Biological Report 13
July 1993

Proceedings of the Symposium on the

Management of Prairie Dog Complexes for the Reintroduction of the Black-footed Ferret

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Management of Prairie Dog Complexes for the Reintroduction of the Black-footed Ferret

Edited by

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Contents

Dedication

George E. Menkens, Jr., 1957–1990

This collection of papers on the management of the prairie dog ecosystem is dedicated to George E. Menkens, Jr. Menkens, his fellow biologist John Bevins of the U.S. Fish and Wildlife Service, and pilot Clifford Minch failed to return from a flight to radio-track polar bears over the Arctic icecap on 11 October 1990. Menkens was a participant in the conservation of the prairie dog ecosystem, and his paper in this workshop was the result of 6 years of research into white-tailed prairie dogs in central and southern Wyoming. Menkens studied the biology of prairie dogs as a graduate student in the Wyoming Cooperative Fish and Wildlife Research Unit, and he received a Ph.D. from the University of Wyoming in 1988. He was an energetic worker, and his research was published in several journals. Menkens was involved in prairie dog and black-footed ferret issues as a scientist and conservationist, and he rallied to the support of the prairie dog ecosystem and the plethora of species that depend on that system.

Introduction

At the beginning of this century, prairie dog (*Cynomys*) colonies covered over 40 million ha of native short and mixed grass prairies in western North America but by 1960 had been reduced to cover only about 600,000 ha (Marsh 1984) or 2% of the area that was formerly occupied by the four species of prairie dogs. A significant part of that reduction was due to the control of prairie dogs for the benefit of the livestock industry. Merriam (1902) once estimated that prairie dogs reduced range productivity by 50–75%. Subsequently, prairie dogs on millions of acres were poisoned (Bell 1921; Day and Nelson 1929; Anderson et al. 1986; Dunlap 1988), although modern research indicated only a 4–7% level of competition between livestock and prairie dogs (Uresk and Paulson 1988). The recent spread of the sylvatic plague, a disease that is probably exotic to North America, further reduced the numbers of prairie dogs.

Regardless of the reason or combination of reasons, loss of prairie dog populations reduces vertebrate biodiversity in the prairie ecosystem. Over 100 vertebrate species use prairie dog colonies as habitat (Clark et al. 1989; Sharps and Uresk 1990), and the prairie dog community supports higher numbers of small mammals and arthropods, more terrestrial predators, higher avian species diversity, and higher avian density than surrounding areas (Hansen and Gold 1977; O'Meilia et al. 1982; Agnew et al. 1986; Krueger 1986; Reading et al. 1989). Prairie dog activity increases nutrient content and digestibility of grasses for herbivores, and bison (*Bison bison*) and domestic cattle preferentially graze on prairie dog colonies (O'Meilia et al. 1982; Coppock et al. 1983; Detling and Whicker 1988).

The reduced number, size, and distribution of prairie dog colonies increase risk for all species associated with that community. Small isolated populations of prairie dogs are more susceptible to disease, inbreeding, and catastrophic events. Highly specialized animals like the black-footed ferret (*Mustela nigripes*) are most vulnerable to the effects of habitat fragmentation.

Black-footed ferrets were historically distributed across the western plains of North America (Anderson et al. 1986). Ferrets are habitat specialists and dependent on prairie dog colonies for survival (Hillman 1968, Biggins et al. 1985). Over 90% of the black-footed ferret's diet comprises prairie dogs (Sheets et al. 1972; Campbell et al. 1987), and ferrets use prairie dog burrows as their sole source of shelter. Once widely distributed, black-footed ferrets are now listed as endangered by the U.S. Fish and Wildlife Service (Federal Register 32:4001, 11 March 1967), and only one population was known to exist in the 1980's. That population, near Meeteetse, Wyoming, collapsed during an epidemic of canine distemper in 1985 (Williams et al. 1988). Surviving ferrets were captured and placed in a captive breeding facility managed by the Wyoming Game and Fish Department. By 1989, successful captive breeding of ferrets and plans for the reintroduction of ferrets into the wild were initiated.

As part of that planning process, the U.S. Fish and Wildlife Service sponsored a two-day workshop in August 1989 on management of prairie dogs. The importance of that topic is obvious. Black-footed ferrets depend on prairie dog communities (Hillman 1968; Biggins et al. 1985) and must be reintroduced into their native habitat for successful recovery. There are also obvious biological and political difficulties. Biologically, prairie dog populations are fragmented and highly susceptible to the sylvatic plague. Politically, efforts to reduce prairie dog numbers through chemical control continue.

The workshop featured a review of current knowledge in the biology of prairie dogs in the context of managing black-footed ferret habitat. The review addressed two main components. The first consisted of a series of papers on prairie dog habitat and biology.

The first paper, by Hanson, provides an historical account of the control of prairie dogs in South Dakota where control operations profoundly reduced prairie dog populations. The next four papers deal with the ecology of prairie dogs in the Great Plains. The presentations by Uresk and Reading were based on timely papers published prior to the workshop. Because they contribute a vital basis for understanding the prairie dog ecosystem, the reference to those papers and a short abstract of the results are included in the proceedings. Uresk's abstract and the paper by Whicker and Detling address interactions between livestock, prairie dogs, and vegetation. The paper by Whicker and Detling, the paper by Munn, and

Reading's abstract address the importance of prairie dogs to the integrity of the grassland ecosystem.

The papers by Barnes, Cully, and Fitzgerald on the plague and prairie dogs are critical to the selection of sites for the reintroduction of black-footed ferrets because plague plays a major role in regulating present prairie dog populations. The paper by Coffeen and Pedersen includes discussion of the relocation of the endangered Utah prairie dog (*Cynomys parvidans*). Indeed, management of black-footed ferrets may ultimately require relocation of prairie dogs from one site to another, particularly if plague reduces the viability of an important site for reintroduction.

The last two papers are evaluations of prairie dog populations. Menkens and Anderson discuss census techniques. Biggins et al. describe the method used by the Black-footed Ferret Interstate Coordinating Committee for evaluating potential habitat for black-footed ferrets.

The second component of the workshop was a summary of the participants' discussion about managing prairie dog complexes. This discussion was based on the previously identified papers and profited from the participants' expertise on the ecology of black-footed ferrets and prairie dogs. The report provides current and comprehensive information about management of habitat for prairie dogs and black-footed ferrets and is a useful guide for agencies and individuals that manage black-footed ferrets.

Participants of the workshop were: Allan Barnes, Dean Biggins, Tom Campbell, Mike Coffeen, Ron Crete, Jack Culley, Jim Detling, Jim Fitzgerald, Louise Forrest, Steve Forrest, Monte Garret, John Grinsten, Lou Hanebury, Rew Hanson, Bob Luce, George Menkens, Brian Miller, Larry Munn, Jordan Pederson, Larry Shanks, Tom Thorne, Dan Uresk, and April Whicker.

We appreciate and acknowledge the assistance of the following: Joan Thielbaud for making arrangements for the workshop; Spencer Amend for facilitating the discussion that resulted in the workshop summary; and Dora Medellin for merging the individual manuscripts into a single style and format.

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Control of Prairie Dogs and Related Developments in South Dakota

by

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The black-tailed prairie dog (*Cynomys ludovicianus*) is a South Dakota native with a long history of controversy about its activities and control. Control of prairie dogs dates back to 1914. Little information about it was recorded, however, until the passage of a rodent control law by the South Dakota Legislature in 1919.

Nine counties west of the Missouri River in South Dakota provided the first reports of control in 1920 when prairie dogs in towns of 161,190 ha were poisoned. Control of the prairie dog has continued to the present time whenever colonies expanded to where they were not tolerated by landowners and managers. Populations of prairie dogs increased in South Dakota during the 1930's as a result of reduced control, drought, and overgrazing during the depression and dust bowl, in the mid-1940's after control was relaxed, and in the late 1970's as a result of a ban on the control of prairie dogs. In 1968, the estimated area occupied by prairie dogs in South Dakota was 24,705 ha; prairie dogs expanded 12-fold to 295,650 ha by 1980. Although many social, economic, political, biological, and climatic conditions influenced these fluctuations, control itself is self-limiting. As control succeeds, concern about prairie dogs decreases.

Organization, Regulations, and Rodenticides

Early controls were organized county-by-county by the county commissioners, the county agent, and the Bureau of Biological Survey of the U.S. Department of Agriculture. The Bureau of Biological Survey provided training, direction, and demonstrations on preparation of bait, application procedures, and other technical aspects of control. After implementation, the supervision of the project was usually delegated to the county agent who became the key figure in the prairie dog control.

In 1930, the Bureau of Biological Survey moved its offices from Rapid City to Mitchell and established the first central bait-mixing plant. From 1914 through the 1940's, strychnine oat bait was the rodenticide of choice. In 1940, the Bureau of Biological Survey was transferred from the Department of Agriculture to the Department of the Interior and became the Fish and Wildlife Service. Beginning in 1950, operational use of Compound 1080 oats under the direct supervision of Predator and Rodent Control personnel of the service was the standard prairie dog control procedure. Strychnine bait, however, was still used by many private landowners. From the late 1940's to the mid-1950's, 8,100–20,250 ha / year were treated with Compound 1080.

From 1955 to 1965, prairie dog populations were maintained at low levels. In 1965, the policy on pre-control surveys of black-footed ferrets (*Mustela nigripes*) was established. This policy required that surveys of ferrets be conducted prior to control of prairie dogs and added considerable costs to control operations.

On February 2, 1972, Executive Order 11643, stopped the use of toxicants on federal lands or by federally-funded programs and placed the control of prairie dogs on hold until 1975. Two decades of using Compound 1080 as the primary control substance for the control of prairie dogs had conditioned ranchers and managers to its efficiency and effectiveness. With its demise in 1972, the only remaining available substance was strychnine that had a long history of use with inconsistent results but could be used on non-federal lands and by non-federal programs. The executive order also mandated the closing of the cooperative bait-mixing plant managed by the U.S. Fish and Wildlife

Service. It was transferred to the South Dakota Department of Agriculture that did not have the background or expertise in plant operation or in the formulation of quality bait. No single action has impaired the management and control of prairie dogs as did Executive Order 11643.

In 1976, zinc phosphide oats became the prescribed bait for prairie dogs on federal lands and by federal agencies, and 12,150 ha / year were treated through 1979. Effectiveness of zinc phosphide was contingent on pre-baiting a prairie dog town and was a most difficult concept to sell to individuals and agencies. However, for effectiveness and consistency, pre-baiting was essential to the successful use of strychnine or zinc phosphide in the control of prairie dogs.

Costs

The following provides a perspective of the economics of the control of prairie dogs in the five counties of Haakon, Fall River, Pennington, Jackson, and Butte during 1922. The counties had the option of purchasing strychnine oat bait at $8 / bushel or of mixing strychnine oat bait for about $4 / bushel following the formula by the Bureau of Biological Survey. Counties also had the option to contract or hire crews to do the baiting or to set up cooperative or community programs for individuals to do their own baiting. Poison was placed on approximately 60,750 ha for the first time and again on 8,100 ha. The five counties used 1,255 bushels of strychnine oat bait at an estimated cost of $4 / bushel, or $5,020. The average applicator baited 30.4 ha of prairie dog-occupied land per day, and his labor cost $3 per day or $0.10 / ha. Labor costs for the 68,850 ha were approximately $6,810. The total cost was $11,830 or about $0.17 / ha. Carbonbisulphide was sometimes used to bait the few remaining active burrows at a cost of $0.01 per burrow.

The registration of zinc phosphide as a rodenticide for prairie dogs in 1976 provided an effective control substance, but effective use of zinc phosphide required pre-baiting. This additional operation more than doubled the time, labor, and cost of control with Compound 1080. Analysis of the 1985 and 1986 control on the Pine Ridge Indian Reservation revealed that operational costs averaged $2.79 / ha for the 2 years. Pre-control surveys of black-footed ferrets came to $0.40 / ha, which brought the total field cost to $3.19 / ha. Except for one zone of 2,025 ha that was not baited properly in 1986, the degree of control during the 2 years averaged over 92%.

Control of Prairie Dogs on the Pine Ridge Indian Reservation A Case Study

In 1922, a survey on the Pine Ridge Indian Reservation revealed at least 56,700 ha occupied by prairie dogs. Organized control of prairie dogs on the reservation and on private, state, and federal lands continued throughout the 1920's, and by 1930 the prairie dog population had been reduced to individuals in widely scattered small towns. Towns were kept at management levels (i.e., small to medium-size colonies with few in excess of a section in size) until the early 1940's, but in 1945, the numbers of prairie dogs increased throughout their range in South Dakota. Operational control with Compound 1080 treated oats maintained populations at manageable levels until the mid-1960's.

Toward the end of this period, prairie dogs again expanded because of reduced cooperator interest, decreased funds for control, and the added cost of pre-control surveys of black-footed ferrets. As previously noted, in 1968, the estimated area with prairie dogs in South Dakota was 24,705 ha, of which 16,200 ha were on the Pine Ridge Indian Reservation. Populations were somewhat reduced by increased control from 1968 through 1970. Baiting by individual ranchers also increased during this period.

The rapid expansion of prairie dogs during droughts or in response to overgrazing is amazing. A vivid example occurred on the Pine Ridge Indian Reservation when 12,960 ha with prairie dogs in 1973 developed into nearly 121,500 ha by 1981, in spite of treatment of over 32,400 ha from 1976 to 1980. In general, 81,000 ha of this expansion were one colony interrupted only by rivers, creeks, highways, buttes, tables, and badlands escarpments. Similar rates of increase occurred across western South Dakota during this same period. In 1981, the area with prairie dogs on the Pine Ridge Indian Reservation peaked at nearly 121,500 ha. During 1980–86, 285,120 ha of prairie dog habitat was baited on the Pine Ridge Indian Reservation. In spite of several complications and delays, by 1988 the prairie dog population on the Pine Ridge Indian Reservation again consisted of small scattered colonies separated by grasslands.

Control of Prairie Dogs and the Black-footed Ferret

Thousands of hours were spent in precontrol surveys of black-footed ferrets. In the process, all kinds of wildlife from spiders to a mountain lion (*Felis concolor*) were identified and recorded and included many coyotes (*Canis latrans*) and badgers (*Taxidea taxus*). With all these efforts, no black-footed ferrets or evidence thereof were found.

Observations by pre-control survey teams during the day and at night indicated that coyotes and badgers consumed more prairie dogs as scavengers than as predators. By the same token, the golden eagle (*Aquila chrysaetos*) seemed to be the most efficient predator of prairie dogs, but like all predators, its effectiveness was limited by appetite.

Much about prairie dogs and their environment is not known. The prairie dogs on the Pine Ridge Indian Reservation today are descendants of the population on 56,700 ha in 1922 and probably use some of the same burrows. One of the key factors is that prairie dog towns are not removed, only the inhabitants. Yet, human nature in true fashion will probably entertain biological, social, economic, political, and judicial exercises in preference to responsible management of this unique wonder of the prairie and its great diversity of wildlife.

Relation of Black-tailed Prairie Dogs and Control Programs to Vegetation, Livestock, and Wildlife[1]

by

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Synopsis

This chapter presents a review of the literature on the control of black-tailed prairie dogs (*Cynomys ludovicianus*) and the economic benefits from increased forage, effectiveness of rodenticides in the control of prairie dogs, secondary effects on nontarget animals, livestock–prairie dog forage relations, and use of prairie dog colonies by other wildlife species.

Production of Plants

The production of forbs is no different from or greater in areas with both prairie dogs and cattle than in areas with only cattle. Responses of grasses are more variable, and some species increase and others decrease with use by prairie dogs. Control of black-tailed prairie dogs to improve forage production is not economically feasible when 10% or more of the total treated area requires annual repetition of treatment.

Control of Prairie Dogs with Rodenticides

Control is greater by zinc phosphide-treated grain than by strychnine-treated grain. Reduction of prairie dogs with zinc phosphide has ranged from 65 to 95%.

Effects on Nontarget Animals

Zinc phosphide does not cause secondary poisoning of predators that eat poisoned prairie dogs and Richardson's ground squirrels (*Spermophilus richardsonii*). Some passerines and small mammals are poisoned by direct consumption of zinc phosphide. Ingestion of strychnine-treated oats has been shown to kill birds but not mammalian predators and had mixed effects on other rodents. In essence, nontarget species are killed when prairie dogs are controlled with toxicants.

Cattle–Prairie Dog Relations

Generally, prairie dogs eat the same forage species as cattle, although consumption of individual plant species varies from region to region. Consumption of plants by prairie dogs causes greater species diversity and delays phenological development of vegetation. As a result, weights of cattle do not differ between areas occupied by prairie dogs and areas not occupied by prairie dogs.

The condition of the range and the composition of plant species affect distribution of black-tailed prairie dogs. Where warm season grasses dominate and grazing by cattle is intense, prairie dogs are likely to expand. Prairie dogs seem to do better in short cover. Expansion can be reduced by resting pastures and by managing for cool season grasses.

Prairie Dogs and Enhancement of Wildlife

Prairie dog-occupied range sites in shortgrass and patchy plant associations tend to have less mulch cover and lower vegetation height than adjacent sites without prairie dogs. This type of site is more suitable than ungrazed sites to some species of wildlife, thus, the diversity of species of birds and mammals is greater in prairie dog colonies.

[1] Pages 312–323 *in* J. L. Capinera, editor. Integrated pest management on rangeland. Westvew Press, Boulder, Colo. Synopsis published with author's permission.

Attributes of Black-tailed Prairie Dog Colonies in North-central Montana, with Management Recommendations for the Conservation of Biodiversity

by

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Synopsis

The dynamics and associated vertebrate species of black-tailed prairie dog (*Cynomys ludovicianus*) colonies were studied in Phillips County, Montana, in 1981, 1984, and 1988. Mean size of 92 prairie dog colonies, measured in each of the 3 years, increased from 37.8 ha in 1981 to 62.1 ha in 1988. Colony size was inversely related to colony expansion rate. However, during the study, mean expansion rate decreased as mean colony size increased. These findings agree with suggestions that the growth of prairie dog colonies is logistic. As colonies grew, expansion was probably limited by a reduction in preferred vegetation at the edges of colonies, by physical barriers such as steep slopes or tall dense vegetation, and by increased shooting of prairie dogs in the area. Expansion rate was not related to nearest colony distance or to the number or area of surrounding colonies. The density of burrow openings was not related to colony size but to adjacent colonies; density was higher in colonies more distant from the nearest colony, but lower in colonies with a larger number of colonies and larger area of colonies within 6.4 km.

