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ON THE STRUCTURE AND FUNCTION OF WHITE-TAILED PRAIRIE DOG BURROWS

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ABSTRACT.—The architecture of burrows of the white-tailed prairie dog (*Cynomys leucurus*) is poorly known. For this reason and for comparative purposes, one recently active burrow of this species was excavated in southern Montana; the detailed methodology is described. Data were compiled on the dimensions of the 29.3 m of excavated passages, and interpretations of several features are discussed. A "turning bay," sleeping quarters, two hibernacula, and a maternity area are described, the last feature for the first time in print. In addition, we report *Cynomys* using their teeth to dig, also for the first time. Further, an inadvertent remodeling of the burrows is ascribed to normal animal traffic and appears to confirm a prediction based on late Pleistocene fossil burrows in Alberta.

The white-tailed prairie dog (*Cynomys leucurus:* Rodentia: Mammalia) may spend almost two-thirds of its life underground (Clark et al. 1971) in laboriously constructed burrows. Burrows provide shelter from inclement weather and predators, and a peaceful place for bearing and rearing young; they are also important to the social structure of the colony (King 1955, 1984). Research on subterranean architecture has concentrated on other *Cynomys* spp. For *C. ludovicianus*, tunnel schematics (Merriam 1901, Scheffer 1937, Wilcomb 1954) and tabular data (Sheets et al. 1971, Whitehead 1927) are available, and for *C. gunnisoni*, schematics (Foster 1924, Longhurst 1944). Clark (1971, 1977) provided the only *C. leucurus* schematics, and these are of only one tunnel and part of a second.

This paper discusses the excavation of one *C. leucurus* burrow in southern Montana, at the northern edge of the range for this species (Flath 1979). It was not a complete system but rather what we could excavate in five days. One of us had recently excavated fossil *Cynomys* burrows in southern Alberta, Canada (Burns and McGillivray 1989), and to facilitate comparison of the fossil and Recent burrows, we employed similar mapping techniques. The fossil burrows are to be described elsewhere (Burns and Young, in preparation).

STUDY AREA

The burrow chosen for study is located in Sec. 31, T9S, R27E, Carbon County, Montana (see Flath 1979). A Carbon County specimen of *C. leucurus* (U.S. National Museum #67369) collected in 1894 attests to the lengthy occupation of the region (R. D. Fisher, personal communication, 1987). Annual precipitation in this northernmost portion of the Bighorn Basin is 15–23 cm (Flath and Paulick 1979). Vegetative ground cover is 40–50%, consisting largely of big sagebrush (*Artemisia tridentata*), saltbush (*Atriplex nuttallii*), and a limited variety of forb species, but little graminoid forage. Although rain is scarce, erosion channels in the bare soil indicate that high rates of erosion can occur with occasional summer rains.

The soil is very hard and is characterized as a dense clay-clayey-saline upland soil (Parker et al. 1975). On the ground and throughout the subsurface soil are vast numbers of fragmentary shells of an undetermined species of Jurassic pelecypod mollusc, *Gryphaea*. These were likely redeposited from Jurassic strata in the Bighorn Mountains during the formation of an early Holocene playa lake in the basin.

METHODS

Flath and Paulick (1979) identified complex (= maternity) and simple burrow mounds. The mound chosen to begin the excavation was classified as simple in this scheme: dome-shaped and featuring a single opening. The moderately pitched tunnel was first probed with a 2.4-m flexible plumber's cable. A rope-filled canvas sack was pushed into the tunnel

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as far as possible to keep the burrow free of loosened earth. A backhoe (Case 580E) with a 0.25-yd^3 (0.19-m^3) bucket was used to remove earth from the surface in small portions. The dig was cleared at appropriate intervals to determine the direction of the tunnel and to measure its dimensions.

