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Perceptual specificity in the alarm calls of Gunnison's prairie dogs

Judith Kiriazis [1], C.N. Slobodchikoff *

Northern Arizona University, Flagstaff, AZ 86011, USA

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Abstract

Gunnison's prairie dogs have a complex alarm communication system. We show that the escape responses of prairie dogs to naturally occurring live predators differed depending upon the species of predator. We also show that playbacks of alarm calls that were elicited originally by the live predators produced the same escape responses as the live predators themselves. The escape responses fell into two qualitatively different categories: running to the burrow and diving inside for hawks and humans, and standing upright outside the burrow for coyotes and dogs. Within these two categories there were differences in response. For hawks, only the prairie dogs that were in the direct flight path of a stooping red-tailed hawk ran to their burrows and dove inside, while for humans and human alarm call playbacks there was a colony-wide running to the burrows and diving inside. For coyotes and coyote alarm call playbacks there was a colony-wide running to the burrows and standing alert at the burrow rims, while for domestic dogs and playbacks of alarm calls for domestic dogs the prairie dogs assumed an alert posture wherever they were feeding, but did not run to their burrows. These responses to both the live predators and to predator-elicited alarm calls suggest that the alarm calls of Gunnison's prairie dogs contain meaningful referential information about the categories of predators that approach a colony of prairie dogs.

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1. Introduction

When detecting a predator, some animals give an alarm call that contains information about the type of predator that has been detected. Such information about an external situation has been termed referential specificity (Marler et al., 1992; Macedonia and Evans, 1993; Evans, 1997). In order to demonstrate referential specificity in an alarm call, two components have been suggested as being necessary (Evans et al., 1993; Macedonia and Evans, 1993; Blumstein and Armitage, 1997): productional specificity and perceptual specificity. Productional specificity suggests that specific information about the predator is encoded in the alarm call by the animal producing that alarm call. Perceptual specificity suggests that the encoded information is perceived by other animals that hear the alarm call, and upon hearing the alarm call, the listening animals take appropriate evasive actions.

A number of animal species have been shown to incorporate some measure of referential specificity into their calls. Some animals have two types of calls, one for terrestrial and and another for aerial predators. Included within this group are: many ground squirrels (*Spermophilus* spp.) (Owings and Hennessy, 1984); chickens (*Gallus gallus domesticus*) (Gyger et al., 1987; Evans and Evans, 1999); tree squirrels (*Tamiasciurus hudsonicus*) (Greene and Meagher, 1998); dwarf mongooses (*Helogale undulata*) (Beynon and Rasa, 1989); suricates *(Suricata suricatta)* (Manser, 2001; Manser et al., 2001). A few species have vocalizations for different predator species or categories of predators. Such referential specificity has been found in: vervet monkeys (*Cercopithecus aethiops*), with calls for three different types of predators, snake or python, large cat species or leopard, and eagle (Cheney and Seyfarth, 1990); Diana monkeys (*Cercopithecus diana*) and Campbell's monkeys (*Cercopithecus campbelli*), with calls for leopards (*Panthera pardus*) and crowned-hawk eagles (*Stephanoaetus coronatus*) (Zuberbühler, 2000, 2001); prairie dogs (*Cynomys gunnisoni*) (Placer and Slobodchikoff, 2000, 2001, 2004).

Escape responses can also differ according to the type of call. For example, in the Belding's ground squirrel (*Spermophilus beldingi*), aerial predators elicit brief single-note whistles, while terrestrial predators elicit longer duration trills (Robinson, 1981; Sherman, 1985). The evasive responses (perceptual specificity) also differ: whistles elicit running to a burrow, while trills elicit

* Corresponding author. Tel.: +1 9285237231; fax: +1 9285237500.
E-mail address: Con.Slobodchikoff@nau.edu (C.N. Slobodchikoff).
[1] Present address: HSS, P.O. Box 4480, Cottonwood, AZ 86326, USA.

