

POSSIBLE FUNCTIONS OF THE ALARM CALLS OF  
BELDING'S GROUND SQUIRRELS AND PRAIRIE DOGS

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## INTRODUCTION

Alarm calls, which are vocalizations that alert other animals of danger, have the appearance of altruism. Altruistic behavior can be defined as behavior that benefits another organism, not closely related, while being apparently detrimental to the organism performing the behavior. Trivers (1971) and Sherman (1977) have written on the possible evolutionary routes leading to the giving of alarm calls as it is related to altruistic behavior.

Before the possible evolutionary routes of alarm calling can be discovered it is necessary to determine the exact function of the calls. Identifying the function of alarm calls is difficult because predation is rarely seen in the field, and it is also difficult, with most species, to identify individuals and their relatedness.

During a three-year field study, Sherman (1977) investigated the function of the alarm call of the Belding's ground squirrel (Spermophilus beldingi) that was given when a terrestrial predator approached. The ground squirrel population he studied contained individually marked animals of known age and familial relationships. This paper is a review of Sherman's work as compared to the literature concerning alarm calls of the prairie dog (Cynomys sp.).

## POSSIBLE FUNCTIONS OF ALARM CALLS

Sherman (1977) listed six hypotheses of the possible functions of alarm calls. They are:

- 1.) Diversion of predator's attention to other prey.
- 2.) Discouragement of predator pursuit.
- 3.) Alerting relatives.
- 4.) Helping the group - relatives and nonrelatives alike.
- 5.) Reduction of the likelihood of later attacks by the same predator.
- 6.) Warning of others likely to reciprocate.

#### STUDY ANIMALS

In order to distinguish between the possible functions of alarm calls it is necessary to understand the life history and social structure of the animals involved.

Belding's ground squirrels - These animals are diurnal rodents that inhabit alpine and subalpine meadows in the West. The population studied by Sherman (1977) is active from May through September, with hibernation taking place the remainder of the year. Conspecific ground squirrels interact daily, but unlike prairie dogs they do not group their burrows into circumscribed aggregations, nor do they produce young synchronously.

Belding's ground squirrels give a segmented alarm call in the 4- to 6-kilohertz range when a predatory mammal approaches and a single-noted, high-pitched whistle on the approach of avian predators (Turner 1973, Sherman 1977).

Female Belding's ground squirrels that are successful in rearing young, are sedentary between years, and the daughters mature and breed near their birthplaces (Sherman 1977). As a result, the genetic relatedness among females occupying a small area is high. The young males, in contrast to their sisters, permanently emigrate from their birthplaces. Males do not return to their natal area to copulate.

Some male Belding's ground squirrels are highly polygynous.

Sherman (1977) reported that in 1976 the most successful male accounted for 31 percent of all completed copulations. Males do not defend mating territories, nor do they appear to behave parentally toward their mate's offspring.

Females are sexually receptive during a 4- to 6-hour period, during which time they mate with an average of 2.1 males (Sherman 1977). Females rear their young alone, and exclude nondescendants from the area around the natal burrow. The males abandon areas where their mates will rear the young, and inhabit burrows elsewhere at about the time their mate's young are born. The males will usually remain at these new burrows until after mating the following spring.

Prairie dogs - Prairie dogs are closely related to ground squirrels. There<sup>are</sup> three species and four subspecies of prairie dogs which are divided into two main forms. These forms are the black- and the white-tailed. The white-tailed forms consist of: Whitetail, (C. leucurus), Utah (C. parvidens), Gunnison (C. g. gunnisoni), and Zuni (C. g. zunnienus). The black-tailed forms consist of: blacktail (C. l. ludovicianus), Arizona (C. l. arizonensis), and Mexican (C. mexicanus). The white-tailed forms live in mountain parks and open shrubland west of the Rocky Mountains. The black-tailed forms live on the plains and grasslands of the central United States and northern Mexico.

None of the alarm calls of any species of prairie dogs have been studied as extensively as the Sherman (1977) study of the Belding's ground squirrels. For the most part, the information that is available on prairie dog alarm calls has come from studies of general behavior. Because of this lack of a detailed study, information from many studies of several species of prairie dogs will be used to make comparisons

with the Belding's ground squirrels.

There are conflicting views in the literature concerning the type of alarm calls given by prairie dogs. Tembrock (1963), and Tileston and Lechleiter (1966) stated that the blacktail prairie dog had different alarm calls for avian predators than for terrestrial predators. The call for avian predators was said to be more "shrill" than the call for ground predators. In contrast to this, Smith et al. (1977) and Waring (1970) reported that there is no difference in the alarm calls given by blacktail prairie dogs for avian and terrestrial predators. A possible explanation for these differences is that the latter researchers used more modern audio recording and sound analysis equipment than the earlier researchers. The latter studies used sound spectrograph analyses which pick up differences in frequency, but not in intensity. It is possible that the calls differed only in loudness or intensity and not in frequency. This would make the two calls sound different to the human ear. It is also possible that different colonies of the same species have slightly different alarm calls. The literature contains no evidence that there are different alarm calls for terrestrial versus avian predators for any species of white-tailed prairie dogs.