Planar coordinates were measured at flagged and numbered "survey points" along the tunnels. Elevations were determined relative to a datum stake with a surveying transit. All measurements were tied into a grid system constructed on magnetic north and laid out in a pattern of squares 5 m on a side. Horizontal position of points was determined from angular coordinates measured from two designated corner-posts within the corresponding 5-meter square using a plumb bob to position the tape measures over the point. In addition to the point coordinates, the vertical and transverse diameters of the tunnel at those points were recorded. A note was made of the portions of the tunnel that were plugged and of the composition of the plugs. After clearing a plug almost 4 m beyond the mouth of the first mound, we identified the second entrance by using a smoke bomb (cf. Stromberg 1975).

RESULTS

The openings of the selected burrow, on mounds A and B, were both of the dome type (cf. King 1955). The shortest distance along the tunnels between openings was 16.5 m. We mapped an additional 12.8 m of lateral tunnels; four other leads could not be completed due to lack of time. Plan and perspective views are given in Figures 1 and 2. At point 4 (hereafter, pt. = point), 13 cm below surface and 65 cm from the opening in mound A, was a two-part chamber similar to Scheffer's (1937) "turning bay." A lower exit led down to pt. 7, where a north-south tunnel intersected. The main tunnel was indistinguishable from the cross-tunnel, as both were plugged with similar plant-rich material. It is uncertain whether the cross-tunnel fortuitously intersected, or was part of, the main system. Lack of time prevented pursuit of the cross-tunnel beyond pt. 10 (Fig. 1).

The main tunnel proceeded west. At pt. 13, a major side-tunnel that branched southward was completely plugged with earth, plant matter, and feces. At pts. 35 and 42, two chambers of modified globular and globular shape, respectively, were filled with semi-fresh plant matter, apparently the roots and shredded bark of *Artemisia*. The chamber at pt. 42 was 24 cm high and 23 cm across and was filled with more than 3 L of plant stuffing but no feces. The side-tunnel ended at pt. 45 in a narrow cul-de-sac 6 cm in width. A chamber of an independent burrow was located above this terminus (Fig. 1). An adult *Cynomys* humerus was found at pt. 39 in the chamber and a tibia and metatarsal at pt. 40. (Only one other bone was found below ground, a *Cynomys* metacarpal at pt. 10). The upper burrow was plugged with old plant matter.

The main tunnel made a sharp northward bend at pt. 16 and continued to an intersection at pt. 19. The area immediately to the north was enlarged but not to full chamber dimensions. Two tunnels branched off at pts. 20 and 21, but time did not allow pursuit of them. The main route led to the bottom, at pt. 30, of an inclined shaft, which then led up to the opening on mound B.

To the north of pt. 30 the entire complex was plugged with earth and feces, including numerous 5-mm-long juvenile pellets. Three tunnels branched off the complex at pts. 54, 49, and 55. The complex contained three subchambers, all of which were clearly modified by shallow, accessory diggings. The tunnel from pt. 55 to pt. 65 and beyond could not be followed due to lack of time. Pts. 49 and 55 led to a common tunnel that terminated in a vertical shaft at pt. 57. The top of the shaft was not seen to reach ground surface anywhere during excavation and is thought to have been a blind vertical terminus. Pts. 54 and 67 were ends of a common tunnel that featured another vertical terminus, at pt. 69. This was carefully uncovered during excavation and could not have reached the surface.

In summary, the system as far as it was excavated, consisted of a 16.5-m-long tunnel connecting mounds A and B. The straight-line distance between mound openings was 11.3 m. The two mounds were simple domes with one opening each. The main tunnel had at least five side-branches, only one of which was completely dug; total length of excavated tunnels was 29.3 m. Three irregular and two globe-shaped structures were defined. One area in the northwest featured a moderately

Fig. 1. Plan map of the burrow system. Numbers refer to the survey points mentioned in the text. Arrows indicate leads that were left unexcavated. The unusual orientation of the north arrow was suggested by Figure 2, which is the optimal orientation for appreciating the features of the burrow system.

