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Prairie dog alarm calls encode labels about predator colors

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Abstract Some animals have the cognitive capacity to differentiate between different species of predators and generate different alarm calls in response. However, the presence of any addition information that might be encoded into alarm calls has been largely unexplored. In the present study, three similar-sized human females walked through a Gunnison's prairie dog (*Cynomys gunnisoni*) colony wearing each of three different-colored shirts: blue, green, and yellow. We recorded the alarm calls and used discriminant function analysis to assess whether the calls for the different-colored shirts were significantly different. The results showed that the alarm calls for the blue and the yellow shirts were significantly different, but the green shirt calls were not significantly different from the calls for the yellow shirt. The colors that were detected, with corresponding encoding into alarm calls, reflect the visual perceptual abilities of the prairie dogs. This study suggests that prairie dogs are able to incorporate labels about the individual characteristics of predators into their alarm calls, and that the complexity of information contained in animal alarm calls may be greater than has been previously believed.

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Introduction

An increasing body of evidence suggests that some animals have referential communication, in which they can incorporate information into their vocalizations or signals about an object or event that is external to the animal (Evans 1997). This kind of communication has sometimes been termed functional reference (Evans et al. 1993; Evans 1997; Evans and Evans 1999) because of the difficulty of determining the meaning of the actual information that is encoded in the signal. The term functional reference has been used in describing alarm calls because the signal functions as if it refers to the predator, and the term sidesteps the difficulties of determining the actual content of the information encoded within the signal.

With alarm calls, for example, the information that is encoded might refer to the species of predator (i.e., a label), or to instructions for escape. Instructions about escape could potentially include information about the urgency of the response required to a particular predator (e.g., run fast, or take your time). Information encoded about response urgency has been documented in yellow-bellied marmots (*Marmota flaviventris*) (Blumstein and Armitage 1997) and in juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) (Warkentin et al. 2001). Some authors (e.g., Kirchhof and Hammerschmidt 2006) consider response urgency to be a part of a graded system of alarm calls given by animals who have only one strategy of escape from predators, and functionally referential calls to be part of an alarm system of animals who have multiple ways of responding to predators. However, response urgency and functionally referential calls do not need to be mutually exclusive. For example, suricates (*Suricata suricatta*) have functionally referential calls for aerial versus terrestrial predators, and also incorporate response urgency into those calls (Manser 2001; Manser et al. 2001).

Functionally referential communication has been described in animals with differing levels of complexity in their alarm vocalizations. A number of animal species, including many species of ground squirrels (*Spermophilus* spp.) (Owings and Hennessy 1984), tree squirrels (*Tamiasciurus hudsonicus*) (Greene and Meagher 1998), chickens (*Gallus gallus domesticus*) (Evans and Evans 1999; Gyger et al. 1987), dwarf mongooses (*Helogale undulata*) (Beynon and Rasa 1989), suricates (*Suricata suricatta*) (Manser 2001; Manser et al. 2001), and tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) (Kirchhof and Hammerschmidt 2006) have alarm calls that differ for aerial versus terrestrial predators. A few species such as the vervet (*Cercopithecus aethiops*), Diana (*Cercopithecus diana*) and Campbell monkeys (*Cercopithecus campbelli*), and Gunnison's prairie dogs (*Cynomys gunnisoni*) have different alarm calls for different predators, such as for leopard (*Panthera pardus*), martial eagle (*Polemaetus bellicosus*), and python (*Python sebae*) for the vervets (Seyfarth et al. 1980), leopard and martial eagle for the Diana and Campbell monkeys (Zuberbühler 2000, 2001), and red-tailed hawk (*Buteo jamaicensis*), human (*Homo sapiens*), coyote (*Canis latrans*), and domestic dog (*Canis familiaris*) for the Gunnison's prairie dogs (Kiriazis and Slobodchikoff 2006; Placer and Slobodchikoff 2000, 2001, 2004; Placer et al. 2006; Slobodchikoff 2002; Slobodchikoff and Placer 2006).

Another level of information that can potentially be encoded into alarm calls involves descriptive features of the predators. Scant evidence of this has been found so far. Black-capped chickadees (*Poecile atricapilla*) have recently been shown to incorporate information into their mobbing vocalizations about the relative size of different predator species such as owls and hawks (Templeton et al. 2005). Gunnison's prairie dogs have been shown to have descriptive elements about individual predators in their alarm calls, but there has been no evidence of how that related to the perceptual abilities of the prairie dogs (Slobodchikoff et al. 1991). Also, Frederiksen and Slobodchikoff (2007) showed that black-tailed prairie dogs (*Cynomys ludovicianus*) appeared to have responses to different-colored shirts that are similar to those of the Gunnison's prairie dogs.

