Cynomys ludovicianus. By John L. Hoogland
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Cynomys ludovicianus Ord, 1815
Black-tailed Prairie Dog

Arctomys ludovicianus Ord, 1815:292 (description on page 302).
Type locality “Upper Missouri River.”

Cynomys sociatus Rafinesque, 1817:45. Type locality “Plains of the Missouri.”

Cynomys griseus Rafinesque, 1817:45. Type locality “On the Missouri.”

Muæs missourianæ Warden, 1819:226. Type locality “The Missouri country.”

Arctomys latrans Harlan, 1823-306. Type locality “Plains of the Missouri.”


Cynomys arizonæs Meares, 1890:305. Type from Point of Mountain, near Wilcox, Cochise County, Arizona.

Cynomys pyræticiliæ Elliot, 1905:139. Type from White Horse Spring, Woods County, Oklahoma.

CONTEXT AND CONTENT. Order Rodentia. Suborder Sciuriformia (=Proteutheria or Sciuromorpha), Family Sciuridae, Subfamily Sciurinae, Tribe Cynomysini (=Marmotini), Subtribe Spermophilina, Genus Cynomys, Subgenus Cynomys (Hoffmann et al., 1993; see also Hafner, 1984; Hollister, 1916). The genus Cynomys has five living species; Cynomys ludovicianus has two subspecies (Hall, 1981; Hollister, 1916). However, Pizzimenti (1975:64) argued that “… there is no reason to support subspecific designation, and C. ludovicianus should be considered monotypic.”

Cynomys ludovicianus ludovicianus Ord, 1815:292, 302. See above.

Cynomys ludovicianus arizonæs Meares, 1890:305. See above.

DIAGNOSIS. The genus Cynomys has five species with non-overlapping geographic ranges: black-tailed (C. ludovicianus), Mexican (C. mexicanus), Gunnison’s (C. gunnisoni), white-tailed (C. leucurus), and Utah prairie dogs (C. parvidens). Because they have long (71–115 mm), black-tipped tails (Fig. 1), Hollister (1916) grouped black-tailed prairie dogs together with Mexican prairie dogs into the subgenus Cynomys, Hollister (1916; see also Clark et al., 1971; Pizzimenti, 1975) grouped the other three species, all with shorter (40–65 mm), white- or gray tipped tails, into the subgenus Leucocicus. Salient differences between the two subgenera include the following: Leucocerusomy is hibernates each year, but Cynomys do not; Leucocerusomy live at altitudes of 1,500–3,000 m above sea level, but Cynomys live at altitudes of 1,200–2,000 m; shrubs and herbs within colonies of Leucocerusomy are commonly 0.5 m high or taller, but vegetation with colonies of Cynomys is rarely taller than 0.3 m (Hollister, 1916; Hoogland, 1995; Pizzimenti, 1975). Further, Leucocerusomy have smaller molar teeth and thinner jugal bones than do Cynomys (Clark et al., 1971; Hollister, 1916; Pizzimenti, 1975). Finally, the territorial and antipredator calls of black-tailed and Mexican prairie dogs are practically identical, but differ markedly from the territorial and antipredator calls of Gunnison’s, white-tailed, and Utah prairie dogs (Clark, 1977; Hoogland, 1995; Pizzimenti and McCleneghan, 1974; Rayor, 1988; Slobodchikoff et al., 1991; Wright, 1970; Wright-Smith, 1978).

Like skulls of other prairie dog species, the skull of C. ludovicianus is broad and angular, with wide zygomatic arches and conspicuous processes (Fig. 2). Distinctive features of the black-tailed prairie dog skull include “… superior surface of maxillary root of zygoma bordering premaxillary and frontal bones narrow, sharply emarginate anteriorly; auricular bullae comparatively small” (Hollister, 1916:15; Merriam, 1892).

Probably because “… both taxa were part of a single reproductive unit in the recent past” (Pizzimenti, 1975), black-tailed and Mexican prairie dogs are remarkably similar in every respect. One conspicuous difference is the non-overlapping geographic ranges (Hall, 1981). Another important difference concerns the color and length of the tail. Only the distal third of the tail of C. ludovicianus is black (Fig. 1), but the tail of C. mexicanus is usually over one-half black distally (Hollister, 1916). The mean ± SD length of the tail of C. l. ludovicianus is 78.6 ± 9.2 mm (n = 212), but the mean ± SD length of the tail of C. mexicanus is 88.7 ± 10.6 mm (n = 61; Pizzimenti, 1975). Ranges in length of tail are 71–115 mm for black-tailed prairie dogs and 93–115 mm for Mexican prairie dogs (Hall, 1981; Pizzimenti, 1975).

With the length of tail being a notable exception, most skeletal and cranial measurements indicate that C. ludovicianus is the largest species of prairie dog, followed by C. mexicanus, C. leucurus, C. parvidens, and C. gunnisoni in that order (Hollister, 1916; Pizzimenti, 1975). However, body masses of adults during the breeding season indicate that white-tailed and Utah prairie dogs are the largest species (Clark 1977; Hoogland, 1995; Wright-Smith, 1978).