sitting up or running to a rock (Sherman, 1985). Owings and Hennessy (1984) suggest that such differences between aerial and terrestrial predator calls may reflect differences in time constraints posed by the rate of predator approach. The attack of aerial predators is very rapid: a brief single-note whistle is all that an animal has time to give while quickly escaping. Attack by terrestrial predators affords more time for a longer trill, as these predators usually can be seen from a relatively long distance and proceed more slowly than an aerial predator. A form of response-urgency based communication has been described for yellow-bellied marmots (*Marmota flaviventris*), where the marmots vary their alarm whistles as a function of their perception of risk (Blumstein and Armitage, 1997). Similarly, juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) appear to have response-urgency based communication (Warkentin et al., 2001; Sloan and Hare, 2004), and Richardson's ground squirrels have different components within the alarm calls that seem to elicit greater vigilance from call recipients (Sloan et al., 2005). The referential information that is encoded in the three different acoustically distinct alarm calls of vervet monkeys elicit different escape responses that are appropriate for evading each category of predator (Seyfarth et al., 1980; Cheney and Seyfarth, 1990).

Another level of referential information is encoded in the alarm calls of Gunnison's prairie dogs (*C. gunnisoni*). Gunnison's prairie dogs have alarm calls for four different species of predator: hawk (*Buteo jamaicensis*), human (*Homo sapiens*), coyote (*Canis latrans*), and domestic dog (*Canis familiaris*) (Placer and Slobodchikoff, 2000, 2001), as well as vocalizations for objects in their environment that are not known to them but could potentially represent a predator (Ackers and Slobodchikoff, 1999). Slobodchikoff et al. (1991) have found that within the call type given for humans, there is a considerable amount of variation that can be ascribed to descriptors of body size, shape, and color of clothes.

However, although such information apparently is encoded in the alarm calls of prairie dogs, there have been no experimental data published previously to show that this information is actually communicated to other prairie dogs, i.e., that it produces a predictable response that is specific to different species of predators. Initial field observations of prairie dogs suggested several possible scenarios might be taking place in response to alarm calls. Prairie dogs reacting to alarm calls might be taking an appropriate evasive action based upon the information content of the call, or, as suggested by Morton's (1977) structural function hypothesis, they might simply be responding because the call is an expression of the internal state of fear or excitement in the calling animal. Alternatively, they might be reacting to some visual cue in the posture of the calling animal (Owings and Hennessy, 1984), in which case the call's only function is to direct attention to the caller.

Our study addresses the first alternative and assesses whether the information contained in the different alarm calls of Gunnison's prairie dogs is communicated to and perceived by conspecific listeners. To do this, we: (1) document the escape behaviors of prairie dogs to naturally occurring hawks, humans, domestic dogs, and coyotes in the field, to show that the evasive responses differ according to the species of predator; (2) show that in the absence of a live predator, playbacks of alarm calls given in response to humans, domestic dogs, and coyotes elicit the same response as that elicited by the live predators.

2. Methods

2.1. Study sites

This study was conducted during the 1989 and 1990 prairie dog reproductive seasons (June–September), at two colonies near Flagstaff, AZ. Prairie dog densities at the two colonies were approximately equal: 40–50 animals, including young, at each colony. All animals at each colony were individually marked with black Nyanzol dye to allow us to identify individual animals at a distance. One colony, HS, was located at an elevation of 2100 m within the Flagstaff city limits; the other, SB, was located 8 km north of Flagstaff at an elevation of 2250 m. Each colony was 1.5 ha in area, and was staked out in a grid system of 120 m × 160 m, with location stakes implanted at each 10 m point. This grid system was used in estimating distances, such as the distance of the prairie dogs from a playback speaker, from a predator, or from one another.

Located at the midpoint along the wide boundary of each colony was a stationary blind, whose viewing platform was approximately 1.5 m above ground level. The contents of the blind were screened from view on three sides by pieces of adjustable earthtone fabric that were left partially in place when the blind was not in use, so as to habituate the animals to them. The observation platforms each were 1 m × 2 m in area, which provided enough room for two observers and recording equipment.