Fig. 2. Perspective view of the burrow system. Negative values accompanying hash marks on the burrow are the elevations below a common datum stake.

complex network of tunnels and interconnections. The greatest depth of the system was 2.0 m below surface, at pt. 33 on the south side-branch. Average vertical and transverse diameters of tunnels were both 10–11 cm. Plugging was extensive throughout.

Discussion

Clark (1971, 1977) noted, based on available data at that time, that there were few if any criteria that distinguish the burrows of white-tailed and black-tailed prairie dogs. The results of the present study do not alter that conclusion but do include some worthy observations.

Tunnel plugging is a notable feature of prairie dog burrows. The purpose of the plugging is variously ascribed to a need for altering tunnel systems (Wilcomb 1954), to sanitary reasons, such as burying dead kin (Smith 1958), to protection from ferret predation (Henderson et al. 1969, Clark et al. 1984, Martin et al. 1984), to keeping winter food moist (Jillson 1871). The results of these studies are not always comparable, as some deal with artificial situations and some deal only with plugs at mound entrances. In the present study the only unplugged portion of the system extended from the opening on mound B eastward along the main tunnel to pt. 9, just west of the cross-tunnel. However, one intriguing feature of the system was that the opening on mound B was partially plugged with slopewash off the mound, resulting from heavy rains in the preceding month or two. Although not wholly occluded, the tunnel was impassable for a prairie dog. The side-branches, at pts. 7, 13, 20, 21, and 23, were occluded with richly organic materials. It is unlikely that the plugging observed near mound A was a protective measure because the cross-tunnel was similarly blocked; there was likely no hibernant beyond pt. 10. The southerly side-branch from pt. 13 to its terminus was entirely blocked, and yet near-fresh, unfouled nest material filled the globular chambers; at pt. 13 itself some recent (bright green interior) fecal pellets were noted, but the remainder of the plug was composed of old, dried pellets, plant matter, and some earth. Likewise, at pts. 20 and 21, old, dried organic plugs were present, and the multi-chambered area at pt. 51 was also filled with old plug material.

It seems that plugging was an effort to remodel. Longhurst (1944) suggested that earth from deeper, second-year passageways was packed into shallow, first-year tunnels, thus economizing on the effort to move it to the surface. Plugging for the purpose of underground food storage (as in Jillson's [1871] experiment) was not corroborated by the present study or others (Scheffer 1937, Longhurst 1944). Free-ranging prairie dogs do not store food below ground.

It may be that our system had been abandoned or that the hibernant was located beyond pt. 20 or 21. The latter option is less likely because plugs in these openings were tightly packed as if from the "near" side. As the prairie dogs were in hibernation in early October when we undertook the study, there was no way to know if the burrow was inhabited or not, short of exhuming an animal. The only signs of activity were the fresh pellets at pt. 13 and relatively fresh-looking "trench" on the surface of mound A (Fig. 1). The trench was worked from above as it did not reach into the lumen of the tunnel. Its purpose is unknown.

To date no studies have identified maternity areas within burrow systems. Flath and Paulick (1979) identified maternity systems based on observations of juvenile play groups frequenting certain mounds. Further, they identified 98% of these systems as having juvenile "accessory digging" in the entrance mounds.

Our mounds were not typical of such maternity burrows. Yet one area in the northwest portion of the system appears to have served a maternity function. The irregular chamber noted above, at pt. 51, with its subchambers, "grassy" nesting material, accessory diggings, and myriad small pellets, is a likely center of maternal/juvenile activity. Several other accessory diggings were noted, at pt. 17A (associated with a possible nest centered on pt. 18) and near pt. 62, just west of the maternity area. This is believed to be the first description of an underground maternity area.

Cynomys ludovicianus, *C. leucurus*, and *C. gunnisoni* can, and do, hibernate (Bakko and Nahorniak 1986, Harlow and Menkens 1986, Rayor et al. 1987); whitetails appear to be obligate hibernators, but blacktails are more variable in this. Nevertheless, the nature of the hibernaculum has never been described because torpid prairie dogs in the wild have never been reported.

