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Cynomys ludovicianus.

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Cynomys ludovicianus Ord, 1815

Black-tailed Prairie Dog

Arctomys ludoviciana Ord, 1815:292 (description on page 302). Type locality "Upper Missouri River."

Cynomys socialis Rafinesque, 1817:45. Type locality "Plains of the Missouri."

Cynomys? grisea Rafinesque, 1817:45. Type locality "On the Missouri."

Monax missouriensis Warden, 1819:226. Type locality "The Missouri country."

Arctomys latrans Harlan, 1825:306. Type locality "Plains of the Missouri."

C[ynomys]. cinereus Richardson, 1829:155. (pro *grisea* Rafinesque, 1817).

Cynomys ludovicianus Baird, 1858:xxxix, 331. First use of present name combination.

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

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

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi (=Protrogomorpha or Sciuromorpha), Family Sciuridae, Subfamily Sciurinae, Tribe Cynomyini (=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 arizonensis Mearns, 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 *Leucocrossuromys*. Salient differences between the two subgenera include the following: *Leucocrossuromys* hibernate each year, but *Cynomys* do not; *Leucocrossuromys* live at altitudes of 1,500–3,000 m above sea level, but *Cynomys* live at altitudes of 1,300–2,000 m; shrubs and herbs within colonies of *Leucocrossuromys* 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, *Leucocrossuromys* 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, 1996; Pizzimenti and McCleneghan, 1974; Rayor, 1988; Slobodchikoff et al., 1991; Waring, 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; audital 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 $\pm$ *SD* length of the tail of *C. l. ludovicianus* is 78.6 $\pm$ 9.2 mm (n = 212), but the mean $\pm$ *SD* length of the tail of *C. mexicanus* is 88.7 $\pm$ 10.6 mm (n = 61; Pizzimenti, 1975). Ranges in length of tail are 71–115 mm for black-tailed prairie dogs and 83–115 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, 1970; 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 irises. 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

FIG. 1. Black-tailed prairie dog, *Cynomys l. ludovicianus*, in South Dakota. Note the long tail whose distal third is black. When involved in a territorial dispute as seen here, black-tailed prairie dogs flare the tail hairs and chatter their teeth. Photo courtesy of Wind Cave National Park.

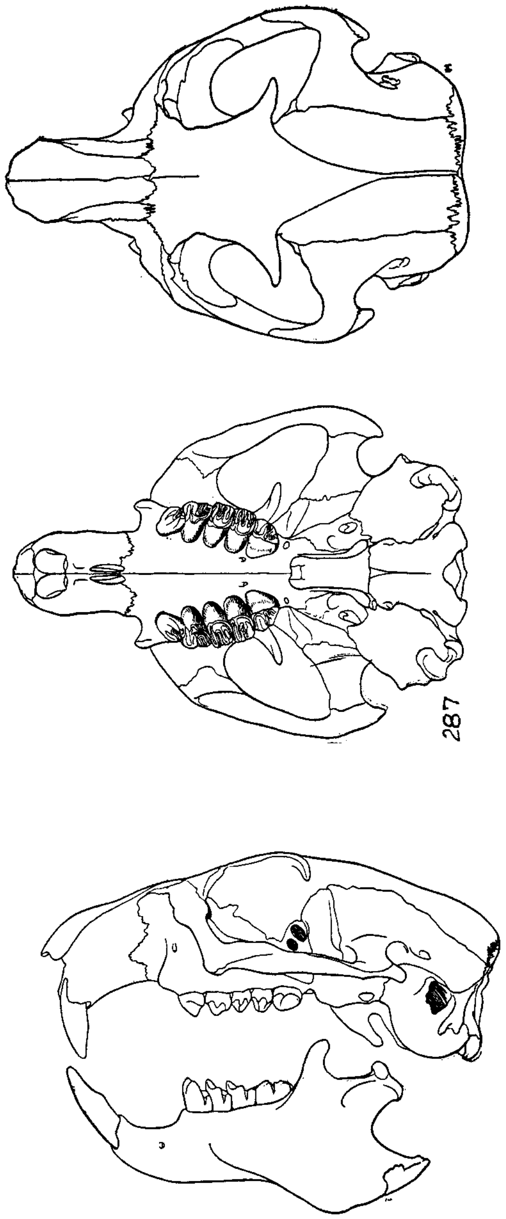

FIG. 2. Ventral, lateral, and dorsal views of cranium and lateral view of mandible of *Cynomys l. ludovicianus*. Greatest length of cranium (this specimen) 61 mm. Photo from Hall (1981).

length of adult and yearling black-tailed prairie dogs ranges from 355 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 = 493–1,147, n = 149) in winter (February–March), and 801 ± 99.0 g (range = 437–1,010, n = 281) in spring (May–June). Comparable body masses for adult females are 819 ± 103 g (range = 470–1,149, n = 430) in autumn, 689 ± 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 = 253–690, 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 = 264–695, 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, 30.7 ± 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, 6.2 ± 0.4 (5.0–6.4); height of foramen magnum, 7.8 ± 0.5 (7.4–8.6); 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); occipital breadth, 21.3 ± 0.9 (20.2–22.2); total length, 373.5 ± 29.3 (354.5–397.8); length of hind foot, 60.2 ± 3.4 (57.5–64.5).

