DISSERTATION

SOUNDS OF BLACK-TAILED, WHITE-TAILED, AND GUNNISON'S PRAIRIE DOGS

Submitted by

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IT IS RECOMMENDED THAT THE DISSERTATION PREPARED BY George H. Waring ENTITLED Sounds of Black-Tailed, White-Tailed, and Gunnison's Prairie Dogs BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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Chairman

Abstract of Dissertation

SOUNDS OF BLACK-TAILED, WHITE-TAILED, AND GUNNISON'S PRAIRIE DOGS

The sounds of black-tailed, white-tailed, and Gunnison's prairie dogs were studied in Colorado and Wyoming from February, 1964 to June, 1966. Observations, photographs, and tape recordings were made in the field and were supplemented by data collected from captive prairie dogs. The sounds were tape-recorded on a battery-powered tape recorder at 15 inches per second and analyzed on a sound spectrograph. An unidirectional dynamic microphone was used with the recorder.

The sounds of the black-tailed prairie dogs were named and had the usual function as follows: (1) "repetitious barks"--alert; (2) "chuckle"--alert; (3) "chatter barks"--threat; (4) "wee-oo song"--contact; (5) "raspy purr"--pleasure; (6) "snarl"--threat; (7) "scream"--distress; (8) "growl"--threat; and (9) "tooth chatter"--threat. In addition, a grunting sound was occasionally heard.

The sounds of the white-tailed prairie dogs were named and had the usual function as follows: (1) "vocal chatter"--alert; (2) "chuckle"--alert; (3) "laughing barks"--contact; (4) "snarl"--threat; (5) "scream"--distress; and (6) "growl"--threat.

The sounds of the Gunnison's prairie dogs were named and had the usual function as follows: (1) "repetitious

barks"--alert; (2) "rapid barks"--apprehension; (3) "chuckle"--alert; (4) "raspy chatter"--contact; and (5) "growl"--threat. In addition, Gunnison's prairie dogs occasionally were heard making snarling, screaming, and tooth chattering sounds.

Each species can be identified by certain sounds unique to it, although, in general, all three species emit sounds under similar circumstances. The same sound may have different uses under different ecological conditions. For this reason, all sounds were named for physical rather than functional characteristics. The "chuckle" sounds are regular alerting sounds altered by the burrow system rather than by the prairie dog. Highly alarmed individuals may give more rapid alerting sounds, and during extreme alarm more than one individual may give these vocalizations. Black-tailed prairie dogs usually give their alarm calls for long periods; the other two species group their alarm barks into sets of sounds. The contact call of the black-tailed prairie dog is often repeated immediately by other individuals; the contact call of the other two species is usually repeated after a delay of several seconds. Tail flicking during vocalization occurs only in the black-tailed prairie dog.

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NOTE

An annotated demonstration tape recording from this research is on file in the Tape-recording Collection at the Colorado State University Library and in the Library of Natural Sounds at Cornell University.

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INTRODUCTION

The purpose of this research was to investigate the sounds produced by three species of social rodents, the prairie dogs, which have long been known for their vocalizations. The following species were studied: the black-tailed prairie dog (Cynomys ludovicianus), the white-tailed prairie dog (C. leucurus), and the Gunnison's prairie dog (C. gunnisoni). The three species are diurnal in above-ground activity, and the latter two are known to become totally inactive above ground during the winter months. All species are monestrous, with one litter a year born in the spring or early summer. The pups appear above ground at approximately one and a half months of age.

Prairie dogs were unknown to zoologists until the Lewis and Clark Expedition made a small collection of skins and one live specimen which they sent to President Thomas Jefferson in 1805. In 1815, Ord used these specimens when he first described and gave a scientific name to the prairie dogs.

Few mammals have ever been named for their vocalizations; however, most common names of the "prairie dog" have referred, at least indirectly, to their sounds. For example, they have been called "barking squirrels," "mound yappers,"

and "barking marmots." The early French trappers called them "petite chien" since to them they were "small dogs." However, the first published name was "ground prairie dog" which appeared in a Baltimore newspaper in 1805 as a letter from William Clark to William Henry Harrison (Jackson, 1962). The somewhat misleading name of "prairie dog" has commonly been used since then. As Kendall (1929) so pointedly wrote in 1844, "it is this short bark alone that has given them the name of dogs, as they bear no more resemblance to that animal, either in appearance, action, or manner of living, than they do to the hyena."

Studies of animal sounds as well as other means of communication are basic to our understanding of social behavior. Without communication (the giving and receiving of information) between individuals of a group, there would be no social interaction, only an aggregation of organisms. Animals that live in close association with one another often have a means of warning others about danger. Frequently, there is an exchange of information among individuals of the group which helps to reduce the amount of competition between them, or causes them to behave as a unit and stay together. When animals live as a social unit, this behavior seems to have survival value for both the individuals and the species.

Since prairie dogs appear to be social animals and are known to emit sounds, it seemed likely that they would have communications, especially those used in warning and

threatening, using vocal and nonvocal sounds. It was the goal of this research to investigate what sounds are emitted by the three species of prairie dogs. Sounds produced under natural conditions were of primary interest.

REVIEW OF LITERATURE

Taxonomy and Distribution

Five species of prairie dogs are recognized today and are unique to North America. Hollister (1916) classified them as follows:

Genus: Cynomys Rafinesque

Subgenus: Cynomys Rafinesque

Cynomys ludovicianus ludovicianus (Ord, 1815)

Black-tailed Prairie Dog (those seen by Lewis and Clark and occurring from Texas to Saskatchewan eastward from the Rocky Mountains to about 97° west longitude)

Cynomys ludovicianus arizonensis Mearns, 1890

Arizona Prairie Dog (occurs from southern New Mexico and Arizona to northern Mexico and west Texas)

Cynomys mexicanus Merriam, 1892

Mexican Prairie Dog (found in the vicinity of northern San Luis Potosi, Mexico)

Subgenus: Leucocrossuromys Hollister

Cynomys leucurus Merriam, 1890

White-tailed Prairie Dog (occurs in Wyoming, northwestern Colorado, and east-central Utah)

Cynomys parvidens Allen, 1905

Utah Prairie Dog (occurs in central Utah)

Cynomys gunnisoni gunnisoni (Baird, 1855)

Gunnison's Prairie Dog (occurs in central Colorado)

Cynomys gunnisoni zuniensis Hollister, 1916

Zuni Prairie Dog (found over southwestern Colorado, northwestern New Mexico, and northeastern Arizona)

Originally, the prairie dogs were classified in the same genus as the marmots; however, later they were given a separate generic grouping. Wade and Gilbert (1940) think they are closer to the Citellus evolutionary line than to that of the Marmota. Fossil evidence of prairie dogs occurs only in western North America and has been found in formations as old as Early Pliocene or Late Miocene (Green, 1960).

Certain morphological characteristics separate the three species studied. The black-tailed prairie dog has a tail averaging more than one-fifth the total body length with the distal third tipped in black. The jugal is thick, and the outer surface at the angle of the ascending ramus presents a broad, triangular surface. The posterior border of the inflected angle of the mandible is at an angle of approximately 45° to the axis of the jaw. The white-tailed and the Gunnison's prairie dog have white-tipped tails averaging less than one-fifth the total body length. The jugal is thin, and the outer surface at the angle of the

ascending ramus is only slightly thickened with the margin rounded and not distinctly triangular. The tail of the white-tailed prairie dog has the terminal half white without a dark center, whereas the tail of the Gunnison's prairie dog has the terminal half with a gray center, bordered and tipped with white (Warren, 1942; Hall and Kelson, 1959).

Social Organization

Black-tailed prairie dogs live in large groups called "towns." The towns are sometimes divided by topographic barriers into "wards," and the wards often contain one to several rigid social groupings of prairie dogs called "coteries." Each coterie usually contains a dominant male (King, 1955).

Little is known about the social organization of the other two species; however, Tileston and Lechleitner (1966) found that "clans" existed among the white-tailed prairie dogs rather than the "coteries" of the black-tailed prairie dogs. The "clan" seemed loosely organized and members of one clan often fed beside members of another clan. In this species the males are apparently unimportant in the social structure of the clan.

Sounds

Black-tailed Prairie Dogs. Many of the early travelers across the Great Plains commented about the sounds of the black-tailed prairie dogs. Thwaites (1959) mentions that William Clark after first seeing the animals on September 7,

1804, wrote that the prairie dogs sat erect and made a whistling noise, whereas Meriwether Lewis later noted in his journal that "their note being much that of the little toy dogs, their yelps are in quick succession and at each they give a motion to their tails upwards." Zebulon Pike (1811, reprinted 1889) noted that as he and his men approached the prairie dog towns they were "saluted" by the cries "uttered in a shrill and piercing manner." Maximilian (1843) thought their sound was "not a bark, but a shrill squeak."

Kendall (1844, reprinted 1929) on his journey to Santa Fe became very interested in the prairie dogs and their behaviors. When he neared the prairie dog town a few "dogs" were seen running for cover,

> their short, sharp yelps giving general alarm to the whole community. The first brief cry of danger from the outskirts was soon taken up in the center of the city, and now nothing was to be heard or seen in any direction but a barking, dashing, and scampering . . . each to his burrow. . . . Gradually a citizen would emerge from the entrance of his domicil, come out upon his observatory, perk his head cunningly, and then commence yelping somewhat after the manner of a young puppy--a quick jerk of the tail accompanying each yelp.

Brackenridge (1816), Merriam (1902), Bailey (1905), Hornaday (1914), Nelson (1918) and Soper (1938) elaborate further on their barking sounds and the associated behaviors. Merriam (1902) best summarizes it as follows:

> When a person approaches a dog town the animals see him a long way off and keep a close watch on his movements. As he comes nearer an alarm note is sounded, at which those away from their burrows rush to the entrance mounds, where they sit or stand erect, nervously twitching their tails and chattering or barking

> excitedly. If he continues to move toward them the excitement increases, and most of the animals on the near side of the colony plunge headlong into their burrows. Some withdraw more slowly, and for some time their heads and eyes may be seen peering up from the funnel-shaped openings of the mounds. Those near by are usually silent, while those at a little distance continue to scold and chatter. This chattering or barking, as it is usually called, can often be heard after the animals have gone down out of sight in their holes.

King (1955) describes the "warning bark" commonly heard by observers in the field as "a short, nasal yip which varies in intensity and frequency in accordance with the stimulus that produces it." He states the barks, which may continue as long as an hour, are usually too fast to count, with the first few sounds more frequent and penetrating than the latter. He concludes that the "warning barks" alert other animals which then must perceive the danger themselves before they respond further. Smith (1958) heard these barks continued for as long as one and a half hours. To him the bark is in two syllables--the first of "a higher pitch and shorter duration than the second."

A more effective warning call is one King (1955) terms the "hawk warning" which is given "faster, more intense, of higher pitch, and of shorter duration" than the "warning bark." It was given as eagles or hawks flew low overhead and when other sudden danger occurred. He found neighboring prairie dogs ran immediately to their burrows upon hearing this call. Smith (1958) thinks this call "consists of the same two syllables as the alarm bark, but because the second syllable maintains a high pitch the two barks are recognizably different." Seton (1926) reports that when one

prairie dog gave a "sharp 'squit-tuck'" they all ran for cover.

Another type of sound was described by Jillson (1871) who heard it given by his captive prairie dogs. He stated,

> They would quickly assume an erect posture, their fore paws hanging in front, their heads raised as high as possible, and with mouth turned upwards, give forth a sound . . . resembling the yelp of a domestic puppy. . . .