GENERAL CHARACTERS. Except for rare albinos (Costello, 1972; Tate, 1947), black-tailed prairie dogs are brown or reddish-brown above and whitish below. Most individual hairs in summer are “black at base, followed by buffy white, then cinnamon, with subterminal band of buff, and, in unworn condition, narrow tip of blackish. Mixed with these are numerous wholly black and half-black hairs, rather longer than the ordinary pelage …” (Hollister, 1916:15). Most individual hairs in winter, by contrast, are “… intense black at bases, then pale buff, with subterminal band of cinnamon and tip of almost pure white” (Hollister, 1916:15). Individuals have black whiskers, black toenails, and dark brown hair. Females have eight gray mammae that are conspicuous only during lactation or shortly after weaning (Hoogland, 1995).

Juvenile black-tailed prairie dogs, also called pups or young, are individuals that first emerged from the natal burrow <8 months prior to observation. Yearlings have been coming aboveground for ≥8 months, but <20 months, prior to observation. Adults have been coming aboveground for ≥20 months (Hoogland, 1995). Total
length of adult and yearling black-tailed prairie dogs ranges from 335 to 415 mm (Hall, 1981).

Black-tailed prairie dog males are usually 10%-15% heavier than females. Mean ± SD body mass of adult males in South Dakota is 905 ± 116 g (range = 613–1,390, n = 217) in autumn (October–November), 750 ± 121 g (range = 496–1,147, n = 149) in winter (February–March), and 861 ± 99.0 g (range = 437–1,010, n = 261) in spring (May–June). Comparable body masses for adult females are 819 ± 103 g (range = 470–1,149, n = 439) in autumn, 669 ± 105 g (range = 406–1,045, n = 276) in winter, and 696 ± 84.1 g (range = 418–982, n = 613) in spring (Hoogland, 1995).

Mean ± SD body mass of yearling males in South Dakota is 476 ± 102 g (range = 253–696, n = 109) in winter (February–March) and 699 ± 107 g (range = 382–968, n = 190) in spring (May–June). Comparable body masses for yearling females are 468 ± 90.8 g (range = 264–605, n = 115) in winter and 636 ± 80.4 g (range = 418–845, n = 208) in spring (Hoogland, 1995).

From 212 adult and yearling specimens of C. l. ludovicianus, Pizzimenti (1975) calculated means ± SD and ranges for the following measurements (in mm): condylobasal length, 59.9 ± 2.4 (57.2–61.8); least cranial breadth behind zygoma, 24.5 ± 0.7 (23.9–25.0); width of external auditory meatus, 4.0 ± 0.4 (3.7–4.6); zygomatic breadth, 50.7 ± 1.8 (29.6–32.3); width of postorbital constriction, 13.6 ± 0.7 (13.0–14.3); least interorbital breadth, 12.9 ± 0.8 (12.4–13.7); height of rostrum, 12.7 ± 0.6 (11.9–13.3); width of rostrum, 11.7 ± 0.5 (11.2–12.2); length of nasals, 23.4 ± 1.2 (22.4–24.8); width of nasals, 6.3 ± 0.4 (5.0–6.4); height of foramen magnum, 7.8 ± 0.5 (7.4–8.0); width of foramen magnum, 8.4 ± 0.5 (8.0–9.2); lambdoidal depth, 18.9 ± 1.1 (17.8–20.3); greatest depth of skull, 27.1 ± 1.3 (25.9–28.3); bital constriction, 13.6 ± 0.7 (13.0–14.3); lambdoidal depth, 21.3 ± 0.9 (20.2–22.2); total length, 373.5 ± 29.3 (354.5–397.8); length of fornal fur, 60.2 ± 3.4 (57.5–64.5).

The dental formula for black-tailed prairie dogs, as for other prairie dog species, is i/1, c/0, p/2, m/3, total 22 (Stockrahm and Seabloom, 1990). Incisors of adults and yearlings are white or pale yellow.

DISTRIBUTION. Black-tailed prairie dogs have a larger geographic range than any other species of prairie dog. About 150 years ago, C. ludovicianus occurred as far north as southern Saskatchewan in Canada, as far south as southern Coahuila in Mexico, as far east as eastern Nebraska, and as far west as western Montana and eastern New Mexico (Fig. 3; Ceballos et al., 1993; Hall, 1981). They probably numbered over 5 billion, and a single colony in Texas contained 400 million residents (Merriam, 1922). However, farmers and ranchers view black-tailed prairie dogs as pests. Shooting and poisoning in combination with destruction of habitat have led to a precipitous decline in numbers—even though financial costs of eradication usually outweigh benefits (Anderson et al., 1986; Clark, 1979; Knowles, 1989a, 1989b; O’Melia et al., 1982; Uresk, 1985). Consequently, black-tailed prairie dogs were on the list of endangered species as recently as 1974. Though still rare, they are no longer in acute danger of extinction. They occur in isolated colonies throughout their former range, and in national parks such as Wind Cave in South Dakota and Theodore Roosevelt in North Dakota; national monuments such as Devil’s Tower in Wyoming; state parks such as Custer in South Dakota; and national wildlife refuges such as Quivira in Kansas and Wichita Mountains in Oklahoma.