Several vertebrate species were associated with prairie dog colonies: 70 species of birds, 12 species of mammals, and 1 reptile. Of these, 30

[1] Pages 13-23 in T. W. Clark, D. Hinckley, and T. Rich editors. The prairie dog ecosystem: managing for biological diversity. Montana Bureau of Land Managment Wildlife Techncial Bulletin 2.

avian and 1 mammalian species had not been previously reported in black-tailed prairie dog colonies. No comparable enumeration was made on sites not colonized by prairie dogs. Black-tailed prairie dog colonies may represent distinct, island-like patches of habitat to many species. Avian species richness correlated with colony size ($R = 0.66, P < 0.001$) and with the area of colonies within 6.4 km ($R = 0.28, P < 0.001$). Together, colony size and the area of colonies within 6.4 km accounted for 47.6% of the variation in avian species richness. These findings were consistent with the theory on island biogeography.

Conservation of prairie dogs and their associated species should be by an ecosystem approach. Complexes (clusters) of prairie dog colonies should be managed as metapopulations of prairie dogs and associated fauna because of the increased biodiversity and reduced likelihood of extinction from stochastic events.

Effects of Prairie Dogs on Physical and Chemical Properties of Soils

by

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Abstract. The literature reveals little quantifying data about the effects of prairie dogs (*Cynomys* spp.) on physical and chemical properties of soils. Black-tailed prairie dogs (*C. ludovicianus*) move more soil material and live in larger and denser social groups than other species of prairie dogs. They are, therefore, more likely to alter soils in their habitat. Prairie dogs alter species composition and biomass of plants, litter, and bare ground in their colony areas. These alterations, in addition to the direct effects of burrowing, may be expected to change soil properties permanently. In general, prairie dogs contribute to patchiness or diversity of the environment. Rates of soil mixing by prairie dogs are more rapid than normal rates of soil formation. On sodium affected soils and on shallow soils, activities by prairie dogs tend to increase plant biomass. Where the prairie dogs bring subsoil with salts and carbonates to the surface of a noncalcareous soil, productivity tends to decrease.

Key words: Soil mixing rates, pedoturbation, *Cynomys* spp.

Much of the literature on the effects of prairie dogs (*Cynomys* spp.) on the properties of the soil is about the building of mounds by the black-tailed prairie dog (*C. ludovicianus*; Koford 1958; Sheets et al. 1971; Potter 1980; White and Carlson 1984; Cincotta 1985, 1989; Carlson and White 1987, 1988). The white-tailed prairie dog (*C. leucurus*) has been studied less intensively by pedologists, perhaps because it does not build large mounds (Koford 1958; Tileston and Lechleitner 1966; Clark 1971, 1977; Stromberg 1978; Flath and Paulick 1979; Schloemer 1991). Most of the literature on the effects of prairie dog activities on soil properties is about the effects of pedoturbation or soil mixing from the burrowing of these animals. Since Thorp (1949) calculated that prairie dogs (species not given) built 54.6 metric tons of mound material per hectare and converted the surface soils on one-third of the Akron, Colorado, Dryland Experiment Farm from silt loam to loam texture, there has been much interest in calculating mixing rates attributable to rodents. White and Carlson (1984) suggest that many of these attempts need to be viewed with caution. Although mixing of subsoil and topsoil layers has been estimated by numerous authors, documentation of short- and long-term effects of prairie dog activity on the chemistry and morphology of soils is scarce. Documentation is particularly scarce of the effects of prairie dog induced changes in plant physiology and community structure on soil properties. The literature also does not address the persistence of prairie dog induced changes in soils after abandonment of the prairie dog town.

Literature Review

Koford's (1958) monograph provides an extensive discussion of the interrelations between prairie dogs, the soil, plant communities, and livestock. He lists additions of organic matter and nutrient salts, improvement of soil structure, and increased water infiltration as beneficial effects of prairie dog activity. Koford calculated that 12 burrows have a volume of 2.7 m^3 (95 cubic feet) and represent the removal of 3.63 metric tons (4 tons) of soil to the surface. He considered this a reasonable estimate for 0.4 ha of an established prairie dog town. White and Carlson (1984) calculated that 550 years are required to cover a hectare with mounds and that 8,800 years are required to create a hectare of burrows, assuming the prairie dogs constructed new burrows each year, which they do not do. They concluded that the effect of soil mixing by rodents may be greatly exaggerated in the literature. Black-tailed prairie dogs mix soil excavated from their burrows with surface soil gathered from the area surrounding their burrows to create a large compact mound (Koford 1958; Smith 1958). The mounds of white-tailed prairie dogs, however, are simply a pile of subsoil removed from the burrows (Clark 1971). The black-tailed prairie dog builds larger, more complex burrows (Tileston and Lechleitner 1966; Sheets et al. 1971) and probably mixes greater volumes of soil over time. However, Clark (1971) concluded that there was no species-specific pattern of tunnel excavation. Seemingly, the burrow system is continuously enlarged and modified while it is occupied (Longhurst 1944). Burrows occupied by female white-tailed prairie dogs with litters are enlarged throughout the period when the young are raised (Flath and Paulick 1979). An additional consideration is the enlargement of prairie dog burrows by badgers (*Taxidea taxus*). Campbell and Clark (1981) reported that 10–27% of the burrows on the sites they studied had been enlarged by badgers in pursuit of prairie dogs.

Potentially harmful effects of prairie dogs on soils include accelerated erosion because of increased bare ground from removal of vegetation (Koford 1958) and the calcification of noncalcareous surface horizons from the mixture of carbonate ($CaCO_3$) rich subsoil material. As an example of the latter effect, soils mapped on the north flank of Sheep Mountain in Albany County, Wyoming, are a complex of Haplargids and Calciorthids where the rodents converted appreciable areas of soils with noncalcareous argillic horizons to soils that are now calcareous throughout the profile (Soil Conservation Service, Casper, Wyoming, unpublished data).

Prairie dogs apparently prefer flat open areas and often colonize old fields (Longhurst 1944; Koford 1958; Dalsted et al. 1981). Dalsted et al. (1981) listed four characteristics of sites that black-tailed prairie dogs prefer:

1. deep soils free from excessive stoniness,
2. minimal flooding hazard,
3. moderate or better productivity of soils, and
4. slopes of less than 9%.

Prairie dogs also dig, however, in gravelly soils and in soils of extremely high density (so high that digging is difficult for a human with a steel shovel), and on soils with only sparse vegetation. White-tailed prairie dogs and Gunnison's prairie dogs (*C. gunnisoni*) inhabit more steeply sloping sites than black-tailed prairie dogs (Longhurst 1944; Koford 1958; Fitzgerald and Lechleitner 1974). In large contiguous towns, the burrows are unevenly spaced, apparently in response to food and soil conditions (Sheets et al. 1971). Density and distribution of prairie dogs are more likely controlled by available food than by edaphic conditions, with the exception of the exclusion of rodents by high water tables (Koford 1958).

Carlson and White (1987) provide detailed data on soil chemistry (pH, N, P) and soil color in two black-tailed prairie dog mounds that they transected in South Dakota. They reported enrichment in P but concluded that effects by prairie dogs on soils were mostly confined to the mound area itself. Cincotta (1985) reported differences in soil organic matter, available phosphorus, and available nitrogen in black-tailed prairie dog towns of varying ages and in adjacent unoccupied areas. Early in the year, available P and N were higher in soils in the prairie dog town than in the adjacent undisturbed soil. Potter (1980) found higher organic matter contents in crater mounds of the black-tailed prairie dog than in dome mounds and in intermound topsoil. Tadzhiyev and Odinoshoyev (1987) reported similar changes as a result of burrowing activities of marmots (*Marmota caudata* Leoff.) in the Pamirs where the rodents excavated 6–8 burrows/ha. The marmots increased soil pH in the mounds by bringing carbonate-rich subsoil to the surface, brought stones to the surface, decreased soil humus (except in Alpine desert where it increased), and altered the

distribution of N and P in the soil profiles. Carlson and White (1988) reported increases in pH in the mounds but not in the nonmound areas in a black-tailed prairie dog town.

Because more soil area is affected by the mound than by the burrow (White and Carlson 1984), changes in soil chemistry probably reach beyond the area directly excavated by the animals. Schloemer (1991) investigated white-tailed prairie dog colonies on soils derived from a Cretaceous age marine shale in the Shirley Basin in Wyoming. He reported that prairie dog colonies can be located visually from distances of 100 m or more because of the enhanced vigor of sagebrush (*Artemisia tridentata*) in the colony area. The dominant soils of this landscape have dense subsoils of clay accumulation and appreciable sodium (Na) on the exchange complex (natric horizons, Soil Survey Staff 1987) and subsurface segregation of carbonates, gypsum, and salts. He attributed the greater productivity of sagebrush in the colony area to several mechanisms:

1. an increase in macroporosity of the soil,
2. the substitution of calcium for sodium on the exchange complex as a result of the transfer of gypsiferous subsoils to the soil surface,
3. deeper penetration of precipitation as a result of increased electrolyte content of infiltrating rain water, and
4. incorporation of organic materials into the soil as plant parts and feces.

The Natragids (soil taxonomy names after Soil Survey Staff 1987) in the Shirley Basin are representative of one type of soil that probably responds positively to pedoturbation. Farmers commonly amend such soils with gypsum and manure to improve infiltration of water.

The literature on the effects of prairie dogs on vegetation is voluminous and dates to Merriam's (1901) calculation that the occupants of one large colony of black-tailed prairie dogs in Texas consumed enough forage each year to support 1.6 million cattle. Recent literature reflects greater realism and consists of reports on the diverse effects on plant community structure, plant physiology, and biomass (Clark and Kinker 1970; Bonham and Lerwick 1976; Bonham and Hannan 1978; Klatt and Hein 1978; Coppock et al. 1983; Ursek 1985, 1987; Agnew et al. 1986). Authors cite prairie dog-induced changes in plant vigor, species composition, plant height, plant nutrient content, biomass and reproduction success, and litter and bare ground characteristics. Virtually all of these changes can be expected to affect soil carbon storage, nutrient cycles, chemistry, and morphology. Agnew et al. (1986) reported that prairie dog activity contributed to species richness and to patchiness of the ecosystem. This ecosystem diversity is exploited by other species of wildlife including bison (*Bison bison*), pronghorns (*Antilocapra americana*), black-footed ferrets (*Mustela nigripes*), and a host of birds, small mammals, and insects (Wilcomb 1954; Coppock et al. 1983; Agnew et al. 1986).

Age and Profile Characteristics of Soils in the High Plains and Wyoming Basins

The age of soils in the high plains and basins of Wyoming is highly variable; soils on steep south facing slopes are kept perpetually young by erosion. In contrast, soils on many flat stable surfaces date to the Pleistocene and some perhaps to the Tertiary period (Mears 1991). Even in the mountains of Wyoming under high rainfall, soils developed on geomorphic surfaces younger in age than Bull Lake (~140,000 years before present [YBP]) typically have not formed noncalcareous subsurface horizons of clay accumulation (argillic horizons). An exception is the coarse-textured parent materials where some soils of post-Pinedale age (~15,000 YBP) may have minimal argillic horizons (Munn 1987). Because many soils on the high plains and intermountain basins are Pleistocene relicts that developed under other than contemporary climatic conditions, burrowing by prairie dogs may effect permanent changes in soil chemistry and morphology.

The Laramie Basin in south central Wyoming is typical of the intermountain basins in the northern Rockies. In the Laramie Basin, soils range in age from young soils on the modern floodplain and eroding slopes to old mature soils on alluvial terraces that are at least 2 million years old. The older surfaces typically are occupied by Haplargids and Paleorthids (Soil Conservation Service, Casper, Wyoming, unpublished data). A representative soil horizon sequence of the Haplargids is E (thin leached surface), Bt (clay accumulation), Bk (carbonate accumulation), By (gypsum accumulation), and Bz (salt accumulation; horizon nomenclature is after Soil Survey Staff 1981). On old alluvial surfaces, the soils show the upward fining characteristic of alluvium–loam or clay loam textures over gravelly sands. Many of the older soils in the Laramie Basin (and other Wyoming basins) show

evidence of cryoturbation during periods of permafrost (Mears 1981; Munn 1987). Complexes of soils occur where Haplargids are apparently converted to Calciorthids (Table 1) as a result of mixing by rodents—both prairie dogs and the Richardson's ground squirrel (*Spermophilus richardsoni*) and an apparent decrease in effective precipitation since the soils originally formed. After excavation of subsoil carbonates to the soil surface by rodents, present-day precipitation is insufficient to leach the carbonates from the surface tier. Mixing by the rodents also distributes gravel from the subsoil throughout the fine-textured surficial layers. The conversion of Haplargids to Calciorthids can profoundly reduce vegetative biomass. For example, the Dalquist series (Borollic Haplargid) has a rated productivity of 1,300 kg / ha compared with 450 kg / ha of the Browtine series (Borollic Calciorthid; Soil Conservation Service).

Prairie dogs frequently dig through the solum of the soil on sideslopes and bring fragments of soft bedrock (often shale or sandstone) to the surface where its weathering is accelerated. Virtually all exposures of soil profiles in grasslands reveal krotovinas, the casts of rodent burrows. These features are assumed by pedologists to persist for long periods (hundreds of years), but their persistence is not well documented (Borst 1968; Allgood and Gray 1974). Observations of the effects of prairie dog removal on vegetation (Bishop and Culbertsen 1976; Uresk 1985, 1987) have generally been conducted for too short a time to allow understanding of the long-term effects of burrowing on soil properties.

Mixing of Soil by Prairie Dogs

Because of the wide range of burrow densities (Table 2) and burrow and mound volumes (Table 3), any calculation of possible turnover or mixing rates by prairie dogs must be prefaced by a careful listing of assumptions. White and Carlson (1984) used 62 burrows per ha, a burrow diameter of 15 cm, and an average mound diameter of 0.6 m. They calculated that prairie dogs could create a hectare of mounds in 550 years and a hectare of burrows in 8,800 years if the animals constructed new burrows each year. This led them to conclude that the effect of the rodents on mixing soil materials described in the literature may often be exaggerated. However, compared with the normal time scale of soil formation, such turnover rates are quite rapid.

For a representative calculation of mixing rates in a white-tailed prairie dog colony, I used 20 burrows / ha, an average burrow volume of 0.15 m^3, and a mound diameter of 0.5 m for nonmaternity burrows and 1.0 m for maternity burrows. Ten percent of the burrows were assumed to be maternity burrows with a volume of 0.30 m^3. Approximately 20% of the burrows were presumed to be excavated by badgers to four times their original volume (0.60 m^3). Finally, new burrow

Table 1. *Comparison of Dalquist (Haplargid) and Browtine (Calciorthid) soil profiles in a prairie dog-affected soil complex, Albany County, Wyoming (Soil Conservation Service 1988).*

Horizon	Depth (cm)	Color-10YR hue[a] (value / chroma)	Fine earth textural class	Coarse fragments (%)	$CaCO_3$ (%)	Effervescence	pH
Dalquist							
A	0–5	6 / 2 d, 4 / 2 m	sl	50	—	—	7.0
BA	5–13	5 / 3 d, 4 / 3 m	scl	50	—	—	7.2
Bt	13–38	5 / 4 d, 4 / 3 m	scl	45	—	—	7.2
Bw	38–50	6 / 6 d, 5 / 4 m	scl	40	6	discontinuous	7.5
Bk1	50–63	6 / 4 d, 5 / 4 m	sl	85	35	violent	8.6
Bk2	63–150	6 / 4 d, 5 / 4 m	sl	55	8	strong	8.2
Browtine[b]							
A	0–8	5 / 3 d, 4 / 3 m	sl	40	7	strong	8.0
AB	8–22	6 / 3 d, 5 / 3 m	sl	55	18	violent	8.2
Bk1	22–35	8 / 2 d, 7 / 3 m	sl	45	37	violent	8.4
Bk2	35–78	8 / 2 d, 7 / 3 m	l	75	36	violent	8.6
C	78–150	6 / 6 d, 5 / 6 m	sl	80	7	strong	8.2

[a] Color: d = dry, m = moist.
[b] 10%–50% surface cover of pebbles, cobbles, and stones.

Table 2. *Average densities of burrows by four species of prairie dogs.*

Species of prairie dog	Burrow density (burrows per hectare)		Source	Comments
Gunnison's[a]	57		Fitzgerald and Lechleitner (1974)	Only 10% had mounds
Gunnison's	2–5	(sagebrush)	Longhurst (1944)	—
	37–49	(fields)		
	74	(maximum)		
Black-tailed[b]	3		Sheets et al. (1971)	43 ha colony, not evenly distributed, 4.1 animals / burrow
Black-tailed	—		Smith (1958)	55–56 animals / ha
White-tailed[c]	—		Flath and Paulick (1979)	Mounds 6 m in diameter, 57 cm tall
White-tailed	9	(grass)	Clark (1977)	Laramie, Wyoming area
Black-tailed (?)	42		Thorp (1949)	Species unspecified
Black-tailed	247		Koford (1958)	Fed by tourists
Black-tailed	54–128		Koford (1958)	15 / ha in a new dog town
White-tailed	54		Tileston and Lechleitner (1966)	—
Black-tailed	103		Tileston and Lechleitner (1966)	—
Black-tailed	84		Bishop and Culbertsen (1976)	—
White-tailed	25	(9–129)	Campbell and Clark (1981)	—
Black-tailed	21	(11–67)	Campbell and Clark (1981)	—
Utah[d]	—		Collier and Spillett (1972)	6 animals / ha
White-tailed	0.7		Stromberg (1978)	—
Black-tailed	0.7–3.7		Stromberg (1978)	—
Black-tailed	8.9		King (1955)	—
White-tailed	59		Clark (1971)	Laramie area

[a] *Cynomys gunnisoni.*
[b] *C. ludovicianus.*
[c] *C. leucurus.*

Table 3. *Volume of prairie dog burrows and mounds.*

Burrow (m^3)	Mound (m^3)	Source	Comments
0.14, 0.23	—	Koford (1958)	Data from Merriam (1901) and Fish and Wildlife Service
0.22	—	Wilcomb (1954)	—
—	0.023	White and Carlson (1984)	Model based on a mound 0.6 m in diameter and 0.3 m high
—	0.014, 0.028	Clark (1977)	Calculated from mound dimensions
0.04, 0.38, (0.15 av.)	—	Sheets et al. (1971)	Calculated for burrows without chambers, 12 cm diameter
—	6.4	Thorp (1949)	Largest mound
0.02, 0.10, (0.05 av.)	—	Stromberg (1978)	Calculated for burrows without chambers, 12 cm diameter
0.12	—	Smith (1958)	Calculated for burrows without chambers, 12 cm diameter
—	5.4	Flath and Paulick (1979)	Largest mound
—	0.13	Fitzgerald and Lechleitner (1974)	Largest mound
—	4, 37	Carlson and White (1987)	Large mound was 14.6 m diameter by 0.67 m high

systems were assumed to be constructed every 10 years and the depth of the burrows, 1.5 m.