Wilder (1872) added that they "stiffen the whole trunk and 'rear' into a very comical attitude." Seton (1926) called this the prairie dog "song." He thought it was made by both sexes of adults "without obvious motive or visible cause." They would suddenly "rear up and with snout to the zenith, utter a soft 'Wee-oo,' then drop down again onto all four feet." Scheffer (1938) adds, "the act seems to be contagious, passing from one to the other, though there is no appearance of excitement or alarm." King (1955) reports the call is long and of two syllables. The first syllable occurs as the animal throws itself up, and the second on the way down, "as if the action provokes a deep, vocalized inspiration which is expired as the animal descends." He heard it given when the animals were standing, running, feeding, and even when part way down a burrow.

The purpose of such a "song" has been elusive. It has been speculated that it indicates anger (Anonymous, 1949). Anthony (1955) and Smith (1958) call it an "all clear" signal. King (1955) terms it the "territorial call"; yet he mentions that it may indicate all-is-well, a threat, victory,

dominance or a challenge. He thinks the spontaneous calls given at intervals while the animals feed can be accounted for because the individuals feel secure in their positions within the social group.

A short sound of the black-tailed prairie dog given during "excitement" had the principal frequencies of 5120 to 7232 cycles per second according to the work of Tembrock (1963).

In 1882, Brons reported an event he and his companions saw several times. One afternoon when passing through a prairie dog town in Kansas, the travelers "heard a most unusual noise and stir (in the town) as though they were holding a bellicose council." The prairie dogs were collected around a burrow entrance into which they were vigorously scraping dirt. Upon investigating, Brons and his party found the prairie dogs were trying to "entomb" a large rattlesnake in the burrow. However, King (1955) found the prairie dogs he observed never barked at snakes.

To Seton (1926), the sound "skr-skirr" indicated "fighting or menace." In addition, he heard "a number of squeaks and chatters that were used in conversation or in squabbling."

The "disputing churr" of King (1955) was made among disputing prairie dogs. It was often "preceded or broken by little barks." He found the "persecuted member" of the dispute was usually the vocalizer.

Anthony (1955) distinguished a "low 'chirr' or fighting bark" which occurred "during aggressive contacts" and was often followed by tooth chattering.

Squire (1925) heard tooth chattering sounds emitted from a pet prairie dog when it was "really angry and ready to bite someone." Griffin (1940) made a similar report; however, Cates (1927) only observed the tooth chatter when it appeared to be playing a role in tooth sharpening. King (1955) noted that "tooth chattering, often accompanied by a soft, high-pitched whistle is a characteristic vocalization of prairie dogs in a dispute," and was given by both individuals. Smith (1958) occasionally heard "low, muffled barks" while the teeth chattered. He heard the chatter from sleeping prairie dogs as well as from "dogs" being groomed.

King (1955) found that prairie dogs released from traps "often ran down a burrow while giving a quick chuckling bark." Tileston (1961) made similar observations and heard the "chuckle" occasionally while he walked through his study area.

A "scream" has been reported by King (1955) and Smith (1958). They agree that it is given as a fear reaction by pups being handled.

"Snarling" also has been reported. King (1955) heard it from prairie dogs being handled while marking them. Smith (1958) heard "a low-pitched snarl" emitted by prairie dogs prior to chasing away thirteen-lined ground squirrels.

Tileston (1961) heard a "growl" from prairie dogs he retained in live-traps.

King (1955) mentions two additional sounds not otherwise reported. The first is the "defense bark" which is a slow, high-pitched call. "Rather than a series of barks, it is a single bark uttered at intervals." It was given by adult females or young defending their present territory against aggressors, such as the dominant male of another coterie. The other sound is the "muffled bark" much like the "defense bark," but softer, as if made with the mouth closed. It occurred in disputes between two females protecting their nesting areas.

Cahalane (1947) claims there is "much loud talk" during the breeding season.

Smith (1958) frequently heard captive prairie dogs "bark in their sleep," but he could never hear any sounds coming from the burrows in the wild at night.

Johnson (1927) found that laboratory-reared young could "bark" at about 40 days after birth--a few days after their eyes opened. King (1955) found the wild pups barked frequently two to three weeks after they first appeared above ground.

From the literature about the sounds of the black-tailed prairie dog, it can be surmised that these prairie dogs emit at least two types of alarm barks above ground and an alarm "chuckle" within the burrow; a "song," "territorial call," or "all clear" vocalization; an "unusual noise" when challenging a snake; a "skr-skirr," "disputing churr," "growl," "low 'chirr,'" or various types of barks when

disputing or fighting; and "tooth chatters," "screams," or "snarls" when threatening or fearful.

White-tailed Prairie Dogs. The literature about the sounds of the white-tailed prairie dog is meager. Cary (1911) says, "the usual note is a peculiar querulous cry very unlike the short, sharp bark of ludovicianus." He mentions that, "chattering alarm notes also are occasionally heard as one walks through a colony."

Tileston (1961) noted four different sounds as the "warning bark," the "all clear," the "growl," and the "chuckle." The "warning bark" consists of a "series of sharp, mechanical sounding 'churcks'" which are spaced at approximately half-second intervals. As the danger approached, "the intensity and rapidity of the warning bark increased." When the number of sounds increased to "three or four per second, many of the prairie dogs ran to their burrows," and at four or five per second there was "a mass rush to the burrows." No particular postures were associated with these barks.

The "all clear" call, Tileston heard, "had a musical quality that closely resembled a flicker (Colaptes auratus) melodic call." It consisted of five components. The first "slurred downward and was followed by four notes of equal tone" resembling "chtaa-chaa-chaa-chaa-chaa." When this call was given it continued "through a greater portion of the population."

The "growl" was a "throaty growl resembling that of a dog." It was "often climaxed by a squeal and was accompanied by a bristling of the hair on the tail." It was given by captured individuals in live-traps.

The "chuckle," Tileston explains, was made up of "a soft 'chucka, chucka, chucka...' rapidly slurred together." It was given by prairie dogs recently released into their burrows from live-traps.

From the literature about the sounds of the white-tailed prairie dog, it can be surmised that these prairie dogs emit a "warning bark" and "chuckle" when alarmed, a "growl" when threatening or fearful, and an "all clear" call.

Gunnison's Prairie Dogs. The literature on the sounds of the Gunnison's prairie dog is also sparse. Burnett and McCampbell (1926) observed that a badger or domestic dog caused the Zuni prairie dogs to bark from their mounds or burrow entrances. Longhurst (1944) noted that as soon as "one dog gave a shrill warning bark every other prairie dog within hearing immediately sat up to locate the source of disturbance." Scheffer (1947) was aware of a difference between the sound of the Zuni subspecies of prairie dog and the black-tailed prairie dog. He thought maybe it was "only a local dialect but distinctively different." He described it as "a short 'bark' with something of a metallic timbre."

The alarm bark has been reported for the Gunnison's prairie dog; however, additional sounds of similar function

to those of the other two species have not been mentioned in the literature. Black-tailed and white-tailed prairie dogs apparently emit more than one type of alarm sound, an "all clear" call, and a "growl." According to previous authors the black-tailed prairie dog, in addition, produces "snarls," "screams," "tooth chatters," and one or more types of disputing or fighting sounds.

Other Ground Dwelling Sciurids. Few detailed descriptions have been made of the sounds of species closely related to the prairie dogs. Seton (1929) compiled numerous reports of sounds and the associated behaviors of sciurids. Linsdale (1946) carefully reported on the sounds of the California ground squirrel (Citellus beecheyi). This species has an alarm call consisting of a mono- or bi-syllabic, sharp chirp followed by a short, rapid chatter. In addition, it often gives a tooth chatter; a growl or a diminuendo chatter when intimidated; a single, high-pitched bark before entering a burrow; a loud or quiet mono- or bi-syllabic, continuous chirping when alerted or slightly uneasy; and several slight variations of these calls.

Balph and Stokes (1962) found that sexually active male Uinta ground squirrels (Citellus armatus) emit "a series of 2-4 charp, 'chirp' sounds given at 0.1-0.2 second intervals at a frequency of 4,000-5,000 cycles per second." A series may be "repeated every 5-15 seconds for as long as 30 minutes." Balph and Balph (1964) reported that of the

five types of calls given by Uinta ground squirrels in the wild, four were used as a threat and one for alarm.

Tembrock (1963) reported that the warning call of the common souslik (Citellus citellus) is principally at 4304-6080 cycles per second.

In 1966, I reported that the warning whistles of the hoary marmot (Marmota caligata) had a duration of 0.564 second and fundamental tone at 3,200 cycles per second; whereas the whistles of the yellow-bellied marmot (Marmota flaviventris) were 0.037 second long and the fundamental tone up to 800 cycles per second higher than the call of the hoary marmot. The yellow-bellied marmot emits tooth chattering and an accelerating whistle chatter when threatening; screams when fearful or in play; a single, loud whistle before entering its burrow; quiet, irregular whistles when apprehensive; "barking whistles" while running; and either slow or rapid, continuous warning whistles when alert or alarmed (Waring, 1966).

Bio-acoustical Techniques

In 1945, Potter introduced to biologists a new instrument, the sound spectrograph, which, along with the tape recorder, revolutionized studies of animal sounds. The sound spectrograph produces a picture (sound spectrogram) of a sound on a special piece of paper. From the sound spectrogram one can estimate the duration of the sound, the relative intensity, frequency components, and the harmonic components (harmonic structure) of the sound. Stein

(1963) mentioned the importance of calibrating the individual sound spectrograph one is using for analysis. The most helpful paper on sound spectrographic analysis was written by Davis (1964). He suggested techniques which can be used to double-check analyses in order to reduce misinterpretations.

METHODS AND MATERIALS

Observations and tape recordings were made in the field in Colorado and Wyoming, although whenever possible, additional data were obtained from captive prairie dogs. The research was begun in February, 1964 and continued until June, 1966. One individual of each species was held captive in outdoor cages for later study. Captive prairie dogs of Dr. R. R. Lechleitner were studied also.

Study Areas

Black-tailed Prairie Dogs. These animals were studied primarily 4 miles southwest of Fort Collins, Larimer County, Colorado, at an elevation of 5,300 feet (SW 1/4 of Section 16, T7N, R69W, 6PM). The study area consisted of a ward separated from the main prairie dog town by a low ridge arcing around the area from the north and east. A high "hogback" ridge of the foothills is on the west side of the study area. The south exposure is relatively level. As many as 16 prairie dogs occupied the ward under study and divided it into two coteries. Observations were made from a vantage point on the ridge top northeast of the ward and also from a burlap blind located within the study area. This area was visited 111 days totaling about 285 hours

during all seasons from April, 1964 to June, 1966. The potential predators seen in this area were man, coyotes, domestic dogs, eagles, hawks, and a bull snake. The captive black-tailed prairie dog, a female, was obtained here as a two-month-old pup.

Another area of study for the black-tailed prairie dogs was located a mile northeast of Timnath, Larimer County, Colorado, at an elevation of 4,900 feet (SE 1/4 of Section 26, T7N, R68W, 6PM). These prairie dogs were at the base of a low hill on the north and west sides. They were studied 7 days for a total of 10 hours from February, 1964 through April, 1964.

White-tailed Prairie Dogs. These animals were studied first in the Laramie River Valley beside Jimmy Creek, 7 miles north of Glendevey, Larimer County, Colorado, at an elevation of 7,950 feet (SE 1/4 of Section 17, T11N, R76W, 6PM). The burrows were on a grassy rise of ground overlooking the creek. This area was studied only 4 days for a total of 15 hours in July, 1964. I observed from a cloth blind. The captive white-tailed prairie dog, a full-grown male, was trapped here.