In prior experiments with prairie dogs, the size and shape of the humans that elicited the calls varied. An earlier study of the alarm calls of Gunnison's prairie dogs (Slobodchikoff et al. 1991) found that the prairie dogs could incorporate significant differences into their alarm calls for four humans wearing blue, green, yellow, and grey t-shirts. However, a possible confounding factor was that the humans differed in height, weight, and sex, and none of the humans wore any other color of shirt. Two of the humans were males, and one wore a blue shirt while the other wore a grey shirt. The other two humans were females, and one wore a green shirt while the other wore a yellow shirt. Similarly, the study with black-tailed prairie dog alarm calls (Frederiksen and Slobodchikoff 2007) had humans that differed in height and sex, and each human only wore one color of shirt.

In the present experiment, we attempted to remove the possible confounding variables of differences in size and sex of the humans wearing the shirts. Three similarly sized human females walked through a prairie dog colony wearing a blue t-shirt, a green t-shirt, or a yellow t-shirt, while we recorded the alarm calls elicited by the humans. This provided a better control on size and shape than the previous study (Slobodchikoff et al. 1991) allowing us to test for the effects of differences in color. Because the escape responses for all of the humans in this experiment were typical of those produced in response to humans (Kiriazis and Slobodchikoff 2006), any differences in acoustic structure of the alarm calls would reflect labels about the physical features of the humans, rather than differences in escape instructions.

Methods

We recorded alarm calls at a Gunnison's prairie dog colony in an undeveloped area in Flagstaff, AZ, USA between 12 July 2004 and 1 August 2004. The colony was 1 ha in size, and contained 55 adult prairie dogs and their juvenile offspring. Three human females (EA, ES, and JV) walked through the colony on one of three paths, randomly determined by a random number generator for each walk-through, wearing a yellow, green or blue t-shirt, blue jeans and sunglasses. During the course of the experiment, all three females wore each of the shirts. All three females were of similar height (EA was 162.6 cm, ES was 160.1 cm, and JV was 157.5 cm tall) and had a similar slender shape. Each person walked at a pace of approximately 20 m/min. A minimum of 10 min passed between the human's exiting the colony and the beginning of the next walk-through. EA walked path one 7 times, path two 13 times, and path three 12 times, for a total of 32 walk-throughs. ES walked path one 11 times, path two 13 times, and path three 14 times, for a total of 38 walk-throughs. JV walked path one 12 times, path two 10 times, and path three 7 times, for a total of 29 walk-throughs. The purpose of walking different paths was to elicit alarm calls from different animals within the colony.

The same observer sat on a hill 30 m away from the edge of the colony to record alarm calls and caller's identity in all of the walk-throughs. Animals had been trapped in squirrel-sized Tomahawk #204 live traps and painted with black Nyanzol D dye in distinctive patterns to allow for the identification of individual prairie dogs.

We recorded the alarm calls of 48 individually marked prairie dogs resulting in 82 calls. Of these animals, nine called to all three shirts (27 calls), 16 called to two shirts (32 calls), and 23 called to one of the shirts (23 calls). During a walk-through, we recorded only the first animal that called, ignoring subsequent calling by other prairie dogs. Because of this, not all walk-throughs yielded a call that we could use for our analysis.

Calls were recorded using a Telinga Pro 5 directional microphone connected to a Sony MZ-R70 mini-disc recorder at distances ranging from 30 to 140 m. When a calling bout consisted of more than one call, the measurements were averaged across all calls from that bout by that individual animal, so that the sample size was not artificially inflated and to avoid pseudoreplication. Each calling bout by an identified individual was analyzed using a RTS Real-Time Spectogram package (Engineering Design, Belmont), with a sample rate of 25 kHz and a frequency resolution of 48.8 Hz. Each alarm call had 13 frequency and time variables measured (Fig. 1). The variables were analyzed with SPSS discriminant function analysis. The resulting classification was tested with cross-validation, or the "leave-one-out" of SPSS.

The reflectance of light from the t-shirts was measured with a FieldSpec UV/VNIR HandHeld Spectroradiometer (Analytical Spectral Devices Inc. Boulder, CO). For each sample, a white light illuminated the sample, and the percentage of light reflecting for each wavelength between 440 and 640 nm was recorded. These percentages were measured five times for each sample and then averaged to reach a final reflectance for each wavelength.

