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Behavioural Processes 73 (2006) 29–35
BEHAVIOURAL PROCESSES
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Perceptual specificity in the alarm calls of Gunnison's prairie dogs

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Received 20 August 2005; received in revised form 20 January 2006; accepted 30 January 2006

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.

Keywords: Alarm calls; Prairie dogs; Referential communication; Perceptual specificity; Ground squirrel

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

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doi:10.1016/j.beproc.2006.01.015

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 elicits 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-