Like Belding's ground squirrels, prairie dogs give a segmented alarm call. Prairie dog alarm calls are in the range of 0.9 to 8 kilohertz, whereas the ground squirrel calls are in the 4- to 6-kilohertz range (Waring 1970, Sherman 1977, Smith et al. 1977).

During the spring breeding season prairie dogs of all species live in groups. These groups usually consist of one male and from two to four females (Longhurst 1944, Koford 1958, Tileston and Lechleitner 1966). The black-tailed species have strong social ties within the

group that remain throughout the year. Family groups (or coteries) of this form actively defend a territory, and the males take the most active part. Contrary to the black-tailed species, males of the white-tailed species live separate from the females except during the breeding season (Longhurst 1944, Tileston and Lechleitner 1966). Burrow systems and feeding areas are the only sites which are defended by white-tailed species.

The females of at least two of the white-tailed species (Zuni and Gunnison) leave their young shortly after they appear above ground. The approximate age of the young at that time is six weeks (Longhurst 1944). The females go to a different area then, and either dig another burrow or clean out an unoccupied burrow. After two or three weeks the young also disperse from the natal burrow. The black-tailed species differ greatly from the white-tailed on this. Both females and males of the black-tailed species stay at the natal burrow. Their young do not disperse until fall, when they are at an age of 12 to 16 weeks (Koford 1958).

White-tailed species of prairie dogs hibernate throughout the winter like Belding's ground squirrels. The actual time of hibernation varies with geographic locations and weather conditions (Tileston and Lechleitner 1966). The black-tailed species do not hibernate. Their activity is noticeably reduced during the winter, but on relatively warm, calm days they will come above ground to feed (Koford 1958, Tileston and Lechleitner 1966).

#### DISCRIMINATING AMONG THE POSSIBLE FUNCTIONS OF ALARM CALLS

Contrary to Sherman's hypothesis number one, it was found that

alarm calls did not cause a diversion of the predators' attention to other prey. This was true for both prairie dogs and Belding's ground squirrels (Sherman 1977, Fitzgerald and Lechleitner 1974). <sup>I observed.</sup> The opposite result ~~was observed~~ with predation by golden eagles (Aquila chrysaetos) on the Utah prairie dog <sup>pers. obs.</sup> (Player 1978). <sup>I</sup> Eagles ~~were~~ often noticed <sup>as they</sup> sitting on rocks in or near dog towns. The prairie dogs would sit up and give an alarm call whenever a vehicle approached. The eagle would take off and circle over the prairie dogs when they were sitting up. It would then dive at the prairie dogs while their attention was on the vehicle. <sup>I never saw</sup> The eagle ~~was never observed~~ catching a prairie dog, but this seemed like a good hunting technique. A similar hunting technique was reported by Fitzgerald and Lechleitner (1974) concerning coyotes and the Gunnison prairie dog. In this case a coyote went through a dog town, and two coyotes followed about 100 meters behind and to the sides of the first. The lead coyote got the attention of the prairie dogs. While they were alarm calling, the other coyotes attempted to sneak up on them. The capture of a prairie dog by a coyote was not observed, but one of the coyotes was shot and its stomach contained the remains of several prairie dogs.

Sherman (1977) reported that neither long-tailed weasels (Mustela frenata), badgers (<sup>e</sup>Taxidea taxus), dogs (Canis familiaris), coyotes (C. latrans), or pine martens (Martes americana) were deterred by ground squirrels giving alarm calls. These examples, along with the two listed above for prairie dogs, suggest that hypothesis number two (discouragement of predator pursuit) is incorrect. All seven of the predators mentioned stalked or chased alarm callers. This suggests that alarm calling may in fact <sup>e</sup> encourage predator pursuit.

Adult female prairie dogs (of both forms) and Belding's ground squirrels are usually the first to sight danger and give an alarm call (Tileston and Lechleitner 1966, Sherman 1977). The methods of rearing young found in Belding's ground squirrels and species of the black-tailed form of prairie dogs supports the hypothesis (number three) that the function of alarm calls is to alert kin. With these species those animals most likely to hear an alarm call from an adult female are the young of the caller. However, there are some discrepancies to this also. First of all, males of the black-tailed form are near the young as much (or nearly so) as females, so why don't the males call alarms as frequently as the females? It could possibly be that the male's main role is to defend the territory from conspecifics, and the female's main role is to give warning of danger from predators. Much more data is needed before any statement can be made concerning this. Another discrepancy is with the fact that the females of the white-tailed species leave the young within a few weeks. Apparently the young are able to detect predators on their own by the time the female leaves them. The young might be being aided in predator detection by other adults nearby (this would support hypothesis number four). Of course, here again, more data is needed concerning this matter before a conclusion could be <sup>drawn.</sup> made.