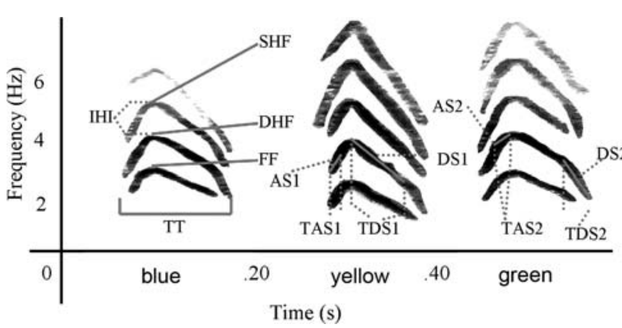

Fig. 1 A spectogram of a typical prairie dog alarm call given in response to the same human wearing either a yellow, green, or blue t-shirt. Variables used in the discriminant function analyses were measured as follows: *FF* fundamental frequency (Hz), *DHF* dominant harmonic frequency (Hz) (measured at top of chevron), *SHF* superharmonic frequency (Hz) (measured at top of chevron), *IHI* interharmonic interval between DHF and SHF (Hz), *TT* total time of call, *AS1* first half of the ascending slope of the dominant harmonic *AS2* second half of the ascending slope of the dominant harmonic, *TAS1* time of ascending slope 1 of the dominant harmonic, *TAS2* time of ascending slope 2, *DS1* first half of descending slope of the dominant harmonic, *DS2* second half of descending slope of the dominant harmonic, *TDS1* time of descending slope 1 of the dominant harmonic, *TDS2* time of descending slope 2. For more detailed information on how the measurements were obtained, see Frederiksen and Slobodchikoff (2007)

Results

The discriminant function analysis showed that the prairie dogs had different time and frequency values in their calls for the different shirt colors. The DFA generated classification functions that could significantly discriminate between calls elicited by yellow and blue and blue and green shirts, but not between calls elicited by green and yellow shirts. The DFA showed a significant difference between the colors (Wilks' $\lambda = 0.815$, $X^2(6) = 15.938$, $P = 0.014$), with a 54.9% correct classification (45 calls correctly identified to shirt color out of 82 calls; chance was 33.3%). The variables that contributed significantly to the discrimination were fundamental frequency (FF) ($P = 0.009$), ascending slope 1 (AS1) ($P = 0.008$), and the time of the ascending slope 1 (TAS1) ($P = 0.014$). Table 1 shows the classifica-

Table 1 Discriminant function analysis classification results of the three color shirt experiment, where original shows the number of calls recorded for each color of shirt, and predicted group membership shows the number and percentage of those calls that were classified by the DFA into yellow, green, and blue shirt groups, and cross-validated shows the results of the "leave-one-out" analysis

Classification results[a, b]	Color	Predicted group membership			
		Yellow	Green	Blue	Total
Original					
Count	Yellow	14	7	7	28
	Green	2	17	8	27
	Blue	6	7	14	27
Percentage	Yellow	50.0	25.0	25.0	100.0
	Green	7.4	63.0	29.6	100.0
	Blue	22.2	25.9	51.9	100.0
Cross-validated[c]					
Count	Yellow	13	8	7	28
	Green	4	13	10	27
	Blue	6	7	14	27
Percentage	Yellow	46.4	28.6	25.0	100.0
	Green	14.8	48.1	37.0	100.0
	Blue	22.2	25.9	51.9	100.0

Chance levels of classification are at 33.3%

[a] 54.9% of original grouped cases correctly classified

[b] 48.8% of cross-validated grouped cases correctly classified

[c] In cross-validation, each case is classified by the functions derived from all cases other than that case

