and AS1 (F = 69.68, df = 1,97).

Table 6.

DFA classification of alarm calls elicited for the feeding person condition: Yellow Shirt vs Green Shirt.

		Predicted Person/Color	
Condition	N	KF/Green	KF/Yellow
KF/Green	48	75%	25%
KF/Yellow	55	4%	96%

Total percentage of calls correctly classified was 86%.

Table 7.

DFA classification of the alarm calls elicited by the BR (Blue)/Weapon Condition (WC) and the BR (Blue)/Non-weapon Condition (NWC).

		Predicted Person/Color	
Condition	N	BR/Blue NWC	BR/Blue WPC
BR/Blue NWC	50	90%	10%
BR/Blue WPC	50	4%	96%

Total percentage of calls correctly classified was 93%.

DISCUSSION

Animal signals have been shown to contain more information than has been previously thought (Leger 1993, Macedonia & Evans 1993, Evans 1997). The results of the present experiments suggest that black-tailed prairie dogs can distinguish individual predators and incorporate information about these predators into their alarm calls. Information about the physical features of humans and the biologically significant conditions of feeding or shooting a weapon appears to be conveyed in these calls. A cautionary note here, however, is that we cannot determine at this point whether this information is actually being utilized by recipients of the calls, in terms of facilitating the prairie dogs' avoidance of, or escape from, these predators. Further studies using playback experiments might elucidate this in greater detail.

Although the results suggest that prairie dogs can discriminate between different colors, it is very difficult to establish under field conditions whether the prairie dogs are responding to differences in color or differences in brightness. Prairie dogs appear to have dichromatic color vision in the range of 460-640 nm that is sensitive to the blue, green, and yellow wavelengths (JACOBS & PULLIAM 1973). Within this range, they have a narrow neutral zone of 2-3 nm in the region of the visible spectrum close to 505 nm, in which they cannot discriminate between chromatic and achromatic light of equal brightness (JACOBS & PULLIAM 1973). The existence of this neutral zone is what suggests that prairie dogs have dichromatic vision, since humans with a similar neutral zone have dichromatic vision in which they are not able to see red colors, and in the neutral zone see white (HURVICH 1981). The parallels between human vision and prairie dog vision are not exact, however, because humans with dichromatic vision see white in a slightly different part of the spectrum (490-505 nm), and usually cannot see green (500 nm) (HURVICH 1981). However, prairie dog spectral sensitivity includes the 500 nm part of the spectrum (JACOBS 1981). In addition to this spectral sensitivity, prairie dogs can detect brightness differences as small as 0.2 log units (JACOBS 1981). Consequently, in our study we are unable to establish whether the prairie dogs were responding to color differences, brightness differences, or a mixture of both.

In the present study, even though most of the discriminations between the humans and their color conditions were significant, black-tailed prairie dogs, when compared to Gunnison's prairie dogs, did not show the high percentages of discrimination for the replicated 4p4c condition. Several explanations of these results could be postulated. First the shade of the grey shirt was much lighter than the one used by the SLOBODCHIKOFF et al. (1991) study (a possible brightness difference), and the colors used in the present study (gray vs green) might have been more difficult for the color vision of prairie dogs to discriminate. Thus, the gray and the green used in the present study might both have had a spectral radiance near the prairie dogs' neutral point, and perhaps that might have accounted for the prairie dogs' relative difficulty in discriminating between TF in a grey shirt and KF in a green shirt. Another variable could have been the size, shape, and other physical features of the human subjects used in the individual studies. These physical attributes may have also have had an effect on the results of the higher discrimination of the female humans in the 4p4c and WCC conditions of this study and the WCC of the SLOBODCHIKOFF study. Even though all persons in the WCC dressed alike, female humans who served as stimuli for alarm calls in both studies elicited calls that were more discriminable in the DFA analysis than were the calls elicited by male humans. Further investigation of human gender discrimination appears to be warranted.

The allusion to levels of 'danger' also appears to have credibility since highest discriminatory ability appeared in the two biologically significant conditions, with the highest discrimination appearing in the Weapon Condition. These results lend credence to the suggestion that prairie dogs may be able to incorporate information about the level of 'danger' of their predators into their alarm calls.

Aside from distinctly different alarm calls for these biologically significant conditions, the prairie dogs displayed extremely different reactions to the researchers after the completion of the two test situations. During and after the feeding period, whenever KF appeared in the field carrying the food bucket, the animals would sit up on hindquarters and wait for their food. Some were so bold as to not withdraw into their burrows, sitting within a few inches of KF while their oats were delivered. However, if BR appeared in the colony wearing the blue shirt anytime over a 4-day period after the weapon trials, the prairie dogs submerged into their burrows and did not emerge until he left the colony. It would seem that from the results of this study, a human who approached a prairie dog wearing a specifically colored shirt has much less significance than the same-shirted person approaching a prairie dog carrying food or firing a weapon.

One question is, why would the prairie dogs incorporate such detailed information into their alarm calls? A possible answer might be that this would allow them to have access to information about individual predators (e.g., individual coyotes), if these predator individuals had different hunting styles. Coyotes (*Canis latrans*) individuals have been observed employing different hunting methods. Some individuals walk through a colony and make a rush at prairie dogs who appear to be slightly farther from their burrows, apparently trying to get the prairie dogs to run away from their burrow entrances, while other coyote individuals lie down next to a burrow and wait for up to an hour for prairie dogs to emerge (SLOBODCHIKOFF 2002). Because prairie dog colonies are in the same plot of land for many years, the same individual predators can hunt in the same colony for months or perhaps years. Knowing the hunting style of individual predators can be advantageous, and perhaps a description of the predator conveys information about that individual's hunting style.

Although it might at first seem surprising that prairie dogs would have alarm calls in response to humans, in actuality humans have been hunting prairie dogs for hundreds if not thousands of years. Native American archeological sites dating to 800 years B.P. reveal the bones of cooked prairie dogs, and there are recipes among Native American groups for the culinary preparation of prairie dogs (SLOBODCHIKOFF et al. 1991). If we assume that the generation time of prairie dogs is 1.5 years (HOOGLAND 1995), and we assume that Native Americans began to hunt prairie dogs only 800 year B.P., then there would have been 533 generations of prairie dogs between now and the present time. This number of generations may well be adequate for selection to act in the evolution of a specific alarm call for humans.

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