The two globular chambers at pts. 35 and 42 may represent hibernacula. They were maximally distant from either mound opening; they were full of unfouled, shredded nesting material; and they do resemble in these features the hibernacula of the Columbian ground squirrel, *Spermophilus columbianus* (Shaw 1925; Burns, personal observations). Although proof requires finding torpid prairie dogs *in hibernaculo*, it is important to distinguish among hibernacula, maternity chambers, and normal sleeping quarters. It is not necessary that all systems possess all three features, but in the current study it seems to be so. The maternal and hibernacular sites are tentatively described above. Further, a widening in the tunnel, at pt. 18, to 18 cm wide may have functioned as sleeping quarters. Wilcomb (1954) encountered numerous such widenings in his study of 14 blacktail burrow systems.

Another feature of this burrow system was the occurrence of two vertical termini at pts. 57 and 69. Similar vertical "blind alleys" have been described in the popular literature as refuges from flooding. Foster (1924) reported casual observations of ranchers who saw a colony inundated for several hours and who claim no subsequent reduction in the prairie dog population. Upon excavation of a burrow, Foster noted several of the vertical termini and proposed the refuge hypothesis. Such a construction might work in the clayey soil of Carbon County, Montana, but only if enough rain fell to test it.

The terminus at pt. 69, 12 cm in mean diameter, extended up 39 cm to a blunt end above the roof of the underlying burrow. Surprisingly, the inner surface of the tube was riddled with the paired, linear gouges of *Cynomys* incisor teeth (Fig. 3A, B). The U-shaped cross sections of the gouges indicate the use of *lower* incisors for the digging. There is a divergence toward the end of the stroke in several of the paired gouges (Fig. 3C), made possible because the mental (mandibular) symphysis is flexible; no such flexibility exists between the premaxillae. The divergence opens upward, indicating motion from bottom to top. In at least 15 instances upper incisors were used to anchor the head in the earth while the lower jaw was being drawn upward and forward. Short, flat impressions of paired upper incisors are visible in these instances a few millimeters above the end of the lowers' stroke (Fig. 3D).

Some burrowing rodents (e.g., Geomyidae; Bathyergidae; Muridae: Spalacinae, Tachyoryctinae; some extinct Castoridae) normally use their teeth to dig (Martin and Bennett 1977, Vaughan 1978). For this they possess some or all of the following features: procumbent upper incisors, lips that prevent loose earth from entering the mouth, and horny nose pads that prevent abrasion on the nose (Martin and Bennett 1977, Vaughan 1978). It is to be noted that all of these species use their upper incisors; our *Cynomys* used their lowers. In any case, prairie dogs are ill adapted to digging with their teeth.

The Carbon County whitetails must have been desperate. The hard earth forced the digging teeth apart and in so doing would have stretched the gingiva painfully; the teeth must have been worn very rapidly, and the lips and nose probably suffered horribly from abrasion. It is difficult to imagine this self-mutilation unless they were in mortal danger. It is unlikely that a predator was threatening, because time would not have permitted such extensive digging. Perhaps there is an explanation in P. J. Young's (1988) observations of radio-tagged *Spermophilus columbianus* emerging from hibernation. He reported that the squirrels did not return to the surface by unplugging existing passages, and the evidence in the ground suggested that new tunnels were excavated straight to the surface from the hibernaculum. If the prairie dogs were emerging from torpor and digging their way out, there must have been a pressing need (hunger?) to get to the surface. Although Foster's (1924) explanation for vertical termini is unproven, it suggests an alternative for our site. Slopewash off mound B, presumably caused by flash flooding, had largely occluded the passage from the mouth down to pt. 30, as noted earlier. It could be that fear of drowning, with no negotiable exit, forced the attempt to burrow straight up, and with some alacrity.