The dental formula for black-tailed prairie dogs, as for other prairie dog species, is i 1/1, c 0/0, p 2/1, m 3/3, 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, 1902). 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, 1986*a*, 1986*b*; O'Meilia 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. spispiza* 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, sparser 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 summer 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 gallstones under laboratory conditions, research with them has led to a better understanding of gall bladder diseases (Broughton et al., 1991). *C. ludovicianus* also has been useful in studies of metabolism (Bakko, 1977; Pfeiffer et al., 1979).

ONTOGENY AND REPRODUCTION. Aging live adult

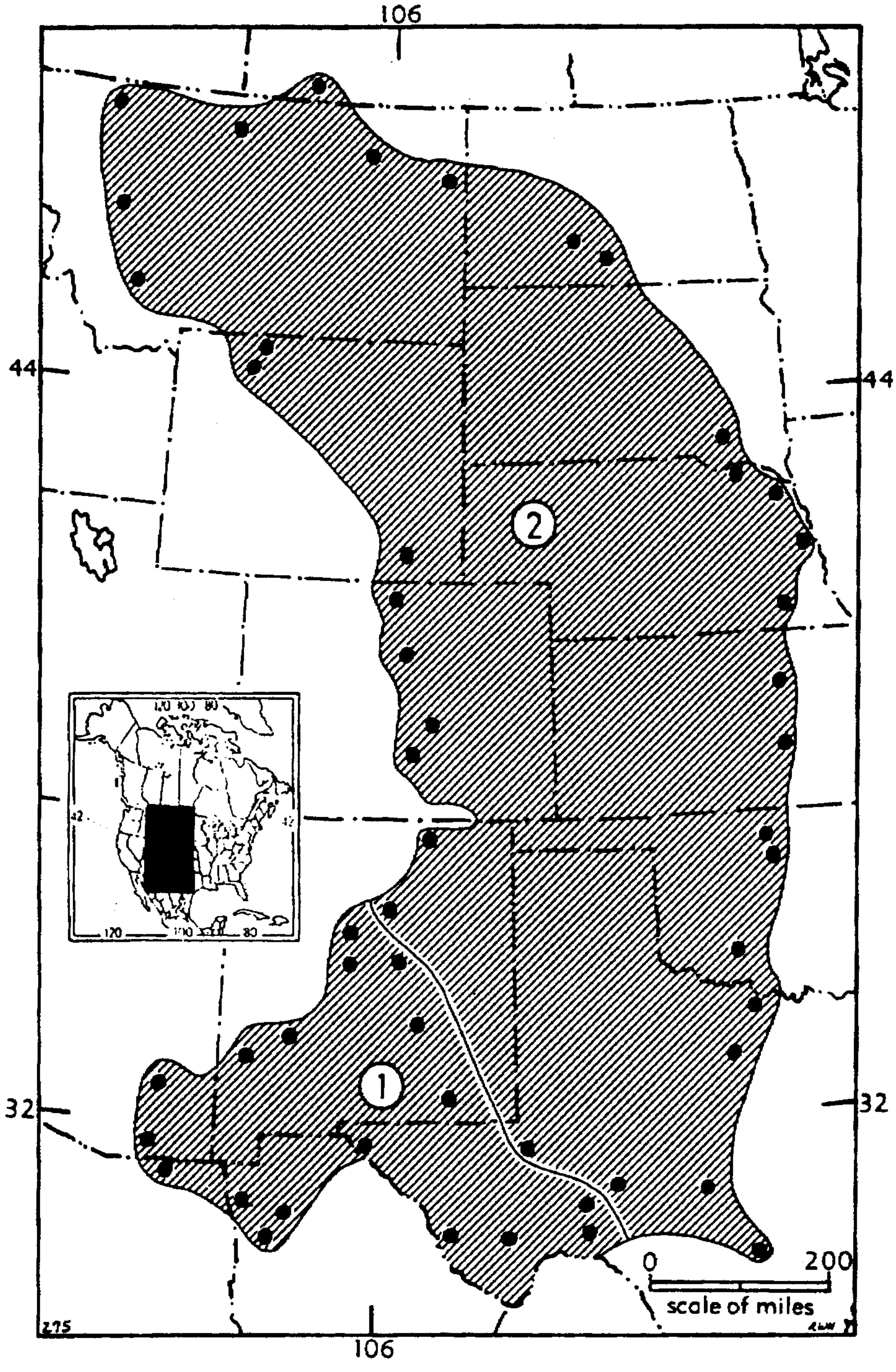

FIG. 3. Geographic range of the two subspecies of black-tailed prairie dogs: 1, *Cynomys l. ludovicianus*; 2, *Cynomys l. arizonensis*. This map shows the range of black-tailed prairie dogs about 150 years ago. In response to shooting, poisoning, and destruction of habitat, black-tailed prairie dogs 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 eartags) as juveniles (Hoogland, 1995). Approximate aging of unmarked 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. ludovicianus* varies curvilinearly with age, but extensive overlap precludes aging from body mass except for the simple distinction between 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 Seabloom, 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, approximately 21 months following first emergence from the natal burrow (Hoogland, 1995; King, 1955; Stockrahm and Seabloom, 1988). However, some individuals first copulate as yearlings (females 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).