Later the white-tailed prairie dogs were studied at a more readily accessible site 3 miles west of Chimney Rock (Camel Rock) along the Colorado-Wyoming line in Larimer County, Colorado, at an elevation of 7,800 feet (NW 1/4 of Section 21, T12N, R75W, 6PM). Their burrows were on a gradual slope facing south and west. The area was visited 15 days for a total of 80 hours from July, 1964 through

August, 1965. Observations were made from cloth blinds and from a deserted shed. Potential predators observed were man, eagles, badgers, and coyotes.

Finally, in order to study these prairie dogs during the months of spring snowfall, a study area was located within reasonable hiking distance from roads plowed free of snow. The colony was one mile north of Tie Siding, Albany County, Wyoming, at an elevation of 7,750 feet (NE 1/4 of Section 18, T13N, R72W, 6PM). The studied portion of this large group of prairie dogs surrounded a shed and board fence. The latter formed a convenient blind. These animals were studied for 6 days for a total of 46 hours from March, 1966 through April, 1966. Domestic dogs and eagles were the potential predators observed.

Gunnison's Prairie Dogs. These prairie dogs were first studied near the type locality of Cochetopa Pass about five miles south of Cochetopa Dome in Saguache County, Colorado, at an elevation of 9,400 feet (SW 1/4 of Section 24 and the NW 1/4 of Section 25, T45N, R2E, New Mexico PM). The study area is on the edge of the open valley floor on an east facing slope. Observations were made from a cloth blind for 4 days for 25 hours in July, 1964. The potential predators found to be present were coyotes and eagles. Sylvatic plague (Pasteurella pestis) was also present.

As the animals in the above mentioned prairie dog colony were beginning to die from sylvatic plague, another group was discovered at the base of Black Mountain, 8 miles

south of Fairplay, Park County, Colorado, at an elevation of 9,950 feet (NE 1/4 of Section 17, T11S, R77W, 6PM). The area is on the west side of the mountain. This group was observed from August, 1964 through August, 1965, on 15 days for a total of 53 hours. Cloth blinds were used. Badgers, man, bobcats, eagles, and hawks were the major potential predators known present at the time of study. Sylvatic plague was discovered in this colony by Dr. R. R. Lechleitner and J. P. Fitzgerald in September, 1965. The captive prairie dog of this species held for subsequent study was trapped here in 1964. It was a female of about three months of age when caught.

During the spring of 1966, a third group was studied. The colony occupied both sides of the South Platte River in Douglas and Jefferson Counties. The study plot is 3 miles downstream from Deckers in Douglas County, Colorado, at an elevation of 6,350 feet (SW 1/4 of Section 10, T9S, R70W, 6PM). Observations were made from a car on 4 days for a total of 28 hours from March, 1966 through April, 1966. Eagles and man were the known predators.

Equipment

The sounds of the prairie dogs were recorded on an Amplifier Corporation of America model W-610-EV TransMagnemite battery-operated tape recorder. A tape speed of 15 inches per second was used. At this speed the recorder had a frequency response from 100 to 12,000 cycles per second ±2.5 db (Fig. 1). One mil, acetate base Scotch recording

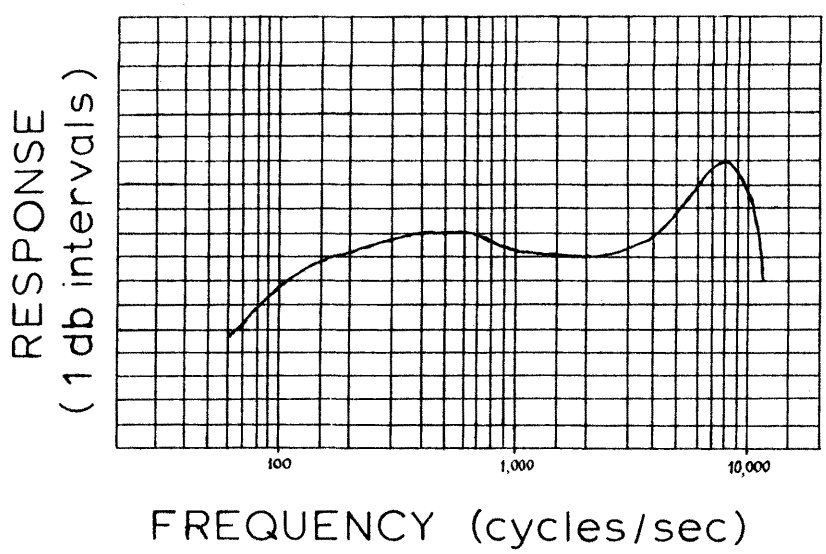

Fig. 1. Recording response of the TransMagnemite tape recorder.

tape was used. An Electro-Voice model 644 "Sound Spot" unidirectional microphone was used; however, I did try to supplement with both 24 and 39 inch aluminum parabolas and a model 666 Electro-Voice dynamic microphone. Since parabolas fail to reflect lower frequencies adequately, I discontinued using them in order to maximize the frequency response I could record. The "Sound Spot" microphone was placed on an Electro-Voice model 423A stand. Headphones were used for monitoring while recording.

A 16mm Bolex H16 reflex movie camera with 25mm and 150mm lenses was used to film many behaviors of the prairie dogs. Also used for filming was a 35mm Hexacon single lens reflex, still camera with a 350-650mm variable lens.

Both 20 and 25 power spotting scopes and 7 power binoculars aided in making observations.

Double door, 6 x 6 x 24 inches National Live Traps were used for trapping the prairie dogs.

Other field instruments utilized were a hand-held Dwyer Wind Meter, a Taylor Instrument Company pocket thermometer, and a Minerva Watch Company stopwatch.

In the laboratory, the tape recordings were analyzed on a sound spectrograph (Kay Electric Company model 661-A Sona-Graph). Type "B" Sona-Graph paper was used. The time scale was calculated and the frequency ordinate determined for the machine used. The original recordings were transferred to the Sona-Graph from an Ampex PR-10 tape recorder. A Hewlett-Packard model 350D attenuator was used in conjunction with the PR-10 recorder.

The working efficiency of my tape recorder was tested, using the following instruments: Hewlett-Packard model 200CD Wide Range Oscillator, Hewlett-Packard model 521A Electronic Counter, Ballantine model 300D Vacuum Tube Voltmeter, and Hewlett-Packard Attenuator Set. The recording characteristics determined for the recorder are shown in Fig. 1. A constant voltage of 0.00015 volts rms at a minimum of -74 dbm (12 dbm above the manufacturer's minimum sensitivity rating) was fed into the microphone input of the recorder during the calibration. The volume control of the recorder was set approximately at mid-range. Pure tones verified by the decade counter were tape-recorded on the recorder then replayed through the voltmeter and again through the decade counter. The speed of the recorder was extremely accurate. For example, pure tones of 100, 1000, 4001 cycles per second were replayed at 100, 999, and 4001 cycles per second, respectively.

The microphone (Electro-Voice model 644) used for the field recordings is claimed by the manufacturer to have a level response from 60 to 10,000 cycles per second. I was unable to verify this due to the lack of the necessary equipment.

Techniques

I strived to make the times of observation representative of all daylight hours during the seasons each species was active above ground. The tape-recording equipment was set up to record during all observations when environmental

conditions allowed it. It was not exposed to heavy rain or snow, nor was it usually set up when the wind constantly exceeded 20 mph. The recorder was turned on only when an animal began vocalizing or when I thought the animals might soon produce sounds. The microphone was pointed toward the sound source with the stand usually on the ground. Thus, the microphone was at an elevation of 9 inches above the surface of the ground.

After making a tape recording, I completed a data form describing the situation existing for that sound sequence (e.g., the environmental conditions, time, date, and instrument settings). Meanwhile, I kept a continuous journal and completed other forms about the activities of the subjects, other animals nearby, weather data, and also described sounds not tape-recorded. For ease in taking notes, I made a map of the study areas and divided each area by burrow groupings or into a pattern of grids which could then be referred to in my notes by initials.

Generally, the most favorable tape-recording conditions occurred during the early morning hours before the wind and background sounds increased in intensity. Poor signal-to-noise ratio was only tolerated and never fully overcome due to wind and other background noise plus the, often great, subject-to-microphone distances.

Photographs were taken to supplement my observations of postures and movements. I was able to study behaviors again in the laboratory by reviewing the films.

Once I entered a blind, I would remain there the entire period of observation for that day, although some days I had separate morning and afternoon observation periods. The prairie dogs would commonly resume activity above ground 15 minutes after I entered the blind if my arrival caused them to retreat underground. My 197 observation periods ranged in duration from 15 minutes to 14 hours and 45 minutes with a mean of 2 hours and 45 minutes.

I captured many of the subjects and marked them with either Nyanzol "A" or "D" dye. The identifying pattern of marks were placed so the animal could be identified from either side.

Pups were studied after they first came above ground at approximately seven weeks of age.

In the laboratory, I made sound spectrograms of the clearest portions of the prairie dog sounds on each recording. Wide band, HS, and original speed analysis was used first. Narrow band and half-speed spectrograms were made for further interpretation when needed. The frequencies analyzed were kept within the limitations and calibrations of the equipment; the range of 100-8000 cycles per second was investigated. The time scale was determined to be 1mm per 0.0076 second at the original speed.

A mean of the time characteristics of all spectrographically similar sounds was determined along with the standard deviation and 95% confidence limits. Frequencies could not be measured adequately to generalize similarly

about them. Actual intensity could not be determined since the animals would not vocalize in audiometric testing chambers. Relative intensity can be estimated from the shading of the sound spectrograms.

The original tape recordings were put on the Ampex PR-10 recorder and transferred to the Sona-Graph at full or one-half original speed from Channel A via a high impedance cable directly into the Sona-Graph input. When the attenuator was needed, a low impedance cable led from Channel A into the attenuator input. A high impedance overload plug preceded the low impedance attenuator output cable leading to the Sona-Graph input.

RESULTS

I feel it is necessary to rename some of the sounds already described by other workers. My approach will be to consistently name the sounds by terms which refer to the physical, rather than the functional, characteristics of the sounds. Naming the sounds by their possible function (e.g., territorial call) only stereotypes the sound to one meaning, whereas the sound might have different functions under different ecological conditions as recognized by Collias (1960) and Waring (1966). Because of the possibility of more than one function per sound, names, such as "warning barks," "all clear call," and "territorial call," have been dropped from the following scheme.

The term "noise" will refer to sounds of multiple frequencies lacking distinct overtones on the sound spectrograms. The "fundamental" of a sound will be used to refer to the first harmonic or lowest frequency component consistently visible on the sound spectrograms of multi-overtone sounds. The "dominant" frequencies or harmonics are those with the greatest amplitude. By the "function" of a sound, I refer to the purpose or evolutionary advantage for the sound being emitted under certain circumstances (e.g., a sound functioning to warn others of danger).

I detected no difference in the sound repertoire of the prairie dogs between different study areas of the same species.

Sounds of Black-tailed Prairie Dogs

Repetitious Barks. The sounds commonly heard by any visitor to a black-tailed prairie dog town are the "repetitious barks." Each sound is a short vocalization which is repeated over and over again. The interval between sounds can vary from one situation to another, but it is shortest during the sudden or close approach of danger. In every instance observed, the vocalizing animal was alerted and remained so while producing the call. Nearby prairie dogs became alert as soon as the "repetitious barks" began; however, what they did next depended upon the situation. If the vocalizer began the call and ran rapidly for its mound, the neighboring prairie dogs ran for their mounds before looking any further. If a prairie dog were some distance from its mound when alerted and began calling without running for cover, nearby individuals looked for the cause of the alarm themselves and then returned to their previous activities if they saw no cause for alarm. If the vocalizer was already on its mound the reaction of the neighboring individuals varied from running for their mounds to alerting temporarily where they were as the sounds began. Prairie dogs that had wandered far from their burrows often ran back to their mounds whenever the "repetitious barks" began.