FOSSIL RECORD. Nine species of Cynomys have been recognized in the fossil record, from the Pliocene (Late Blancan) to Recent (Goodwin, 1993, 1995; see also Black, 1963; Bryant, 1945; Hay, 1921; Hibbard, 1937; Wood, 1933). Six of these species are extinct (C. churcherii, C. hibbardi, C. meadensis, C. niobrarius, C. spipiza, and C. vetus), and the other three are extant (C. gunnisoni, C. leucurus, and C. ludovicianus; Goodwin, 1995).

FORM AND FUNCTION. Means and ranges (in mm) of bacular measurements from 10 adult and yearling specimens of C. l. ludovicianus are: greatest length, 4.38, 4.02–4.76; width of distal end, 1.34, 1.02–1.67; width of base, 1.47, 1.15–1.78; least width of shaft, 0.45, 0.37–0.54; number of teeth on left side, 2.90, 2–4; number of teeth on right side, 2.10, 1–3; total number of teeth, 5.00, 4–6 (Pizzimenti, 1975).

Despite Hollister’s (1916) claim of only one molt per year, adult and yearling black-tailed prairie dogs molt the entire pelage twice each year (Hoogland, 1995). In the switch from long, thick winter fur to shorter, summer fur, molting starts on the underside. Molting then moves to the dorsal side, where it starts near the eyes and progresses posteriorly. In the switch from summer to winter pelage, the progression reverses: from tail to eyes to underside. The initiation and duration of molting vary with latitude, altitude, and individual condition. In South Dakota, nonbreeding yearlings begin to molt the winter fur as early as mid-April, but some older breeding females do not begin to molt until early June (Hoogland, 1995). Molting of winter fur in South Dakota is more synchronous, with most individuals beginning in late August or early September and finishing about 10–14 days later (Hoogland, 1995). Fast-growing C. ludovicianus juveniles molt the entire pelage two or more times in their first summer before acquiring the winter fur in late August or September (Hollister, 1916).

Because black-tailed prairie dogs frequently develop gall-bladder diseases (Broughton et al., 1991). C. ludovicianus also has been useful in studies of metabolism (Bakko, 1977; Pfeiffer et al., 1979).
FIG. 3. Geographic range of the two subspecies of black-tailed prairie dogs: 1, Cynomys l. ludovicianus; 2, Cynomys l. arizonensis. This map shows the range of black-tailed prairie dogs about 150 years ago. In response to shooting, poisoning, and destruction of habitat, black-tailed prairie dogs are now rare or extinct in some areas of their former range. Map from Hall (1981).

and yearling C. ludovicianus with complete reliability is possible only if they are first permanently marked (e.g., with numbered ear­
tags) as juveniles (Hoogland, 1995). Approximate aging of un­
marked black-tailed prairie dogs as yearlings, 2-year olds, or ≤3-
year olds is possible from estimates of molar attrition (Cox and
Franklin, 1990; Hoogland and Hutter, 1987). Body mass of C. lu­
dovicianus varies curvilinearly with age, but extensive overlap pre­
cludes aging from body mass except for the simple distinction be­
tween adults and yearlings (Hoogland, 1995).

The sequence of eruption in the permanent cheek teeth of C. ludovicianus, from first to last, is “... M1 and m1, M2 and m2,
M3 and m3, P3, p4, followed by P4 lagging somewhat behind the
other premolars” (n ≥ 300 juvenile skulls; Stockrahm and Sea-
bloom, 1990:107). Within 2–3 months after first emergence from
the natal burrow, juveniles acquire complete permanent dentition.

Most black-tailed prairie dogs first become sexually mature and copulate in the second February or March following birth, ap­
proximately 21 months following first emergence from the natal
burrow (Hoogland, 1995; King, 1955; Stockrahm and Seabloom,
1988). However, some individuals first copulate as yearlings (fe­
males 35%, males 6%). The probability of a yearling’s producing
emergent juveniles is low for both sexes, but is higher for females
than males (9% versus 2%). Conversely, some individuals delay
sexual maturation until the third year. Again a sexual asymmetry
prevails, with males being more likely than females to delay (24%–
versus 5%—Hoogland, 1995).
Juveniles first appear aboveground is 3.08. The probability of giving birth after copulation is higher for adults. The mean ± SD length of gestation for black-tailed prairie dogs is 34.6 ± 0.73 days (range = 33-38, n = 225 gestations). These precise numbers are longer than previous estimates, for which researchers were unable to pinpoint the date of copulation. Parturition always occurs underground, usually in the morning (Hoogland, 1995).

At birth, juveniles are about 70 mm long, have a body mass of about 15 grams, are blind, and have no fur. Fur appears about 3 weeks after parturition, and the eyes open about 2 weeks later (Johnson, 1927).