Wilcomb (1954) noted blacktails using claws in the construction of tunnels in crumbly clay-loam soil. Under captive conditions, *C. gunnisoni* was observed using its front feet (i.e., claws) to burrow (Longhurst 1944). The present study is the first, to our knowledge, in which *Cynomys* has been shown to dig with teeth.

Loose soil on burrow floors is expected. Its depth is variable, from 0.5 cm (Wilcomb 1954) to as much as 5 cm (Clark 1971, 1977). Our study revealed the floors to be bare or slightly blanketed. However, in cross sections cut well below the lumina of the tunnels, dark stains traced out vague, semicircular outlines (Fig. 4). The dark subfloor soil was sometimes pasty in texture and, though organic, contained only grossly recognizable material (feces, plant stems, etc.). Survey flags could be driven into the floors easily, whereas the enclosing matrix was much too hard. This feature was predicted to occur in the modern context because it is well developed in the Pleistocene burrows of southern Alberta (Burns and Young, in preparation). Constructed in uncemented sands of Miocene age, the in-filled fossil burrows with normal 13–15-cm diameters show cross sections with vertical heights of up to 80 cm.

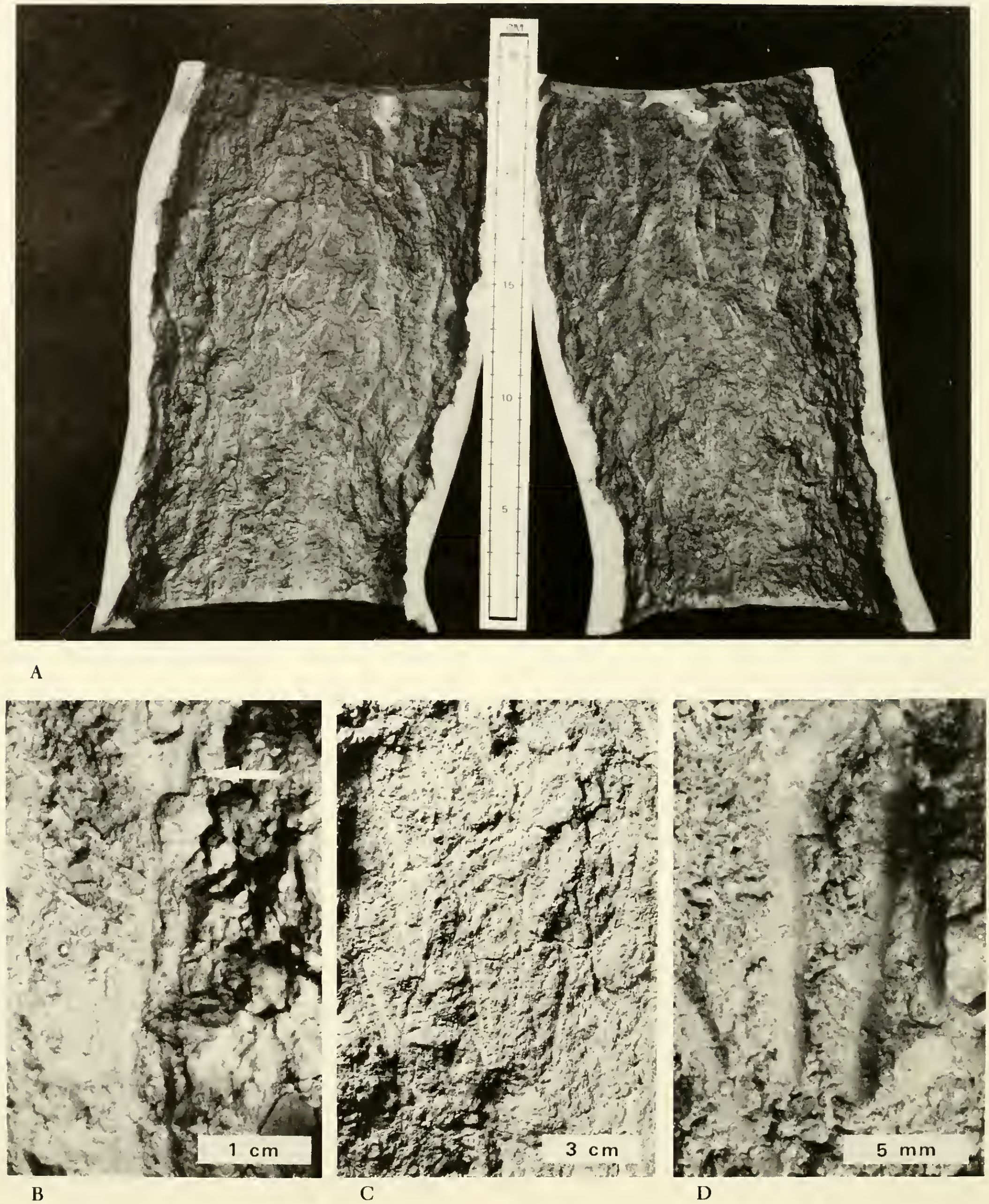

