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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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32 Cognition and Communication in Prairie Dogs

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My central research question concerns the relationship between the complex communication system of Gunnison's prairie dogs and their cognitive abilities. Gunnison's prairie dogs (*Cynomys gunnisoni*) are social, colonial animals that are found in the American Southwest, within the states of Arizona, New Mexico, Utah, and Colorado. There are four other species of prairie dogs: the black-tailed prairie dog (*Cynomys ludovicianus*), found in the midwestern United States; the Utah prairie dog (*Cynomys parvidens*), found in the state of Utah; the white-tailed prairie dog (*Cynomys leucurus*), found in the states of Montana and Wyoming; and the Mexican prairie dog (*Cynomys mexicanus*), found in the state of Chihuahua in Mexico.

Gunnison's prairie dogs typically spend the winter in a state of torpor inside extensive underground burrow systems, then emerge in the spring to set up territories (Slobodchikoff 1984; Rayor 1988). Each territory is defended by the group living on it, and the social structure can vary considerably within the same colony. Some territories are occupied by a single male or female; others are occupied by a single male and a single female; still others are occupied by a single male and several females; and some are occupied by several adult males and several adult females (Slobodchikoff 1984; Travis and Slobodchikoff 1993). The structure of the social system within a territory seems to be correlated with the distribution of food resources: uniformly distributed food resources correlate with single male–single female territories, while patchily distributed food resources correlate with single male–multiple female and multiple male–multiple female territories (Slobodchikoff 1984; Travis and Slobodchikoff 1993). The colonies are spatially fixed, and the extensive burrow systems can persist for perhaps hundreds of years.

The spatial concentration of prairie dogs into colonies means that a number of predators can encounter a dependable food source throughout much of the year. Prairie dogs are preyed upon by coyotes, foxes, badgers, golden eagles, red-tailed hawks, ferruginous hawks, harriers, black-footed ferrets, domestic dogs, domestic cats, rattlesnakes, and gopher snakes. Also, prairie dogs are hunted extensively by humans for target practice and sport. Prior to the introduction of rifles, prairie dogs were hunted as a source of meat by Native American peoples for at least 800 years (Slobodchikoff et al. 1991).

Such predation pressure was probably important for the evolution of antipredator defenses. Prairie dogs have dichromatic color vision (Jacobs and Pulliam 1973) and can detect the presence of a predator from long distances. They also have an alarm call system that allows them to advertise the approach of a potential predator. The alarm calls are very loud and can carry for distances of more than a kilometer (Hoogland 1996). The burrows provide an escape route from most terrestrial and aerial predators. The burrow architecture within a territory has several openings to the surface which are connected to a series of underground tunnels that can run a horizontal distance of more than 10 m below the ground's surface (Fitzgerald and Lechleitner 1973).

The alarm call system has proven to be a Rosetta stone for deciphering the information encoded in the prairie dog vocalizations. When a prairie dog detects a predator, he or she emits a call that alerts other prairie dogs to the presence of danger. The call can be given as a single bark or as a series of barks that comprise a calling bout. The external referent, the predator, can be seen and videotaped by field observers, as can the escape behaviors of the prairie dogs in response to the predator. The alarm calls can be recorded on audiotape and brought back to the laboratory for analysis. The calls can be analyzed through fast Fourier transform to assess the acoustic structure of the vocalizations. Different parts of the waveforms of the calls can be measured, and statistical analyses or fuzzy logic neural net analyses can be performed to determine whether calls elicited by different predators are similar to one another or different from each other (Slobodchikoff et al. 1991; Placer and Slobodchikoff 2000). The calls recorded for each predator can be played back to the prairie dogs when no predator is present and when no prairie dog is calling. The escape behaviors of the prairie dogs can be recorded on videotape, allowing comparisons of escape behaviors elicited by a predator with escape behaviors elicited by the playback of the alarm calls (Kiriazis 1991). Field experiments can be designed that expose prairie dogs to different predators or different attributes of individual predators, and the calls elicited can be recorded and analyzed. All of the prairie dogs can be marked with black fur dye, using a code of letters and numbers that allows observers to identify the individual prairie dog who is calling. Also, several colonies are available for study, and repeating experiments at multiple colonies can increase the external validity of the experiments.