Estrous black-tailed prairie dog females are sexually receptive on a single day each year. Rarely, females that do not conceive in the first estrus will come into a second estrus about 13 days later. The breeding season (i.e., the period of 2–3 weeks during which copulations occur) varies with latitude. For example, black-tailed prairie dogs usually copulate in January in Oklahoma, in late February in Colorado, in late February through March in South Dakota, and in late March and early April in Montana (Hoogland, 1995). Dates of first juvenile emergences also indicate that southern black-tailed prairie dogs breed earlier. Juveniles usually first appear aboveground in late April and early May in Oklahoma and Texas, in mid- and late May in Colorado and South Dakota, and in late May and June in North Dakota and Montana (Hoogland, 1995).

Probably to avoid male–male competition for estrous females, black-tailed prairie dogs usually copulate underground (98% of 546 estrous females). Aboveground behaviors that indicate an underground copulation include (1) frequent co-submergence of a breeding male and the estrous female into the same burrow during daylight hours, (2) unusually high frequency of interactions between the estrous female and breeding male(s), (3) self-licking of the genitals, (4) taking nest material underground by the breeding male, (5) a unique male mating call, and (6) late final submergence at the end of the day by the estrous female. Rare aboveground copulations show these same behaviors that are characteristic of underground copulations (Hoogland, 1995).

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; Knowles, 1987). 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 juvenile emergence for *C. ludovicianus,* an estimate of the length of lactation, is 41.3 ± 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, 1987; Tileston and Lechleitner, 1966) 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 = 1–6, n = 361 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 556 ± 98.0 g for males (range = 243–964, n = 189) and 532 ± 87.3 g for females (range = 270–819, n = 178—Hoogland, 1995).

Sixty-seven percent of estrous black-tailed prairie dog females (365/542) copulate with a single male, and 84% (457/542) copulate exclusively with the resident breeding male(s) in the home coterie (or harem; see below). Females in multi-male coteries are more likely than females in one-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, 1982*a*). These males most commonly disperse as yearlings in May and June, when juveniles are once again first appearing aboveground (Garrett and Franklin, 1988). 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 end up in the same coterie territory. When this happens, genetic relatives usually resort to other mechanisms to avoid extreme inbreeding (Hoogland, 1982*a*, 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 dogs 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 1.61 ± 1.74 (range = 0–6, n = 581 females). The mean ± *SD* number of emergent juveniles sired in one year by males that copulate 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 ± 3.85 (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 7.06 ± 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. Heavy 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 to emergence than do later-copulating females. Female ARS correlates negatively, but male ARS correlates positively, with coterie size. For females, 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 herbivorous 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 *Leucocrossuromys,* black-tailed prairie dogs appear aboveground 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; Halpin, 1987; Hoogland, 1995; King, 1955; Knowles, 1985; 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 livetraps baited with whole oats (Hoogland, 1995). A conical, cloth bag facilitates handling. National fingerling eartags 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 70 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 a single breeding adult male, two or three adult females, and several nonbreeding yearlings and juveniles. The mean ± *SD* coterie size (adults and yearlings only) in South Dakota in April is 6.13 ± 3.53 (range = 1–26, n = 273 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, 1986*b*; 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 (Agnew et al., 1986; Klatt and Hein, 1978; Koford, 1958; Whicker and Detling, 1988). Certain plants, such as scarlet globemallow (*Sphaeralcea coccinea*), black nightshade (*Solanum nigrum*), pigweed (*Amaranthus retroflexus*), and the appropriately named prairie dog weed (*Dyssodia papposa*), almost never occur outside colonies of *C. ludovicianus* (King, 1955).

Most dispersing black-tailed prairie dogs move to other 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, antipredator-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 length of the body nearly vertical, an 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-to-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 dog non-kin from different coteries meet, they engage in a flagrant territorial dispute that involves staring, tooth 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 chases as well (Hoogland, 1995).

Animals that prey on *C. ludovicianus* include coyotes (*Canis latrans*), bobcats (*Lynx rufus*), badgers (*Taxidea taxus*), black-footed ferrets (*Mustela nigripes*), golden eagles (*Aquila chrysaetos*), prairie falcons (*Falco mexicanus*), accipiter and buteo hawks (*Accipiter* sp. and *Buteo* sp.), bullsnakes (*Pituophis melanoleucus*), and rattlesnakes (*Crotalus* sp.). Faced with so many predators, individuals spend about one-third of their time scanning for enemies (Hoogland, 1979*b*). Upon detecting a predator, black-tailed prairie dogs commonly give loud, repetitious antipredator calls. Individuals call not only to warn offspring, but also to warn nondescendant kin such as siblings, aunts and uncles, and nieces and nephews (Hoogland, 1983, 1995). The superb protection from predators that results from so many individuals scanning and giving antipredator calls is 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, 1979*a*). The most common species of fleas are *Opisocrostis hirsutus*, *O. tuberculatus*, *O. labis*, *Pulex simulans*, *P. irritans*, and *Leptopsylla segnis* (Ecke and Johnson, 1952; Pizzimenti, 1975; Smit, 1958). The most common species of ticks are *Ixodes kingi* and *Atricholaelaps glasgowi* (King, 1955; Pizzimenti, 1975; Tyler and Buscher, 1975). No information is available regarding the species of lice that infest *C. ludovicianus*. Fleas transmit bacteria (*Pastuerella* [*Yersinia*] *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; Pollitzer and Meyer, 1961). Entire colonies quickly disappear after the initial introduction of plague (Barnes, 1993; 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 dog 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 Biggins and Schroeder, 1988; Hoogland, 1995; Sparks, 1973; Stuart and Christensen, 1973; Torres, 1973). Coloniality 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 nocturnal, burrow-entering black-footed ferrets (Hoogland, 1982*b*). 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 (*Agopyron* 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.), thistle (*Cirsium* sp.), and underground roots. Common plants within colonies that black-tailed prairie dogs usually avoid include sagebrush (*Artemisia* sp.), threeawn (*Aristida* sp.), prairie dog weed, and horseweed (*Conyza ramosissima*; Costello, 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 sometimes live as long as eight years under natural conditions in South Dakota, but males never live longer than five years (Hoogland, 1995).