The "repetitious barks" can be of one or two syllables (Figs. 2A and 2B). Often it was difficult to determine the syllabic number of the sounds (Fig. 2C); therefore, they have been grouped as one type of sound. There seems to be no uniform difference in the function or purpose between the two extremes. However, frequently under extreme alarm the prairie dogs gave the more obvious two syllable sounds. The first syllable was always of equal frequency or higher than that of the second. Specific characteristics of these sounds are listed in Table 1.

TABLE 1. Characteristics of the "repetitious barks" of the black-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Individual sound duration (sec)	0.0304-0.1216	157	0.0171	0.0674 ±0.0027
Intersound interval (sec)	0.1520-1.4668	121	0.0610	0.3959 ±0.0109

Other characteristics--

Fundamental:	
syllable one	1500-2300 cycles/sec
syllable two	1400-2200 cycles/sec
Interharmonic interval:	1400-2300 cycles/sec
Dominant frequencies:	second harmonic
Relative intensity:	greatest mid-syllable

After they were two months old, black-tailed prairie dogs of either sex gave these barks for prolonged periods of

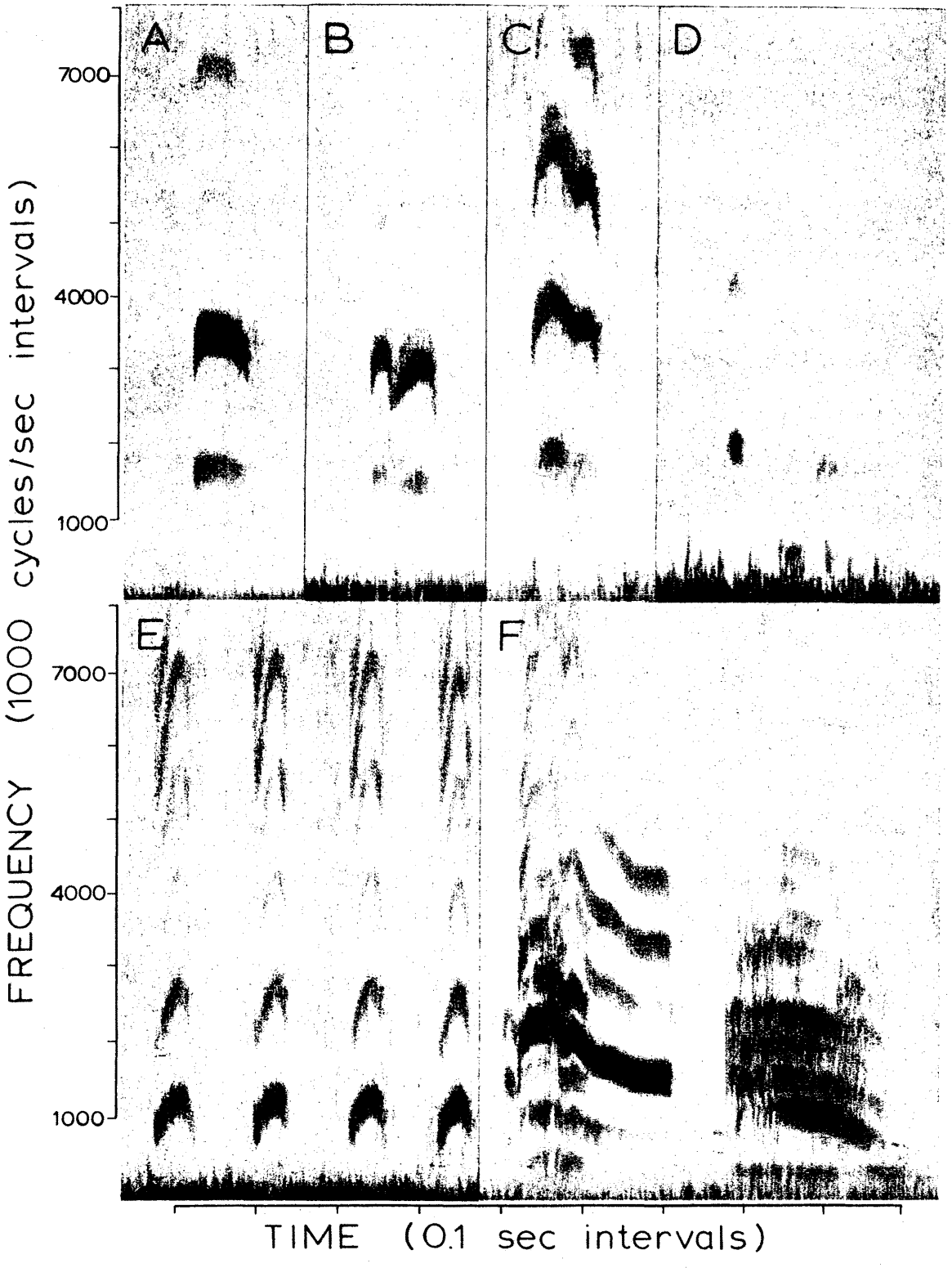

Fig. 2. Sound spectrograms of sounds of the black-tailed prairie dog. A. Mono-syllable Repetitious Bark. B. Bi-syllable Repetitious Bark. C. Indefinite-syllable Repetitious Bark. D. Chuckle. E. Chatter Barks. F. Wee-oo Song.

time whenever alarmed or disturbed by a strange object in the vicinity. The vocalizing posture was usually sitting up on their haunches or standing on all four legs; however, they were observed to stand up on their hind legs, sit, crouch, and even lie prone while vocalizing. The head was held erect, facing commonly to one side of the intruder and looking at it with monocular vision. The tail commonly was flicked in a vertical plane with each bark. Tail flicking was done frequently by nearby prairie dogs when alert but not vocalizing. As the intruder neared, the prairie dogs moved into the crater of their mounds and peered over the rim, so that only their heads and flicking tails showed as they continued to bark.

If there was sudden or imminent danger, more than one prairie dog in the neighborhood sometimes gave the barks; however, commonly only the first individual to see the intruder gave the barks and continued until the danger was gone or the intruder no longer caused a fear response.

Occasionally, a seemingly uneasy black-tailed prairie dog gave these barks when there was no disturbance apparent to this observer. The animal sometimes continued the sounds with only a few short pauses for close to an hour, although the call was normally given for less than 30 minutes. The intensity and intersound intervals became variable during the long barking sequences.

Black-tailed prairie dogs gave these sounds with the mouth only partially opened and showed contraction of abdominal muscles with each bark.

Chuckle. The barks emitted by male and female black-tailed prairie dogs while in, or as they ran down, their burrows sounded like a "chuckle" to me and other observers. The barks emitted by the prairie dog were a brief series of the "repetitious barks"; however, the barks sounded different from the "repetitious barks" because the higher frequencies were lost in the burrow system and the fundamental became the more dominant audible frequency (Fig. 2D). If the animal were running, the duration of each bark and intersound interval were often irregular. These sounds were heard commonly after a prairie dog was released from a live-trap and ran into its burrow. During these instances the intersound interval was usually short since the individual was highly alarmed.

Chatter Barks. Sometimes the black-tailed prairie dogs emitted barks so rapidly that the sound was like a barking chatter; hence, I shall call them "chatter barks" (Fig. 2E). These sounds were often given by an adult female which had retreated from a male during the reproductive season. The sounds were directed to the male if he continued to approach her. Prairie dogs before and after chasing another prairie dog sometimes made these sounds. One August, some pups made the "chatter barks" when they appeared fearful of an adult male. See Table 2 for further details.

TABLE 2. Characteristics of the "chatter barks" of the black-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Individual sound duration (sec)	0.0076-0.0684	77	0.0141	0.0270 ±0.0032
Intersound interval (sec)	0.0228-0.5396	70	0.0965	0.1241 ±0.0230

Other characteristics--

Fundamental:	900-1350 cycles/sec
Interharmonic interval:	900-1350 cycles/sec
Dominant frequencies:	1st, 2nd, or 3rd harmonic
Relative intensity:	greatest mid-duration

Wee-oo Song. The most unusual of all the vocalizations of the black-tailed prairie dogs was the two syllable call which sounded like "wee-oo" (Fig. 2F). The prairie dogs made the first syllable as they extended their heads up and back and raised onto their hind legs with their backs arched. The forelegs were extended out and upward above the horizontal. Finally, the animals were in a quasi-opisthotonos position for a fraction of a second before they relaxed and came down to stand on all four feet. On the way down, they emitted the second syllable of the "song." The whole act occurred rapidly. See Table 3 for further characteristics.

The situations where the "wee-oo song" was given varied greatly. Some black-tailed prairie dogs periodically gave it as they paused during feeding or from their resting

TABLE 3. Characteristics of the "wee-oo song" of the black-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Duration (sec)	0.0912-	11	0.0918	0.2393
syllable one	0.3952			±0.0616
syllable two	0.0760-	11	0.0912	0.2273
	0.3496			±0.0612
Intersyllable	0.0076-	11	0.1113	0.1274
interval (sec)	0.3800			±0.0747

Other characteristics--

Fundamental:	
syllable one	500-1800 cycles/sec; may undulate
syllable two	400-2200 cycles/sec; may undulate
Interharmonic interval:	
syllable one	500-1800 cycles/sec
syllable two	400-2200 cycles/sec
Dominant frequencies:	lower four harmonics
Relative intensity:	greatest in early part of each syllable usually

place on the mounds. Two individuals sometimes suddenly stopped and gave the "song" after one had been chasing the other. Often they gave the sounds soon after first peeking out of their burrow entrances early in the morning. They frequently gave the call immediately after a dive by an aerial predator. Captive prairie dogs once habituated to their new surroundings gave the "wee-oo song" occasionally after hearing a human cough. My pet prairie dog gave these sounds whenever our domestic dog shook itself and rattled the metal tags attached to its collar. Once a male pup made

five of these "songs" within its burrow immediately after being released from several days in captivity.

Raspy Purr. A captive female black-tailed prairie dog began making "raspy purring" sounds at one year of age when it was scratched by a human being. Pet prairie dogs seem to appreciate having their body rubbed and scratched. The sounds were rather short and low in amplitude and pitch (Fig. 3A). Often the "wee-oo song" followed the "purr." Further details are listed in Table 4.

TABLE 4. Characteristics of the "raspy purr" of the black-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean
Duration (sec)	0.0836-0.2356	3	0.1416	0.1571

Other characteristics--

Frequency range:	primarily below 700 cycles/sec; sounds occur in pulsations
Harmonic structure:	lacking
Resonance:	lacking
Relative intensity:	greatest below 500 cycles/sec

Epimeletic grooming was observed only twice in my study areas; I could not detect any sounds on either occasion. Therefore, I am unable to say whether the "raspy" purr" occurs in the wild.