Not every black-tailed prairie dog female that copulates gives birth. Failure to give birth results either from failure to conceive or from abortion of all embryos (with or without resorption) after conception (Anthony and Foreman, 1951; Knobles, 1967). Of 301 copulating females scored for parturition, 82% (248) gave birth. The probability of giving birth after copulation is higher for adults than for yearlings (89% versus 54%; Hoogland, 1995).

After parturition, black-tailed prairie dog juveniles remain underground for several weeks before the first emergence from the natal burrow. Pre-emergent juveniles depend primarily on their mother’s milk for nourishment, but sometimes eat plants brought underground by the mother as well. Conversely, emergent juveniles depend primarily on their own foraging for nourishment, but sometimes receive additional nourishment from nursing. These patterns make it difficult to specify the exact day of weaning and the exact length of lactation. The mean ± SD length between parturition and first emergence for C. ludovicianus is 43.1 ± 2.46 days (range = 37-51, n = 149 litters—Hoogland, 1995). The length of lactation varies inversely with litter size at first juvenile emergence; the length of gestation, however, is unrelated to litter size (Hoogland, 1995).

Because parturition occurs underground, information on litter size at birth is scarce for C. ludovicianus. Laboratory studies (Anthony and Foreman, 1951; Foreman, 1962; Wade, 1928) and necropsies of pregnant and lactating females (Knowles, 1907; Tileston and Lechleiter, 1960) indicate that litter size at birth ranges from one to eight. The mean ± SD litter size about 6 weeks later when juveniles first appear aboveground is 3.08 ± 1.06 (range = 1-4, n = 578 litters—Hoogland, 1995).

Upon first emergence from the natal burrow in May or June, the mean ± SD juvenile body mass in South Dakota is 147 ± 31.8 g for males (range = 68-288, n = 587) and 141 ± 31.2 g for females (range = 60-258, n = 521). Several months later in October, the mean ± SD juvenile body mass is 356 ± 98.0 g for males (range = 543-964, n = 109) and 532 ± 87.5 g for females (range = 270-819, n = 176—Hoogland, 1995).

Sixty-seven percent of estrous black-tailed prairie dog females (363/542) copulate with a single male, and 84% (457/542) copulate exclusively with the resident breeding male(s) in the home coterie (or haven, see below). Females in multi-male coteries are more likely than females in non-male coteries to copulate with a second male (Hoogland, 1995).

Male-biased dispersal precludes most types of extreme inbreeding for C. ludovicianus. For example, young black-tailed prairie dog males disperse from the natal coterie territory sometime before sexual maturation, and thereby avoid copulations with mothers and sisters (Hoogland, 1982a). These males most commonly disperse between May and June, when they first again find success underground (Garrett and Franklin, 1989). In addition, older males do not remain in the same breeding coterie territory for more than two consecutive years, and thus avoid copulations with their two-year old daughters (Hoogland, 1995).

Despite the regular dispersal of young and older black-tailed prairie dog males, sexually mature close kin of the opposite sex sometimes copulate end up in the same coterie territory. When this happens, genetic relatives usually resort to other mechanisms to avoid extreme inbreeding (Hoogland, 1982a, 1995). For example, some females do not come into estrus when the only resident breeding male is a father, brother, or son. Other females come into estrus, but only copulate with unrelated males from outside the home coterie. Although they avoid extreme inbreeding with parents, offspring, and siblings, black-tailed prairie dog males copulate regularly with more distant kin such as full and half first and second cousins (Hoogland, 1992, 1995).

The mean ± SD number of emergent juveniles produced in one year by females that copulate is 1.01 ± 1.74 (range = 0-6, n = 581 females). The mean ± SD number of emergent juveniles produced in one year by males is 4.17 ± 4.22 (range = 0-21, n = 219 males). The mean ± SD number of emergent juveniles produced by females over their entire lifetimes is 4.25 ± 3.05 (range = 0-18, n = 178 females that copulated at least once). The mean ± SD number of emergent juveniles produced by males over their entire lifetimes is 7.66 ± 7.67 (range = 0-45, n = 124 males that copulated at least once). Because variance in lifetime reproductive success is greater for males than for females, the mating system of C. ludovicianus is appropriately described as polygynous.

Female C. ludovicianus evidently do not adaptively vary the sex ratio of their emergent litters in response to variables such as populational sex ratio, maternal or paternal age, maternal body mass, paternal reproductive success, local mate competition, local resource competition, or local resource enhancement (Hoogland, 1995).

Several factors significantly promote annual and lifetime reproductive success (ARS and LRS) among black-tailed prairie dogs. For example, middle-aged males and females survive and reproduce better than older and younger individuals. When a female copulates with two or more males, the first male to copulate sires more offspring than later-copulating males. Female ARS varies directly with litter size, which correlates positively with precipitation in the previous summer. Healthy individuals of both sexes are more likely to copulate and rear offspring than are lighter individuals. Females that copulate early in the breeding season rear more juveniles than later-copulating females. Female ARS correlates negatively, but male ARS correlates positively, with litter size for females. For males, ARS is highest in multi-male coteries. For males, on the other hand, ARS is highest for those dominant individuals that can monopolize all the females of two adjacent coteries. More than any other factor, longevity enhances male and female LRS. Male copulatory success is a good predictor of male reproductive success (Hoogland, 1995).