Based on the described assumptions, prairie dogs produced 5.1 m^2 of mound basal area, which if renewed every 10 years covered a hectare in 19,600 years. Mixing of the 1.5 m of soil by the rodents occurred in 29,760 years during continuous occupation of the colony. This estimate is low because the rodents were redigging some of the same soil material each time. Because of their usual greater burrow density, black-tailed prairie dogs mixed soil at a greater rate (perhaps as much as five fold). Episodic depopulation of the colony slowed the rate of change. However, even if the final estimate is doubled or tripled (100,000 years for soil mixing and 20,000 years for coverage of the ground with subsoil [mound] material), the time period is still relatively short compared with the age of many soils in the intermountain basins of Wyoming and the high plains.

Horizons of alluvial clay accumulation on Pleistocene surfaces are probably relicts in soils with more than 15% clay in the surface (E) horizons under the present climate in Wyoming's basins (<35 cm annual precipitation). Textural stratification with depth is a relict condition inherited from the parent material in soils developed in alluvium and in soils developed in interbedded sedimentary rocks of contrasting texture (e.g., sandstone over shale). In these situations, admixture of calcareous and gypsiferous subsoil to the surface of the soil creates a permanent change in soil chemistry, and admixture of subsoil materials to surface horizons permanently changes soil texture. These changes cause a patchiness in the vegetation on the site until virtually all of the site is affected by rodent activity. Despite the apparently irreversible nature of some of these effects, prairie dog colonies are irregularly distributed in the landscape and their populations fluctuate markedly over time. The net effect of their activity is to increase diversity in the environment—diversity in soil properties and in plant community characteristics.

Where goals of management call for expansion of existing prairie dog towns or reintroduction of prairie dogs to sites from which they were eliminated in the past, prediction of the probable effects of prairie dog burrowing on soils and associated vegetation may be desirable. In the intermountain basins of the Rocky Mountains and adjacent high plains, major changes in plant growth will probably occur as a result of burrowing by prairie dogs. These changes are expected:

1. on alluvial soils with abrupt contrast in texture between horizons (loamy layers over gravelly layers);
2. on Haplargid profiles where noncalcareous surface layers (E and Bt horizons) overlie carbonate and salt-rich Bk, By, and Bz horizons;
3. on Natragid profiles where the sodium affected Btn horizon is underlain by gypsum (By horizon);
4. on shallow Torriorthents (young, poorly developed soils) where soft bedrock is brought to the surface and weathering accelerated; and
5. on favored sites where burrow density is greatest.

Least affected will be soils of extremely uniform texture (e.g., Psamments) and soils with very thick A horizons (pachic and cummulic Subgroups of Mollisols) on sites with high water tables (aquic Suborders and Subgroups).

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Control of Grassland Ecosystem Processes by Prairie Dogs

by

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Abstract. Prairie dogs cause intense disturbance of the grassland community. The patches (colonies) they create differ from the unmodified grassland in many ways, including vegetation structure, nutrient cycling, and animal use patterns. However, most management policies have encouraged the elimination of prairie dogs because they are viewed as competitors of cattle. In this paper, we address some of the changes by prairie dogs in ecosystems of the Wind Cave National Park, South Dakota, and the relation between those changes and management and research. Because this paper is a review of research during a 15-year period, portions of this paper were excerpted from other manuscripts published by the authors.

Key words: Black-tailed prairie dog, *Cynomys ludovicianus*, grassland ecosystem, herbivore, nutrient cycling, patch structure.

Disturbance can change structural and functional properties of an ecosystem and create recognizable, well-defined patches (White and Pickett 1985). The affected properties and the extent of their change are directly related to the nature of the disturbance and the nature of the ecosystem. Prairie dogs (*Cynomys* spp.) are a source of disturbance that results in one of the largest and most distinct patches in North American grasslands.

There are several reasons why prairie dogs have had such an important effect on North American grasslands. Historically, the most abundant and widely distributed species, the black-tailed prairie dog (*C. ludovicianus*), was common throughout the short- and mixed-grass prairies of the Great Plains. Although the average size or density of prairie dog colonies in presettlement times cannot be estimated accurately, prairie dog colonies covered about 40 million ha in 1919 (Nelson 1919, cited in Summers and Linder 1978). This is more than 20% of the potential area of natural short- and mixed-grass prairies (Lauenroth 1979). Although control has reduced the number of prairie dog populations to fewer than 2% of those several decades ago (Summers and Linder 1978; Uresk 1987), where populations are relatively uncontrolled by humans, colonies may range from tens to hundreds of hectares (Dahlsted et al. 1981; Knowles 1986) at average densities of 10–55 animals / ha (O'Meilia et al. 1982; Knowles 1986; Archer et al. 1987).

Areas inhabited by prairie dogs receive continual and intense disruption by burrowing. A typical burrow system (Sheets et al. 1971) has two entrances, a depth of 1–3 m, a total length of 15 m,

and a diameter of 10–13 cm. We calculated that prairie dogs mix approximately 200–225 kg of soil/burrow system. Much of this subsoil is deposited around the burrow entrances, creating soil mounds of 1–2 m in diameter. These burrow entrances may number 50–300 / ha (King 1955; O'Meilia et al. 1982; White and Carlson 1984; Archer et al. 1987), are small patches in a colony, and have physical and chemical properties that may remain altered for hundreds or thousands of years (Carlson and White 1987).

Although it frequently denudes the zone surrounding entrances to their burrow systems, grazing by prairie dogs affects the entire area of the colony. Prairie dogs forage aboveground throughout the year and may also clip and fell herbaceous vegetation, nipping it near ground level but not eating it. This behavior presumably facilitates detection of predators (King 1955).

The effects of prairie dogs on ecosystem structure and dynamics have been ignored or overlooked by investigators of disturbance and patch dynamics (Pickett and White 1985). About 15 years ago, we and our colleagues began research in the mixed grass prairie at Wind Cave National Park, South Dakota. This 11,355 ha site is about 75% grassland and 25% ponderosa pine (*Pinus ponderosa*) forest. In 1978, the site contained 11 major prairie dog colonies ranging from 5 to 250 ha (Dahlsted et al. 1981). Our objectives were to determine how black-tailed prairie dogs influence structural and functional properties of the grasslands over time and how they and other herbivores respond to grazing-induced changes in the ecosystem. This paper summarizes that research and the results of other research on grasslands and prairie dogs to provide a description of how prairie dogs affect the prairie ecosystem and other wildlife, including the black-footed ferret.

Prairie Dog–Plant Interactions

Plant Biology

Morphological and physiological changes often occur in intensively grazed plants. For example, plants grazed by domestic herbivores are often shorter and more prostrate than ungrazed individuals (Hickey 1961). Changes in morphology from grazing sometimes disappear quickly following release from grazing (Quinn and Miller 1967), or they may persist, indicating genetic differentiation into distinct ecotypes.

We investigated differences in populations of western wheatgrass (*Agropyron smithii*) from an intensively grazed prairie dog colony and from a large, permanent grazing exclosure (Detling and Painter 1983; Detling et al. 1986; Cid et al. 1989). Sod blocks containing western wheatgrass were collected on and off prairie dog colonies and were transplanted to a common greenhouse environment. After 9 months, plants from the prairie dog colonies had more tillers per plant, fewer leaves per tiller, shorter and narrower leaves, higher blade to sheath ratios, and a more prostrate growth form than plants from ungrazed populations. Polymorphism and persistence of these characteristics suggested that these populations were genetically distinct. Heavy grazing by prairie dogs and other herbivores apparently has modified the selection pressures and competitive balance that existed in the ungrazed populations, causing a shift in dominance to an ecotype that may be more resistant to grazing or be less intensively grazed because of its shorter stature (Jaramillo and Detling 1988).

Several responses to simulated grazing by the two ecotypes of western wheatgrass were compared (Detling and Painter 1983). Photosynthetic rates were similar and partial defoliation enhanced net photosynthesis equally in the remaining leaves in the two ecotypes. However, net primary production (relative to undefoliated plants) was essentially unaffected by defoliation in plants from the prairie dog colony but decreased by 20% following defoliation of exclosure plants. These differences may have resulted from greater photosynthetic rates of leaf blades than sheaths and greater blade to sheath ratios in plants from the prairie dog colony. Therefore, although they are less productive, these grazing morphs may be more resistant to subsequent grazing than seldom grazed plants.

Another response to grazing is increased accumulation of silica in leaves of grasses. Silica accumulation may be a defense against herbivores (McNaughton 1985) because silica decreases digestibility and palatability of plants and promotes tooth wear in herbivores (Van Soest 1982). Brizuela et al. (1986) found higher concentrations of silicon in tillers of western wheatgrass and little bluestem (*Schizachyrium scoparium*) from heavily grazed prairie dog colonies than from lightly grazed areas. Because leaf blades contain higher concentrations of silicon than leaf sheaths (Cid et al. 1989), the higher concentrations of silicon in tillers from heavily grazed prairie dog colonies

would be explained by the higher blade to sheath ratios in colony plants (Detling and Painter 1983).

In general, as plants mature, their nutritive value declines (Van Soest 1982). Grazing removes aging leaves and may stimulate growth of new tissue. This new tissue usually has a higher nitrogen concentration and digestibility than ungrazed plants (McNaughton 1984). Part of our research at the Wind Cave National Park involved examination of the effect of prairie dog colonization and grazing on nutrient dynamics of plants (Coppock et al. 1983a). A prairie dog colony was divided into three ages or states of colonization: (1) an older area (colonized more than 25 years); (2) a young area (occupied 3–8 years); and (3) a recently (<2 year) colonized edge. The uncolonized prairie

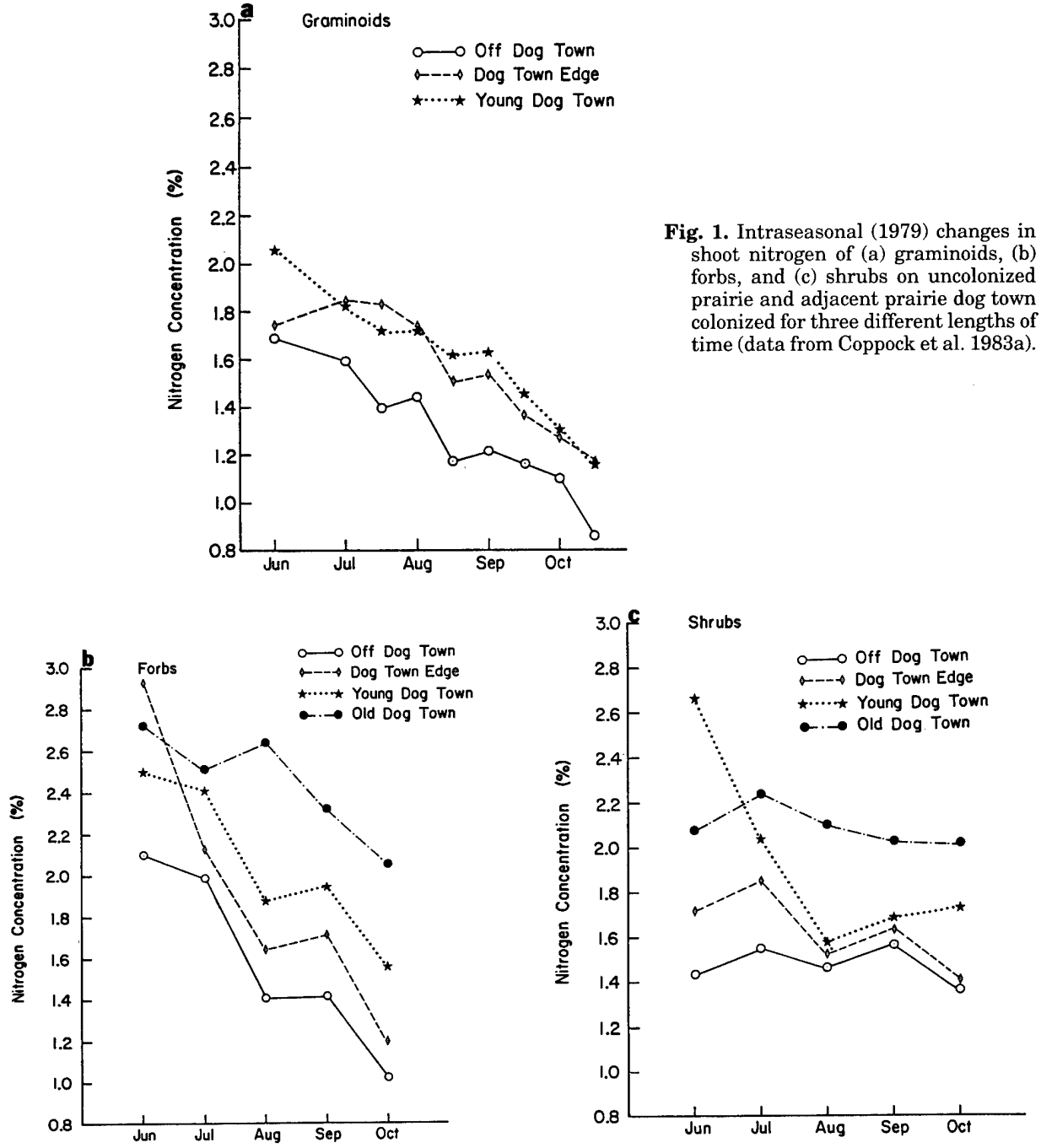

Fig. 1. Intraseasonal (1979) changes in shoot nitrogen of (a) graminoids, (b) forbs, and (c) shrubs on uncolonized prairie and adjacent prairie dog town colonized for three different lengths of time (data from Coppock et al. 1983a).

(Fig. 1) was used as a control site. During the growing season, live material of six grass species (three cool and three warm season species), a composite of forbs, and a dwarf shrub (fringed sage; *Artemisia frigida*) were collected monthly from each site and analyzed for nitrogen concentration and digestibility.

Nitrogen concentrations in shoots typically were lowest in plants from the uncolonized grassland and increased with the length of time an area had been occupied by prairie dogs. Similar results in western wheatgrass were observed at the Wind Cave National Park (Krueger 1986). On average, cool season grasses had higher concentrations of nitrogen throughout the season than did warm season species for each age of colonization. Although it declined as the season progressed, digestibility of grasses followed a pattern similar to concentration of nitrogen. Grasses from the uncolonized area had lower digestibility than grasses from the recently colonized edge and the young colony, and cool season grasses were more digestible than warm season grasses. These results indicate that grazing by prairie dogs positively influences plant nutrition and forage quality.

Plant Community Changes

When prairie dogs invade an area, they crop the vegetation to a height of a few centimeters and maintain it at that height, creating microclimatic changes in the canopy and soil. Archer and Detling (1986) found that temperature and moisture content of soils were generally higher on than off prairie dog colonies. These abiotic changes can directly influence rate of microbial activity and nutrient cycling in soils and water balance and production of plants. These modifications of the microhabitat alter the competitive balance of plants in the colony that changes the plant community.

Following occupation by prairie dogs, overall canopy height decreases (Fig. 2) and grasses are replaced by forbs (Fig. 3). In one of our research colonies, the mean canopy height decreased 62% in the first 2 years of colonization and changed little thereafter (Archer et al. 1987). Change in canopy structure can be achieved in several ways: (1) plants that are clipped repeatedly never reach full growth; (2) genetically determined taller morphs are replaced by grazing tolerant, shorter,

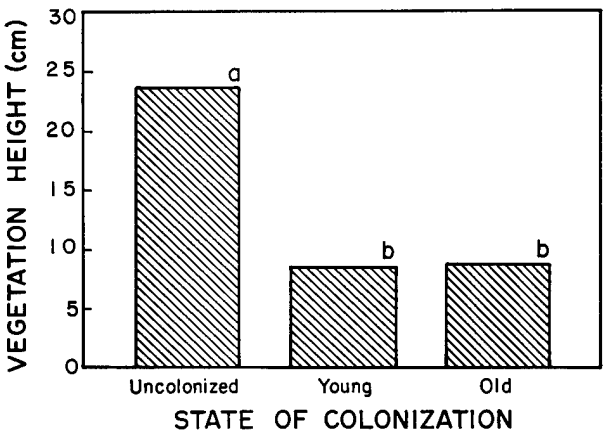

Fig. 2. Mean vegetation height as a function of state of colonization. Data are from two prairie dog colonies sampled in June, July, and August of 1987. *Bars* with different letters are significantly different at $P \leq 0.05$ (from Whicker and Detling 1988b).

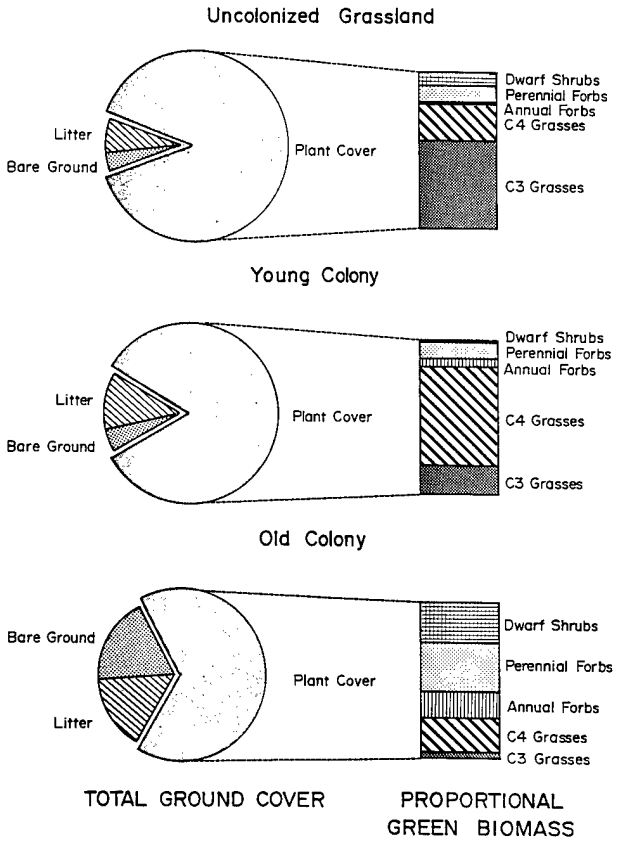

Fig. 3. Pie diagram indicating proportion of ground covered by standing plant material and litter. Of the total green biomass, *bar graphs* indicate the relative contribution by each of several plant functional groups. Data are seasonal means in June, July, and August 1987 on two sites of uncolonized grassland and nearby prairie dog colonies at different states of colonization (from Whicker and Detling 1988b).