Using these techniques, we have shown that the calls contain a variety of information. A call can identify the category of predator, such as coyote, human, domestic dog, or red-tailed hawk (Slobodchikoff et al. 1986; Placer and Slobodchikoff 2000). Each category of predator-specific calls elicits different escape responses (Kiriazis 1991), just as the different alarm calls of vervet monkeys elicit different escape responses (Cheney and Seyfarth 1990). The escape responses are of two different types, unlike other ground squirrels that seem to have only one response, running to their burrows (Owings and Morton 1998). Among the prairie dogs, hawk and human alarm calls elicit running to the burrows and diving inside. For a human-elicited call, running to the burrows is a colony-wide response, and for a hawk-elicited call, only the animals in the immediate flight path of a diving hawk run to their burrows. Coyote and domestic dog alarm calls elicit either a running to the lip of the burrow and standing at the burrow (coyote) or standing in place where the animal was feeding (domestic dog). In both of the latter cases, other animals emerge from their burrows and watch the progress of the predator through the colony (Kiriazis 1991).

The predator-specific calls appear to be referential, describing objects or events external to the animal. [See Evans (1997) for a discussion of referential signals.] Such categorizations functionally serve as nounlike elements in the alarm calls. In addition, within a predator category, the prairie dogs can incorporate information about the physical features of a predator, such as color, size, and shape (Kiriazis 1991; Slobodchikoff et al. 1991). For example, with humans, the calls contain information about the color of clothes that the humans are wearing, and the general size and shape of the humans (Slobodchikoff et al. 1991). These categorizations serve as adjectivelike elements in the alarm calls. Finally, the prairie dogs can incorporate information about the relative speed of travel of a predator, or the relative urgency of the response, by shortening the time interval between individual alarm barks in a calling bout, in direct proportion to the speed of travel of the predator (Kiriazis 1991). The time element between barks thus serves as a verblike element.

These sources of information in alarm calls appear to function as a primitive grammar, composed of nounlike, adjectivelike, and verblike elements (figures 32.1–32.4). For example, if a coyote appears and is moving slowly, one prairie dog will produce a single bout of calls that contains descriptive information about the size, shape, and color of the coyote. If the coyote starts to run, a number of prairie dogs start to call, each providing a description of the coyote. In addition, the interval between each alarm bark in a bout is shortened proportionately to the speed of travel of the coyote (Kiriazis 1991). The information that is encoded into the alarm calls could let other prairie dogs know who the individual

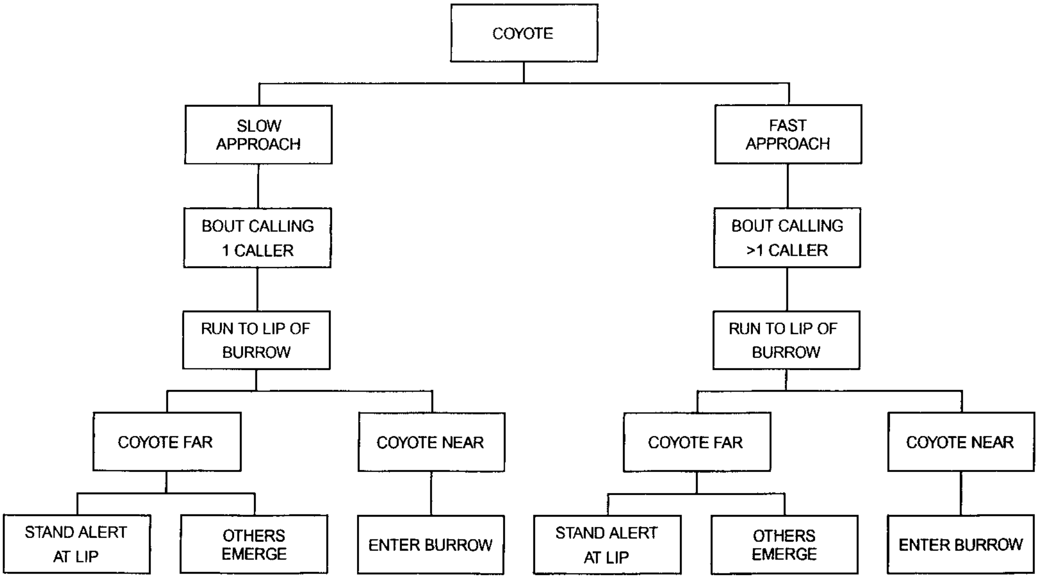

Figure 32.1
Responses of prairie dogs to an approaching coyote. If the coyote is approaching quickly, a single animal will produce a multiple-note bout of alarm calls. If the coyote is approaching slowly, several animals will simultaneously produce multiple-note bouts of alarm calls. All animals run to the lips of their burrows, and animals below ground emerge to watch the progress of the coyote through the colony.