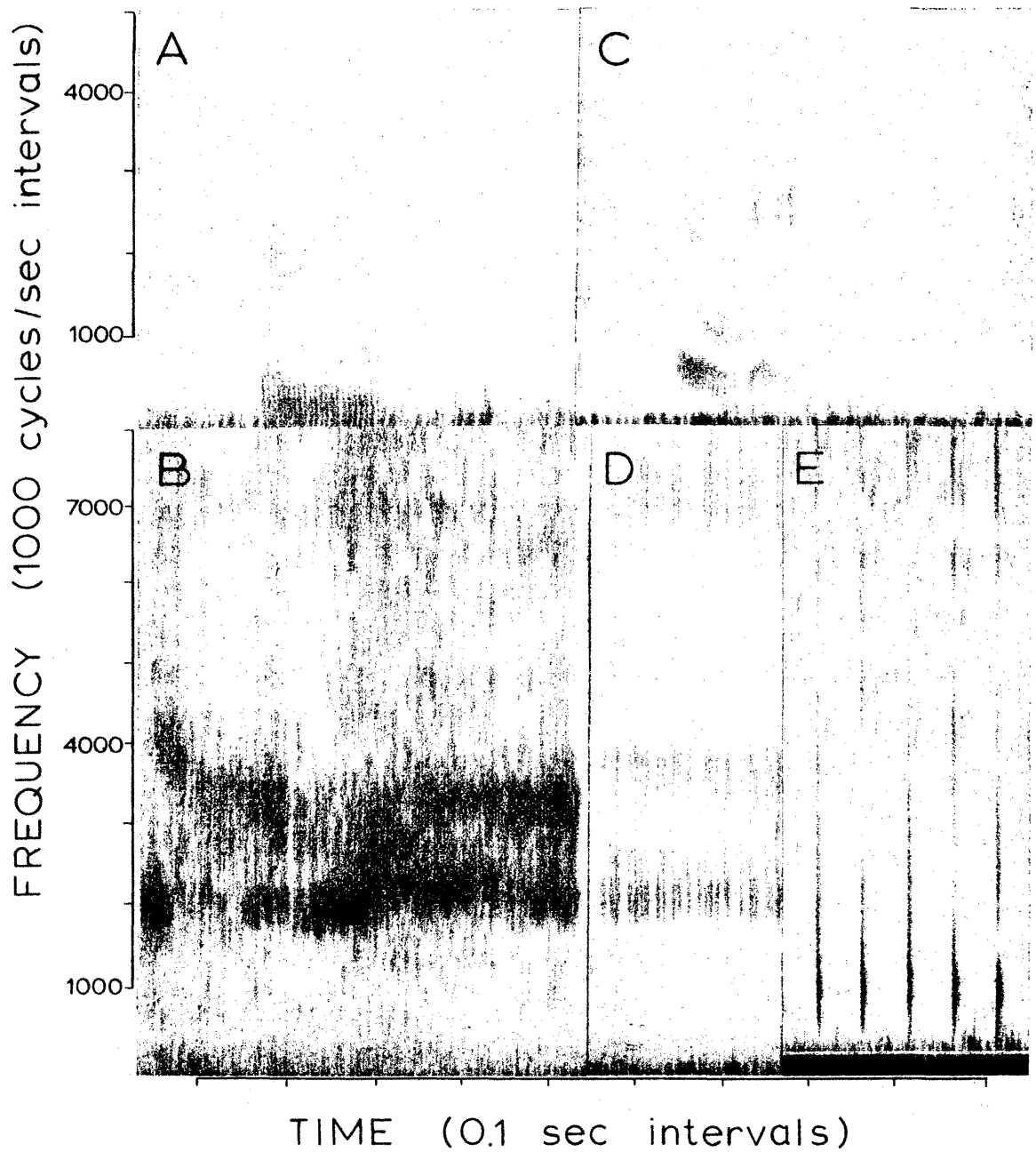

Fig. 3. Sound spectrograms of sounds of the black-tailed prairie dog. A. Raspy Purr. B. Snarl. C. Scream. D. Growl. E. Tooth Chatter.

Snarl. When male and female black-tailed prairie dogs were threatening or attempting to bite a menace close by, they gave a "snarl" sound. Prairie dogs in a live-trap often "snarled" when a hand was repeatedly waved past the side of the trap. Adults, especially, gave these sounds and resumed a posture of sitting, mouth opened, ready to bite, and often raised one foreleg. Some individuals lay partially on one side as they "snarled" at an overhead object. Free ranging prairie dogs have been heard giving a brief "snarl" when threatening another that persisted in attempting to mount or paw the unreceptive individual. The vocalizer often feigned an attack. A prairie dog held in the talons of a hawk repeatedly "snarled" as it wiggled and fought to free itself.

The "snarl" is characterized by being a prolonged noise with resonance bands. Often some undulation in pitch occurs. For further details refer to Table 5 and Fig. 3B.

TABLE 5. Characteristics of the "snarl" of the black-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Duration (sec)	0.2508-0.4940	10	0.0953	0.3344 ±0.0682

Other characteristics--

Frequency range:	less than 100 to over 8000 cycles/sec
Harmonic structure:	lacking
Resonance:	variable around 700, 2000, and 3500 cycles/sec
Relative intensity:	varies throughout duration

Scream. Immediately following a "snarl," captive black-tailed prairie dogs on a few occasions made a low amplitude, musical, abbreviated "scream." As can be seen from the sound spectrogram (Fig. 3C), the sound has harmonics and is primarily of low frequencies. See Table 6 for more details; however, the data presented in this table are from only one individual. I would expect the duration and even the pitch to vary somewhat with individuals and circumstances.

TABLE 6. Characteristics of the "scream" of the black-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Duration (sec)	0.0912-0.1292	5	0.0156	0.1155 ±0.0193

Other characteristics--

Fundamental:	300-1000 cycles/sec
Interovertone interval:	300-1000 cycles/sec
Dominant frequencies:	1st, 3rd, or 4th harmonics
Relative intensity:	varies throughout duration

Growl. Another sound of black-tailed prairie dogs often associated with the "snarls," but different on the sound spectrograms and to the human ear, is the "growl." This also was given by both sexes and by captive or free ranging individuals when the menace was not too close or too annoying. For example, when a hand was passed directly over a captive prairie dog, "snarls" were given, but when the hand

was moved away or was not yet close to the captive, "growls" were commonly heard. When a prairie dog appeared annoyed by the presence of another nearby, it occasionally made the "growls." Quiet "chatter barks" sometimes followed.

See Fig. 3D and Table 7 for characteristics of the "growls" recorded. It should be noticed that the "growl" is pulsed and has no undulation of the resonance bands.

TABLE 7. Characteristics of the "growl" of the black-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Duration (sec)	0.0684-0.7752	14	0.2612	0.3127 ±0.1509

Other characteristics--

Frequency range:	less than 100 to over 8000 cycles/sec in rapid pulsations
Harmonic structure:	lacking
Resonance:	about 2000 and 3700 cycles/sec
Relative intensity:	greatest at resonance and at each pulsation

Tooth Chatter. The most audible nonvocal sound the black-tailed prairie dogs made was the "tooth chatter." By anteroposterior and posteroanterior movements of the lower jaw, the prairie dog clicked the tips of the lower incisors against the upper incisors. The result was a rapid clicking or chattering sound.

Both sexes produced these sounds; however, during the reproductive season captive males especially produced the "tooth chatter" toward their usual human handlers and were hostile toward them. Occasionally a pet prairie dog being scratched emitted the "tooth chatters," although the chatters were barely audible.

Each clicking sound is an extremely brief, wide frequency range noise, and, as shown in Fig. 3E, there is resonance in the lower frequencies possibly due to the oral cavity. For further details refer to Table 8.

TABLE 8. Characteristics of the "tooth chatter" of the black-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Intersound interval (sec)	0.0304-0.0532	136	0.0046	0.0412 ±0.0005

Other characteristics--

Duration:	0.0076 sec or less
Harmonic structure:	lacking
Frequency range:	less than 100 to over 8000 cycles/sec
Resonance:	about 800 cycles/sec
Relative intensity:	greatest below 1500 cycles/sec

These sounds could only be heard when the animal was close to the blind. Sometimes the subject was sitting alone on the mound; other times the sound was given as two prairie dogs were alert and close together. I never was certain that I heard it during disputes between two prairie dogs.

Other Sounds. Some other sounds from black-tailed prairie dogs were heard only on a few occasions, but tape-recording them was unsuccessful. Thus, I am not able to present evidence that they are truly different sounds. One of these was a single sound which seemed to be the first syllable of the "wee-oo song." It was produced especially by pups during peaceful situations.

On a few occasions single barks were heard which alerted nearby prairie dogs. These sounded identical to components of the "repetitious barks."

One September morning a young prairie dog appeared with one or both hind legs lame. I watched it groom its left hind foot. Then it wandered on, feeding, and attempted to keep its weight off that foot. Suddenly it shrieked, seemingly in pain, as it darted 3 feet away. The vocalization was a three syllable, high-pitched scream lasting one second. Possibly it reinjured itself, for it groomed both hind legs and then limped away. The sounds seemed like more prolonged forms of the "scream" mentioned earlier.

Black-tailed prairie dogs of both sexes held around the back of the neck sometimes produced a grunting or quiet coughing noise. It was of low intensity and varied from one individual to the next in pitch and duration. In general, it was low-pitched and short. The prairie dogs seemed in discomfort due to the constriction by my hand.

Black-tailed prairie dogs annoyed by others of their species but not directing any attack toward them sometimes

made one to three squeaking or chirping sounds. This seeming scolding note sounded like rapidly saying the word "cheek." This may have been a short version of the "chatter barks."

In summary, the sounds emitted by free-ranging or captive prairie dogs were: the repeated barks called "repetitious barks"; the "chuckle" which consists of barks emitted within the burrow; the rapidly repeated "chatter barks"; the bi-syllabic, complex "wee-oo song"; the pulsated "growl"; the nonvocal "tooth chatter"; and a grunting sound.

Sounds of White-tailed Prairie Dogs

Vocal Chatter. The white-tailed prairie dogs produced a very short, vocal sound which was repeated so rapidly it became a chattering sound. Pups after a few days above ground and the older male and female prairie dogs emitted this series of sounds whenever they were alarmed. Immediately the neighboring prairie dogs became alert and looked for the cause of the alarm. If they saw others run for their mounds and burrow entrances or were some distance from safety themselves, they ran for their burrow entrances. After looking about, if they did not see any danger, they soon returned to their previous activities, even when the vocalizer continued to emit the sounds. Occasionally, seemingly uneasy prairie dogs gave the "vocal chatter" when to this observer there was no cause for alarm. The tail was motionless and down during alarm behavior.

Unlike the functionally homologous "repetitious barks" of the black-tailed prairie dogs, the "vocal chatter" was not given continuously but in sets of about 30 sounds each. After one set, there was a pause of about 1-15 seconds then another set of sounds was given. As can be seen from Table 9, there is only a slight variation in the sound durations and in the intersound intervals. The first sounds of each set were the clearest for harmonic structure; later sounds became more noisy (Fig. 4A).