Perhaps because cumulative experience is so important to reproductive success, costs of reproduction among black-tailed prairie dogs are absent or subtle. When compared with unsuccessful individuals, for example, individuals that produce emergent offspring in one year do not differ in the next year regarding survivorship, probability of reproduction, or number of emergent juveniles produced (Hoogland, 1995).

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 5 to 10 m long and 2 to 3 m deep, but some are as long as 33 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 50 cm wide (Gunderson, 1978; Sheets et al., 1971). Most black-tailed prairie dog burrows have only one or two entrances. 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 usually 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, like those under dome craters, are commonly suitable for seeking safety from predators, spending the night, and rearing offspring (Hoogland, 1995). Especially 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 dogs enter their burrows at about 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 Collier, 1975; Tileston and Lechleitner, 1966; Wright-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. In addition, the mounds facilitate underground ventilation via 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 coteries 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 not only their own offspring, but the offspring 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 7% of litters, occurs when male immigrants kill weaned or unweaned juveniles after taking over a coterie territory. The four types of infanticide together account for the partial or total demise of 39% of litters born into prairie dog colonies. Infanticide occurs among myriad species (Hausfater and Hrdy, 1984; Hrdy, 1979; Sherman, 1981), including sciurid species (Brody and Melcher, 1985; Dobson, 1990; McLean, 1983; Trulio et al., 1986; Vestal, 1991), but only rarely at the high frequency observed within colonies of black-tailed prairie dogs.

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 natal burrow (Hoogland, 1995).

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., 1983*a*, 1983*b*; 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 commonly prefer to forage at colony sites (Carr, 1973; Knowles, 1986*b*; Koford, 1958; O'Meilia 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 should be able to co-exist. 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 harvester ants (*Pogonomyrmex occidentalis*) to mountain plovers (*Eupoda 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, 1968; Hillman and Linder, 1973). Finally, research with *C. ludovicianus* has contributed significantly to our understanding of natural selection and the evolution of social behavior (Garrett and Franklin, 1988; Halpin, 1987; Hoogland, 1995; King, 1955; Knowles, 1985; Loughry, 1988; Smith, 1967; Tileston and Lechleitner, 1966). For these and other reasons (Hoogland, 1995; McNulty, 1971), wildlife biologists should continue to emphasize the conservation and longterm survival of black-tailed prairie dogs (Oldemeyer et al., 1993; Seal et al., 1989).

GENETICS. Black-tailed prairie dogs have a diploid number (2n) of 50 chromosomes, as do all other prairie dog species except *C. gunnisoni* (2n = 40). The biarmed autosomes consist of 15 pairs of metacentrics and 9 pairs of submetacentrics. The X chromosome is a small- or medium-sized submetacentric, and the Y chromosome is a small acrocentric (Nadler et al., 1971; Pizzimenti, 1975).

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 polymorphism. At least seven of these loci are polymorphic: esterase-1, esterase-4, mannose phosphoisomerase, 6-phosphogluconate dehydrogenase, transferrin, nucleoside phosphorylase, phosphoglucomutase-2; the first four of these loci have two alleles, the next two have three alleles, and phosphoglucomutase-2 has four alleles (Daley, 1992; Foltz and Hoogland, 1983; Foltz et al., 1988; see also Chesser, 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).

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LITERATURE CITED

AGNEW, W., D. W. URESK, AND R. M. HANSEN. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. Journal of Range Management, 39:135–139.

ANDERSON, E., S. C. FORREST, T. W. CLARK, AND L. RICHARDSON. 1986. Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851. Great Basin Naturalist Memoirs, 8:11–62.

ANTHONY, A., AND D. FOREMAN. 1951. Observations on the reproductive cycle of the black-tailed prairie dog (*Cynomys ludovicianus*). Physiological Zoology, 24:242–248.

BAIRD, S. F. 1858. Mammals. Reports of exploration and surveys . . . for a railroad from the Mississippi River to the Pacific Ocean, volume 8. United States War Department. Washington, D.C., 757 pp.

BAKKO, E. B. 1977. Field water balance performance in prairie dogs (*Cynomys leucurus* and *C. ludovicianus*). Comparative Biochemical Physiology, 56:443–451.

BARNES, A. M. 1982. Surveillance and control of bubonic plague in the United States. Symposia of the Zoological Society of London, 50:237–270.

———. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pp. 28–37, *in* Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of black-footed ferrets (J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, eds.). United States Fish and Wildlife Services, Biological Report, 93:1–96. Washington, D.C.

BARNES, A. M., L. J. OGDEN, AND E. G. CAMPOS. 1972. Control of the plague vector, *Opisocrostis hirsutis*, by treatment of prairie dog (*Cynomys ludovicianus*) burrows with 2% carbaryl dust. Journal of Medical Entomology, 9:330–333.

BIGGINS, D., AND M. H. SCHROEDER. 1988. Historical and present status of the black-footed ferret. Pp. 93–97, *in* Eighth Great Plains wildlife damage control workshop proceedings (D. W. Uresk, G. L. Schenbeck, and R. Cefkin, tech. coords.). General technical report RM-154. Fort Collins, Colorado, 231 pp.

BLACK, C. C. 1963. A review of the North American Tertiary Sciuridae. Museum of Comparative Zoology, Harvard University, Bulletin, 130:109–248.

BRODY, A. K., AND J. MELCHER. 1985. Infanticide in yellow-bellied marmots. Animal Behaviour, 33:673–674.

BROUGHTON, G., A. TSENG, R. FITZGIBBONS, S. TYNDALL, G. STANISLAV, AND E. RONGONE. 1991. The prevention of cholelithiasis with infused chenodeoxycholate in the prairie dog (*Cynomys ludovicianus*). Comparative Biochemical Physiology, 99A:609–613.

BRYANT, M. D. 1945. Phylogeny of nearctic Sciuridae. American Midland Naturalist, 33:257–390.

CAMPBELL, T. M., AND T. W. CLARK. 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. American Midland Naturalist, 105:269–276.

CAMPBELL, T. M., T. W. CLARK, L. RICHARDSON, S. C. FORREST, AND B. R. HOUSTON. 1987. Food habits of Wyoming black-footed ferrets. American Midland Naturalist, 117:208–210.

CARR, J. F. 1973. A rancher's view towards prairie dogs. Pp. 168–170, *in* Proceedings of the black-footed ferret and prairie dog workshop (R. L. Linder and C. N. Hillman, eds.). South Dakota State University, Brookings, South Dakota, 208 pp.

CEBALLOS, G., AND D. E. WILSON. 1985. Cynomys mexicanus. Mammalian Species, 248:1–4.

CEBALLOS, G., E. MELLINK, AND L. HANEBURY. 1993. Distribution and conservation status of prairie dogs (*Cynomys mexicanus* and *Cynomys ludovicianus*) in Mexico. Biological Conservation, 63:105–112.

CHESSER, R. K. 1983. Genetic variability within and among populations of the black-tailed prairie dog. Evolution, 37:320–331.

CLARK, T. W. 1977. Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*). Publications in biology and geology, Milwaukee Public Museum, Milwaukee, Wisconsin, 3: 1–97.

———. 1979. The hard life of the prairie dog. National Geographic, 156:270–281.

———. 1989. Conservation biology of the black-footed ferret, *Mustela nigripes*. Special Scientific Report 3:1–175. Wildlife Preservation Trust International, Philadelphia, Pennsylvania.

CLARK, T. W., R. S. HOFFMANN, AND C. F. NADLER. 1971. *Cynomys leucurus*. Mammalian Species, 7:1–4.

CLARK, T. W., L. RICHARDSON, D. E. CASEY, T. M. CAMPBELL, AND S. C. FORREST. 1984. Seasonality of black-footed ferret diggings and prairie dog burrow plugging. The Journal of Wildlife Management, 48:1441–1444.

CLARK, T. W., L. RICHARDSON, S. C. FORREST, D. E. CASEY, AND T. M. CAMPBELL. 1986. Descriptive ethology and activity patterns of black-footed ferrets. Great Basin Naturalist Memoirs, 8:115–134.

COPPOCK, D. L., J. K. DETLING, J. E. ELLIS, AND M. I. DYER. 1983*a*. Plant–herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia, 56:1–9.

COPPOCK, D. L., J. E. ELLIS, J. K. DETLING, AND M. I. DYER. 1983*b*. Plant–herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. Oecologia, 56:10–15.

COSTELLO, D. F. 1970. The world of the prairie dog. Lippincott, Philadelphia, Pennsylvania, 160 pp.

COX, M. K., AND W. L. FRANKLIN. 1990. Premolar gap technique for aging live black-tailed prairie dogs. The Journal of Wildlife Management, 54:143–146.

DALEY, J. G. 1992. Population reductions and genetic variability in black-tailed prairie dogs. The Journal of Wildlife Management, 56:212–220.

DOBSON, F. S. 1990. Environmental influences on infanticide in Columbian ground squirrels. Ethology, 84:3–14.

ECKE, D. H., AND C. W. JOHNSON. 1952. Plague in Colorado. United States Public Health Monograph, 6, Part I:1–37.

Elliot, D. G. 1905. Descriptions of apparently new mammals of the genera *Ovibos*, *Cynomys*, and *Mustela*. Proceedings of the Biological Society of Washington, 18:135–140.

Eskey, C. R., and V. H. Haas. 1940. Plague in the western part of the United States. United States Public Health Bulletin, 254:1–83.

Ferrara, J. 1985. Prairie home companions. National Wildlife, 23:48–53.