2.2. General methods

Prairie dog behaviors were recorded with a video camcorder (Panasonic model #PV430), which had an 8:1 zoom lens and an internal onscreen digital clock. After arriving and setting up equipment at the blind, we initiated a 15–30 min habituation period to allow subject animals to emerge from their burrows and resume their normal activities. At this point, the camera was focused on at least one prairie dog who was visible within the approximately 70 m range of the camera. Focal animals were chosen at random at the beginning of each observation period (Altmann, 1974), but an effort was made to avoid repeated recording of the same animals over the season. The camera was then left running during an observation period or a test, and the field of view was deliberately left wider than necessary so as not to lose sight of focal animals should they move a short distance from their original position. In this way, it was possible to videotape prairie dog movements within a 15–20 m radius of their burrow openings. Additionally, one or two observers kept visual track of the animals, which were marked with individually distinct codes.

Videotapes of field experiments and of natural observation periods (recording of natural events over a 15-min sampling period) were then used to determine counts of prairie dog behav-

iors. If a predator appeared during a natural observation period, recording would continue until the predator left the colony. If no predators were evident during the natural observation period, we would turn off the camera and wait for a predator to appear, usually spending a minimum of 2 h in the blind each time. Accurate measures of focal animal behaviors were possible only if the camera was already focused on prairie dogs before a predator arrived, and only these instances were used for data analysis. Videotapes were analyzed using a video cassette recorder (Mitsubishi model #HS-U70), with a real-time counter for elapsed time.

Simultaneous with the videotaping of each observation period, an independent audio recording was made using a cassette recorder (Uher model #CR160 AV) and a shotgun microphone (Sennheiser model #ME88), boosted by a small, on-line amplifier powered by a 9-V battery. This audio equipment was used to obtain recordings of prairie dog vocalizations. Fieldwork was usually conducted during a period between 07:00 and 10:30 MST, when the prairie dogs were active. Verbal notations of pertinent events were dictated into the microphone on the video camera. During the 1989 and 1990 field seasons, a total of 214 h was spent either in actual observation or experimentation.

Escape responses were recorded as the first response (the initial response of a prairie dog to a predator or playback), and second response (the response that followed the initial response within 30 s of the beginning of the first response). Possible first responses were: Run to Burrow; Go Down in Burrow; Stand Alert at Burrow; Stand Alert in Place; No Response. Possible second responses were the same as the above first responses, except that instead of No Response there was No Change, indicating that the behavior did not change from that of the first response within the 30 s observation period.

2.3. Experimental methods

In addition to natural observations, experiments were conducted involving playbacks of alarm calls. These playbacks were designed and conducted as follows.

2.3.1. Playbacks of alarm calls

To determine whether prairie dog alarm calls have referential content, an experiment was designed to play back alarm calls during times when no predator or calling prairie dog was evident. A pool of pre-recorded alarm calls given by prairie dogs in response to three categories of live predators at the SB study colony was recorded onto broadcast tapes. From this pool, calls were accessed randomly for playback. Each playback was 11 s in duration. Three categories of playbacks were used as a test: recordings of alarm calling bouts for a dog, a coyote, and a human. Additionally, a control sound was played; the control playback was a recording of a rubber toy squeezed repeatedly for 11 s to produce a nonsense sound with a rhythm, frequency range and amplitude similar to prairie dog alarm vocalizations. Sound intensity was adjusted to that comparable to a calling prairie dog, as measured in dB from a distance of 40 m. The recorded pool consisted of 9 human, 15 dog, 12 coyote, and 9
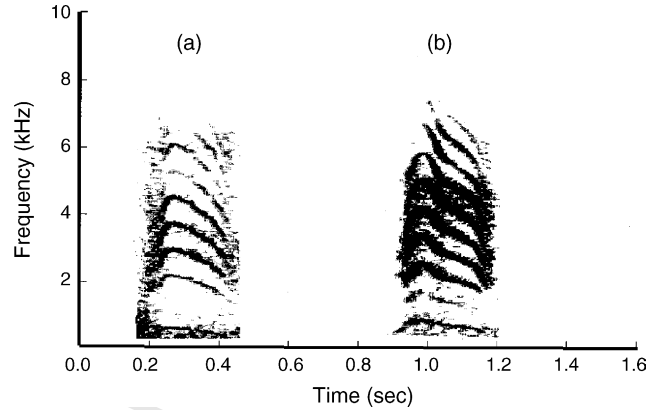

Fig. 1. Sonograms of prairie dog alarm calls in response to different species of predators: (a) alarm call elicited by a coyote; (b) alarm call elicited by a domestic dog. Sonograms were generated with a Signal 3.0 (Engineering Design) system.

nonsense calls. Sonograms of representative calls are shown in Figs. 1 and 2.