Longterm research has shown that practically every measurable variable shows substantial annual variation for black-tailed prairie dogs, except the sex ratio of litters at first juvenile emergence. For example, litter size, adult and juvenile survivorship, juvenile body mass at first emergence, colony size and colony density (i.e., the number and density of resident adults and yearlings), and dates for copulation, parturition, and first juvenile emergence all vary significantly across years (Hoogland, 1995).

ECOLOGY AND BEHAVIOR. Black-tailed prairie dogs are diurnal, burrowing rodents. Coloniality is perhaps the most striking feature of these heritable squirrels that forage from dawn until dusk. Undisturbed colonies contain thousands of residents and extend for kilometers in all directions. Colonies of C. ludovicianus are usually larger and more densely populated than those of other species of prairie dogs (Hoogland, 1995).

Like Mexican prairie dogs but unlike prairie dogs of the subgenus Leucocrossomys, black-tailed prairie dogs appear above-
ground throughout the year (i.e., do not hibernate). During extremely cold weather, however, black-tailed prairie dogs sometimes remain underground for several consecutive days (Hoogland, 1995).

*Cynomys ludovicianus* has been the focus of at least eight detailed studies with marked individuals under natural conditions (Garrett and Franklin, 1988; Halpia, 1987; Hoogland, 1995; King, 1955; Knowles, 1965; Loughry, 1988; Smith, 1967; Tileston and Lechleitner, 1966). *Cynomys ludovicianus* is consequently the best studied of all the prairie dog species.

Researchers capture black-tailed prairie dogs with 15 cm by 15 cm by 60 cm Tomahawk double-door liveness baited with whole oats (Hoogland, 1995). A conical, cloth bag facilitates handling. Numerous studies, using ear tags work well for permanent identification, as does Nyanzol-D fur dye for visual identification from a distance (Hoogland, 1995).

Within colonies, black-tailed prairie dogs live in contiguous, territorial, harem-polygynous family groups called coteries (King, 1955). A coterie's territory covers about one-third of a hectare, contains about 20 burrow entrances, and usually remains constant from generation to generation. Following the emergences of juveniles from their natal burrows, as many as 40 individuals sometimes live in one coterie territory. Most coteries, however, contain only one breeding adult male: two or three adult females, and several non-breeding yearlings and juveniles. The mean ± SD coterie size (adults and yearlings only) in South Dakota in April is 6.13 ± 3.39 (range = 2–15, n = 233 coteries), and the mean ± SD number of emergent juveniles per coterie each year is 4.24 ± 3.98 (range = 0–19, n = 265 coteries). Large coteries sometimes contain two breeding males, which are commonly brothers. Conversely, one male sometimes controls two contiguous, small coteries (Hoogland, 1995).

Unlike the more nomadic males, females usually spend their entire lives within the natal coterie territory. Consequently, females within a coterie are invariably close kin (Hoogland, 1995).

Vegetation differentiates black-tailed prairie dog colonies from surrounding areas in two ways. First and more conspicuous, the height of vegetation is markedly shorter within colonies (Koford, 1958; Tileston and Lechleitner, 1966). This shortness results not only from normal foraging, but also because black-tailed prairie dogs prefer to colonize areas where the vegetation is already low (Clark, 1979; Knowles, 1966; Koford, 1958; Snell, 1985). In addition, black-tailed prairie dogs use their teeth to clip down certain tall (>20 cm) plants without consuming them (King, 1955). Such clipping facilitates the detection of predators (Hoogland, 1995). Second, the composition of the plant community is radically different within colonies (Agnello et al., 1986; Clat and Hein, 1978; Koford, 1958; Whicker and Deling, 1986). Certain plants, such as scarlet globemallow (*Sphaeralcea coccinea*), black nightshade (*Solanum nigrum*), pigweed (*Amaranthus retroflexus*), and the appropriately named prairie dog weed (*Dysosida paposa*), almost never occur outside colonies of *C. ludovicianus* (King, 1955).

Most black-footed ferrets prefer black-tailed prairie dog coterie territories of the same home colony, but others move farther in search of a new colony (Hoogland, 1995). The latter strategy is more dangerous, mainly because intercolonial dispersers are so vulnerable to predation while away from burrows and scanning, anti-predator-calling conspecifics (Garrett and Franklin, 1988). Consequently, successful migration of black-tailed prairie dogs from one colony to another is rare, so that immigrants usually account for only 1–3% of colony residents (Garrett and Franklin, 1988; Hoogland, 1995; King, 1955).