Fitzgerald, J. P., and R. R. Lechleitner. 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. American Midland Naturalist, 92:146–163.

Foltz, D. W., and J. L. Hoogland. 1981. Analysis of the mating system of the black-tailed prairie dog (*Cynomys ludovicianus*) by likelihood of paternity. Journal of Mammalogy, 62:706–712.

———. 1983. Genetic evidence of outbreeding in the black-tailed prairie dog (*Cynomys ludovicianus*). Evolution, 37: 273–281.

Foltz, D. W., J. L. Hoogland, and G. M. Koscielny. 1988. Effects of sex, litter size, and heterozygosity on juvenile weight in black-tailed prairie dogs (*Cynomys ludovicianus*). Journal of Mammalogy, 69:611–614.

Foreman, D. 1962. The normal reproductive cycle of the female prairie dog and the effects of light. Anatomical Record, 142: 391–405.

Garrett, M. G., and W. L. Franklin. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. Journal of Mammalogy, 69:236–250.

Goodwin, H. T. 1993. Subgeneric identification and biostratigraphic utility of late Pleistocene prairie dogs (*Cynomys*, Sciuridae) from the Great Plains. Southwestern Naturalist, 38: 105–110.

———. 1995. Systematic revision of fossil prairie dogs with descriptions of two new species. Miscellaneous Publications, University of Kansas Natural History Museum, 86:1–38.

Gunderson, H. L. 1978. Under and around a prairie dog town. Natural History, 87:57–66.

Hafner, D. J. 1984. Evolutionary relationships of the Nearctic Sciuridae. Pp. 3–23, *in* The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, Nebraska, 459 pp.

Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 2:601–1180 + 90 pp.

Halpin, Z. T. 1983. Naturally occurring encounters between black-tailed prairie dogs (*Cynomys ludovicianus*) and snakes. American Midland Naturalist, 109:50–54.

———. 1987. Natal dispersal and the formation of new social groups in a newly established town of black-tailed prairie dogs (*Cynomys ludovicianus*). Pp. 104–118, *in* Mammalian dispersal patterns: the effects of social structure on population genetics (B. D. Chepko-Sade and Z. T. Halpin, eds.). University of Chicago Press, Chicago, Illinois, 342 pp.

Harlan, R. 1825. Fauna Americana being a description of the mammiferous animals inhabiting North America. Anthony Finley Press, Philadelphia, Pennsylvania, 318 pp.

Hausfater, G., and S. B. Hrdy (eds.). 1984. Infanticide: comparative and evolutionary perspectives. Aldine, New York.

Hay, O. P. 1921. Description of Pleistocene Vertebrata, types of specimens of which are preserved in the United States National Museum. Proceedings of the United States National Museum, 59:617–638.

Henderson, F. R., P. F. Springer, and R. Adrian. 1969. The black-footed ferret in South Dakota. Technical Bulletin 4:1–37. South Dakota Department of Game, Fish, and Parks, Pierre, South Dakota.

Hibbard, C. W. 1937. *Cynomys ludovicianus ludovicianus* from the Pleistocene of Kansas. Journal of Mammalogy, 18:517–518.

Hillman, C. N. 1968. Field observations of black-footed ferrets in South Dakota. Transactions, North American Wildlife and Natural Resources Conference, 33:433–443.

Hillman, C. N., and R. L. Linder. 1973. The black-footed ferret. Pp. 10–23, *in* Proceedings of the black-footed ferret and prairie dog workshop (R. L. Linder and C. N. Hillman, eds.). South Dakota State University, Brookings, South Dakota, 208 pp.

Hoffmann, R. S., C. G. Anderson, R. W. Thorington, and L. R. Heaney. 1993. Family Sciuridae. Pp. 419–465, *in* Mammal species of the world: a taxonomic and geographic reference (D. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., 1,206 pp.

Hollister, N. 1916. A systematic account of the prairie dogs. North American Fauna, 40:1–37.

Hoogland, J. L. 1979*a*. Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae: *Cynomys* spp.) coloniality. Behaviour, 69:1–35.

———. 1979*b*. The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). Animal Behaviour, 27:394–407.

———. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). Ecology, 62:252–272.

———. 1982*a*. Prairie dogs avoid extreme inbreeding. Science, 215:1639–1641.

———. 1982*b*. Reply to a comment by Powell. Ecology, 63: 1968–1969.

———. 1983. Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). Animal Behaviour, 31: 472–479.

———. 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. Science, 230:1037–1040.

———. 1986. Nepotism in prairie dogs (*Cynomys ludovicianus*) varies with competition but not with kinship. Animal Behaviour, 34:263–270.

———. 1992. Levels of inbreeding among prairie dogs. American Naturalist, 139:591–602.

———. 1995. The black-tailed prairie dog: social life of a burrowing mammal. The University of Chicago Press, Chicago, Illinois, 557 pp.

———. 1996. Why do Gunnison's prairie dogs give anti-predator calls? Animal Behaviour, 51:871–880.

Hoogland, J. L., and D. W. Foltz. 1982. Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). Behavioral Ecology and Sociobiology, 11:155–163.

Hoogland, J. L., and J. M. Hutter. 1987. Aging live prairie dogs from molar attrition. The Journal of Wildlife Management, 51:393–394.