coyote is, from the description of the predator and the speed of its travel through the colony.

The identity of the individual coyote may be important to the prairie dogs because different coyote individuals hunt prairie dogs in different ways (Leydet 1977). Some coyotes walk or run through the colony in a straight path, and then lunge at any prairie dog that appears to be away from the lip of its burrow. Other coyotes lie down next to a burrow that contains prairie dogs and wait for more than an hour by the side of the burrow. Knowing the identity of the individual coyote might provide some information about the type of hunting style that that individual typically adopts.

The categorization and description of predators implies a sophisticated cognitive function. This cognitive function can be achieved through genetic hardwiring into the brains of prairie dogs, through cultural transmission of learned information, or a combination of both. Some measure of cultural transmission of information might exist in the alarm calls because the calls vary somewhat from colony to colony in what has been described as dialects (Slobodchikoff and Coast 1980; Slobodchikoff et al. 1998). Within a local area, such as the vicinity of Flagstaff, Arizona, colonies separated by less than 2 km can have differences in frequency and time components within a category of call, such as that elicited by a human. All of the calls elicited by a human from these colonies recognizably fall into the structure of the human category, but significant differences exist. On a broader regional basis, such as over the entire range of the Gunnison's prairie dogs, dialect differences are more

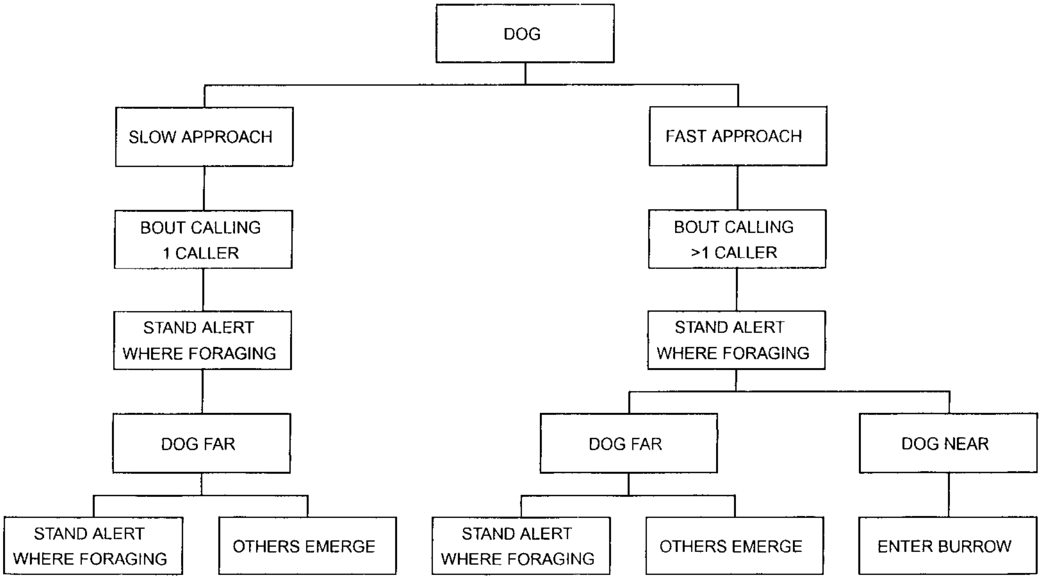

Figure 32.2
Responses of prairie dogs to an approaching domestic dog. As with a coyote, different rates of approach elicit calling by either one or several prairie dogs. However, unlike the coyote response, the prairie dogs do not run to their burrows, but stand upright in an alert posture wherever they were foraging. Other prairie dogs emerge from their burrows to watch the progress of the dog through the colony.

pronounced, although even there a human-elicited call still retains the basic structure of the human category. Although some genetic differences exist between colonies at the local level, these differences are relatively slight (Travis et al. 1997), suggesting that genetic differences alone might not explain the existence of dialects.