Perhaps the most ostentatious behavior of *C. ludovicianus* is the territorial call, or “jump-yip display.” While stretching the lenated, nearly vertically, and individual throws the forefeet high into the air as it calls. A single jump-yip usually starts a chain reaction among black-tailed prairie dogs of the home and adjacent coteries (Smith et al., 1976, 1977; Waring, 1970). Other salient behaviors include at least 11 other distinctive vocalizations; scratching to remove fleas; pushing, kicking, and pounding dirt to enhance burrow mounds; and collecting mouthfuls of dry grass for underground nests (Hoogland, 1995; King, 1955).

Behavioral interactions among black-tailed prairie dogs are conspicuous and frequent. Within coteries, interactions are amicable and include play, allogrooming, and mouth-mouth contacts that resemble kisses. Amicability gives way to hostility in February through April, however, when pregnant and lactating females vigorously defend burrows for rearing offspring (i.e., their nursery burrows). Amicability returns in May when juveniles first emerge from their natal burrows and appear aboveground (Hoogland, 1986; King, 1955).

When black-tailed prairie dogs non-kin from different coteries meet, they engage in a flagrant territorial dispute that involves staring, teeth chattering, flaring of the tail, bluff charges, unique vocalizations called “defense barks,” and reciprocal anal sniffing (King, 1955). Territorial disputes commonly persist for more than 30 minutes, and sometimes include fights and chase as well (Hoogland, 1995).

Animals that prey on *C. ludovicianus* include coyotes (*Canis latrans*), bobcats (*Lynx rufus*), badgers (*Taxidea taxus*), black-footed ferrets (*C. gunnisoni*), golden eagles (*Aquila chrysaetos*), prairie falcons (*Falco mexicanus*), avocet and buteo hawks (*Accipiter sp.* and *Buteo sp.*), bullsnakes (*Pituophis melanoleucus*), and rattlesnakes (*Crotalus sp.*). Faced with so many predators, interspecific differences in the availability of protective cover have probably been the primary benefit of coloniality for *C. ludovicianus* (Hoogland, 1981).

As a cost of their extreme coloniality, black-tailed prairie dogs frequently harbor numerous fleas, lice, and ticks (Hoogland, 1979a). The most common species of fleas are *Ospocristosis hissuta*, *O. tuberculatus*, *O. labis*, *Pulex simulans*, *P. irritans*, and *Leptopsylla segnis* (Ecke and Johnson, 1952; Pizzimenti, 1975; Smith, 1958). The most common species of ticks are *Ixodes kings* and *Aretobolaegus glazogenei* (King, 1955; Pizzimenti, 1973; Tyler and Bascher, 1975). No information is available regarding the species of lice that infest *C. ludovicianus*. Fleas transmit bacteria (*Pasterella* [*Verrunza* *pestis*] that cause sylvatic (bubonic) plague, an introduced disease to which black-tailed prairie dogs are highly susceptible (Barnes, 1982, 1993; Eskey and Haas, 1940; Pizzimenti and Meyers, 1961). Entire colonies quickly disappear after the initial introduction of plague (Barnes, 1995; Barnes et al., 1972).

On the basis of Hall's (1981) range map for the black-footed ferret, Powell (1982) suggested that ferrets prey on black-tailed prairie dogs but not on the other four species of prairie dogs. If so, then black-footed ferrets might ultimately explain why colonies of *C. ludovicianus* are larger and more densely populated than colonies of other prairie dogs species. However, Hall's (1981) range map shows that black-footed ferrets also occur in habitats of white-tailed and Gunnison's prairie dogs (see also Biggs and Schroeder, 1988; Hoogland, 1995; Sparks, 1973; Stuart and Christiansen, 1973; Torres, 1973). Colony size of all prairie dog species has probably evolved primarily in response to more diurnal predators such as coyotes, bobcats, and raptors, with the secondary consequence that individuals are especially vulnerable to more nocturnal predators, entering black-footed ferrets (Hoogland, 1982b). Interspecific differences in the availability of protective cover have probably been more important than interspecific differences in predation by black-footed ferrets in the evolution of coloniality in the different prairie dog species (Hoogland, 1981, 1995).

Black-tailed prairie dogs are selectively herbivorous. Favorite foods in the summer include wheatgrass (*Agropyron sp.*), grama (*Bouteloua sp.*), buffalo grass (*Bromus sp.*), scarlet globemallow, and rabbitbrush (*Chrysothamnus sp.*; Koford, 1958; Summers and Linder, 1978). Preferred forage in the winter includes prickly pear cactus (*Opuntia sp.*), whistle (*Cirsium sp.*), and underground roots. Competing plants within colonies of black-tailed prairie dogs usually avoid saltbush (*Artemisia sp.*), treevase (*Aristida sp.*), prairie dog weed, and horseweed (*Conyza ramosissima*; Costelle, 1970; King, 1955; Summers and Linder, 1978).

Survivorship during the first year after emergence from the natal burrow is 54% for females and 47% for males of *C. ludovicianus*. Females that survive the first year usually live as long as their golden anniversary in the wild. Males, on the other hand, may live only as long as their second year (Garrett and Franklin, 1988; Summers and Linder, 1978).
Burrows of black-tailed prairie dogs are integral to both defense against predators and protection from the weather. Burrows are typically 10 to 30 cm in diameter at the entrances, but narrow somewhat underground (King, 1955, 1984; Merriam, 1902; Sheets et al., 1971). Burrows are usually about 2 to 3 m deep, but some are as long as 35 m and as deep as 5 m.