Hoogland, J. L., R. H. Tamarin, and C. K. Levy. 1989. Communal nursing in prairie dogs. Behavioral Ecology and Sociobiology, 24:91–95.

Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethology and Sociobiology, 1:13–40.

Johnson, G. E. 1927. Observations on young prairie dogs (*Cynomys ludovicianus*) born in the laboratory. Journal of Mammalogy, 8:110–115.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. Contributions from the Laboratory of Vertebrate Biology, University of Michigan, 67:1–123.

———. 1984. Historical ventilations on a prairie dog town. Pp. 447–456, *in* The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, Nebraska, 459 pp.

Klatt, L. E., and D. Hein. 1978. Vegetative differences among active and abandoned towns of black-tailed prairie dogs (*Cynomys ludovicianus*). Journal of Range Management, 31:315–317.

Knowles, C. J. 1985. Observations on prairie dog dispersal in Montana. Prairie Naturalist, 17:33–40.

———. 1986*a*. Population recovery of black-tailed prairie dogs following control with zinc phosphide. Journal of Range Management, 39:249–251.

———. Some relationships of black-tailed prairie dogs to livestock grazing. Great Basin Naturalist, 46:198–203.

———. 1987. Reproductive ecology of black-tailed prairie dogs in Montana. Great Basin Naturalist, 47:202–206.

Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs, 3:1–78.

Lechleitner, R. R. 1969. Wild mammals of Colorado. Pruett Publishers, Boulder, Colorado, 254 pp.

Loughry, W. J. 1988. Population differences in how black-tailed prairie dogs deal with snakes. Behavioral Ecology and Sociobiology, 22:61–67.

Martin, S. J., and M. H. Schroeder. 1978. Black-footed ferret surveys on seven coal occurrence areas in southwestern and southcentral Wyoming, June 8 to September 25, 1978: final report. United States Fish and Wildlife Service, Denver, Colorado, 37 pp.

———. 1980. Black-footed ferret surveys on seven coal occurrence areas in Wyoming, February–September, 1979: final report. Wyoming State Office, United States Bureau of Land Management, Cheyenne, Wyoming, 34 pp.

McLean, I. G. 1983. Paternal behaviour and killing of young in arctic ground squirrels. Animal Behaviour, 31:32–44.

McNulty, F. 1971. Must they die? The strange case of the prairie dog and the black-footed ferret. Doubleday, Garden City, New York, 86 pp.

Mearns, E. A. 1890. Description of supposed new species and subspecies of mammals, from Arizona. Bulletin, American Museum of Natural History, 2:277–307.

Merriam, C. H. 1892. Description of a new prairie dog (*Cynomys mexicanus*) from Mexico. Proceedings of the Biological Society of Washington, 7:157–158.

———. 1902. The prairie dog of the great plains. Pp. 257–270, *in* Yearbook of United States Department of Agriculture (1901). Washington, D.C., 600 pp.

Nadler, C. F., R. S. Hoffmann, and J. J. Pizzimenti. 1971. Chromosomes and serum proteins of prairie dogs and a model of *Cynomys* evolution. Journal of Mammalogy, 52:545–555.

Oldemeyer, J. L., D. E. Biggins, B. J. Miller, and R. Crete, eds. 1993. Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of black-footed ferrets. United States Fish and Wildlife Services, Biological Report 93:1–96. Washington, D.C.

O'Meilia, M. E., F. L. Knopf, and J. C. Lewis. 1982. Some consequences of competition between prairie dogs (*Cynomys ludovicianus*) and beef cattle. Journal of Range Management, 35:580–585.

Ord, G. 1815. North American Zoology. Pp. 291–361, *in* A new geographical, historical, and commercial grammar, volume 2: 1–600 (W. Guthrie, ed.). Second ed. Lippincott, Philadelphia, Pennsylvania.

Pfeiffer, E. W., L. N. Reinking, and J. D. Hamilton. 1979. Some effects of food and water deprivation on metabolism in black-tailed prairie dogs *Cynomys ludovicianus*. Comparative Biochemical Physiology, 63:19–22.

Pizzimenti, J. J. 1975. Evolution of the prairie dog genus *Cynomys*. Occasional papers of the Museum of Natural History, University of Kansas, 39:1–73.

Pizzimenti, J. J., and G. D. Collier. 1975. Cynomys parvidens. Mammalian Species, 52:1–3.

Pizzimenti, J. J., and L. R. McCleneghan. 1974. Reproduction, growth and development, and behavior in the Mexican prairie dog, *Cynomys mexicanus* (Merriam). American Midland Naturalist, 92:130–145.

Pollitzer, R., and K. F. Meyer. 1961. The ecology of plague. Pp. 433–501, *in* Studies of disease ecology (J. M. May, ed.). Hafner Press, New York, 613 pp.

Powell, R. A. 1982. Prairie dog coloniality and black-footed ferrets. Ecology, 63:1967–1968.

Rafinesque, C. S. 1817. Museum of Natural Sciences. 9. Synopsis of four new genera and ten new species of Crustacea, found in the United States. American Monthly Magazine, 2: 40–46.

Rayor, L. S. 1988. Social organization and space-use in Gunnison's prairie dog. Behavioral Ecology and Sociobiology, 22: 69–78.

Richardson, J. 1829. Fauna Boreali-Americana; or The zoology of the northern parts of British America, volume 1:1–300. John Murray Press, London, England.