Sherman (1977) stated that there was a lack of evidence supporting hypothesis number four (alarm calling functions to help the group) with Belding's ground squirrels. The lack of evidence he referred to is the fact that there were no non-calling groups or populations of ground squirrels near his study site. This lack of non-calling groups certainly does not mean that alarm calling does not function to warn

the group as a whole. As mentioned above, for species of white-tailed prairie dogs there is evidence that the alarm calling functions by aiding the group. If this were not the case, it seems that the prairie dogs of these species would call less after dispersal of the females and young. There was no mention that white-tailed species did this.

Reduction of the likelihood of later attacks by the same predator (hypothesis five) seems to be a logical function of alarm calls. Predators are known to practice reward following by returning to the same site or sites similar to where they last succeeded in capturing prey (Trivers 1971). When a prey species warns its conspecifics by calling alarms of approaching danger, this likely reduces the probability of a predator being successful. The chance of that predator returning to the same site is greatly reduced if it was unsuccessful there previously. Sherman (1977) said that predators did not preferentially return to the exact sites of previous successes on his study sites. He apparently overlooked the fact that the predators returned to the same general area. Sherman used his limited data to refute all the other literature on reward following. He concluded that alarm calls did not reduce the likelihood of later attacks. Sherman may be correct, but there is more evidence supporting the hypothesis than there is against it. Again, no positive conclusion can be made without more data.

It is difficult to distinguish hypothesis <sup>6</sup> three and four from hypothesis six (warning of other who are likely to reciprocate). In order for reciprocation to take place, individual recognition must take place, and the individuals must be closely associated with each other.

The animals must also be able to remember their indebtedness. It is known that the first two conditions exist for prairie dogs and Belding's ground squirrels (Fitzgerald and Lechleitner 1974, Sherman 1977). Proving the third condition would be very difficult, if not impossible. Sherman (1977) found that nonreciprocators (those squirrels not giving warning calls) were not obviously discriminated against. The reciprocators still called even if only nonreciprocators were present. While this does not prove or disprove hypothesis six, it does support hypothesis four. Warning of others likely to reciprocate is a possible function of alarm calls, but much more data are necessary before a valid conclusion can be made.

#### CONCLUSION

From Sherman's work on alarm calls of Belding's ground squirrels and the literature dealing with the alarm calls of prairie dogs, it is possible to begin determining the possible functions of alarm calls. There is a limited amount of evidence available that refutes hypotheses one and two. These two hypotheses say that alarm calls divert or discourage predator pursuit. Sherman stated that hypothesis number three (alerting relatives) is the most likely function of alarm calls. However it seems that hypotheses four (helping the group) and six (warning of others likely to reciprocate) are also likely functions. More research is needed before further conclusions can be drawn. No direct evidence has been found in support of hypothesis five (reduction of later attacks by the same predator). However, indirect evidence, such as reward following by predators, shows that this hypothesis is possibly correct. More information is necessary before it can be determined if alarm calling is an altruistic act.

# LITERATURE CITED

- Fitzgerald, J. P., and R. R. Lechleitner. (1974). Observations on the biology of Gunnison's prairie dog in central Colorado. Am. Midl. Nat., 92, 142-163.
- Koford, C. B. (1958). Prairie dogs, whitefaces, and blue grama. Wildl. Monog., 3, 1-78.
- Longhurst, W. (1944). Observations on the ecology of the Gunnison prairie dog in Colorado. J. Mammal., 25, 24-36.
- Flayer, R. L. (1978). Personal observation on the Awapa Plateau, Wayne county, Utah, July, 1978.
- Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. Science, 197, 1246-1253.
- Smith, J. W., S. L. Smith, E. C. Oppenheimer, and J. G. Devilla. (1977). Vocalizations of the blacktail prairie dog Cynomys ludovicianus. Am. Beh., 25, 152-164.
- Tembrock, G. (1963). Acoustic behavior of animals. In: R. G. Busnel ed. Acoustic behavior of animals, Elsevier Publishing Co., New York. pp. 751-786.
- Tileston, J. V., and R. R. Lechleitner. (1966). Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. Am. Midl. Nat., 75, 292-316.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. Quarterly Rev. of Biol., 46, 35-57.
- Turner, L. W. (1973). Vocal and escape response of <sup>U.</sup>Spermophilus beldingi to predators. J. Mammal., 54, 990-993.
- Waring, G. H. (1970). Sound communications of black-tailed, white-tailed, and gunnison's prairie dogs. Am. Midl. Nat., 83, 167-185.