TABLE 9. Characteristics of the "vocal chatter" of the white-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Individual sound duration (sec)	0.0152-0.0380	181	0.0047	0.0226 ±0.0007
Intersound interval (sec)	0.0760-0.1748	168	0.0187	0.1147 ±0.0028

Other characteristics--

Fundamental:	2000-2200 cycles/sec
Interovertone interval:	500-700 cycles/sec
Dominant frequencies:	rather uniform throughout
Relative intensity:	greatest mid-duration

The first prairie dog to see danger began the "vocal chatter" while running to its mound or from a standing, sitting up, or standing up posture with the head alert. Monocular vision was used except for distant objects. If the

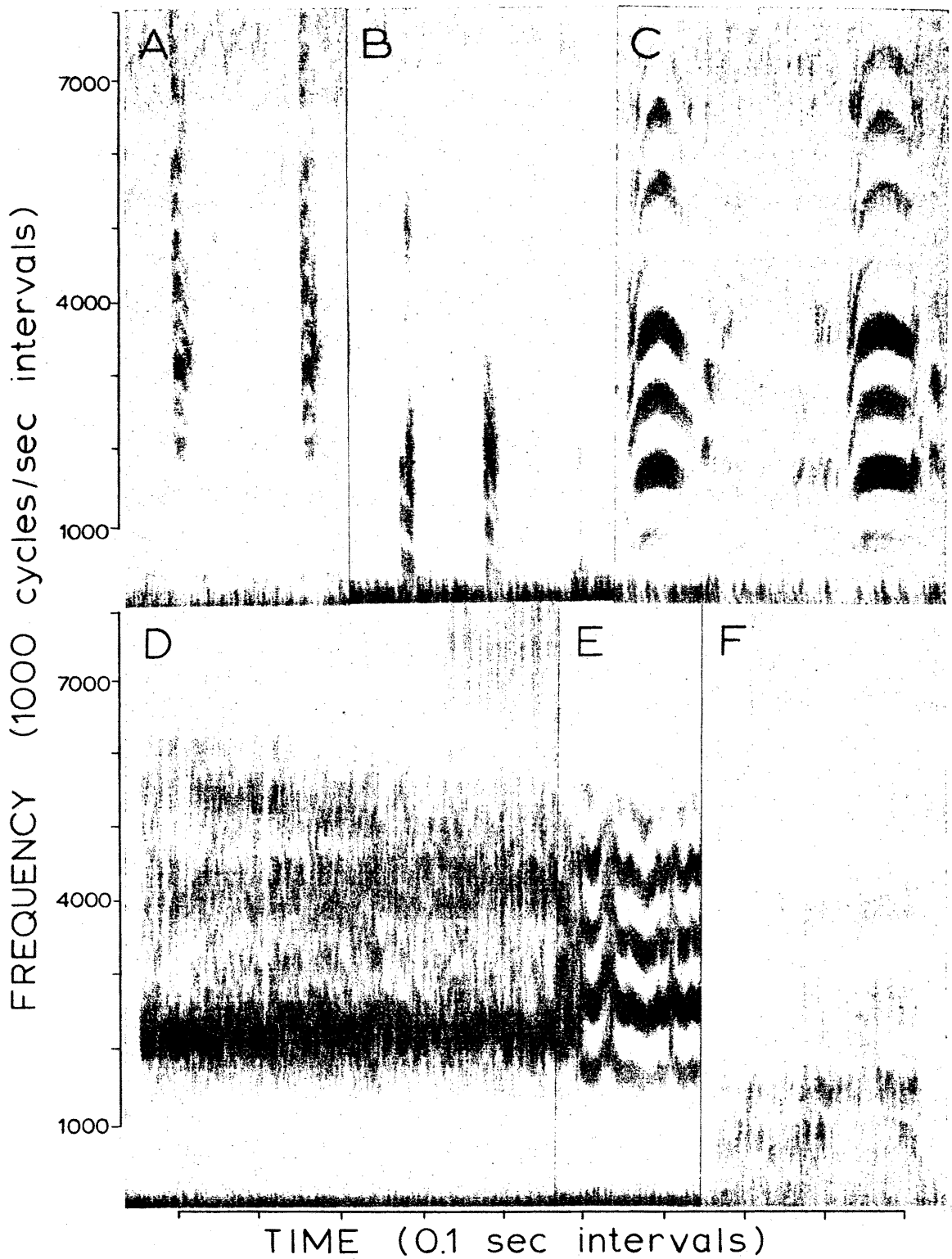

Fig. 4. Sound spectrograms of the sounds of the white-tailed prairie dog. A. Vocal Chatter. B. Chuckle. C. Laughing Barks. D. Snarl. E. Scream. F. Growl.

intruder greatly alarmed nearby prairie dogs, they often vocalized also.

The mouth was opened completely with each sound then partially closed before again opening for the next sound emission. The tongue was obvious in a side view and bulged outward at each sound. The abdominal muscles contracted with each emission of the sound.

Chuckle. The "chuckle" of the white-tailed prairie dog consisted of the sound emitted within the burrow. The prairie dogs produced the "vocal chatter," but again as with the "chuckle" of the black-tailed prairie dog, all but the lower frequencies were lost in the burrow system. The sound heard was of lower pitch; hence, it appeared different. The intersound interval was shorter than the average for the "vocal chatter" since the animal was usually in a higher state of alarm. In Fig. 4B, a sound spectrogram is shown of a prairie dog vocalizing while it descended its burrow. Both sexes and individuals older than two months of age produced these sounds as they were released from live-traps.

Laughing Barks. When white-tailed prairie dogs were undisturbed and the environment seemed peaceful, both sexes periodically emitted a rather short set of vocalizations which sounded like "laughing barks." Males tended to make these sounds more frequently than the females. The animals often stood, sat up hunchbacked, or were slowly running when they emitted the sounds. The head was outstretched causing the

mouth to be extended forward and up. Others continued their activities and soon made the sounds themselves. Though the call was somewhat "contagious," the allelomimetic response of others was not usually immediate.

The "laughing barks" were given in sets of 2-15 sounds per set. See Table 10 and Fig. 4C for further characteristics of the sounds. The first one or two sounds were often more prolonged than the following sounds in the set.

TABLE 10. Characteristics of the "laughing barks" of the white-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Individual sound duration (sec)	0.0304-0.3116	93	0.0145	0.0896 ±0.0030
Intersound interval (sec)	0.0228-0.9120	75	0.1001	0.1507 ±0.0231

Other characteristics--

Fundamental:	800-1000 cycles/sec
Interharmonic interval:	800-1000 cycles/sec
Dominant frequencies:	2nd, 3rd, 4th harmonics
Relative intensity:	greatest when harmonics reach peak frequencies

Snarl. When seriously threatening something that is menacing them, white-tailed prairie dogs emitted a "snarl." The sound was a loud, prolonged, moderately high-pitched noise with two or more resonance bands above 1500 cycles per second (Fig. 4D). Prairie dogs of both sexes in live-traps

often gave this sound with their mouth opened as if preparing to bite when a hand threatened them. The animals often raised one or both forelegs as they faced the threatening object. Adult males readily gave the "snarls" when threatened in captivity. This sound was not heard among free-ranging prairie dogs. Refer to Table 11 for further details.

TABLE 11. Characteristics of the "snarl" of the white-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Duration (sec)	0.1064-0.6460	24	0.1178	0.3056 ±0.0497

Other characteristics--

Frequency range:	less than 100 to over 8000 cycles/sec
Relative pitch:	high and may fluctuate
Harmonic structure:	lacking
Resonance bands:	two or more between 1500 and 5500 cycles/sec
Relative intensity:	rather constant throughout duration

Scream. Adult female white-tailed prairie dogs and pups of either sex often produced a "scream" when held captive by my hand. I was unable to record a "scream" emitted by adult males. Occasionally the sounds were made within the live-traps. The "scream" was a short to prolonged sound undulating in pitch and having clear harmonic structure (Fig. 4E). It frequently was preceded or followed by the noisy "snarls"

or "growls." In Table 12, I have listed further characteristics.

TABLE 12. Characteristics of the "scream" of the white-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Duration (sec)	0.0456-0.1520	6	0.0399	0.0887 ±0.0419
Other characteristics--				
Fundamental:	600-1800 cycles/sec; undulates throughout duration			
Interovertone interval:	600-900 cycles/sec			
Dominant frequencies:	2nd-4th harmonics			
Relative intensity:	variable throughout duration			

Growl. The "growl" of white-tailed prairie dogs was occasionally associated with the "snarl" and was given by pups and adults of either sex. It was a low-pitched, low intensity sound with resonance below 1500 cycles per second (Fig. 4F). Refer to Table 13 for the characteristics of the few "growls" tape-recorded. The animals observed making this sound were held captive and made the sounds when threatening my hand or a probing stick.

Other Sounds. Once a white-tailed prairie dog emitted a squeaky bark when seemingly scolding another prairie dog after they greeted each other. They leaped apart as the one emitted the sound.

TABLE 13. Characteristics of the "growl" of the white-tailed prairie dog

Feature	Range	No.	Standard Deviation	Mean
Duration (sec)	0.1368-0.4028	3	0.1334	0.2635

Other characteristics--

Frequency range:	primarily below 4000 cycles/sec
Relative pitch:	low
Harmonic structure:	lacking
Resonance:	700 and 1500 cycles/sec
Relative intensity:	weak throughout

In summary, the sounds emitted by free-ranging or captive white-tailed prairie dogs were: the "vocal chatter" which consists of many brief, repeated tones; the chatter emitted within the burrow sounding like a "chuckle"; the set of prolonged barks called "laughing barks"; the high-pitched, noisy "snarl"; the musical "scream"; and the low-pitched, noisy "growl."

Sounds of Gunnison's Prairie Dogs

Repetitious Barks. Gunnison's prairie dogs produced their own type of "repetitious barks" when alarmed or when they sighted a strange object in the distance. Each of these barks had a rather long duration (Fig. 5A) compared to the functionally homologous sounds of the other two species. The sounds were repeated at approximately three per second and were grouped into short sets of 2-25 per set with a

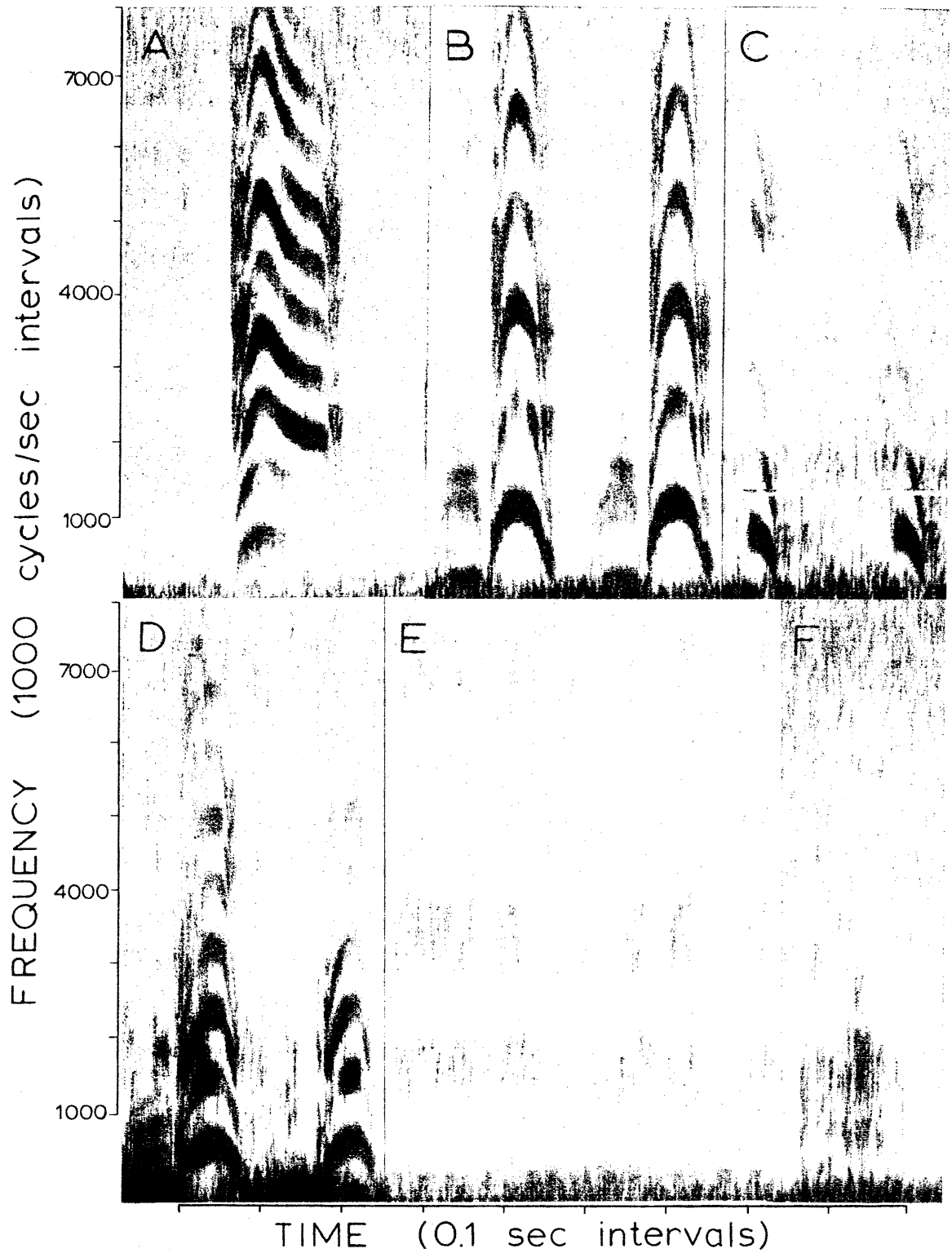

Fig. 5. Sound spectrograms of the sounds of the Gunnison's prairie dog. A. Repetitious Barks. B. Typical Rapid Barks. C. Modified Rapid Barks. D. Chuckle. E. Raspy Chatter. F. Growl.

pause of 3-15 seconds between each set. Table 14 gives further details. The intersound intervals were shortest upon extreme alarm. The first sets commonly had the most sounds per set.