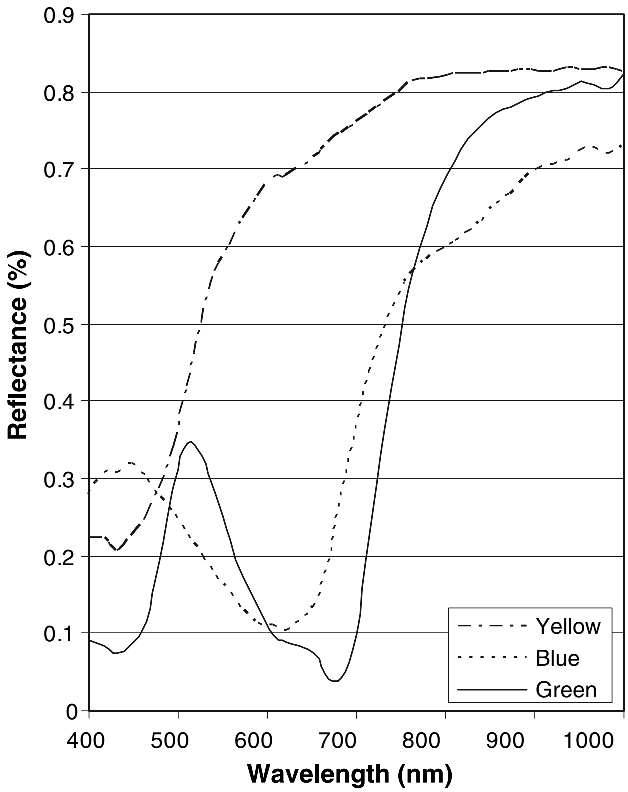

Fig. 2 Reflectance properties of the three colored shirts

tion provided by the DFA. Pairwise group comparisons showed that calls for yellow versus blue shirts were significantly different ($F_{1,79} = 5.522$, $P = 0.021$), calls for green versus blue were significantly different ($F_{1,79} = 9.121$, $P = 0.003$), but the calls for yellow versus green were not significantly different ($F_{1,79} = 0.487$, $P = 0.487$). A MANOVA analysis showed no significant differences in the calls for the three individual humans (Wilks' $\lambda = 0.807$, $F_{24,136} = 0.642$, $P = 0.897$), nor for the three different paths (Wilks' $\lambda = 0.819$, $F_{24,136} = 0.595$, $P = 0.930$).

A reflecting spectrophotometric analysis of the reflected wavelengths of the t-shirts that we used in our experiment showed that while the peak for blue was distinct from the green and yellow peaks, the green peak was almost entirely subsumed by the reflectance values for the yellow shirt (Fig. 2).

Discussion

The results show that prairie dogs have acoustically distinct calls for blue and for yellow/green shirts, but not acoustically distinct calls for yellow and for green shirts. These results appear to reflect the visual perceptual abilities of prairie dogs. Prairie dogs have dichromatic color vision in which they see wavelengths that are in the blue and yellow part of the perceptual visual spectrum, but have a more difficult time discriminating between wavelengths that are close to one another in the green–yellow part of the color spectrum (Jacobs and Pulliam 1973).

These findings suggest that prairie dogs have the cognitive capacity to recognize individual differences in the appearance of possible predators and are able to incorporate information about these differences into their vocalizations. This in turn suggests that the prairie dogs are labeling the predators according to some cognitive category, rather than merely providing instructions on how to escape from a particular predator or responding to the urgency of a predator attack. Each of the humans walked at the same pace and followed one of three predetermined paths through the colony. Consequently, there were no differences in urgency, and the escape behavior in all cases was typical of the escape behavior that has been described for prairie dogs responding to humans, namely running to the burrows and diving inside (Kiriazis and Slobodchikoff 2006).

It should be noted that a study of referential communication is often split into two parts: demonstrating productional specificity and demonstrating perceptual specificity (Evans 1997). Productional specificity refers to the callers' production of signals that refer to external objects or events. Perceptual specificity refers to the receivers of signals being able to interpret the signals as meaningful information. Perceptual specificity is usually tested by playbacks of calls or sounds (e.g., Kiriazis and Slobodchikoff 2006). In the present study, we have demonstrated productional specificity. Demonstrating perceptual specificity has been more challenging, because the prairie dogs responded to all different shirt colors in the same way as they respond to any human, i.e., running to their burrows and diving inside. However, we consider it unlikely that the animals would encode information about different shirt colors into their alarm calls without being able to recognize this information at the perceptual end.

The usefulness of this ability of prairie dogs to label the individual features of possible predators may be for two reasons. One is that because the colonies are spatially fixed, predation or predation attempts occur frequently, often by the same individual predators whose home range includes a colony (Verdolin and Slobodchikoff 2002). The other is that individual predators within a predator category may differ in their hunting styles. For example, some individual coyotes have been observed to walk-through a prairie dog colony and put on a burst of speed when they see a concentration of prairie dogs standing at their burrows, apparently trying to separate one or more animals away from the safety of their burrows. Other individual coyotes have been observed lying down near a burrow and waiting for up to an hour for an unwary prairie dog to emerge (Leydet 1977). Labeling the characteristics of individual predators may allow the prairie dogs to become familiar with the hunting styles of individual predators and take evasive action that matches a particular hunting style.

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