In order to describe the individual features of predators, the prairie dogs might have an innate rule-based cognitive system. This rule-based system might have a template of different time and frequency components that correspond to differences in color, shape, and size, stored in the brains of the prairie dogs. As an individual predator appears, the prairie dogs might pull out of that stored repertoire the components that correspond to the physical description of the individual predator.

A rule-based system is suggested by the experiments done by Ackers and Slobodchikoff (1999). Although earlier work showed that each prairie dog consistently incorporated into its call information about a predator in the same way as other prairie dogs calling to warn of the same predator, such incorporation could come about through cultural transmission. To address this, Ackers and Slobodchikoff (1999) used three kinds of plywood models as stimuli that elicited alarm calls. All of the models were painted black and were presented as silhouettes. One model was an oval, one was a realistic silhouette of a coyote, and one was a realistic silhouette of a skunk. The models were presented to a colony of prairie dogs by having the model come from concealment and travel across a part of the colony on a pulley system.

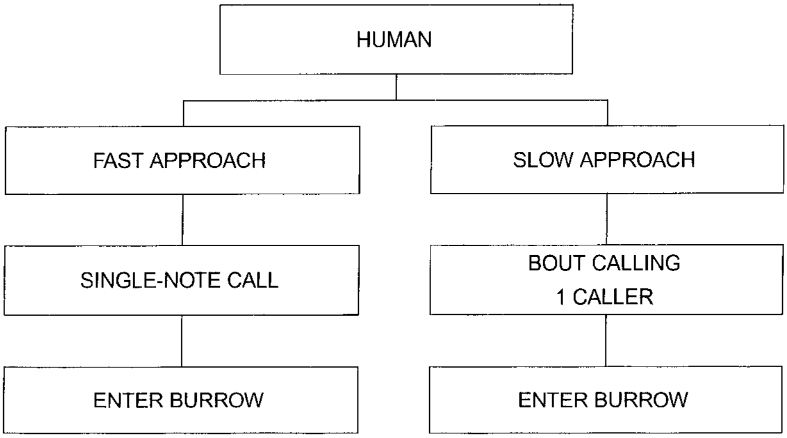

Figure 32.3
Responses of prairie dogs to an approaching human. Depending on the rate of approach of the human, a single animal will give either a one-note call if the human is approaching quickly, or a multiple-note bout of calls if the human is approaching slowly. In either case, all the prairie dogs run to their burrows and disappear inside.

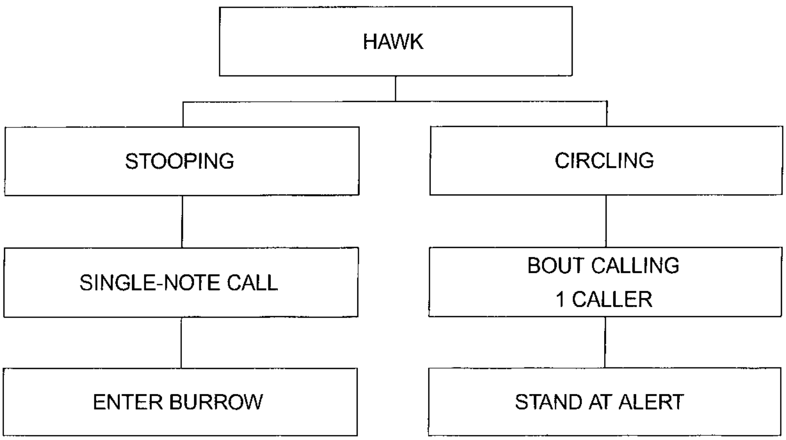

Figure 32.4
Responses of prairie dogs to an approaching hawk. If the hawk is stooping or diving, a single animal will give a single-note call, eliciting running to burrows and disappearing inside. If the hawk is circling overhead, a single animal will give a multiple-note bout of calls. In response to this signal, other prairie dogs do not run to their burrows, but stand upright in an alert posture wherever they were foraging.