TABLE 14. Characteristics of the "repetitious barks" of the Gunnison's prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Individual sound duration (sec)	0.0684-0.1824	93	0.0250	0.1171 ±0.0052
Intersound interval within set (sec)	0.2432-0.4408	76	0.0389	0.3133 ±0.0089

Other characteristics--

Fundamental:	peaks early at 900-1200 cycles/sec
Interharmonic interval:	900-1200 cycles/sec
Dominant frequencies:	3rd and 4th harmonics
Relative intensity:	greatest at peak harmonic frequencies during duration

The vocalizer was alert and viewed the intruder with monocular vision unless it was at a great distance. It normally stood, sat up, or stood up on its hind legs. The tail remained down. The mouth was opened completely and closed partially between sounds. The tongue showed in side view and was protruded slightly with each sound. The abdominal muscles contracted with each sound emission.

Nearby prairie dogs were alerted immediately upon hearing the "repetitious barks," but before taking further

action they awaited visual cues from the vocalizer, other prairie dogs, or their own observations. If another prairie dog ran for a mound, others did likewise. If no further acts of alarm occurred, the nonvocalizing prairie dogs looked about and then returned to their previous activities if no danger were apparent, even when the vocalizer continued to bark. As with the other two species, some prairie dogs vocalized when I could see no reason for alarm. Two-month-old pups, as well as older prairie dogs of either sex, emitted these barks. More than one individual in the same area often gave the "repetitious barks" if the individuals became greatly alarmed.

Rapid Barks. Gunnison's prairie dogs sometimes gave a long series of "rapid barks" when seemingly alarmed or apprehensive. The intersound interval and sound duration were less than for the "repetitious barks" (Table 15). There commonly was an obvious, low-pitched gular or some type of inhalation sound between barks (Fig. 5B). These sounds were heard when male and female prairie dogs were transported in a car or were held captive in live-traps at camp. A captured female pup made these sounds for several minutes at a time when strong winds preceded an approaching storm. She crouched in the live-trap with her head held low. A male pup in another live-trap nearby made a weak series of somewhat similar barks during the strong winds. However, each sound was only the last half of the usual "rapid bark." The mean duration of 12 sounds was 0.0260±0.0082 SD, and the mean of

TABLE 15. Characteristics of the "rapid barks" of the Gunnison's prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Individual sound duration (sec)	0.0228-0.0988	83	0.0120	0.0638 ±0.0026
Intersound interval (sec)	0.0836-0.3648	79	0.0368	0.1113 ±0.0082

Other characteristics--

Fundamental:	peaks at 1000-1300 cycles/sec
Interharmonic interval:	1000-1300 cycles/sec
Dominant frequency:	fundamental
Relative intensity:	greatest mid-duration

11 intersound intervals was 0.1575±0.0141 SD. Modified in this way, the sounds seemed to be a repetitious whimper (Fig. 5C). The following day, this animal was dying apparently from sylvatic plague. I never heard the whimper sounds again. Without further evidence, I consider them as a type of "rapid barks."

Another prairie dog produced the "rapid barks" upon seeing my microphone beside its mound as it came out of its burrow. A nearby prairie dog became alerted, then went down its burrow.

Chuckle. The "chuckle" of the Gunnison's prairie dog consisted of the barks emitted within the burrow (Fig. 5D). As with the other two species, it was a sound altered by the burrow system rather than the prairie dog. The sounds

emitted were the "rapid barks" but only the lower frequencies were heard due to the loss of the higher frequencies in the burrow. These sounds were often heard after releasing a prairie dog into its burrow from a live-trap. Pups and adults of both sexes gave these sounds.

Raspy Chatter. When male and female Gunnison's prairie dogs were feeding peacefully and wandering about, they periodically produced a "raspy chatter." These were low intensity, rather noisy sounds repeated with irregular intersound intervals 2-15 times in a short sequence (Fig. 5E). The vocalizer sat up hunchbacked or stood on all four legs. Also, the sounds were made while the prairie dog loped to another location. The head was outstretched with mouth and snout slightly upward. Nearby individuals often gave the sounds as if in response. They seldom repeated the sounds immediately; therefore, the call was not as "contagious" as the "wee-oo song" of the black-tailed prairie dog.

Since the "raspy chatter" was of low intensity, it was usually necessary to be within 100 feet of the subject in order to record these sounds. In Table 16, I list the features of the "raspy chatters."

Growl. The "growl" of Gunnison's prairie dogs was similar to the "growl" of the other two species. It was a short to prolonged, low-pitched, noisy sound (Fig. 5F). The pitch seemed constant. A captive subject often gave this sound when threatening an approaching stick or hand. However,

TABLE 16. Characteristics of the "raspy chatter" of the Gunnison's prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Individual sound duration (sec)	0.0288-0.1368	42	0.0335	0.0523 ±0.0104
Intersound interval (sec)	0.0288-0.1292	38	0.0357	0.0738 ±0.0117

Other characteristics--

Frequency range:	at least up to 8000 cycles/sec
Harmonic structure:	slight to lacking
Resonance:	2000 and 4000 cycles/sec
Relative intensity:	variable throughout call

compared to the other two species, the Gunnison's prairie dog was generally silent when live-trapped and handled. The "growling" prairie dog was usually sitting ready to bite and often raised one or both forelegs. Either sex made the "growl"; I only heard captive prairie dogs emit it. Refer to Table 17 for the characteristics of the "growls" analyzed on the sound spectrograph.

Other Sounds. The threatening sound heard between free-ranging Gunnison's prairie dogs had a snarl characteristic with undulation of pitch. It sounded similar to the "snarl" of the other two species. There was some undulation in pitch, and it was of higher pitch than the "growl." I was unsuccessful in tape-recording this sound. A female caught in a trap with a male snarled at the male whenever he

TABLE 17. Characteristics of the "growl" of the Gunnison's prairie dog

Feature	Range	No.	Standard Deviation	Mean ±95% Confidence Limits
Duration (sec)	0.0456-0.2812	8	0.0871	0.1349 ±0.0728
Intersound interval (sec)	0.1672 0.7372	5	0.2426	0.3450 ±0.3007

Other characteristics--

Frequency range:	primarily below 3000 cycles/sec
Relative pitch:	low
Harmonic structure:	lacking
Resonance:	1000 and 2000 cycles/sec
Relative intensity:	rather weak and in pulsations

crowded or crawled over her. Another female snarled briefly while attempting to free herself from the grasp of a male during copulation.

A male Gunnison's prairie dog in a live-trap when threatened with my hand made a number of "tooth chatters" which sounded identical to those of the black-tailed prairie dog. The intensity was so low the sounds were almost inaudible.

Gunnison's prairie dogs sometimes produce a squeaky bark or barks when seemingly trying to scold another prairie dog. The sounds were of low intensity and short in duration. They may have been modifications of the "rapid barks."

A screaming sound was made by one prairie dog as a digit was removed for identification purposes. The rather musical sound was like a prolonged bark of high and variable pitch.

In summary, the sounds emitted by free-ranging or captive Gunnison's prairie dogs were: the "repetitious barks" emitted in short sets; the long series of "rapid barks"; the low-pitched "chuckle" given within the burrow; the irregular interval, noisy "raspy chatter"; the low-pitched, noisy "growl"; a noisy snarling; a musical screaming, and a nonvocal tooth chattering.

DISCUSSION

General Comparisons with Previous Studies

It is difficult to characterize animal sounds so that a reader can recognize the sounds upon hearing them in the field. However, one can eliminate doubt by making his own recordings and sound spectrograms, and then comparing his spectrograms with those accompanying a previous description. Since earlier observers of prairie dogs have not published sound spectrograms nor given a detailed description of the sounds, I have had difficulty knowing whether I have heard the same sounds. However, in Table 18, I have attempted to list the names of the sounds given by previous authors which seem synonomous with mine.

Black-tailed Prairie Dogs. The sounds of black-tailed prairie dogs mentioned frequently in the writings of early travelers are most likely the "repetitious barks."

King (1955) and Smith (1958) were able to distinguish both a "warning bark" and a "hawk warning." The sounds I heard during alarm due to aerial predators were the same as those emitted for ground predators. However, since more than one individual would often vocalize as a hawk or an eagle made a dive and since the call was made only during the rapid maneuver of the bird, the call seemed very rapid

TABLE 18. Synonomous names of the sounds of prairie dogs

Name used in this paper	Previous name with original author
Black-tailed Prairie Dog:	
Repetitious Barks	Alarm note (Merriam, 1902) Squit-tuck (Seton, 1926) Warning Bark (King, 1955) Hawk Warning (King, 1955) Alarm Bark (Smith, 1958)
Chuckle	Chuckle (King, 1955)
Chatter Barks	? Muffled Barks (King, 1955) ? Little Barks (King, 1955) ? Chirr (Anthony, 1955)
Wee-oo Song	Yelp (Jillson, 1871) Cry (Wilder, 1872) Song (Seton, 1926) Territorial Call (King, 1955) All Clear (Anthony, 1955)
Snarl	Snarl (King, 1955)
Scream	Scream (King, 1955)
Growl	Skr-skirr (Seton, 1926) ? Churr (King, 1955) Growl (Tileston, 1961)
Tooth Chatter	Tooth Chatter (Squire, 1925)
White-tailed Prairie Dog:	
Vocal Chatter	Alarm Notes (Cary, 1911) ? Warning Bark (Tileston, 1961)
Chuckle	Chuckle (Tileston, 1961)
Laughing Barks	Querulous Cry (Cary, 1911) All Clear (Tileston, 1961)
Growl	Growl (Tileston, 1961)
Gunnison's Prairie Dog:	
Repetitious Barks	Warning Bark (Longhurst, 1944)

and consisted of only a few barks. Without seeing the sound spectrograms, I would have called it another sound. If the barks given during extreme alarm had two syllables, I found that the harmonics of the first syllable may be of slightly higher frequencies than those of the second syllable. In any case, I found no reason to separate the "repetitious barks" into two or more distinct types of calls. All my observations have suggested to me that the prairie dogs seek the protection of their burrows because of visual cues and not because they heard the "repetitious barks." Although, if they have wandered far from their burrows, they may run to their mounds at the slightest sound or rapid motion of another prairie dog.

There seems little doubt that the "chuckle" I have described is the same as the "chuckle" mentioned by King (1955) and Tileston (1961).

The "chatter barks" seem not to have been described by previous observers, unless they are what King (1955) terms the "muffled barks" or possibly the "little barks" which are given among disputing prairie dogs. They may be the sounds Anthony (1955) described as a "low 'chirr.'"