Fig. 3. Evidence of tunneling by *Cynomys leucurus* using the teeth: A, resin cast produced from the section of vertical tunnel at pt. 69; B, detail of a portion of the cast showing a number of the gouges produced mostly by the lower incisors; C, example of the divergence of the tooth gouges; ligaments of the mental symphysis were stretched as the jaw was drawn through the hard earth; D, example of the use of the upper incisors (arrow) to anchor the head while the mandible is adducted in the digging stroke.

One may postulate that, as the animals pass through the tunnels, they rub matrix from the walls and roof. The detritus falls down, becomes incorporated with scattered organic waste, and is then compacted by the traffic. As time passes the tunnel is remodeled. In effect, the tunnel "migrates" upward through the soil profile. Can such a scenario be taken

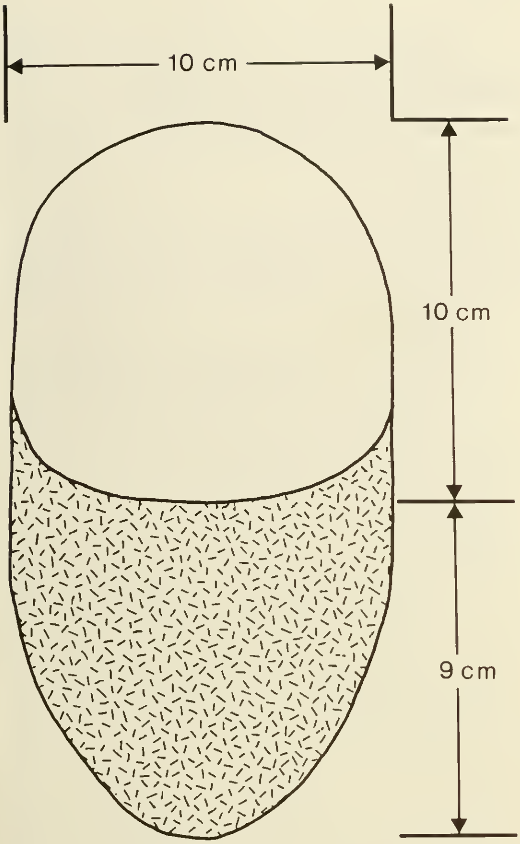

Fig. 4. Schematic of the tunnel profile at pt. 54. Typical of many loci in the system, this shows a patent passageway above a trace of the former passage. The process of upward "migration" of the passage is explained in the text.

seriously? Given that the soils are very hard, can casual contact promote remodeling? It is eminently possible given time. Although the age of this burrow is unknown, the colony is at least 93 years old. If economy of effort is a factor in the construction of burrows in the unyielding soil of this arid, scantily vegetated environment, then a burrow may be inhabited for several years at least. The resulting traffic of years could produce the alterations.

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