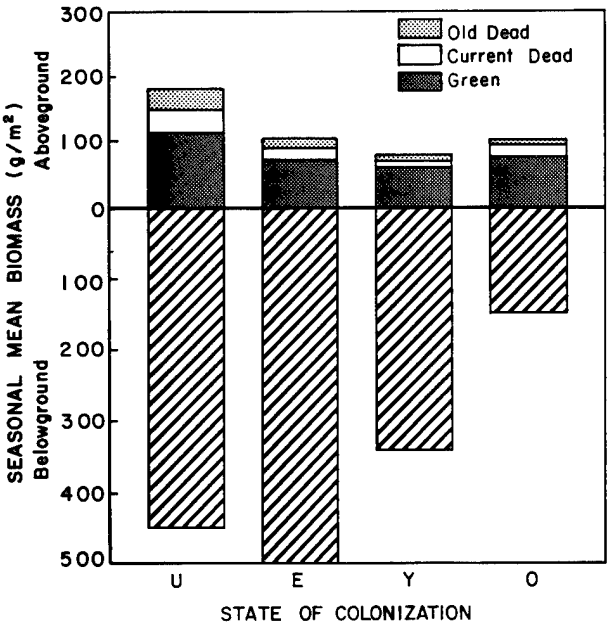

Fig. 4. Mean aboveground and belowground plant biomass of uncolonized grassland (U), and the colony edge (E), young colony (Y), and old colony (O) portions of the Research Reserve in the Wind Cave National Park during the 1984 growing season. *Current dead* refers to plant material that died during the 1984 growing season, and *old dead* material died before that time (from Whicker and Detling 1988a).

prostrate ecotypes of the same species (Detling and Painter 1983); and (3) the plant community changes such that many of the taller species are replaced by shorter species (Koford 1958; Coppock et al. 1983a; Archer et al. 1987).

These same factors may contribute to concomitant decreases in standing crop following colonization (Fig. 4). In one site, the maximum live standing crop (190 g / m^2) was found in uncolonized prairie, where grasses comprised 85% of the biomass (Coppock et al. 1983a). Similar biomass was in the oldest portion of the colony; however, less than 3% was grass. The grass-dominated young area of the colony produced only about one-third the live standing crops of the uncolonized area. However, there was a greater proportion of live to standing dead plant material in the colonized areas than in the uncolonized prairie. Because prairie dogs are continually clipping vegetation, very little matures and dies; thus, standing dead material does not accumulate. As a result, the amount of vegetation that eventually falls to the ground as litter is reduced, and bare ground increases (Coppock et al. 1983a). For example, Archer et al. (1987) found that by the third year after colonization by prairie dogs, bare ground had increased by 25% and litter cover had decreased by about 10% in the colony.

Change in plant species composition after prairie dog colonization has been widely noted (Osborn and Allan 1949; King 1955; Koford 1958; Bonham and Lerwick 1976), but rate of change seldom was documented (Cincotta et al. 1989). In separate colonies at the Wind Caves National Park, Coppock et al. (1983a) and Archer et al. (1987) studied the rate of plant species change, replacement, and diversity. Although rate of change is controlled by several factors in addition to grazing pressure, trends were similar between the two colonies. In the most recently colonized areas (<2 years), plant species composition changed little relative to uncolonized prairie. In areas of the colonies that had been affected more than 3 years, shifts in plant dominance and composition had begun (Coppock et al. 1983a) or had rapidly progressed (Archer et al. 1987). The dominant species in the uncolonized prairie, the midgrasses, were replaced by shortgrasses and annual forbs. Species diversity was highest in parts of the colonies occupied an intermediate time (Fig. 5). Diversity in the oldest portions of each colony declined to levels similar to the uncolonized prairie because of the final dominance by a few species of annual and perennial forbs and dwarf shrubs.

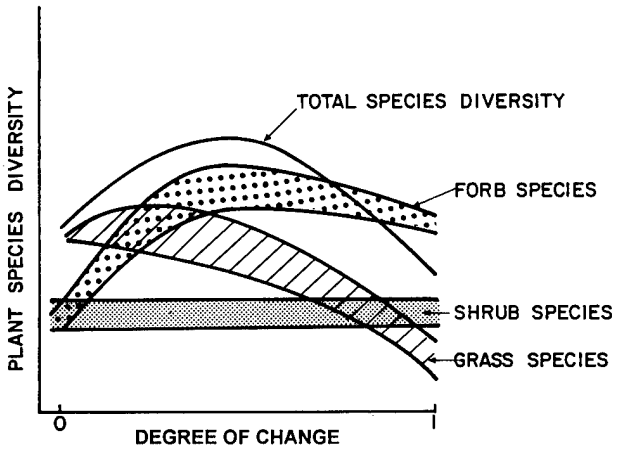

Fig. 5. Changes in plant species diversity on prairie dog colonies with increasing disturbance. An undisturbed state is represented at 0 on the x-axis, and a severely disturbed and highly modified system is at 1. Total species diversity is maximized at intermediate disturbances because forb diversity increased, but grass diversity has not yet substantially decreased. Based on data of Coppock et al. (1983a) and Archer et al (1987); figure from Whicker and Detling (1988a).

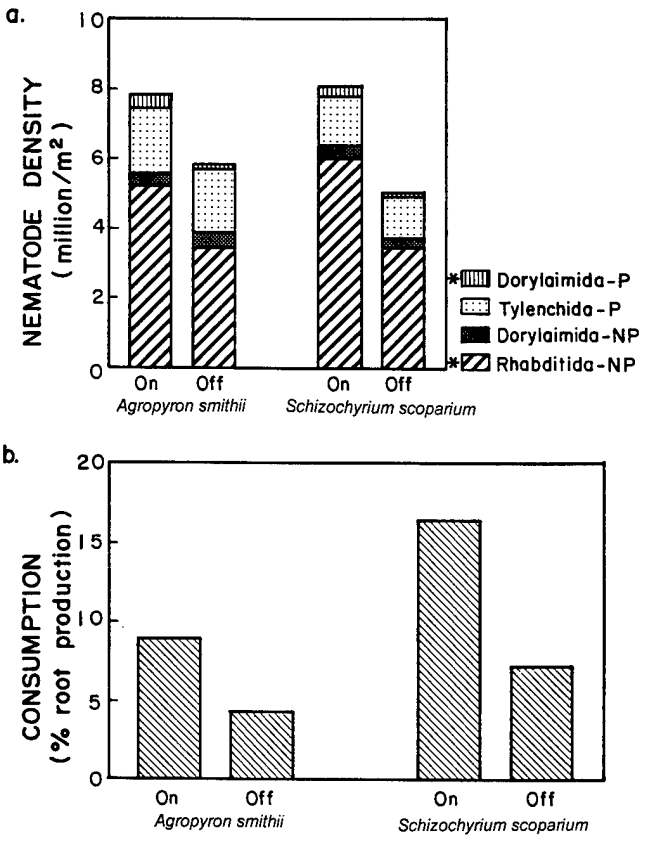

Fig. 6. (A) Densities of four groups of plant parasitic (P) and non-parasitic (NP) nematodes from on and off a prairie dog colony. *'s indicate significant density differences between populations on and off the colony, $P \leq 0.05$. (B) Relative consumption of root production of two grass species by nematodes on and off a prairie dog colony. Data redrawn from Ingham and Detling (1984) by Whicker and Detling (1988b).

Prairie Dogs and the Belowground Ecosystem

Much of the dynamics of plant systems occur belowground, and prairie dogs may influence the belowground responses of both plants and animals. It has been reported that most of the energy flow in grassland systems occurs belowground (Coleman et al. 1976). Soil invertebrates, largely nematodes, may consume as much or more plant biomass than cattle on the mixed grass prairie (Smolik 1974). Because the root system provides a link for transport of materials from the soil to the shoot system of plants, factors that affect the root system generally influence the aboveground plant dynamics as well.

Grazing typically reduces biomass of roots (Schuster 1964) because of reallocation of material from roots to the regrowing aboveground shoots and because of the reduction in net primary production. There is a marked decline in total root biomass from uncolonized prairie to older parts of prairie dog colonies (Fig. 4). In one study (Ingham and Detling 1984), soil cores were taken monthly from beneath western wheatgrass and little bluestem from a heavily affected section of a prairie dog colony and from uncolonized prairie. Roots and nematodes were extracted from the cores. The seasonal mean root biomass from the colony was 70–80% of that of uncolonized prairie, and total nematode densities (Fig. 6) were 45% higher on than off the colony. Nematode densities may reflect changes in plant chemistry or in microclimate and chemistry of soils. Annual net production of roots on the colony was about 60% of that off the colony; however, the percent of annual net production of roots consumed by nematodes was 2.5 times higher on than off the colony. Therefore, the combination of lower production of roots, higher densities of nematodes, and greater consumption of roots on the colonies by nematodes indicates a substantial change in belowground dynamics caused by activities of prairie dogs.

Prairie Dogs and Ungulates

Free-ranging populations of native grassland ungulates in the Wind Caves National Park include about 370 bison (*Bison bison*), 160 prong-

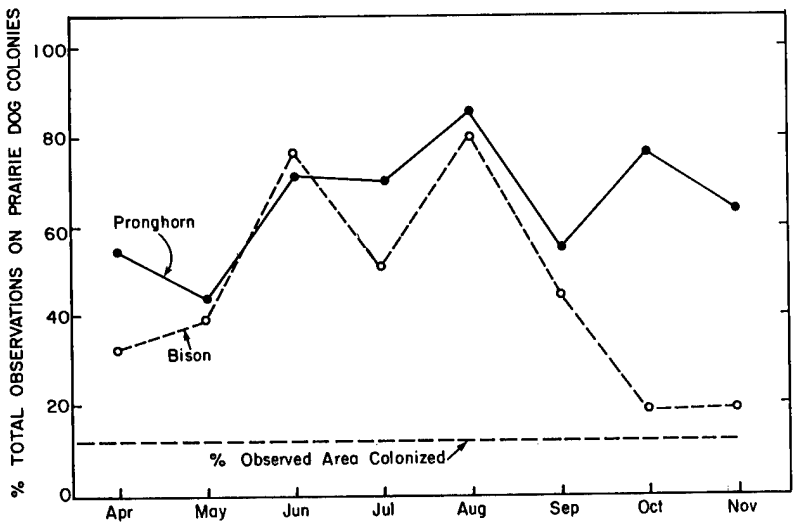

Fig. 7. Use of prairie dog colonies for feeding by bison and pronghorns. Points above the *horizontal dashed line* (random use) indicate selection of colony site. Data redrawn from Krueger (1986) by Whicker and Detling (1988b).

horns (*Antilocapra americana*), 400 elk (*Cervus elephus*), and 120 mule deer (*Odocoileus hemionus*) (Krueger 1986). Early observations suggested that the bison and pronghorn were frequently associated with prairie dog colonies (King 1955; Koford 1958). At the Wind Caves National Park, Wydeven and Dahlgren (1985) reported heavy summer utilization of prairie dog colonies by bison, elk, and pronghorns during 1976 and 1977. Our research verified that bison and pronghorns (Fig. 7) select prairie dog colonies and that ungulates that feed at colony sites may incur some nutritional advantage (Coppock et al. 1983b; Vanderhye 1985; Krueger 1986).

In conjunction with studies of plant response to colonization by prairie dogs, Coppock et al. (1983a, 1983b) investigated the park-wide selection of prairie dog colonies by bison, the pattern of use by bison in a colony, and the resulting dynamics of the plant communities on and off colonies. Approximately 8% of the grasslands in the park consist of prairie dog colonies. If animals use habitat randomly, then the frequency of observations of those animals in a habitat approximate the proportion of that habitat in the park. Coppock et al. (1983a, 1983b) found that bison predominately use the grasslands and prairie dog colonies and, in summer, the use of colonies was much higher than expected by chance. During the growing season, bison used the younger, grass-dominated portion of the colony for both grazing and resting, edge primarily for grazing, and forb–dwarf-shrub-dominated older areas for resting (Coppock et al. 1983b). Bison used the adjacent uncolonized prairie only 20% of the expected time for resting or grazing, indicating that this area was avoided in preference of the colony. Similar patterns by bison and pronghorns have been observed on other colonies (Krueger 1986).

Although unlike other herbivores, bison are nonselective feeders (Schwartz and Ellis 1981), they can choose the habitat in which they prefer to feed. When possible, an animal is expected to feed in the most favorable locations, such as where levels of nutrients and availability of the forage are high (Stephens and Krebs 1986). Because prairie dogs modify grasslands such that plant material from colonies has a greater live-to-dead ratio (albeit lower standing crop), a higher nitrogen level, and a greater digestibility than plant material from uncolonized prairie, grazers obtain more nutrition. The moderately disturbed, grass-dominated areas of the colonies are especially representative of these features. Thus, it seems reasonable to assume that prairie dogs modified the environment, making it a favorable feeding and resting habitat for other animals.

Vanderhye (1985), using Swift's (1983) ruminant model to simulate weight changes based on diet quality, investigated nutritional benefits to bison from selectively feeding on plants in prairie dog colonies. Diet quality in the model was based on values measured on and off colonies. Various patterns of use in colonies by bison were simulated, including random, typical, none, and 100%. Based on data from the Wind Caves National Park, random use by bison was set at 12%, the percent of land covered by prairie dog colonies in the study area, and typical use of colonies during the growing season was 39% (Krueger 1986). The model output suggested that, if mature bison cows used the colonies randomly for feeding, they would gain 2 kg (7%

of seasonal weight gain) more body weight than if they did not feed on colonies. Typical usage of colonies confers an additional 5 kg (18%) weight gain over not feeding on colonies. Body weight of yearling bison can be 4 kg (14%) greater from random feeding on colonies or 13 kg (46%) greater from regular feeding on colonies than the expected body weight of yearling bison that do not feed on colonies. The nutritional advantages are realized only from June through August when differences in forage quality between on and off colonies are maximal. Results such as these might also be expected if parameters for other ruminants, such as cattle, were used in Swift's (1983) model. However, the pattern of use of the prairie dog colonies would have to be known for each group of tested animals.

Pronghorns also preferentially use prairie dog colonies (Krueger 1986). Although both bison and pronghorns preferentially used colonies in summer (Krueger 1986), their location of use in the colonies differed (Fig. 7). Bison preferentially used the grass-dominated portions of the colonies, whereas 57–97% of the feeding by pronghorns was on the forb-shrub dominated centers of the colonies. In a preferred feeding area of the colony, dietary overlap between bison and prairie dogs and between pronghorns and prairie dogs was high. However, rather than competing for forage, the relation seemed to be mutually positive between bison and prairie dogs and mostly neutral between pronghorn and prairie dogs (Krueger 1986).

Implications for Management

As a part of natural ecosystems, prairie dogs enhance certain features of the vegetation and create favorable habitat patches for other animals, such as birds and small mammals (Agnew et al. 1986). Thus, in situations such as those described for the Wind Caves National Park, the presence of a limited number of prairie dog colonies scattered throughout the native grassland may improve the health and increase the diversity of other wildlife species, including the black-footed ferret (*Mustela nigripes*; Clark 1987). The size and spatial patterning of the colonies also may be important to habitat requirements, home ranges, and dispersal characteristics of other species of wildlife.

Extensive use of prairie dog colonies by ungulates, such as bison, may accelerate changes in the vegetation from increased consumption rates of plants and disruption and compaction of soils by trampling and wallowing. These can reduce suitability of these sites for both bison and prairie dogs. However, research at the Wind Caves National Park revealed that extensive use by bison of prairie dog towns can be reduced by creating additional suitable bison habitat with controlled fires (Coppock and Detling 1986). These fires should be sufficiently far from prairie dog colonies so that the burned areas do not provide additional habitat for immigrating prairie dogs.

Caution should be exercised in extrapolating the results of our studies in natural areas managed for wildlife to rangelands managed for livestock. The relation between prairie dogs, bison, and the production and availability of forage may not directly apply to cattle. Although prairie dogs may improve quality of forage for cattle just as they do for bison at the Wind Caves National Park, the quantity of forage may not be sufficient, depending on the number of cattle using the range (O'Meilia et al. 1982; Uresk 1987; Whicker and Detling 1988a). Furthermore, significant portions of prairie dog colonies frequently are dominated by forbs, dwarf shrubs, or species of grass that are less palatable to livestock. Thus, increased quality of forage can come with a sizeable reduction in the total standing crop of forage available for cattle. Although this may not be a problem for managing for wildlife populations at densities well below the carrying capacity of the land, it may conflict with private ranching operations where livestock may be stocked at levels closer to the carrying capacity.

Another consideration in managing for prairie dogs is one of scale. Much of the western rangeland is divided into paddocks or pastures, and the amount of land available to cattle or other livestock is often not as extensive as that available to bison and other ungulates in parks such as the Wind Caves National Park. Because large portions of individual paddocks may be covered by prairie dog colonies, far less forage may be available than in a natural area like our study areas (Coppock et al. 1983a, 1983b; Coppock and Detling 1986; Krueger 1986). Management policies for domestic animals and prairie dogs should address several factors including ownership of the land, occurrence of other wildlife species, juxtaposition of colonies, area available for wildlife and livestock, density of animals, condition and trend of the range, season of use, and potential patterns of multi-species interactions.