These recordings were played back in the field as follows. Attached to the Uher recorder was an amplification system composed of a 20-W amplifier (Realistic model #MPA-25), powered by an 8-V motorcycle battery (Interstate Cyclatron). From the amplifier, a 50 m spool of stereo wire was unwound to hook up to an 8-Ω speaker (Realistic Super Powerhorn, model #40-1251), which had been placed on the ground and partially concealed by a clump of vegetation where possible. The frequency response was 275–14,000 Hz, and the mean SPL from 15 cm above the ground at a distance of 50 m was 45 dB. This equipment outside the blind was arranged upon arrival at a colony; every effort was made to vary the placement and broadcast direction of the speaker from test to test so that the responses of different focal animals could be videotaped each time.

After the equipment was set up, a 30-min habituation period was initiated, during which time no recordings or observations were made. Following this period, when prairie dogs emerged from their burrows, focal animals were selected based upon their location relative to the speaker. Animals in the direct path of
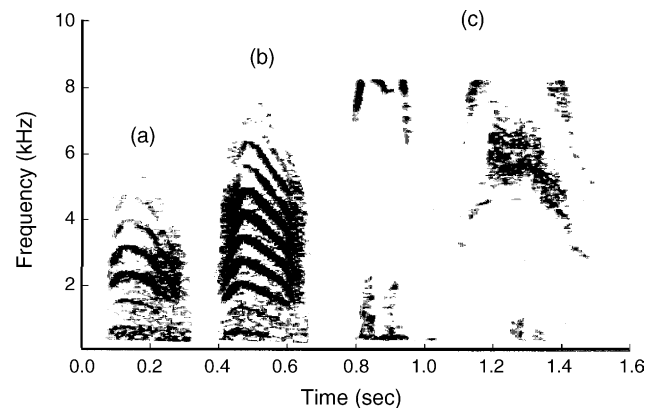

Fig. 2. Sonograms of prairie dog alarm calls in response to different species of predators: (a) alarm call elicited by a red-tailed hawk; (b) alarm call elicited by a human; (c) sonogram of a nonsense sound used in the playback experiments. Sonograms were generated with a Signal 3.0 (Engineering Design) system.

Table 1
Patterns of response of prairie dogs to live predators: first and second behaviors in response to the appearance of a predator

Predator	First response	Second response
Human	Run to Burrow	Go Down in Burrow
Diving hawk	Run to Burrow	Go Down in Burrow
Dog	Stand Alert in Place	Stand Alert in Place
Coyote	Run to Burrow	Stand Alert at Burrow

Fig. 3. First and second responses of prairie dogs to live coyotes (predator) and to playbacks of coyote-elicited alarm calls (playback). The behavioral categories show the different escape responses: RTB, Run to Burrow; GDIB, go down into burrow; AAB, alert at burrow; ANR, alert but not run; NR, No Response. In the second response, NR denotes No Change from the first response behavior. Numbers above columns denote number of prairie dogs responding in each category.

the playback emission and approximately 30–40 m away from the speaker were in the best position, but as prairie dogs did not always choose to occupy such a location, sometimes focal animals were located at a slightly greater distance (40–50 m), or off to one side (10–20°) of the direct line of playback. However, even though these conditions were not ideal, the amplitude of the playback was adequate to elicit a response from prairie dogs within a 60 m radius of the front and sides of the speaker. A videotape recording was made of focal animal activities for at least 2 min before the playback, during the playback itself, and 2 min after the playback.