Nursery burrows and burrows used for final submergence at sunset contain one or two elliptical nest chambers packed with dry grass; each chamber is approximately 30 cm high and 30 cm wide (Gunderson, 1973; Sheets et al., 1971). Most black-tailed prairie dog burrows are narrow; only one or two entrances are present. However, some have three, and a few have as many as five or six entrances (Hoogland, 1995; Sheets et al., 1971). Probably to deter invasions, burrow entrances in different coterie territories never connect (Hoogland, 1995).

Burrow entrances of *C. ludovicianus* are of three general types. First, some entrances, usually found near the colony's periphery, have no conspicuous mound. Individuals do not spend the night or rear offspring in burrows with these entrances, but use them for escape during a surprise predatory attack or for short periods to avoid midday heat. A second type of entrance has wide, rounded, unstructured mounds of dirt called dome craters (King, 1955, 1984). Dome craters sometimes have a diameter of 2-3 m, but are no higher than 0.2-0.3 m. The third and most conspicuous type has a high mound of dirt molded into a distinctive cone called a rim crater, which resembles a miniature volcano. Rim craters usually have a diameter of 1.0-1.5 m and are sometimes as high as 1.0 m. Burrows under rim craters, those under dome craters, are commonly suitable for seeking safety from predators, spending the night, and rearing offspring (Hoogland, 1995). Especilly when the ground is wet after rain, individuals, or groups containing as many as four, reshape the mounds of rim craters by digging, scraping, pushing, and piling the surrounding soil with their noses and front and rear legs (King, 1955, 1984).

Black-tailed prairie dog enters their burrows at sunset and remain there, presumably asleep, until about sunrise the following day (King, 1955). Except under extraordinary circumstances related to either copulation or attempted predation, black-tailed prairie dogs do not switch burrows during the night (Hoogland, 1995).

Both dome craters and burrow entrances with no associated mound are common in colonies among all five species of prairie dogs (Clark, 1977; Fitzgerald and Lechleitner, 1974; Pizzimenti and Coli, 1990; Hoogland and Lechleitner, 1966; Wadge-Smith, 1978). Rim craters, however, are unique to black-tailed and Mexican prairie dogs (Ceballos and Wilson, 1985; Hoogland, 1995; King, 1955; Trevino-Villarreal, 1990).

The mounds of dome and rim craters help to prevent flooding after rainstorms and also provide vantage points to scan for predators, the mounds facilitating the use of Bernoulli's Principle (Vogel et al., 1973). Such improved ventilation might be important when burrows are especially long and deep or when as many as 14 members of a coterie spend the night in the same tunnel (Hoogland, 1995).

By pushing dirt from the burrow mound, black-tailed prairie dogs sometimes close entrances to tunnels that contain either black-footed ferrets or snakes (Clark et al., 1984; Halpin, 1983; Henderson et al., 1969). In addition, a mother sometimes plugs one of the auxiliary entrances to the nursery burrow containing her unweaned offspring (King, 1955).

For most of the year, all coterie members have equal and unchallenged access to the numerous burrow entrances within the home coterie territory during the day. Sharing of burrows at night is also common. Two circumstances temporarily terminate equal access to all burrows. First, in large coherent containing two breeding males, each male defends a subset of burrows within the home coterie territory from the other male. Second, as noted above, females defend their nursery burrows from all coterie members during pregnancy and lactation.

Perhaps in response to the ease of excavating in different types of soil, the density of burrow entrances within black-tailed prairie dog colonies varies from 10 to 250 per hectare (Campbell and Clark, 1981; Hoogland, 1981; Martin and Schroeder, 1978, 1980). Perhaps as a function of either the availability of forage or the density of predators, colony density also varies widely, from fewer than 10 adults and yearlings per hectare to more than 35. The number of burrow entrances per colony resident also varies greatly (Hoogland, 1981). Consequently, neither the number nor density of burrow entrances accurately predicts colony size or colony density for *C. ludovicianus* (Hoogland, 1995; King, 1955).

The major cause of juvenile mortality within colonies of *C. ludovicianus* is infanticide. In the most common type of infanticide that ravages 22% of litters (Type I), lactating females kill and cannibalize the unweaned offspring of close kin. Certain females specialize as killers, and other females are especially likely to lose their litters to infanticide in consecutive years (Hoogland, 1985, 1995). Following emergences of juveniles from their natal burrows, however, mothers suckle their own offspring. However, some have three, and a few have as many as five or six entrances (Hoogland, 1995; Sheets et al., 1971). Probably to deter invasions, burrow entrances in different coterie territories never connect (Hoogland, 1995).