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A Review of Plague and Its Relevance to Prairie Dog Populations and the Black-footed Ferret

by

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Prairie dogs (all four species of *Cynomys*) are considered major amplifying hosts of plague (*Yersinia pestis* infection) in the western United States where the disease is endemic and often epizootic (Barnes 1982). Mortality from plague among prairie dogs during epizootics is extremely high, often near 100% among Gunnison's prairie dogs (*C. gunnisoni*; Eskey and Haas 1940; Lechleitner et al. 1962, 1968; Rayor 1985) and black-tailed prairie dogs (*C. ludovicianus*; Ecke and Johnson 1952; Barnes et al. 1972; Centers for Disease Control, Fort Collins, Colorado, unpublished 1980 records). During a 4-month observation period, Clark (1977) reported 85% mortality in white-tailed prairie dogs (*C. leucurus*) in Wyoming. An epizootic was confirmed by isolation of *Y. pestis* from tissues at the Centers for Disease Control (CDC) in Fort Collins, Colorado, and was reported by the Utah State Health Department to have killed 100% of a small Gunnison's prairie dog colony in Garfield County (Centers for Disease Control, Fort Collins, Colorado, unpublished 1981 records).

Interest in plague and prairie dogs by personnel from CDC stems from the public health perspective: Our primary function is to reduce human morbidity and mortality from any cause. From this perspective, prairie dogs are unimportant; fewer than 3% of the infections of humans with plague in the United States are acquired from prairie dogs or their fleas (Centers for Disease Control, Fort Collins, Colorado, unpublished records). From an ecological perspective, however, prairie dogs play an extremely important role by amplifying the magnitude of plague in the environment, broadcasting the disease to other animal populations, and extending its distribution, at least temporarily, into areas and even regions where plague is not enzootic.

The importance of prairie dog populations as the prey base for the black-footed ferret (*Mustela nigripes*) adds another important ecological dimension to CDC personnel's interest in plague. Plague and loss of its food resource are not the only hazards to this already endangered species but are extremely important. Periodic epizootic forays can render uninhabitable large areas of otherwise favorable habitat.

Based on the published literature and data collected at CDC, I present a brief review of plague in the western United States to provide a conceptual picture of its epizootiology and, as points of discussion, several questions about epizootic plague and its effect on the future of the black-footed ferret.

Background

Plague is a flea-transmitted disease of rodents caused by the bacterium *Yersinia pestis* that exists in widespread, discontinuous foci in parts of Africa, Asia, and the Americas (Poland and Barnes 1979; Velimirovic 1979). In its natural foci, the organism circulates among moderately to highly resistant rodent species with little or no overt disease (Baltazard 1953; Kartman et al. 1958; Baltazard et al. 1963); its persistence is dependent on a complex set of interrelations among reservoir hosts, flea vectors, the organism itself, and external environmental factors that influence its circulation. Each plague focus has its discrete and unique rodent reservoirs, flea vectors, the external environmental factors that influence transmission of the pathogen,

[1] Deceased.

and its epizootic manifestations (Pollitzer and Meyer 1961; World Health Organization 1980). In these respects, plague is typical of zoonoses as characterized by Audy (1958) and Pavlovsky (1966).

The disease in animals is characterized by explosive and often devastating sporadic or periodic epizootics among susceptible and receptive rodent and flea populations. During epizootic amplification, it tends to expand its distribution geographically, often for great distances, involving chance victims among ecologically associated animal species, including humans, who enter or live in the affected areas. Epizootics among wild and commensal rodents are self-limiting (Meyer 1942) and ultimately move on or recede to focal areas, at times seeding new pockets of infection that may persist for varying periods of time or occasionally remain as new nidi of infection.

Bubonic plague has existed in North America since 1900. Its introduction to ports on the Pacific and Gulf coasts, the commensal rodent-borne epidemics that followed, and its ultimate discovery among native wild rodent populations near San Francisco in 1908 (McCoy 1908, 1911; Wherry 1908) are well-documented episodes of the latest world pandemic (Meyer 1942; Pollitzer 1954; Link 1955). Whether or not plague already was present among wild rodents in North America at the time of its discovery has not been proven. Its behavior and devastating effect on rodent populations gives every indication that the disease was introduced as discussed by Elton (1958). The last urban epidemic in North America occurred in Los Angeles, California, in 1924–25 (California Board of Health, unpublished report) and involved commensal rats and California ground squirrels (*Spermophilus beecheyi*) and their fleas as sources of human infection (Link 1955). The episode in Los Angeles is also the last known person-to-person spread of pneumonic plague in the United States. Since 1925, all reported human cases in North America have had their zootic origins from native wild rodents and their fleas, although wild and domestic animals associated with an epizootic source at times played an intermediary role as sources of infection of humans.

After futile attempts to eradicate plague from California ground squirrels in California, the disease eventually spread across much of the state, not only among California ground squirrels but also in other rodent species (Meyer 1942). The first reported case of human plague of wild rodent-flea origin occurred in southern Oregon near the California border in 1934. The case in Oregon was eventually followed by first cases in Utah (1936), Nevada (1937), Idaho (1940), New Mexico (1949), Arizona (1950), Colorado (1957), Wyoming (1978), Washington (1984), and Montana (1987). The apparently rapid spread of plague across the western United States is readily explainable (although not proven) by the host-seeking behavior of fleas and the prey-seeking behavior of carnivores who depend on a rodent population that was eradicated by plague. Fleas migrate to burrow entrances where they are picked up by carnivores that then transport them to previously uninfected rodent colonies.

The U.S. Public Health Service conducted extensive surveys of animal plague through the 1930's and 1940's to determine the distribution of plague and the possibility of its expansion into the more populous eastern states (Eskey and Haas 1940; Meyer 1942; Ecke and Johnson 1952; Miles et al. 1952; Link 1955). These surveys, depending entirely on bacterial isolations (from fleas and rodent tissues), revealed animal plague in 15 western states extending eastward to about the 101st meridian in western Texas, Oklahoma, Kansas, and North Dakota. No cases of human plague of wild rodent origin were reported from Kansas, Oklahoma, or North Dakota through 1988.

During 1925–64, cases of human plague in the United States averaged about two per year (Fig. 1).

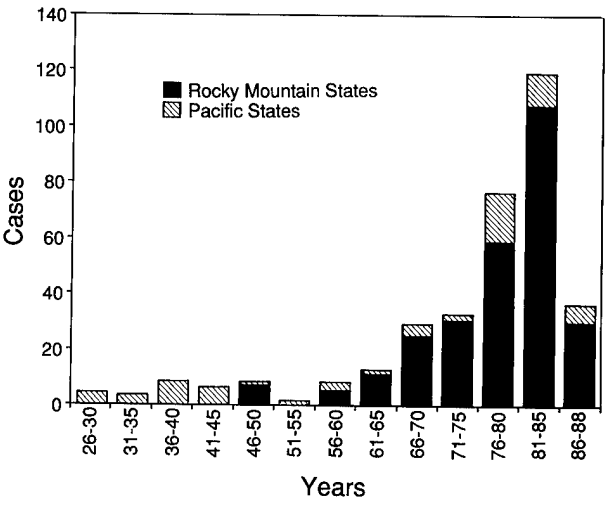

Fig. 1. Reported cases of plague in humans in the United States by 5-year periods, 1926–85, and by 3-year periods, 1986–88. Centers for Disease Control, Fort Collins, Colorado.

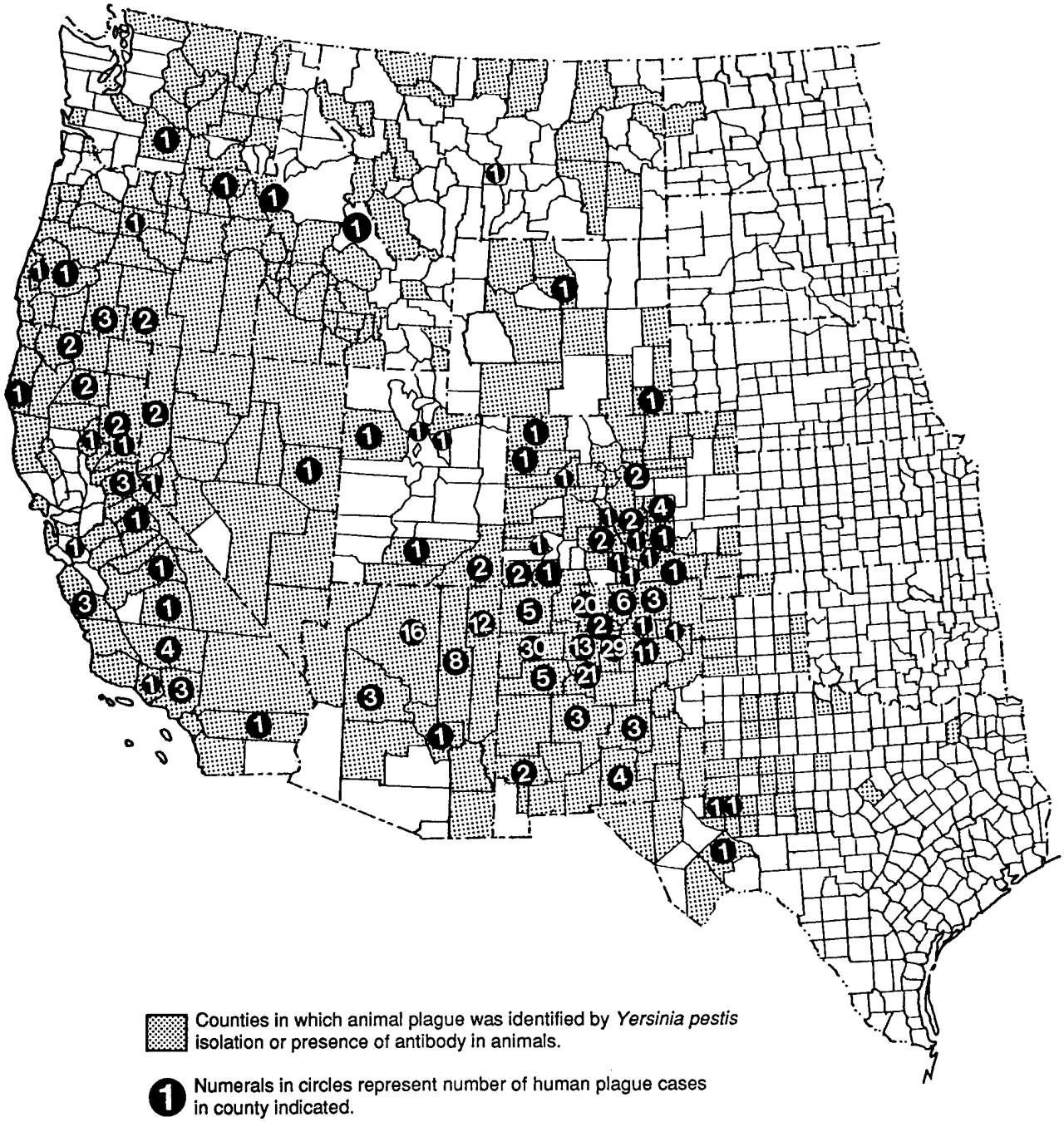

Fig. 2. Geographic distribution of plague in humans and other animals in the United States by county of origin, 1970–88. Centers for Disease Control, Fort Collins, Colorado.

Most were reported from California. In 1965, six Navajo Indian residents of New Mexico were infected (Collins et al. 1967). Since that time, the annual number of human cases has consistently increased, and most are in the Southwest, particularly New Mexico. With this geographic shift, the occurrence of human plague initially seemed to peak each 5 years, suggesting periodicity. Since 1975, the number of cases per year has ranged from 10 to 40 with an average of about 16.

Distribution of Rodent Plague in the United States

During 1971–88, *Yersinia pestis* activity was identified by isolation of the organism from flea vectors and animal tissues and also by the presence of plague antibodies in the sera of animals, primarily rodents and carnivores (Fig. 2).

Data from 1971–88 reconfirm the geographic range of plague in the United States as described by Eskey and Haas (1940), extending it somewhat eastward from the 101st to about the 97th meridian. Serologic positives from border counties in Montana, Washington, California, and Texas strongly suggested its presence, at least on occasion, in Canada and Mexico, and the organism was recently (1988) isolated from rodents in British Columbia (Centers for Disease Control, Fort Collins, Colorado, unpublished records).

Other new records (Centers for Disease Control, Fort Collins, Colorado, unpublished records) include areas in the temperate rain forest in northwestern California and southwestern Oregon. Although plague is well known in the inland areas of both states, the plague organism was assumed not to occur in the cool, wet environment of the coastal area. Plague was not discovered by earlier surveyors in hot desert areas of the Southwest, and CDC personnel were not able to discover evidence of plague in extensive surveys of antibodies among wild carnivores in the deserts of southern Arizona in 1975–80.

As shown by earlier workers (Eskey and Haas 1940; Kartman et al. 1958), the data (Fig. 2) indicate that the plague organism remains widespread and strongly entrenched among wild rodent populations in the western United States. However, quantitative changes in antibody prevalence from year-to-year among wild carnivores (Centers for Disease Control, Fort Collins, Colorado, unpublished data) indicate that in much of its distribution,the appearances of plague are short-lived and consist of amplification and geographic expansion that are followed by regression to focal areas. For example, during longitudinal studies at Fort Collins, personnel from CDC identified plague among carnivore and rodent populations (not only prairie dogs) along the Colorado Front Range every year in 1971–80. Conversely, carnivore populations on the bordering eastern plains from the Rocky Mountains eastward to Kansas had positive antibody titers during only the year or so after identified epizootics among black-tailed prairie dogs.

Hosts and Vectors of Plague Infection

Evidence of plague infection has been found in a multitude of mammalian species. Poland and Barnes (1979) note that globally members of eight orders, 95 genera, and well over 200 species are plague-positive or have antibodies indicating prior infection. In the United States during 1970–88, CDC investigators found evidence of plague infection in 76 species of six mammalian Orders (Rodentia, Lagomorpha, Insectivora, Artiodactyla [deer and antelope], Carnivora, and Primates [humans]). Whereas some of the represented species may function as maintenance hosts and others as epizootic hosts of infection, many others (e.g., humans and deer) are dead-end hosts from which no further transmission is expected. Researchers know nothing about the roles of some rodent genera in plague cycles. Infections in some species may be of transient importance and are passed on by a few individuals even though the host–flea population complex by itself is incapable of sustaining a transmission cycle. Such individuals may at times play a key intermediary role between an epizootic source of infection and other receptive individuals or populations, including humans, either by transport of infective rodent fleas or by serving as a direct source of infection such as domestic cats and humans (Kaufmann et al. 1981; Werner et al. 1984).

Epizootic Host–Flea Complexes

Based on data at CDC, plague epizootics at any time usually involve one or sometimes two rodent–flea complexes that play principal roles in the dynamics of amplification and without which the epizootic would collapse. If two susceptible rodent populations coexist in time and place, plague infection in one almost inevitably transfers to individuals of the other. If population density, flea vector abundance, and other factors of epizootic amplification are receptive, the second popu-

lation becomes centrally involved in its own epizootic. If one or more key factors are not receptive, infection may be confined to individuals that acquire it directly from the first population. To further complicate the situation, time and season of receptivity vary among species and populations. In this complex and shifting milieu, it is often difficult to determine if fleas or rodents are most important because their roles may change with time, space, and circumstance.

Table 1. *Host–flea complexes that were prominent in epizootic plague amplification in western North America by geographic region.*[a]

State and regions	Principal rodent hosts and flea vectors	
	Rodent species	Flea vectors
Arizona, New Mexico, southern Colorado, southern Utah	*Spermophilus variegatus*	*Oropsylla (Diamanus) montana, Hoplopsyllus anomalus*
Arizona, New Mexico, Colorado, Utah (Rocky Mountains and west)	*Cynomys gunnisoni*	*O. (Opisicrostis) hirsutus, O. (O.) tuberculatus cynomuris*
Colorado (east of Rocky Mountains, western Texas, Oklahoma, Kansas	*C. ludovicianus*	*O. hirsutus, O. t. cynomuris*
Wyoming, northwestern Colorado, *northeastern Utah (high plains)*	*C. leucurus*	*O. t. cynomuris, O. hirsutus, O. labis*
Colorado, Idaho, Montana, Wyoming, (mountain parks, high plains grasslands)	*S. richardsoni*	*O. labis, O. idahoensis* (Rocky Mountains), *O. t. tuberculatus, Thrassis bacchi*
California, Oregon, northern Nevada, southeastern Idaho (montane meadows, Great Basin sagebrush–grasslands)	*S. beldingi*	*O. francisi, O. pandorae, O. petiolatus, O. tuberculatus*
Southern Idaho, eastern Oregon, Nevada, Utah (Great Basin sagebrush)	*S. townsendi*	*O. francisi*
Idaho, Utah, Wyoming (Great Basin and montane, 4,000–8,000 ft)	*S. armatus*	*O. pandorae, O. francisi*
California, Oregon, Washington, western Nevada (valleys, foothill savanna, open pine forest, to temperate rain forest edge)	*S. beecheyi*	*O. montana, H. anomalus*
Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon (montane areas, open pine forest)	*S. lateralis*	*Oropsylla idahoensis, O. montana* (Sierra–Cascade), *O. labis* (Rocky Mountains)
Western United States from Rocky Mountains westward	*Tamias* spp.[b] 16 species	*Eumolpianus eumolpi, Monopsyllus eutamiadis, M. fornacis*, and *Ceratophyllus cilliarus* (last three from the Pacific States only)
Western United States from Texas to the Pacific States (desert to high montane shrubby habitats)	*Neotoma* spp.[c] 8 species	*Orchopeas sexdentatus, O. neotomae, Anomiopsyllus* spp.
New Mexico, Arizona, southern California, Utah, Colorado (desert plateau regions)	*Ammospermophilus leucurus*	*Oropsylla bacchi*
Colorado, Wyoming, California (urban residential and rural environments)	*Sciurus niger*[d]	*Orchopeas howardi*

[a] Centers for Disease Control, Fort Collins, Colorado.

[b] Individuals of nine species were found to have been plague-infected or carried plague-positive fleas.

[c] Individuals of five species were found to have been plague-infected or carried plague-positive fleas.