The responses used for analysis were a sequence of two behaviors that each focal animal engaged in as soon as the play-back of an alarm call began. The sequence was obtained from the videotapes. The total number of first and second responses to each category of playback was analyzed using Chi-square goodness-of-fit tests, and, where expected values within cells were too small to permit Chi-squares, a Fisher's Exact Test was performed instead. Chi-squares were performed using a Minitab program, while Fisher's Exact Test was done using BMDP (Program 4F) (Dixon, 1983). When the same data set was used to make several comparisons, the *P*-value was adjusted for each such comparison, using Bonferroni's procedure for mul-tiple hypothesis tests (Sachs, 1984). Analysis of the data sets from the two colonies showed no statistically significant differ-ences between colonies, so the data from the two colonies were pooled.
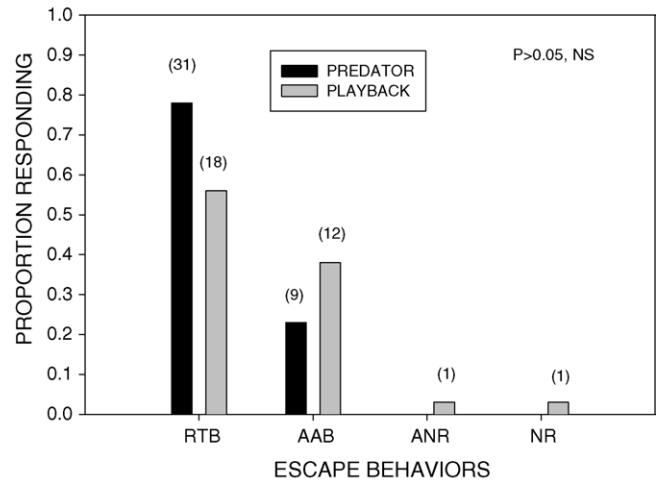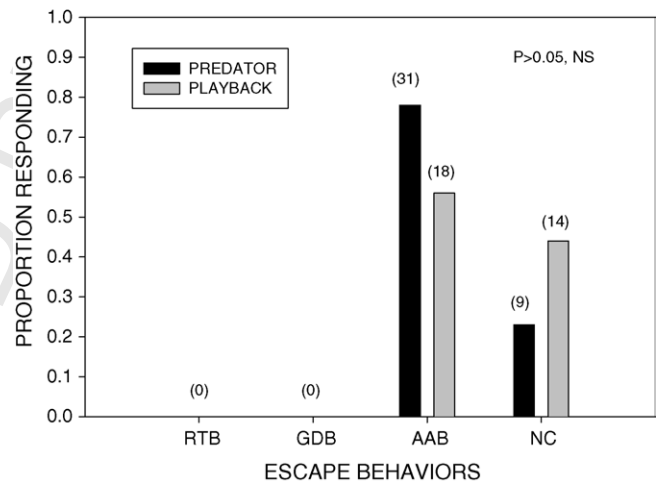
3. Results

3.1. Prairie dog responses to live predators

Based on a comparison of five different escape behaviors (Run to Burrow, Go Down in Burrow, Stand Alert at Burrow, Stand Alert in Place [Not Run], and No Response), prairie dog initial responses to the appearance of live predators differed, depending upon whether the predator was a human, a red-tailed hawk, a dog, or a coyote. Second responses to these three preda-tor types differed as well. Patterns of response to these predators are summarized in Table 1.

These escape responses differed significantly between most categories of predators (Figs. 3–5). Specific escape responses to humans were significantly different from the responses to dogs (first response, Fisher's Exact Test, $P < 0.001$; second response, Fisher's Exact Test, $P < 0.001$) and to coyotes (first response, Fisher's Exact Test, $P = 0.006$; second response, Fisher's Exact Test, $P < 0.001$). Patterns of response also differed signifi-

cantly when prairie dogs were approached by a dog and when they were approached by a coyote (first response, Fisher's Exact Test, $P < 0.001$; second response, Fisher's Exact Test, $P < 0.001$).