Seal, U. S., E. T. Thorne, M. A. Bogan, and S. H. Anderson (eds.). 1989. Conservation biology and the black-footed ferret. Yale University Press, New Haven, Connecticut, 302 pp.

Sheets, R. G., R. L. Linder, and R. B. Dahlgren. 1971. Burrow systems of prairie dogs in South Dakota. Journal of Mammalogy, 52:451–453.

Sherman, P. W. 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals. Pp. 311–331, *in* Natural selection and social behavior (R. D. Alexander and D. W. Tinkle, eds.). Chiron Press, New York, 532 pp.

Slobodchikoff, C. N., J. Kiriazis, C. Fischer, and E. Creef. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. Animal Behaviour, 42:713–719.

Smit, F. G. A. M. 1958. A preliminary note on the occurrence of *Pulex irritans* and *Pulex simulans* in North America. Journal of Parasitology, 44:523–526.

Smith, R. E. 1967. Natural history of the prairie dog in Kansas. Miscellaneous Publications, Museum of Natural History, University of Kansas, 49:1–39.

Smith, W. J., S. L. Smith, J. G. deVilla, and E. L. Oppenheimer. 1976. The jump-yip display of the black-tailed prairie dog, *Cynomys ludovicianus*. Animal Behaviour, 24:609–621.

Smith, W. J., S. L. Smith, E. C. Oppenheimer, and J. G. deVilla. 1977. Vocalizations of the black-tailed prairie dog, *Cynomys ludovicianus*. Animal Behavior, 25:152–164.

Snell, G. P. 1985. Results of control of prairie dogs. Rangelands, 7:30.

Sparks, E. A. 1973. Prairie dogs and black-footed ferrets in Utah. Pp. 102–104, *in* Proceedings of the black-footed ferret and prairie dog workshop (R. L. Linder and C. N. Hillman, eds.). South Dakota State University, Brookings, South Dakota, 208 pp.

Stockrahm, D. M. B., and R. W. Seabloom. 1988. Comparative reproductive performance of black-tailed prairie dog populations in North Dakota. Journal of Mammalogy, 69:160–164.

———. 1990. Tooth eruption in black-tailed prairie dogs from North Dakota. Journal of Mammalogy, 71:105–108.

Stuart, J. E. B., and A. G. Christensen. 1973. The status of black-footed ferrets and prairie dogs in New Mexico. Pp. 47–50, *in* Proceedings of the black-footed ferret and prairie dog workshop (R. L. Linder and C. N. Hillman, eds.). South Dakota State University, Brookings, South Dakota, 208 pp.

Summers, C. A., and R. L. Linder. 1978. Food habits of the black-tailed prairie dog in western South Dakota. Journal of Range Management, 31:134–136.

Tate, G. H. H. 1947. Albino prairie dog. Journal of Mammalogy, 28:62.

Tileston, J. V., and R. R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. American Midland Naturalist, 75:292–316.

Torres, J. R. 1973. The future of the black-footed ferret in Colorado. Pp. 27–33, *in* Proceedings of the black-footed ferret and prairie dog workshop (R. L. Linder and C. N. Hillman, eds.). South Dakota State University, Brookings, South Dakota, 208 pp.

Trevino-Villarreal, J. 1990. The annual cycle of the Mexican prairie dog (*Cynomys mexicanus*). Occasional Papers, Museum of Natural History, University of Kansas, 139:1–27.

Trulio, L. A., W. J. Loughry, D. F. Hennessy, and D. H. Owings. 1986. Infanticide in California ground squirrels. Animal Behaviour, 34:291–294.

Tyler, J. D., and H. N. Buscher. 1975. Parasites of vertebrates inhabiting prairie dog towns in Oklahoma. I. Ectoparasites. Proceedings of the Oklahoma Academy of Science, 55:166–168.

Uresk, D. W. 1984. Black-tailed prairie dog food habits and forage relationships in western South Dakota. Journal of Range Management, 37:325–329.

———. 1985. Effects of controlling black-tailed prairie dogs on plant production. Journal of Range Management, 38:466–468.

Vestal, B. M. 1991. Infanticide and cannibalism by male thirteen-lined ground squirrels. Animal Behaviour, 41:1103–1104.

Vogel, S., C. P. Ellington, and D. L. Kilgore. 1973. Wind-induced ventilation of the burrow of the prairie-dog, *Cynomys ludovicianus*. Journal of Comparative Physiology, 85:1–15.

Wade, O. 1928. Notes on the time of breeding and the number of young of *Cynomys ludovicianus*. Journal of Mammalogy, 9:149.

Warden, D. B. 1819. A statistical, political, and historical account of the United States of North America from the period of their first colonization to the present day, volume 1:1–552. George Ramsey and Company, Edinburgh, Scotland.

Waring, G. H. 1970. Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. American Midland Naturalist, 83:167–185.

Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. Bioscience, 38:778–785.

Wood, A. E. 1933. Pleistocene prairie-dog from Frederick, Oklahoma. Journal of Mammalogy, 14:160.

WRIGHT-SMITH, M. A. 1978. The ecology and social organization of *Cynomys parvidens* (Utah prairie dog) in south central Utah. M.S. thesis, Indiana University, Bloomington, Indiana, 44 pp.

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