[d] This periodomestic species has been introduced to western cities as a park squirrel along with its flea, *O. howardi.*

Regional Epizootic Centers

As shown earlier (Fig. 2), the greatest proportion 83%) of wild rodent-associated cases of human plague in the United States during the past 20 years originated in the Southwest in an area that includes most of New Mexico, northeastern Arizona, southern Colorado, and southernmost Utah. Two major amplifying host–flea complexes exist in the area and overlap in ecotonal situations: one is composed of Gunnison's prairie dogs and the fleas *Oropsylla (Opisocrostis) hirsuta* and *Oropsylla (Opisocrostis) tuberculata*; the other, of rock squirrels (*Spermophilus variegatus*) and the fleas *Oropsylla (Diamanus) montana* and *Hoplopsyllus anomalus*. The prairie dog complex occurs in semi-arid grasslands throughout the Southwest; the rock squirrel complex, also widespread, occurs in uplands characterized by open to closed pinon–juniper and Gambel oak woodland at elevations of about 1,500–2,500 m.

Because of their involvement with human plague, these host–flea associations have been given far more attention than others. Many others (Table 1) support plague epizootics and in some instances have a great effect on rodent populations. For example, a bubonic plague epizootic was identified in 1978 among two of the smaller ground squirrel species, Richardson's (*Spermophilus richardsoni*) and Townsend's (*S. townsendi*) ground squirrels, in southern Idaho when high plague antibody titers appeared among coyote (*Canis latrans*) populations. In 1976, only 7 of 160 coyote sera collected in the entire state were antibody positive and in 1977, only 8 of 211. In each year, the titers of positive animals did not exceed 1:256. In 1978, 91 of 300 carnivores collected in Idaho had antibody titers ranging from 1:32 to 1:4096. The epizootic centered in the southern part of the state where ground squirrels are abundant, particularly in Twin Falls County where 68 of 136 coyotes had significant titers. By 1979, plague had invaded ground squirrel populations in adjacent counties in northern Nevada where epizootics among Belding's ground squirrel (*S. beldingi*) were widespread and devastating. Plague subsided in southern Idaho in 1979, and by 1980, only 4 of 327 captured coyotes had antibody titers; the highest was 1:256. An increased incidence of plague titers among carnivores in eastern Oregon led to the discovery of epizootic plague there among Belding's ground squirrel in 1981. This suggests that the epizootic first discovered in southern Idaho in 1978 had moved through populations of these small ground squirrels distributed over much of the northern Great Basin region in about 3 years, leaving little residual evidence of infection where it was first noted. No studies of the recovery of the squirrel populations or of the peripheral effects among associated animals were done. Epizootics among Gunnison's prairie dogs described by Kartman et al. (1962) and Lechleitner et al. (1962, 1968) involved populations in high mountain parklands in Colorado and the flea *Opisocrostis tuberculatus cynomuris* as the predominant transmitter. Subsequent observations by Maupin (1970) of plague in black-tailed prairie dogs revealed that at lower elevations the flea *O. hirsutus* is dominant in summer and is replaced by *O. t. cynomuris* in winter. Both species seem to transmit the disease equally well among prairie dogs; however, an epizootic involving *O. tuberculatus* in the spring seems to continue at a more rapid pace as *O. hirsutus* becomes abundant and numbers of *O. tuberculatus* diminish with the onset of summer.

Devastating plague epizootics are common among Gunnison's prairie dogs, having been reported from one locality or another in the Southwest in each of the past 20 years. Mortality in a colony during a plague epizootic often approaches 100%. Epizootics may be sporadic and localized in small colonies, but in large continuous colonies may sweep across hundreds of square kilometers. Small, isolated colonies may not recover. On the other hand, colonies that do recover usually require about 4–5 years to regenerate to their former levels and to once more become receptive to a plague epizootic. Many colonies under observation as a surveillance measure regenerated only to be attacked again and nearly eradicated. Similar epizootics have been observed among black-tailed prairie dogs. Epizootics among black-tailed prairie dogs in Boulder, Denver, and Adams counties, Colorado, occurred in recent years. Far less is known about plague in white-tailed and Utah prairie dogs (*C. parvidens*), although CDC has records of plague in both species.

Factors that Govern or Influence the Course of Plague in Prairie Dog Populations

Obviously, the factors that govern the receptivity to plague infection and its epizootiology in a prairie dog colony are many (Table 2). Here I discuss only those that are the most important to our questions, recognizing that the interrelations

Table 2. *Factors of receptivity to plague and the course of epizootics among prairie dog populations.*[a]

Intrinsic Factors
Prairie dogs:
Host susceptibility
Host population density
Nutritional status of the colony
Distribution and separation of colonies
Hibernation and seasonal period of activity
Fleas:
Flea species present
Flea population density
Transmission capability
Survival once infected
Seasonal distribution
Extrinsic Factors
Climate and weather:
Seasonal moisture, temperature regimes, and fluctuations as they affect the burrow microclimate (fleas), the growth of the plague organism in fleas and their ability to transmit (blockage), and the behavior of prairie dogs.
Other rodent involvement:
(Same intrinsic factors that affect prairie dogs)
Other flea involvement (from other animals):
Host preferences and flea exchange.
Proximity to enzootic focus or to another epizootic source of infection.
Availability of predators (mammalian or avian) for intercolonial spread of infected fleas.

[a] Centers for Disease Control, Fort Collins, Colorado.

among them are at least as complex as those in any other ecological community.

Susceptibility of Hosts

The question of prairie dog susceptibility to plague has been well answered. Evidence from countless epizootic investigations during the past 25 years (Centers for Disease Control, Fort Collins, Colorado, unpublished records) revealed that prairie dogs are exquisitely sensitive to naturally occurring plague and that mortality frequently reaches 100% in affected black-tailed and Gunnison's prairie dog colonies, often eradicated in one season or faster (Rayor 1985). The evidence is less clear for white-tailed and Utah prairie dogs. Nevertheless, Clark (1977) reported 85% mortality in white-tailed prairie dogs in Wyoming during a 4-month observation period, and reports and plague isolations support the occurrence of high mortality in the Utah prairie dog during epizootics. More recently, laboratory studies (E. Williams, University of Wyoming, personal communication) identified white-tailed prairie dogs as highly susceptible. No evidence of resistance to plague has been observed as noted by Nelson (1980) among California ground squirrel populations recurrently subjected to epizootic plague.

Population Density and Distribution of Colonies

The density of a host population has obvious importance to disease transmission and also affects the nutritional status, growth, reproduction, dispersal, and other attributes of a population as discussed for prairie dogs by Rayor (1985). According to Nelson (1980), epizootics among California ground squirrels tend to be more violent and rapid in dense and widespread colonies than in smaller and more dispersed aggregations. High population densities among hosts provide greater opportunities for the exchange of fleas and affect the rapidity with which plague can move through a population.

Similarly, the distribution and distance between colonies seem to affect the course of epizootic plague in any area. Years of epizootic investigations revealed that isolation (or separation) plays a major role in the survival of individuals that remain to regenerate colonies and also in the survival of colonies missed by infection during regional epizootics. Surviving individuals and members of surviving colonies rarely have antibodies to plague. As an added note, CDC investigators frequently observed that survivors of a decimated colony are individuals who pioneered new and less favorable habitat as the colony population reached and exceeded the carrying capacity of the available optimum habitat. CDC personnel also observed that plague can move great distances between colonies with the involvement of other animal species, particularly predators, either as infected disease carriers or as passive carriers of infected fleas.

Hibernation and Seasonality

Whether or not species hibernate and how long specific populations do so undoubtedly are major factors in the course, continuation, and end results of epizootics. According to Prince and Wayson (1947), the plague organism in hibernating golden-mantled ground squirrels (*Spermophilus lateralis*) remains dormant with its host during hibernation and becomes active as the host's body temperature increases with emergence. *Yersinia pestis* grows at

temperatures as low as 4°C and survives much lower temperatures, thus plague epizootics among hibernating species seem to simply hibernate along with their hosts to emerge in the spring. Among non-hibernating species such as black-tailed prairie dogs, fleabite transmission and epizootics continue through the winter, but at a seemingly slower pace. The length of the hibernation season, affected by climate, in turn may affect length of time or season during which flea populations may expand and transmission may occur, affecting in turn the course and intensity of epizootic plague in the rodent population.

Flea Species and Their Importance

The ability of fleas of wild rodents to transmit plague varies considerably between species as shown experimentally by Eskey and Haas (1940), Wheeler and Douglas (1945), Kartman and Prince (1956), and others. Some flea species seem to be unable to transmit at all; the capability to transmit by others runs the spectrum from poor to fair; and transmission by most species has not been studied. Factors of transmission capability include how many individuals become infected; how many of those that become infected also become blocked so that they cannot ingest a blood meal and instead regurgitate organisms into the bite wound; how rapidly individuals block, how long they survive after blocking, and how many times they can transmit when blocked; and the abundance of fleas. These are affected in turn by climate and weather that largely determine reproductive rate, survival, abundance, and also the likelihood of blockage by the effect of temperature on the growth and behavior of the plague organism in the flea gut. The briefly mentioned factors could be added to and expanded upon endlessly. However, it should now be apparent that the manifestation of plague in animal populations depends as much on the kinds of involved fleas, their ecologies, and their abundance as on the characteristics of the host population. Ignorance in this area of interest is profound. For example, researchers do not know how many and what kinds of fleas maintain an epizootic, much less determine its course. Not only that, they do not know how to measure flea population density except in a very relative way. How many fleas can be collected on a burrow swab depends on a multitude of factors at any given time. During and following an epizootic, fleas migrate to burrow entrances and can be captured in large numbers. When prairie dogs are alive and healthy, fleas tend to remain in the nest where they are not reachable. Unqualified data on flea abundance in one circumstance has little relevance for comparisons with data collected in other circumstances. Researchers also are uninformed about the relative vector efficiencies of the fleas prominently involved in prairie dog epizootics. Research into this is severely inhibited because of our inability up to now to successfully colonize the vectors.

Plague and Black-footed Ferrets

Plague in prairie dogs is a major impediment to the reintroduction and establishment of black-footed ferrets in the western United States, particularly in the ranges of the Gunnison's and black-tailed prairie dogs. Plague in prairie dogs occurs every year somewhere in the southwestern focus (Fig. 2) and is only somewhat less frequent in the Colorado Front Range and the plains to the east. A great deal more information is needed about plague in white-tailed prairie dogs, but available information indicates that the occasional epizootics in the species are sufficient to reject it as a potential prey base for reintroduced black-footed ferrets. For the same reason, neither Montana and the western most Dakotas where plague was recorded in recent years nor western Oklahoma and Texas where epizootic plague in prairie dogs was recently rampant (1989) should be considered.

This leaves the possibility of successful introductions and establishment of ferrets (barring other barriers) only along the northeastern edge of the black-tailed prairie dog range in Nebraska and in parts of the Dakotas where plague has never been recorded. These areas have not been surveyed for plague since the early 1980's and then only superficially when CDC investigators tested 160 coyote sera from South Dakota for antibodies to *Y. pestis* and obtained negative results. Substantive studies should be conducted in prospective areas for reintroductions to evaluate flea vector populations, associated small mammal populations, and other factors of the ecology of plague. In conducting such studies, the fact that epizootic plague moves through animal populations, then recedes, should be kept in mind; its absence in one year does not indicate its absence or preclude its presence in another.

Plague is the only disease that causes epizootics with high mortality in prairie dogs. Tularemia is rarely found in prairie dogs. In more than 20 years, CDC personnel have not found tularemia in prairie

dogs even though tissues tested for plague were also tested for tularemia.

Control of Plague in Prairie Dogs

Control of fleas on prairie dogs is frequently used to prevent exposure of people in high risk areas, for example, where prairie dog colonies impinge on areas of high human activity such as yards and playgrounds. The general approach involves the dusting of burrows with an acceptable and effective pulicide. Carbaryl (5–10% dust) applied at a rate of 28–56 g (1–2 ounces) of dust / burrow has been the standard successful, but at times unsuccessful, treatment during the past 15 years. Its checkered results and short half-life in soil revealed that newer materials are needed. Personnel at CDC and Fairfield–American, Inc., developed and tested a micronized dust formulation of 0.5% permethrin in silica gel designed specifically for control of fleas on wild rodents. The formulation has been extremely effective against *Oropsylla (O.) hirsuta* and *O. (O.) tuberculatus cynomuris* in prairie dog burrows in Boulder County and Adams County, Colorado, giving excellent control for more than 3 months when used at a rate of 7 g / burrow. It is now licensed in five states under 24C (Special Local Needs Registry) and is currently applied operationally in Colorado and New Mexico. Permethrin, when used as directed, is safe for use around a wide array of domestic animals and humans. The toxicant is also formulated as a liquid and licensed for use on clothing to repel ticks, chiggers, and other blood-sucking arthropods. The cost by weight is considerably greater for permethrin than for carbaryl but, because far less is used (<25%), the cost per burrow is about the same. Should insecticidal control be considered for maintaining prairie dog populations, I strongly recommend permethrin micronized dust as a replacement for carbaryl.

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Plague, Prairie Dogs, and Black-footed Ferrets

by

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Abstract. The historic range of black-footed ferrets (*Mustela nigripes*) roughly corresponds with the range of black-tailed (*Cynomys ludovicianus*), white-tailed (*C. leucurus*), and Gunnison's prairie dogs (*C. gunnisoni*) in western North America. Prairie dog numbers declined drastically between 1900 and 1970, largely from governmental pest control and probably from plague epizootics that have swept through prairie dog colonies over extensive areas since the late 1930's.

Concomitant with the reduction in area of prairie dog colonies, the black-footed ferret, which depends on prairie dogs for prey, also disappeared from most of its range. Because of the black-footed ferret's dependence on prairie dogs for food and prairie dog burrows for shelter, plague epizootics in prairie dog colonies are one of the most serious problems in the management and recovery of the black-footed ferret.

This paper presents a review of the literature on plague in prairie dogs. Known differences in responses to plague between prairie dog species and several plague related management problems are described. The most important questions that plague in prairie dogs pose for the management of black-footed ferrets are (1) How is plague maintained in the prairie dog ecosystem between epizootics? (2) How are plague epizootics in prairie dog colonies started? and (3) Once plague epizootics begin, how can their effects be minimized? Answers to these questions are instrumental for the selection of sites for reintroductions of ferrets and for the stabilization of prairie dog populations when ferrets are released.

Key words: Prairie dogs, *Cynomys*, plague, *Yersinia pestis*, epizootic, black-footed ferret, recovery.

In the late 1800's, an estimated 283 million ha were occupied by prairie dogs (*Cynomys* spp.) in the western United States. By 1971, that area had declined to 600,000 ha (Cain et al. 1971, in Fagerstone and Biggins 1986). Black-footed ferret (*Mustela nigripes*) populations declined, and the species range became restricted at the same time (Hillman and Clark 1980). Although eradication of prairie dogs by government agencies greatly reduced prairie dog numbers, the simultaneous introduction of plague (*Yersinia pestis*) may have been of equal importance. Plague, a disease of wild rodents, came to the United States in 1899 (Link 1955; Barnes 1982; Gregg 1985). The combined effects of the government's eradication and plague, which often kills more than 99% of prairie dogs in affected colonies, have had a devastating effect on populations of Gunnison's (*C. gunnisoni*), black-

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tailed (*C. ludovicianus*), and white-tailed prairie dogs (*C. leucurus*).

Prairie dog populations have increased in many areas since control was reduced in 1972 (Hanson 1993; Hubbard and Schmitt 1984). However, in the western United States, plague epizootics continue to devastate populations of Gunnison's (Rayor 1985; J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data), black-tailed (Barnes 1982), and white-tailed prairie dogs (Ubico et al. 1988) at intervals as short as 3 years (J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data) or more commonly at 5–10 year intervals (Barnes 1982). "Although people disagree on how management should be carried out, most agree that management of the black-footed ferret is dependent upon management of the prairie dog" (Linder 1973:171). An integral part of management of prairie dogs where plague is prevalent will be an understanding of community-wide dynamics of plague to predict the onset of epizootics and retard the spread of plague between prairie dog colonies after epizootics begin.

In this paper, I address (1) the reason plague is an important component of the ecology of black-footed ferrets, (2) the literature on plague that provides insights for management of prairie dogs, (3) plague epizootics in prairie dogs and the roles that other rodent species might play in the long-term maintenance of plague foci, and (4) urgent research into specific aspects of the ecology of plague.

Plague of Wild Rodents in the United States

Plague is found primarily in wild rodents and is transmitted by fleas. The etiologic agent is *Yersinia pestis*, "a gram-negative, bipolar staining coccobacillus of the family Enterobacteriaceae" (Poland and Barnes 1979). Rodents range in their susceptibility to plague from highly resistant species (*Dipodomys*) to highly susceptible species (*Cynomys*). Among the susceptible rodents, the effects of plague vary by the rapidity of death. Among species of *Cynomys*, death occurs so quickly that antibodies and overt signs of pathology do not always develop (Poland and Barnes 1979).

Plague-infected fleas are the primary vectors of plague and are probably responsible for infecting most prairie dogs after an onset of an epizootic. Infected fleas have a long survival in the laboratory where they have survived for more than 1 year at room temperature in dark conditions (Prince and Wayson 1947a, 1947b; Pavlovsky 1966). Infected fleas have been removed from prairie dog burrows more than a year after the beginning of epizootics and at least several months after the disappearance of susceptible prairie dogs (Fitzgerald 1970; J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data). Precise survival times under natural conditions in the field have not been determined because when the last prairie dog in a colony dies or emigrates is difficult to determine and because, as epizootics wane, the immune status of the survivors is unknown.

Plague was probably introduced to the United States from Asia circa 1899 (Link 1955; Barnes 1982; Gregg 1985). The first record of plague in native mammals in North America was near Berkeley, California, in 1908 among California ground squirrels (*Spermophilus beecheyi*; McCoy 1908; Wherry 1908). Since then the disease has spread throughout the western states west of the 100 meridian (Poland and Barnes 1979; Barnes 1993) in 76 species of 5 mammalian orders: Rodentia, Lagomorpha, Insectivora, Artiodactyla, and Primates (Barnes 1982).

The potential for humans to contract plague resulted in considerable research into the ecology of plague during the past 80 years. The disease occurs in foci (or nidi; Pavlovsky 1966) at various locations around the world, including North America, where the disease is recurrent and seems to be persistent. There are also non-focal areas where plague seems to be periodically reintroduced from outside and then disappears between epizootics (Poland and Barnes 1979). Terms in disease ecology that may not be familiar to wildlife ecologists are defined in the Appendix.