There were no significant differences in the escape responses of prairie dogs to a human and to a stooping (diving) red-tailed hawk (first response, Fisher's Exact Test, $P = 1.00$; second response, Fisher's Exact Test, $P = 0.11$). In a qualitative sense, however, the responses to humans and to stooping hawks were different. The response to humans was a colony-wide response, with every animal running to a burrow and diving inside. The response to stooping red-tailed hawks was a more local response, with only the animals within 10–20 m of the flight path of the stooping hawk responding by running to a burrow and diving in, while other animals outside this distance stood at alert.

DOGS VS. DOG PLAYBACKS - FIRST RESPONSE

HUMAN VS. HUMAN PLAYBACK -- FIRST RESPONSE

DOG VS. DOG PLAYBACK -- SECOND RESPONSE
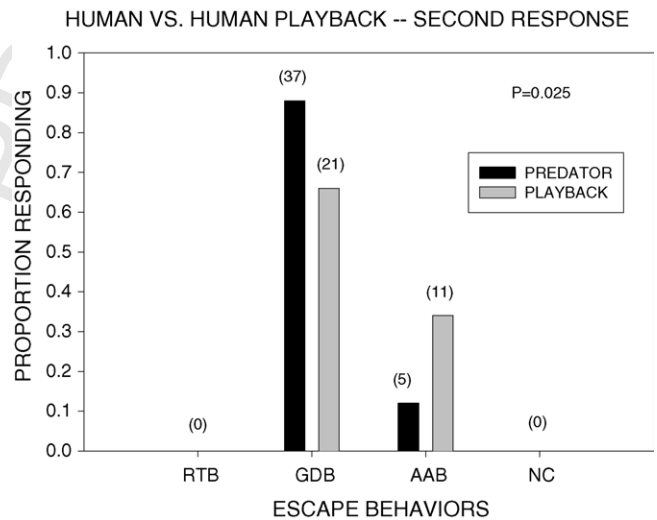
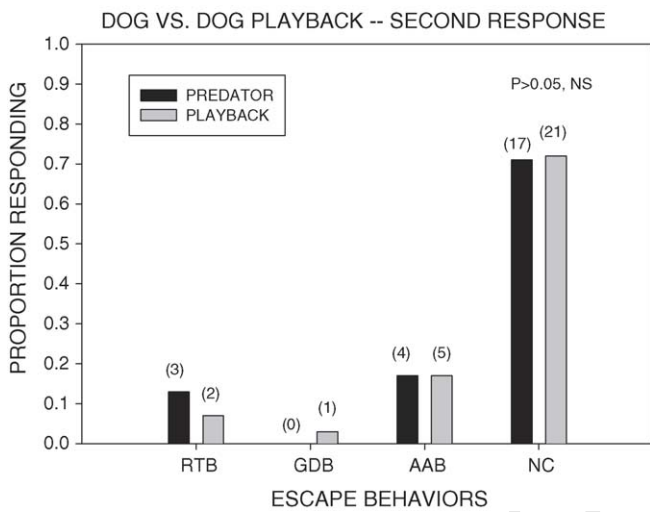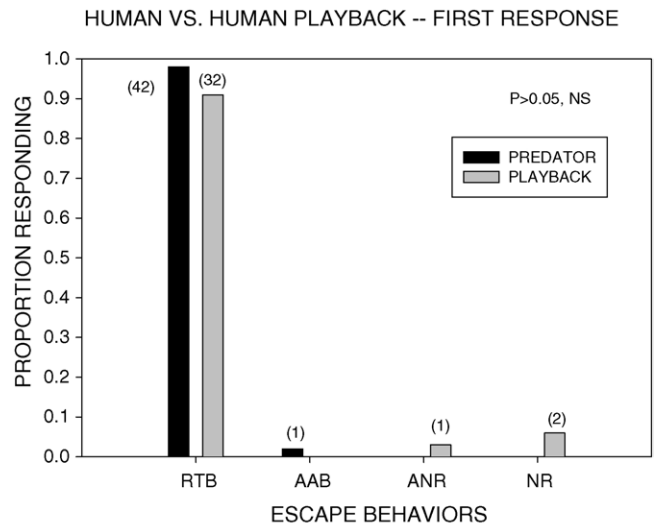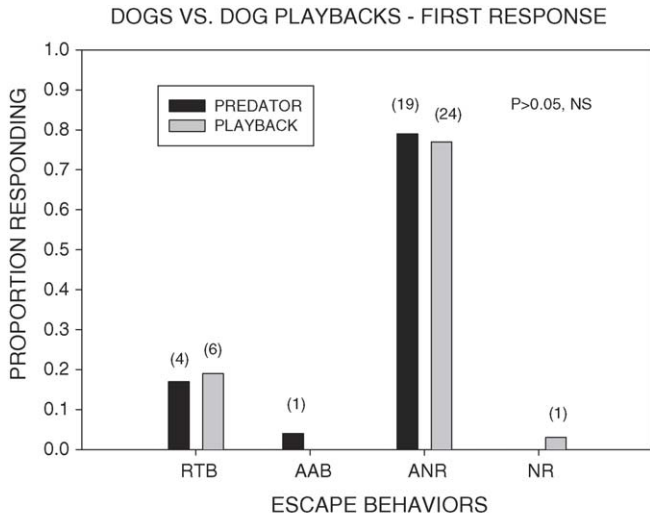HUMAN VS. HUMAN PLAYBACK -- SECOND RESPONSE