Burrow entrances of *C. ludovicianus* occur in three different contexts (Hoogland, 1985, 1995). Type II infanticide occurs when female immigrants from another colony kill weaned or unweaned juveniles after invading a coterie territory. Because female immigration is so rare, Type II infanticide eliminates fewer than 1% of litters. In Type III infanticide, which terminates 9% of litters, mothers abandon their offspring shortly after parturition and allow members of the home coterie to kill and cannibalize them. Type IV infanticide, which destroys 2-3 weeks before the spring of close kin as well, including juveniles they had tried to kill only 2-3 weeks before (Hoogland et al., 1989). Such communal nursing promotes formation of large multi-litter groupings in which a foster mother's own offspring are safer from predation.

Besides Type I, infanticide within colonies of *C. ludovicianus* occurs in three other contexts (Hoogland, 1985, 1995). Type II infanticide occurs when female immigrants from another colony kill weaned or unweaned juveniles after invading a coterie territory. Because female immigration is so rare, Type II infanticide eliminates fewer than 1% of litters. In Type III infanticide, which terminates 9% of litters, mothers abandon their offspring shortly after parturition and allow members of the home coterie to kill and cannibalize them. Type IV infanticide, which destroys 2-3 weeks before the spring of close kin as well, including juveniles they had tried to kill only 2-3 weeks before (Hoogland et al., 1989). Such communal nursing promotes formation of large multi-litter groupings in which a foster mother's own offspring are safer from predation.

Although they clearly discriminate between kin and non-kin, black-tailed prairie dogs seem unable to discriminate between close and more distant kin. For example, individuals groom nieces and nephews as often as offspring and full siblings and infanticidal females victimize offspring of their daughters as often as the offspring of their nieces and cousins. Further, individuals seem unable to recognize kin with whom they have never previously associated. Rather, kin recognition among *C. ludovicianus* seems to require direct social learning during a critical period of about one month following a juvenile's first emergence from the parental burrow (Hoogland, 1985).

Ranchers worry that their domestic horses (*Equus caballus*) and cows (*Bos taurus*) will suffer broken legs after falling into burrows of *C. ludovicianus*. Although possible, leg fractures attributable to burrows are exceedingly rare (Carr, 1973; Hoogland, 1995). Ranchers also worry that black-tailed prairie dogs compete with their livestock for food, however, despite some overlap, black-tailed prairie dogs avoid numerous plants that livestock prefer and prefer numerous plants that livestock avoid (Coppock et al., 1983a, 1983b; Uresk, 1984). Further, excavations and clipping by black-tailed prairie dogs, as well as their aboveground scats, enhance the growing conditions for certain plants, so that American bison (*Bison bison*), pronghorn antelope (*Antilocapra americana*), and livestock prefer to forage at colony sites (Carr, 1973; Knowles, 1986b; Koford, 1958; O'Melia et al., 1982). Finally, ranchers seem to forget that millions of American bison lived sympatrically with billions of black-tailed prairie dogs as recently as 150 years ago. Because the habits and dietary requirements of cattle and American bison are so similar, large numbers of cattle and black-tailed prairie dogs are inapplicable. The inescapable conclusion is that recent attempts to eradicate black-tailed prairie dogs have been misguided and inappropriate. By their foraging and clipping of tall vegetation, black-tailed prairie dogs radically alter the plant communities of western North America. Because their colonies attract predators and so many other animals, black-tailed prairie dogs also have a major impact on wildlife ranging from black widow spiders (*Latrodectus mactans*) and harvest ants (*Pogonomyrmex occidentalis*) to mountain plovers (*Eudocima montana*) and wapiti (*Cervus elaphus*) (Hoogland, 1995).

Further, black-tailed prairie dogs are important prey items for black-footed ferrets, the rarest mammals in North America (Campbell et al., 1987; Clark, 1989; Clark et al., 1986; Hillman, 1984).
Using blood samples from C. ludovicianus sampled at Wind Cave National Park, South Dakota, researchers have used starch-gel electrophoresis to examine over 60 loci for genetic polymorphisms. At least seven of these loci are polymorphic: esterase-1, esterase-4, mannose phospho-2-mannose-6-phosphate dehydrogenase, transferase, nucleoside phosphorylase, phosphogluco-2, the first four of these loci have two alleles, and phosphogluco-2 has four alleles (Daly, 1992; Foltz and Hoogland, 1983; Foltz et al., 1988; see also Cheeser, 1983). In combination with behavioral observations of estrus and copulations, these polymorphisms show that the minimal frequency of multiple paternity (i.e., same mother, different father) among litters of black-tailed prairie dogs is 5%. The minimal frequency of cuckoldry (i.e., the siring of offspring by a male from a different coterie) is 8% (Hoogland, 1995; see also Foltz and Hoogland, 1981; Hoogland and Foltz, 1982).

REMARKS. If captured when young, black-tailed prairie dogs make excellent, engaging pets that are easily house-trained (Ferrara, 1985). Obtaining young pets is difficult, however, because black-tailed prairie dogs do not readily breed in captivity (Hoogland, 1995). For help with figures and photographs, I thank Ray Morgan and Bob Timm. This paper is contribution number 2763-AEL from the National Geographic Society.


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