Plague epizootics frequently involve diurnal rodents, mostly ground squirrels or prairie dogs of the family Sciuridae. Many sciurids, including prairie dogs, reach high population densities and, because they are easily visible, epizootics in these species are noted and investigated. Epizootics in prairie dogs may spread over hundreds of square kilometers (Barnes 1982). Furthermore, cases of plague in humans occur most frequently during or shortly after epizootics (Weber 1978). Consequently, the epizootic phase of the plague cycle has received a great deal of attention from researchers

in public health and is the source of most of the current knowledge about the ecology of plague.

The enzootic or maintenance species are probably "moderately to highly resistant rodent species with little or no overt disease (Baltazard 1953; Kartman et al. 1958; Baltazard et al. 1963)" (Barnes 1982:238). California voles (*Microtus californicus*) in San Mateo County, California, fit these criteria. Although the response varies between individuals, California voles carried plague bacteremia without overt symptoms (Goldenberg et al. 1964; Hudson et al. 1964). Despite many years of research, this California vole population is the only verified example of an enzootic system. Other North American species, which are moderately to highly resistant to plague and which may serve as enzootic hosts, are kangaroo rats (*Dipodomys* spp.), deermice (*Peromyscus maniculatus*; Holdenried and Quan 1956), and northern grasshopper mice (*Onychomys leucogaster*; Thomas et al. 1988). All occur in prairie dog colonies and may serve as reservoirs for plague between the epizootics in prairie dogs.

In other vector-borne diseases, such as La Crosse encephalitis, the pathogen is maintained by the insect vector, and the mammalian hosts are thought to serve primarily to infect new insects (DeFoliart 1983). Given that plague-infected fleas may survive more than a year whereas their rodent hosts die after only a few days, plague, like La Crosse, might be a flea parasite that is amplified by prairie dogs and other rodents.

There is evidence that some mammal species are evolving a reduced susceptibility to plague (Williams et al. 1979; Shepherd et al. 1986; Thomas et al. 1988). For example, during epizootics in some areas of California, California ground squirrels began to have higher rates of survival than early in the century (Meyer et al. 1943; Nelson 1980). Rock squirrels (*Spermophilus variegatus*) also developed resistance where contact with plague has been continuous, but not in areas in Utah where plague has not been identified in this species (Marchette et al. 1962 [in Quan et al. 1985]). Variance in susceptibility to plague in rock squirrels (Quan et al. 1985), California ground squirrels (Williams et al. 1979), and northern grasshopper mice (Thomas et al. 1988) is also great.

The ecology of plague in North America may be changing because of evolutionary changes in resistance in the host mammal community. As resistance develops, species' roles may shift from epizootic to enzootic status. If that happens, populations in areas where plague has been infrequent could become enzootic foci in the future. This change has obvious implications for the management of prairie dogs.

Plague in Prairie Dogs

Plague was first observed in Gunnison's prairie dogs in northwestern Arizona in 1932, in eastern Arizona in 1937, and in New Mexico in 1938 (Eskey and Haas 1940). It was first recorded in Utah prairie dogs (*C. parvidens*) in Utah and in white-tailed prairie dogs in Wyoming in 1936 (Eskey and Haas 1940). Ten years later, plague had reached black-tailed prairie dogs in Texas (Miles et al. 1952). In Colorado, the first report of plague in prairie dogs was between 1945–49 when an epizootic occurred in Gunnison's prairie dogs at South Park (Ecke and Johnson 1952). Today plague has spread throughout the range of Gunnison's prairie dogs in Arizona, Utah, New Mexico, and Colorado (Barnes 1982). It also persists in white-tailed prairie dogs in Wyoming (Clark 1977; Clark et al. 1985; Ubico et al. 1988), in Utah prairie dogs in Utah, and in black-tailed prairie dogs in Colorado, New Mexico, Texas, and Oklahoma (Barnes 1982).

The rate of spread of epizootics may be a function of host population density (Barnes 1982; J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data), flea species, flea density, and host susceptibility. With the exception of host density, there are no experimental data on the effects of any of these factors on the rate of epizootics in prairie dogs. White-tailed prairie dogs, which occur in much lower-density colonies than black-tailed or Gunnison's prairie dogs (Eskey and Haas 1940; Clark et al. 1985; Menkens and Anderson 1989, 1991), seem to experience slower rates of spread and less consistent population declines.

The mean density of prairie dogs at four white-tailed prairie dog colonies at Meeteetse, Wyoming was 3.8 / ha (Clark et al. 1985), which compares well with 3.4 / ha in southern Wyoming (Clark 1977) and 3.6 / ha in Colorado (Tileston and Lechleitner 1966). A plague epizootic in white-tailed prairie dogs in 1967 in southeastern Wyoming killed 85% of the prairie dogs in 4 months (Clark 1977). At Meeteetse, Wyoming, a plague epizootic swept through 4 of 37 prairie dog colonies (Menkens and Anderson 1991), but these four colonies included 1,521 ha of the 2,995 ha of active prairie dog colonies in the complex (Clark et al.

1986). Plague-positive fleas continue to be collected from prairie dog burrows at these colonies after 4 years (G. Menkens, U.S. Fish and Wildlife Service, personal communication). The prairie dog population there is slowly declining, and the epizootic is gradually spreading to other colonies. At this time, the prairie dog population at Meeteetse is below the necessary minimum for the reintroduction of black-footed ferrets (B. Miller, U.S. Fish and Wildlife Service, personal communication).

At Meeteetse, the plague epizootic in white-tailed prairie dogs waned while many prairie dogs were alive. The density of prairie dogs was low, burrows were widely dispersed (compared with Gunnison's and black-tailed prairie dogs), and more than 100,000 burrows were dusted to stop the epizootic (G. E. Menkens and S. H. Anderson, University of Wyoming, unpublished manuscript). Although plague-positive fleas continued to be found in burrows, dusting may have reduced the flea population below the vector transmission threshold (MacDonald 1957).

A laboratory study demonstrated that white-tailed prairie dogs are highly susceptible to plague, and therefore the epizootic probably did not stall because the prairie dogs were resistant (E. Williams, University of Wyoming, undated report to the U.S. Fish and Wildlife Service). If fleas are maintaining plague and low rates of transmission to prairie dogs are adequate to amplify plague in the fleas, the white-tailed prairie dog complex at Meeteetse may be an enzootic plague system. Researchers of plague at Meeteetse should consider this possibility.

Miles et al. (1952) described epizootics of plague in black-tailed prairie dogs near Lubbock, Texas, during 1945–49, and plague epizootics still occur there today (R. Chesser, Savannah River Ecology Laboratory, personal communication). Plague epizootics in black-tailed prairie dogs have been extensive in eastern Colorado (Barnes 1982), but apparently plague has not occurred in this species north of Colorado. Reports of plague epizootics are not as detailed for black-tailed as for Gunnison's prairie dogs, but mortality rates and rate of spread seem to be similar in the two species (see below). The most detailed long-term studies of the behavior and ecology of black-tailed prairie dogs were at the Wind Cave National Park in South Dakota where plague has never been reported in prairie dogs (King 1955; Koford 1958; Hoogland 1979, 1981a, 1981b; Hoogland and Foltz 1982; Garrett and Franklin 1988; Garrett et al. 1982). The reason plague has not struck northern black-tailed prairie dogs is unknown. Plague has been identified in species other than prairie dogs in eastern Montana and Wyoming in counties where black-tailed prairie dogs occur (Barnes 1982). Epizootics in black-tailed prairie dogs may have occurred but have not been noticed because of the remote locations of the colonies.

The densities of Gunnison's prairie dogs are often as high as densities of black-tailed prairie dogs, and like the colonies of black-tailed prairie dogs, colonies of Gunnison's prairie dogs often cover very large areas (Ecke and Johnson 1952). In South Park, Colorado, colonies of Gunnison's prairie dogs covered more than 370,000 ha in 1941. At that time, the U.S. Fish and Wildlife Service began control of prairie dogs, and workers reported that some disease (probably plague) killed prairie dogs on more than 97,000 ha prior to poisoning. Between 1947 and 1949 in South Park, plague reduced colonies of Gunnison's prairie dogs to less than 5% of their former extent (Ecke and Johnson 1952).

Although the epizootic at South Park was the most drastic reported for prairie dogs, colonies of Gunnison's prairie dogs do not have to be large to become the focus of an epizootic. Lechleitner et al. (1962) watched the extinction of a colony of about 275 Gunnison's prairie dogs in an isolated mountain meadow near South Park between June and September 1959. Likewise, Lechleitner et al. (1968) observed the passage of a plague epizootic through a complex of seven colonies of Gunnison's prairie dogs in Saguache County, Colorado, during 1964–66. Two of the colonies were eliminated during the first summer, and three had become extinct by 1966. A few prairie dogs remained at two colonies when the epizootic ended in 1966. Fitzgerald (1970) studied Gunnison's prairie dogs in 1965 at a small colony that was isolated by 12.8 km from other Gunnison's prairie dogs. The colony covered 4.74 ha and consisted of 68 prairie dogs in summer 1965. After 2 years, mortality from a combination of plague and winter kill resulted in the extinction of the town.

Rayor (1985) observed a plague epizootic in a marked population of Gunnison's prairie dogs at the Curecanti National Recreation Area near Gunnison, Colorado. She reported the annihilation of a colony of 1,000–1,500 prairie dogs during a 2 month epizootic in spring 1981. However, some animals were still present in shrubby habitat surrounding her Blue Mesa study area after the epi-

zootic (A. Barnes, Centers for Disease Control, Fort Collins, Colorado, personal communication), and when I visited the site in July 1986, prairie dogs were again abundant despite attempts by the National Park Service to control them.

An epizootic in Gunnison's prairie dogs swept through the Moreno Valley in north-central New Mexico during 1983–87 (J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data). The epizootic probably began near the town of Eagle Nest (Figure) where a human had plague in August 1983. Surveillance by the New Mexico Environmental Improvement Division and the Centers for Disease Control revealed plague-positive fleas of species that associate with Gunnison's prairie dogs, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and deermice. In October 1984, few prairie dogs were found near Eagle Nest; however, prairie dogs were abundant in the west and south of the valley. At a study area between Eagle Nest Lake and U.S. Highway 64 (Midlake) where prairie dogs were marked and trapped in October 1984, their density was 30/ha. With the marked population as a guide to density at other areas and from a survey of colonies in the valley, J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin (University of Notre Dame, unpublished data) estimated that the population of Gunnison's prairie dog in the Moreno Valley at that time numbered more than 100,000.

In October 1984, prairie dogs were as abundant north of Six-mile Creek and west of Moreno Creek as at Midlake. In March and April 1985, few prairie dogs emerged from hibernation in the north, and by 1 July 1985, the density was less than 0.1/ha. Subsequent serology tests of survivors indicated that plague had been present (J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data).

There were no indications of plague in prairie dogs at Midlake until July 1985. However, a large, but uncounted population of thirteen-lined ground squirrels that had been present in October 1984 was reduced to two animals in April 1985. In July 1985, an adult female prairie dog had a weak serum antibody titer, and in August, plague-positive fleas were collected from prairie dogs and their burrows. By 1 October 1985, the marked prairie dog population, which consisted of 168 animals in July, was reduced to about 25. Only seven prairie dogs emerged from hibernation in March 1986, and all had disappeared by 1 July of that year. On 1 September 1986, a careful search of 200 ha between Eagle Nest Lake and Highway 64 revealed two prairie dogs (J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data).

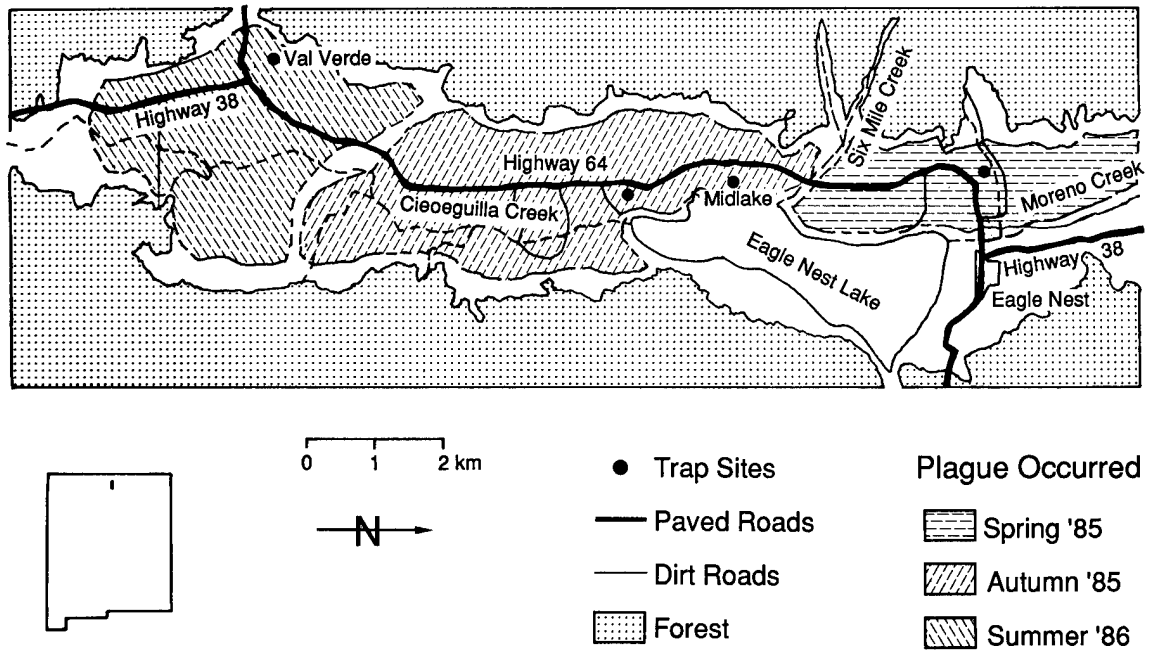

Figure. Moreno Valley in north-central New Mexico.

The pattern at the north and center of the valley was repeated in the south with only minor differences during 1986–87. After the epizootic had spread through the Moreno Valley in June 1987, the entire population of Gunnison's prairie dogs in the valley consisted of 250–500 prairie dogs (J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data). This figure includes several colonies in the north that had undergone 2 years of post-plague population growth at that time. Using the conservative estimates of 100,000 prairie dogs in October 1984 and 250–500 in June 1987, plague reduced the population of Gunnison's prairie dogs by 99.5–99.8%.

All of the described studies of plague in Gunnison's prairie dogs were of isolated colonies or colonies that were in isolated complexes. Climatic conditions and prairie dog flea species (*Oropsylla hirsuta, O. labis, O. tuberculata cynomuris*) were similar in every case, and in all cases, the declines of prairie dog populations were between 95 and 100%. At the end of the epizootics, many prairie dog fleas were infectious for plague. In the Moreno Valley, fleas that associate with other rodent species were taken from prairie dog burrows (J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data): *O. bacchi*, associated with thirteen-lined ground squirrels; *Rhadinopsylla sectilis* and *Aetheca wagneri*, associated with deermice (Haas et al. 1973).

Gunnison's prairie dogs are clearly not the maintenance species for plague. At most, the species spreads the disease rapidly over large areas and possibly allows plague to infect new, potentially enzootic populations of other species. White-tailed prairie dogs are able to maintain sizeable populations much longer during plague epizootics (G. Menkens, U.S. Fish and Wildlife Service, personal communication), whereas the more social black-tailed and Gunnison's prairie dogs suffer rapid, intense die-offs (Miles et al. 1952; Lechleitner et al. 1962, 1968; Fitzgerald 1970; Barnes 1982; Rayor 1985; J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data). The simplest explanation for this difference is that the higher population densities and higher rates of social contact of Gunnison's and black-tailed prairie dogs enhance the spread of plague-positive fleas. Other explanations are less likely because the flea vector species are the same, and all the prairie dog species seem to be similarly susceptible to plague in laboratory studies.

The current ideas of plague epidemiology assume that enzootic populations are spatially homogeneous. That is, there is no spatial structure in the habitat that can affect the rates of contact between individuals in subpopulations or patches. This assumption is clearly unrealistic in natural rodent communities where contact between individuals inside patches is more likely than contact between individuals from different patches. Cully (1986) developed a hypothetical model for the enzootic maintenance of plague in the Moreno Valley, New Mexico, that does not depend on resistant maintenance populations. In that model deermice or meadow voles are enzootic at that focus. Both species are abundant inside some patch types and rare in others. Social contacts by individuals inside patches are frequent, thus enhancing transmission of plague. If there are time lags between colonization of patches by healthy individuals and the appearance of plague at those patches from immigration of infected individuals, plague might be maintained by highly susceptible species. If the model is correct, detection of enzootic plague could be very difficult even at known foci because it would only be present in a given patch at unpredictable times. Because deermice and voles are not conspicuous, epizootics in these species could go unnoticed.

Black-footed Ferrets

Black-footed ferrets were once in prairie dog colonies from Canada to Mexico through the high plains of the western United States. Black-footed ferrets are nearly obligate predators on prairie dogs and use their burrows for shelter (Sheets et al. 1971; Gates 1973; Hillman and Clark 1980; Hillman and Linder 1973; Stromberg et al. 1983; Clark 1986). Black-footed ferrets may occasionally take other prey, but except for transients, they are always found in association with prairie dogs. During the first half of the twentieth century, the species disappeared from most of its former range (Hillman and Clark 1980) as the range of prairie dogs contracted.

At Meeteetse, Wyoming, the colonies of white-tailed prairie dogs that supported ferrets underwent a plague epizootic that began during the winter of 1984–85. At that time, black-footed ferrets began to disappear, presumably as a result of either starvation because of the disappearance of

prairie dogs or of canine distemper that subsequently reached epizootic proportions in the black-footed ferret population (Forrest et al. 1988; Williams et al. 1988). Plague is not thought to be directly responsible for the loss of ferrets because many carnivore species, including domestic ferrets (*Mustela putorius*) and Siberian polecats (*M. eversmani*), seem to be resistant to plague (E. S. Williams, undated. Experiemental infection of white-tailed praire dogs [*Cynomys leucurus*] with plague [*Yersinia pestis*]. Unpublished report to U.S. Fish and Wildlife Service. 11 pages).

Ultimately it makes no difference if plague kills black-footed ferrets directly or by destroying their prey base. If black-footed ferrets are to be successfully restored to their historic range, they must have a prey base that is sufficiently consistent to secure long-term survival. Stable prairie dog populations may exist in areas outside the range of plague or where the transmission of plague is sufficiently slow to allow populations to maintain themselves through an epizootic. Such maintenance might be possible where critical flea vector species are rare or missing and where prairie dogs occur at sufficiently low density that contact with infected conspecifics is unlikely or if prairie dogs can develop resistance to plague.