All of the models elicited alarm calls. The calls were recorded and each prairie dog's alarm call in response to each model was noted. For each type of model, all of the prairie dogs consistently called the same for that model, using the same frequency and time components. Although none of the prairie dogs had ever seen a large black oval before, they all had a call that corresponded to the presentation of black oval, and this call was significantly different from their calls for either the coyote silhouette or the skunk silhouette. Similarly, the calls for the coyote silhouette were significantly different from those for the skunk silhouette. The coyote silhouette elicited calls that were mostly similar to those elicited by a live coyote, but differed in several components. Neither the oval silhouette nor the skunk silhouette represented potential predators, yet each elicited its own model-specific calls. If the calls elicited by the oval and the skunk were just expressing the novelty of the stimulus, the calls for the two models might have been expected to be either the same or at least very similar. Instead, they were very different in terms of their acoustic frequency and time components. This suggests that the prairie dogs were describing their perception of the attributes of each silhouette, rather than the novelty of the stimulus. These results suggest that prairie dogs may have an internal cognitive representational system that they can utilize to encode information about external events.

The alarm calls of prairie dogs can be viewed as an intentional system (Allen and Bekoff 1997). The elements of this representational system allow the coding of information about known objects in the environment, such as predators, as well as unknown objects that the prairie dogs have not previously experienced. We can postulate that prairie dogs might have an internal lexicon corresponding to a set of external conditions. This lexicon might be innate or it might be a combination of innate and learned elements. Upon the occurrence of an external event, such as the appearance of a predator, the prairie dogs might apply a series of transformational rules (as defined by Chomsky, 1965). These transformational rules convert a base structure (elements of the lexicon) into an output structure (the alarm call) that provides a message for other prairie dogs to decode with their own internal lexicon.

In terms of future work, two immediate questions arise. One is related to the lexicon. The Ackers and Slobodchikoff (1999) experiments suggest that prairie dogs can utilize novel combinations of descriptors. Of interest here is how many different external objects the sender can encode and the receiver decode. Are there instances when related objects are grouped together into a single type of call? How fine scaled is the discriminatory ability of both the sender and the receiver? These questions can be addressed with further experiments using the methodology described here.

The other question is that of states of mind (as defined by Cheney and Seyfarth 1990 and Dennett 1987, 1996). This one question leads to a whole host of other questions. Are prairie dogs aware of their own danger when they see a predator? Can they assess the risk and decide to either call or not call? Can they categorize to themselves the different predators that they encounter? Are they aware of communicating a message to another prairie dog, or is their message produced without any awareness?

In terms of Dennett's (1987) intentional systems, prairie dogs could have a zero-order intentional system, in which the calls are simple expressions of fear. This appears to be unlikely, given the complexity of the calling system. Alternatively, the prairie dogs could have a first-order intentional system, in which they have beliefs, and when giving a call they believe that a predator is nearby and want other prairie dogs to take evasive action. It is also possible that prairie dogs might have higher-order intentional systems, with beliefs about the beliefs of other prairie dogs. These are all questions that are relatively difficult to address. Cheney and Seyfarth (1988, 1990) have used with vervet monkeys a habituation-dishabituation experimental design that had been successfully used previously with preverbal children to assess the degree to which representational mental states might exist. Such experiments have not proven to be successful with prairie dogs because of the rapid habituation that the prairie dogs showed to playbacks of alarm calls (Ackers 1997). Another methodology has to be designed to address these questions.

From the standpoint of cognitive ethology (Allen and Bekoff 1997), we can ask the question: Why do prairie dogs have such a complex system of communication? Although the primates are our closest evolutionary relatives, so far no primate species is known to have such a complex referential communication system. One of the best examples of a referential system in primates is that of the vervet monkeys, and they have only three categories of calls: leopard, eagle, and snake. Within these categories, the calls can be given for a variety of different predators and nonpredators (Seyfarth et al. 1980). Perhaps the prairie dogs evolved such a complex system because of the ecological circumstances in which they live. They are a social species occupying spatially fixed colonies that attract the same predator individuals day after day. Since natural selection favors mechanisms that improve an animal's fitness, perhaps phylogenetic relatedness is less important than the ecological conditions in which an animal species lives.

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