Several authors have discussed the "wee-oo song." I adopted the name from Seton's (1926) description. It is a difficult call to label with a single function; for as King (1955) aptly points out, it is given in a variety of circumstances. I conclude that it is a contact or group-cohesion call--one of social familiarization as discussed

by Etkin (1964) serving to maintain the social bonds among the group. Other mammals have sounds of similar function (Tembrock, 1963), although rarely is there such a ritualized act as seen during the "wee-oo song" of the black-tailed prairie dog.

The "snarl" I have described seems to be the same as the "snarl" mentioned by King (1955) and Smith (1958).

The "scream" I heard might be similar to or a slightly modified version of what King (1955) and Smith (1958) call a "scream." I would expect such a sound to vary greatly from one situation to another depending on the state of fear or distress of the animal.

What Tileston (1961) and I name the "growl" might be the sounds King (1955) labels as "disputing churr" or what Seton (1926) describes as a "skr-skirr" sound. The sounds serve as one type of auditory threat.

The "tooth chatter" I described seems similar to that mentioned by others. The function is variable. Dr. R. R. Lechleitner (personal communication) has heard "tooth chatter" from males caged side by side during the period the testes were in the scrotum.

No distinct sounds were heard that could be identified as those King (1955) named "defense barks." I did not witness unusual behavior or sounds toward a bull snake in the town.

White-tailed Prairie Dogs. The "vocal chatter" I have described appears to be the same as the "chattering alarm

notes" mentioned by Cary (1911). The "warning bark" Tileston (1961) described seems to be the same as the "vocal chatter" except for the intersound interval. His description of intersound intervals of 0.5 second is far longer than the data I collected.

The "chuckle" described by Tileston (1961) is doubtlessly the "chuckle" mentioned in this paper.

The "laughing barks" are probably made up of what Cary (1911) called the "querulous cry" and seem also to be the "all clear" mentioned by Tileston (1961).

The "growl" is no doubt the same as described by Tileston (1961).

Gunnison's Prairie Dogs. Burnett and McCampbell (1926), Longhurst (1944), and Scheffer (1947) all seem to have been referring to the "repetitious barks" when discussing the sounds of the Gunnison's or Zuni subspecies of prairie dogs. None of the other sounds have been mentioned previously in the literature.

Other Ground Dwelling Sciurids. I found no evidence in the vocalizations that the genus Cynomys is more closely related to the Citellus than to the Marmota evolutionary line as suggested by Wade and Gilbert (1940). The "tooth chatter" seems to be the sound of greatest similarity among the three genera. They all have various sounds of alarm and of a threatening nature. At our present stage of investigation, only the genus Cynomys appears to have a contact call;

it should be studied, however, in conjunction with the calls of the other two genera of these rather closely related animals.

Comparisons and Contrasts Between the Three Species of *Cynomys* Studied

The sounds of the prairie dogs are a useful tool for identification of species in the field. Certain sounds are unique to each species; therefore, an experienced observer needs only to listen to the sounds of alarm or to the contact calls to identify which species of prairie dog is before him.

Most of the sounds of each species are functionally homologous to sounds of the other two species. In Table 19, I have briefly summarized the characteristics of the sounds of each species and listed the function I most commonly observed.

The sounds given with alarm behavior are rapidly repeated sounds for the white-tailed prairie dog and are repeated more slowly for the other two species. The individual sounds of alarm are shortest in the white-tailed and longest in the Gunnison's prairie dog. The black-tailed prairie dog continues its warning barks over several minutes, whereas the other two species give their alerting sounds for short periods then pause before repeating the sounds in another sequence. Sounds of alarm of the black-tailed prairie dog vary in syllabic and harmonic structure; the alarm sounds of the Gunnison's prairie dog vary primarily in the

TABLE 19. A summary of the sounds of the black-tailed, white-tailed, and Gunnison's prairie dogs and their most commonly observed functions

Name of Sound	Characteristics	Common Function
Black-tailed Prairie Dog:		
Repetitious Barks	Mono- or bi-syllabic Fundamental: 1400-2300 cycles/sec Duration: 0.0674 sec Intersound interval varies about 0.3959 sec Prolonged repetitions	Alert others of danger
Chuckle	Lower harmonics of repetitious barks Short sequence of rapid repetitions	Alert others of danger near burrow
Chatter Barks	Fundamental: 900-1350 cycles/sec Duration: 0.0270 sec Intersound interval: 0.1241 sec	Threat
Wee-oo Song	Contagious Bi-syllabic Fundamental: 400-2200 cycles/sec Total duration approx. 0.59 sec	Social familiarization
Raspy Purr	Low-pitch noise Below 700 cycles/sec	Pleasure
Snarl	Wide freq. range noise Resonance varies in cycles/sec	Threat
Scream	Fundamental: 300-1000 cycles/sec Pitch varies during duration	Distress
Growl	Pulsed noise of wide freq. range	Threat
Tooth Chatter	Nonvocal clicking	Threat

TABLE 19. (continued)

White-tailed Prairie Dog:		
Vocal Chatter	Multi-overtoned over 2000 cycles/sec Duration: 0.0226 sec Repeated in sets	Alert others of danger
Chuckle	Low-pitched vocal chatter	Alert others of danger near burrow
Laughing Barks	Prolonged barks given in single sets Fundamental: 800-1000 cycles/sec	Social familiarization
Snarl	High-pitch, prolonged noise Resonance above 1500 cycles/sec	Threat
Scream	Fundamental: 600-1800 cycles/sec Pitch undulates	Distress
Growl	Low-pitch noise Resonance below 1500 cycles/sec	Threat
Gunnison's Prairie Dog:		
Repetitious Barks	Fundamental: 900-1200 cycles/sec Duration: 0.1171 Repeated in sets	Alert others of danger
Rapid Barks	Fundamental: 1000-1300 cycles/sec Intersound interval: 0.1113 sec	Apprehension
Chuckle	Lower harmonics of rapid barks	Alert
Raspy Chatter	Irregular interval noise Resonance distinct	Social familiarization
Growl	Low-pitch noise Low freq. resonance	Threat

sound duration; alarm sounds of the white-tailed prairie dog are relatively constant. The black-tailed prairie dog opens its mouth only partially and appears to make its sound with less effort than the other two species. The Gunnison's and white-tailed prairie dogs open their mouths to the extreme and emit the alarm sounds with strong contractions of the abdominal muscles. Only the black-tailed prairie dog flicks its tail while vocalizing.

"Chuckles," which are always emitted in the burrows, are specific for each species. They are similar in that they are all modified by the burrow structure from other alarm sounds.

Each of the three species studied emitted a contact or group-cohesion call. The "wee-oo song" of the black-tailed prairie dog is the most interesting to an observer, since it is accompanied by a spectacular toss upward of the head and forelegs. However, the "laughing barks" and "raspy chatter" of the white-tailed and Gunnison's, respectively, also serve the function of maintaining group cohesion. The calls are unique to each species; however, the individual sounds of the "laughing barks" of the white-tailed prairie dog appear somewhat similar in sound structure to the "repetitious barks" of the Gunnison's prairie dog.

The "snarls" of the black-tailed and white-tailed prairie dogs are similar in structure and in function, as are the "growls" of the three species. The "screams of the

white-tailed and black-tailed prairie dogs differ slightly, although the function is the same.

The "tooth chatter" was heard only from the Gunnison's and black-tailed prairie dogs. I do not doubt, however, that the white-tailed prairie dog does produce a "tooth chatter" similar to those of the other two species.

The "chatter barks" of the black-tailed and the "rapid barks" of the Gunnison's prairie dog are somewhat similar in sound structure, although apparently the function of the sounds are different. The "chatter barks" are a type of vocal threat, whereas the "rapid barks" are given when the animal is apprehensive or is giving an alert.

The captive white-tailed and Gunnison's prairie dogs were never successfully tamed; thus, I had no opportunity to hear any sounds functionally homologous to the "raspy purr" of the pet black-tailed prairie dog. Further investigation may find care-soliciting sounds or sounds of pleasure for these two species.

Members of each species studied had some vocal method of scolding another prairie dog. Some of these were described; yet others were brief, of low intensity, and occurred only rarely. The latter were inadequately studied by the techniques used for this research.

If a tape recorder could be operated continuously during the observation periods, one could obtain recordings of some of the sounds that I failed to tape-record. A technique of using numerous microphones placed at different

sites in the study area with multi-channel tape-recording would solve some of the problem of not being close to all the subjects. A study of this kind could best be done by a team of observers and technicians. Each member of the team could either tape-record, photograph, or take notes during the same sequence. Later, they could combine their data.

With the basic knowledge from this research that prairie dogs emit sounds for alarm, contact, intra- and interspecies threat, distress, apprehension, and of pleasure, further investigation of the sounds and their meaning to the animals can be pursued. Playbacks of the sounds and their various components to the animals, and observations of the resulting behavior of these animals may answer more conclusively what the sounds mean to other members of the social group, and which components of the sounds are necessary to convey the meaning of the communication. Experimentation in the field or laboratory could test further which stimuli cause certain sounds to be emitted by the prairie dogs. A colony maintained in an echo-free enclosure would enable further study of low intensity sounds produced during disputes. Studies on the mechanisms of sound production and the hearing range of the animals, as well as the importance of high frequency sound in their communications, should be investigated to further understand the sound communications of the prairie dogs.

SUMMARY

The sounds of black-tailed, white-tailed, and Gunnison's prairie dogs were studied in Colorado and Wyoming from February, 1964 to June, 1966. Observations, photographs, and tape recordings were made in the field and were supplemented by data collected from captive prairie dogs. The study areas of the black-tailed prairie dog were in Larimer County, Colorado; those of the white-tailed prairie dog were in Larimer County, Colorado, and Albany County, Wyoming; those of the Gunnison's prairie dog were in Saguache, Park, and Douglas Counties, Colorado. The sounds were tape-recorded on a battery-powered tape recorder at 15 inches per second and analyzed on a sound spectrograph. An unidirectional dynamic microphone was used with the recorder.

The sounds of the black-tailed prairie dogs were named and had the usual function as follows: (1) "repetitious barks"--alert; (2) "chuckle"--alert; (3) "chatter barks"--threat; (4) "wee-oo song"--contact; (5) "raspy purr"--pleasure; (6) "snarl"--threat; (7) "scream"--distress; (8) "growl"--threat; and (9) "tooth chatter"--threat. In addition, a grunting sound was occasionally heard.

The sounds of the white-tailed prairie dogs were named and had the usual function as follows: (1) "vocal

chatter"--alert; (2) "chuckle"--alert; (3) "laughing barks"--contact; (4) "snarl"--threat; (5) "scream"--distress; and (6) "growl"--threat.

The sounds of the Gunnison's prairie dogs were named and had the usual function as follows: (1) "repetitious barks"--alert; (2) "rapid barks"--apprehension; (3) "chuckle"--alert; (4) "raspy chatter"--contact; and (5) "growl"--threat. In addition, Gunnison's prairie dogs occasionally were heard making snarling, screaming, and tooth chattering sounds.

Each species can be identified by certain sounds unique to it, although, in general, all three species emit sounds under similar circumstances. The same sound may have different uses under different ecological conditions. For this reason, all sounds were named for physical rather than functional characteristics. The "chuckle" sounds are regular alerting sounds altered by the burrow system rather than by the prairie dog. Highly alarmed individuals may give more rapid alerting sounds, and during extreme alarm more than one individual may give these vocalizations. Black-tailed prairie dogs usually give their alarm calls for long periods; the other two species group their alarm barks into sets of sounds. The contact call of the black-tailed prairie dog is often repeated immediately by other individuals; the contact call of the other two species is usually repeated after a delay of several seconds. Tail flicking during vocalization occurs only in the black-tailed prairie dog.

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