Fig. 4. First and second responses of prairie dogs to live domestic dogs (predator) and to playbacks of domestic dog-elicited alarm calls (playback). The behavioral categories are the same as in Fig. 3.

Fig. 5. First and second responses of prairie dogs to live humans (predator) and to playbacks of human-elicited alarm calls (playback). The behavioral categories are the same as in Fig. 3.

3.2. Prairie dog responses to broadcasts of alarm calls

For the playbacks of alarm calls versus playbacks of nonsense sounds, prairie dogs responded significantly to alarm call broadcasts and ignored nonsense sounds (Fisher's Exact Test: $P < 0.001$). When alarm calls were played back, prairie dog responses varied, depending upon which type of alarm call was broadcast—for human, for dog, or for coyote (Figs. 3–5). When nonsense calls were played, the prairie dogs showed No Response to the playbacks.

To test whether a message about a specific category of predator was actually being communicated through an alarm call vocalization, response patterns of the prairie dogs to each type of live predator were compared with their responses to alarm call playbacks for the same type of predator. In all but one case, there were no significant differences between responses to live predators versus playbacks (Fisher's Exact Test for all comparisons: $P > 0.05$, NS for: first response to live humans versus human playbacks; first and second response to live dogs versus dog playbacks; first and second response to live coyotes versus coyote playbacks). The only significant difference was in the prairie dogs' second response to live humans versus human playbacks: they tended to split their second response to the playback between going down into a burrow and remaining alert just outside it, whereas, if a human were visible, they would not delay going down into the burrow (Fisher's Exact Test: $P = 0.025$).

4. Discussion

The results of this study suggest that the alarm calls of Gunnison's prairie dogs not only have productive specificity, but that this information is communicated to listening prairie dogs, even when a predator is not physically present. This information seems to relate to an external referent. Macedonia and Evans (1993) and Evans (1997) have argued that the term "functional reference" should be used in most situations, because there is no way of distinguishing whether an animal is incorporating

information about a category of predator (e.g., coyote), or incorporating information about instructions to evade the predator (e.g., run to your burrow and stand on the lip of it), or incorporating information about behavioral attributes of the calling animal. In this particular case, we suggest that the animals are incorporating information about the category of predator (e.g., coyote) rather than other kinds of information. While there is no way of determining this from the response of the animals to playbacks, the earlier results of Slobodchikoff et al. (1991) showing that prairie dogs are able to incorporate information about the size, shape, and color features of individual predators suggests that the alarm calls contain either information about the category of predator, or at least some description of it, which would satisfy the criteria for external reference.

Our results show that prairie dogs have two qualitatively different kinds of responses to the predators we observed. When hawks and humans appear, the escape response is to run to the burrow and dive inside. When coyotes and domestic dogs appear, the escape response typically is to run to the burrow and stand at the lip of the burrow (for coyotes), or stand alert where foraging (for domestic dogs). In that sense, these qualitatively different responses are similar to the responses of vervet monkeys for different categories of predators (Cheney and Seyfarth, 1990). Previously, Macedonia and Evans (1993) and Evans (1997) have suggested that ground squirrels have only one plane of escape response, the horizontal distance to their burrows, while vervets have two planes of response, the horizontal distance to a tree and the vertical plane of climbing into the branches. Consequently, ground squirrels had only one form of escape behavior, and all that varied was the speed with which the animals ran to their burrows, a form of response-urgency. However, our results show that prairie dogs, and probably other ground squirrels as well, have two dimensions of response, a horizontal one of running to their burrow, and a vertical one of going down into their burrow, and that while the speed of running to the burrows might vary, the form of the response to different predators varies as well.

Although these responses are qualitatively different, they might incorporate elements of response-urgency (Owings and Hennessy, 1984; Warkentin et al., 2001). As discussed below, each category of predator hunts prairie dogs in different ways, and some predators require more immediate responses than others. Such elements of response-urgency do not obviate the possibility that semantic information can be encoded in the alarm calls, perhaps to ensure that the prairie dogs respond appropriately to the different hunting styles of their predators. Similarly, the alarm calls might incorporate structural features consistent with Morton's (1977) motivational structure–function rules, without obviating the possibility of referential encoding of information as well.

Our results show that the escape responses of prairie dogs to various predators are different in a predictable way and are not merely random "panic" responses. These escape behaviors seem to serve the prairie dogs well. Verdolin and Slobodchikoff (2002) studied the incidence of predation at eight different prairie dog colonies and found that although predators hunted at the colonies quite frequently, the success rate at catching prairie dogs was quite low, with 3% of the predation events resulting in kills of prairie dogs. Of these predators, red-tailed hawks and coyotes kill the most prairie dogs (Lewis-Wellman, 1982; Verdolin and Slobodchikoff, 2002), suggesting that if the prairie dogs were merely responding to a gradation of fear of the predator, their responses to hawks would be most similar to their responses to coyotes. In actuality, these responses are very different.

Each category of response seems to be appropriate to its corresponding category of predators. Humans often walk around the edges of prairie dog colonies with rifles and can shoot any prairie dog within several hundred meters. While humans hunting with rifles are relatively new to prairie dog colonies, appearing within the last 150 years (or approximately 100 prairie dog generations if we estimate a generation as 1.5 years), Native Americans have probably hunted prairie dogs with bows and arrows for at least 800 years (Slobodchikoff et al., 1991). An appropriate response to this kind of predation from a distance is a colony-wide one: run to a burrow and dive inside. Red-tailed hawks stoop with great speed at their potential prey, but once committed to a dive cannot capture prairie dogs outside the immediate dive trajectory. An appropriate response to this is a more localized one: run to a burrow and dive inside, if within the immediate approach path of the hawk. Coyote hunting styles differ from individual to individual (personal observation; Leydet, 1977). Some coyotes walk through a colony slowly, then make a rapid run at prairie dogs who might have let the coyote come too close. Other individuals use a different strategy: they lie down next to a burrow, and wait for up to an hour in a lying-down position. If a prairie dog emerges from the burrow, the coyote leaps up and pounces on the prairie dog. An appropriate response to this kind of variable hunting strategy is to run to the burrow and stand at the burrow entrance, watching the progress of the coyote through the colony, so that every prairie dog would know the exact location of the coyote while it is on the colony. That way, it is possible for individual animals to see when the coyote leaves the colony and is no longer a potential threat. Domestic dogs seem to be less methodical than coyotes in hunting prairie dogs. A typical hunting strategy of dogs seems to consist of running around frantically, barking, and running at random prairie dogs (personal observation). Under these circumstances, the prairie dogs have sufficient time to run to their burrows if a domestic dog approaches them. Otherwise, there seems to be little threat from a domestic dog—we have not observed any domestic dogs using the coyote strategy of lying down and waiting at a burrow. As such, an appropriate prairie dog response seems to be standing alert in place and watching the progress of the domestic dog through the colony.

Acknowledgements

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