Management Problems

Some of the management problems created by plague in prairie dogs are: (1) predicting whether a complex of prairie dog colonies with sufficient numbers to support a population of black-footed ferrets persists through time, (2) knowing in advance when an epizootic occurs so that ferrets can be moved or other mitigation can be started, (3) understanding how plague is spread inside and between colonies so that the rate of epizootics and the probability of spread to adjacent colonies inside a complex can be reduced.

The first and most serious gap in knowledge of plague ecology is what happens to the disease between epizootics. Plague has been recorded in non-epizootic rodents, but except for the California vole system described earlier, plague is present in populations for a time and then seemingly disappears (Poland and Barnes 1979; Barnes 1982). The Plague Branch of the Centers for Disease Control in Fort Collins, Colorado, monitored plague antibodies in badgers (*Taxidea taxus*) and other carnivores; but after 8 years of positive records, the disease disappeared. During that time, deermice were thought to be the maintenance hosts (A. Barnes, Centers for Disease Control, Fort Collins, personal communication). Lechleitner et al. (1968) and Fitzgerald (1970) implicated deermice as an enzootic species. Richardson's ground squirrels (*S. richardsoni*; Lechleitner et al. 1962), woodrats (*Neotoma* spp.; Miles et al. 1952; Barnes 1982), and meadow voles (J. F. Cully, Jr., A. M. Barnes, T. J. Quan, and G. O. Maupin, University of Notre Dame, unpublished data) have also been implicated, but no direct evidence that any of these species maintains the disease has been reported.

The most plausible mechanism for the maintenance of plague at foci between sciurid epizootics is the involvement of other mammalian host species. The California vole example cited above is a case in point. At San Bruno Mountain, San Mateo County, California, California voles may become infected like other rodents and attain sufficient numbers of bacteria in their blood to infect fleas, yet show no overt symptoms of the disease (Hudson et al. 1964). Presumably after initial infection, these animals are immune to further infection. Survivors produce young naive voles that provide a susceptible host population. In that system, the rodents can produce several litters of offspring per year, therefore infected fleas can probably maintain plague during short periods when susceptible voles are not available. Such clear enzootic systems have not been identified elsewhere, and the process of maintaining plague in other areas may be different.

The second problem in plague ecology is lack of information on how, when, and why plague is transmitted to prairie dog populations to start epizootics. Knowing the enzootic species is obviously critical to understanding how prairie dogs initially become infected. Transmission to prairie dogs at the beginning of epizootics could be by contact with fleas that were infected when feeding on other bacteremic rodent species; by contact with prairie dog fleas transported from distant prairie dog colonies by dispersing prairie dogs, raptors, wild carnivores (Fitzgerald 1970; Poland and Barnes 1979), or domestic dogs (Rust et al. 1971a, 1971b); by consumption of plague-infected carrion (Rust et al. 1972); or by pneumonic transmission from other species (Rollag et al. 1981). Assuming that plague is maintained by enzootic rodents and transmitted to prairie dogs by fleas, variables that increase the risks of transmission between species have to be known. Data on flea densities prior to epizootics in prairie dogs or other rodent species

are few, but variance in flea density could alter the likelihood of interspecific transmission. Data on the population dynamics of potential enzootic mammal species prior to epizootics or on the changes in habitat overlap that occur with changing rodent density are also few. As the density of enzootic or epizootic species increases, habitat overlap with other species may increase and in turn increase the probability of interspecific contact and exchange of fleas.

The third problem is minimization of the effects of plague in prairie dogs after the onset of an epizootic. There are no published data that demonstrate effective control of plague epizootics. Fitzgerald (1970) attempted to control fleas by dusting prairie dog burrows on half of the colony he studied, but the population was small and after 2 years went extinct. At Meeteetse, burrows were dusted to control fleas, and the epizootic seemed to stabilize. Because long-term maintenance of plague in prairie dogs has not been described from other sites, dusting may have been partially effective. It is also possible that the epizootic was not affected by the attempted flea control but instead was slowed by the long distances between prairie dogs and burrows typical of colonies of white-tailed prairie dogs. Additional controlled experiments with replication could elucidate the effectiveness of flea control. Barnes (1993) described a successful effort to end an epizootic in Gunnison's prairie dogs at the Curecanti National Recreation Area in Colorado. Under some circumstances, plague epizootics can seemingly be modified by flea control after onset of the epizootic, but the necessary conditions and techniques have not been well defined.

If flea control is an effective method for controlling epizootics, the effects will be manifest in individual colonies. A separate problem is the spread of plague between colonies in a prairie dog complex. Such spread could occur in several ways but most likely by dispersing prairie dogs or flea-carrying predators moving among colonies.

A variety of flea controls should be tested at selected prairie dog complexes to determine better flea control prior to epizootics and to identify the most cost-efficient methods. Experiments should be conducted to determine whether the reduction of inter-colony dispersal of prairie dogs is possible by controlling prairie dog density, by manipulating spatial distribution of colonies, or by creating dispersal barriers with vegetation between colonies.

The ecology of plague in most areas probably is affected by a complex interplay of the described factors. Focusing on only one aspect of the system probably does not provide useful insight for management. Flea density may be a function of host population density, and interspecific transmission of plague may depend on spatial overlap of the rodent species and density of fleas on enzootic or epizootic rodents.

Finally, I iterate that, because of the broad spectrum of habitats and the extensive geographic range of prairie dogs, details of the ecology of plague may differ between populations or species. Prairie dogs occupy a wide variety of habitats, each with unique rodent species. Because different rodent species have different habitat associations, the degree of overlap varies. Each rodent species carries different species of fleas, and different fleas may affect transmission by being more or less host specific or effective as plague vectors. In some systems, plague might be transmitted directly from enzootic to epizootic species, whereas in other systems, intermediate hosts may be necessary. Thus, broad generalities about the ecology of plague that can be translated into broad management plans may never be possible. Nevertheless, site specific information from monitoring may be useful for determining whether reintroductions of black-footed ferrets will be successful.

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Appendix. Definitions of epidemiological terms as they are used in this paper[a]

Amplifier A host that serves to infect additional vectors or hosts. It amplifies the infected portion of the population.

Disease Pathology caused by microparasites or macroparasites.

Enzootic Refers to a species or animal that maintains a disease system with little temporal change in intensity for a long time.

Epizootic An explosive outbreak of disease with rapid transmission in non-human animals. An epizootic species supports an epizootic. Because susceptible hosts are quickly used up, epizootics are short-lived.

Focus A geographic area where an enzootic disease system is maintained through time.

Immunity A state following infection in which the host has circulating antibodies that eliminate infections.

Infection A state in which an organism, with or without disease, has reproducing parasites in its body.

Microparasite Virus, rickettsia, bacteria, or protozoa that cause disease in susceptible hosts.

Resistance Used here in the context of resistance to disease, the ability to survive infection.

Susceptibility The ability to become infected by disease causing organisms.

Vector An animal, usually an arthropod, that transmits disease, causing the transfer of organisms between hosts. Fleas are vectors of plague because they transmit plague from one mammal to another.

[a] Some can be defined differently in other contexts.

The Ecology of Plague in Gunnison's Prairie Dogs and Suggestions for the Recovery of Black-footed Ferrets

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Several challenges face biologists attempting recovery of black-footed ferrets (*Mustela nigripes*) in view of the recent outbreak of plague in white-tailed prairie dogs (*Cynomys leucurus*) and distemper in ferrets at Meeteetse, Wyoming. This paper is about the history of plague (*Yersinia pestis*) in prairie dogs, the ecology of plague in Gunnison's prairie dogs (*Cynomys gunnisoni*) in Colorado, the recent epizootic in white-tailed prairie dogs at Meeteetse (Ubico et al. 1988), and recommendations for the recovery of the black-footed ferret.

History of Plague in North America and in Cynomys

Plague is a disease of a wide variety of wild rodents (Kartman et al. 1958; Barnes 1982), many of which are responsible for its maintenance, amplification, and spread under varying sylvatic conditions. Plague exists over much of its global range as an enzootic, not readily detected disease (Kartman et al. 1958; Barnes 1993). Under certain conditions, plague may produce localized epizootics or, more rarely, enter human populations where it is capable of producing epidemic outbreaks. The historic black death that periodically swept parts of the Old World undoubtedly was linked to wild mammalian and flea reservoirs infecting commensal rodents and humans (Pollitzer 1954).

In North America, plague was recorded first in 1899 from two sailors aboard a Japanese ship in San Francisco. In 1900, an epidemic of plague hit Chinatown in San Francisco, and 118 deaths were recorded during a 4-year period (Link 1955). From 1900 to 1966, 547 cases of human plague and 349 deaths occurred in the continental United States, and most of those deaths (284) were associated with epidemics and epizootics in Norway rats (*Rattus norvegicus*) prior to 1925 (Caten and Kartman 1968). Since the 1920's, cases of human plague have been consistently linked to plague in wild mammals, especially rodents, including at times Gunnison's prairie dogs in the southwestern states. Since plague was first recognized in the United States, it has been isolated from wild rodents and their fleas in 15 western states and can be considered endemic over much of the land west of the 100 meridian (Kartman et al. 1958; Caten and Kartman 1968). Plague has not become established east of the 100 meridian. The general lack of plague east of the Mississippi drainage was attributed by Wayson (1947) to lack of ground-dwelling sciurid rodents.

Whether plague was established in the western United States prior to the recorded incidences in 1899 and the early 1900's is conjectural. Some (Meyer 1947; Pollitzer 1954) suggest introductions as early as during Pleistocene times via the Bering land bridge or perhaps by Spanish explorers. If plague was introduced to this country in 1900, it made astonishing progress in 45 years, spreading over 3,108,000 km^2 and across or around deserts, mountain ranges, and similar zoogeographic barriers. By the late 1940's, the disease was widespread over thousands of kilometers from California to Oklahoma, Texas, northern Mexico, and southern Canada (Link 1955).

In the western states, plague was first recorded in fleas and in prairie dogs in 1936 (Table 1; Fig. 1). By the mid-1940's, plague was established across the entire distributional range of the genus *Cynomys* and its predator, the black-footed ferret (Fig. 2). The Gunnison's prairie dog has been more frequently implicated in recurrent epizootic plague than the other three species of prairie dogs in the

Table 1. *Pre-1950 records of plague isolations by state, county, date, and source.*[a]

State	County of location	Date	Isolated from
Arizona	Apache	09-27-38	98 fleas from *Cynomys gunnisoni*
Colorado	San Miguel	07-14-41	30 fleas from *Marmota*
	Larimer	06-21-43	70 fleas from *C. ludovicianus*
Kansas	Cheyenne	06-02-45	105 fleas from *Reithrodontomys Microtus, Peromyscus* (pooled)
	Scott	07-20-46	312 fleas from *C. ludovicianus*
Montana	Beaverhead	07-25-36	153 fleas from *Marmota*
	Garfield	08-04-43	173 fleas from *C. ludovicianus*
New Mexico	Catron	08-09-38	10 *Cynomys* and 1,158 fleas from *C. gunnisoni*
North Dakota	Divide	06-23-41	159 fleas from *Spermophilus richardsoni*
Oklahoma	Cimarron	06-08-44	4 fleas from *Peromyscus*
Texas	Cochran	04-27-46	12 fleas from *S. tridecemlineatus* 81 fleas from *C. ludovicianus* 15 fleas from *Onychomys*
Utah	Beaver	07-16-36	1 *S. variegatus*
	Garfield	08-06-36	2 *C. parvidens* (shot)
Wyoming	Yellowstone	07-27-36	101 fleas from *S. armatus*
	Unita	06-27-38	18 fleas from *C. leucurus*

[a] First isolations from prairie dogs are noted (data from Centers for Disease Control files).

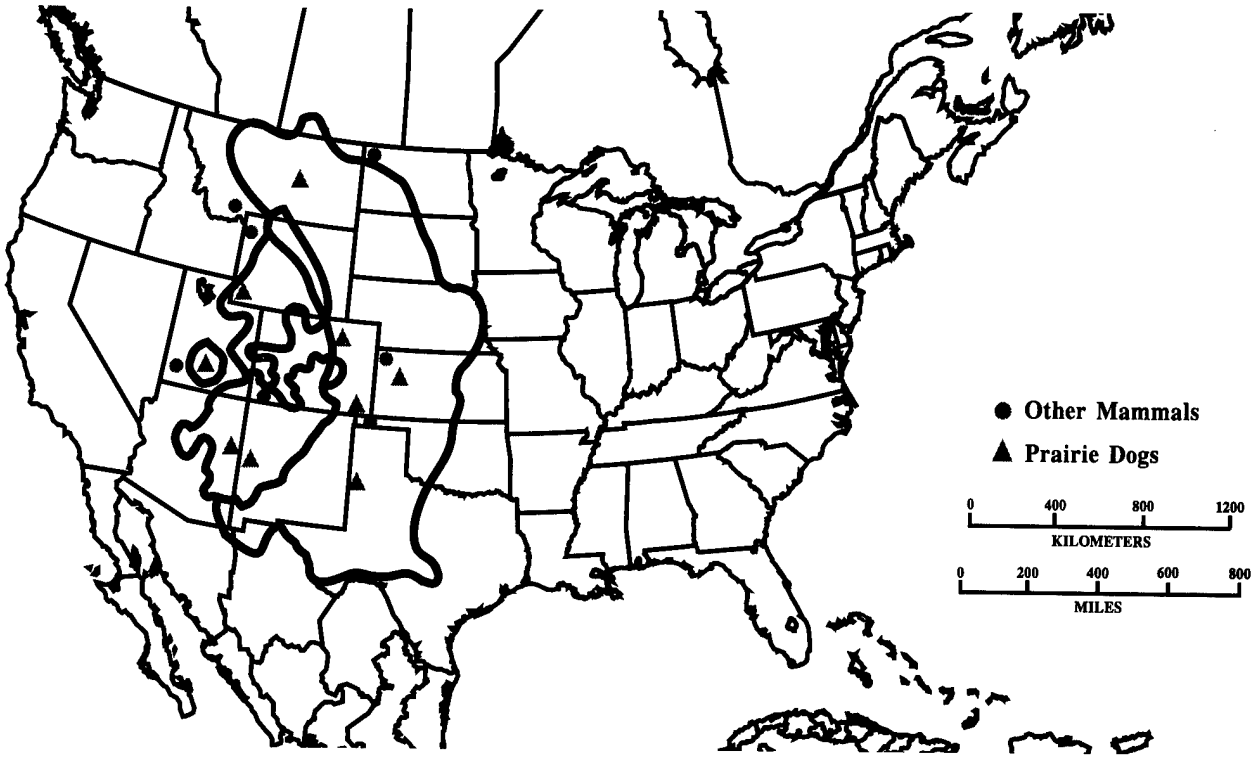

Fig. 1. Distribution of the genus *Cynomys* in the United States and pre-1950 plague isolations. *Triangles* are isolations from prairie dogs or their fleas. *Dots* are from other mammals.

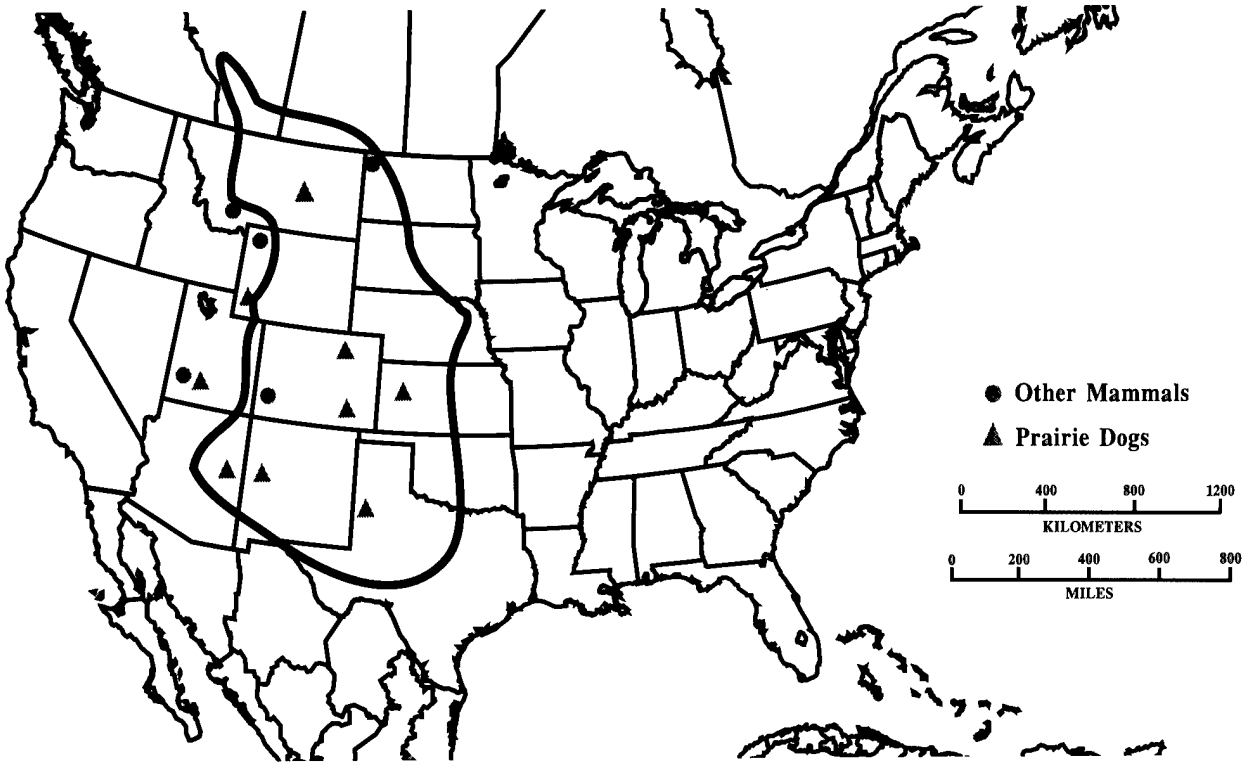

Fig. 2. Distribution of the black-footed ferret in the United States and pre-1950 plague isolations. *Triangles* are isolations from prairie dogs or their fleas. *Dots* are from other mammals.

United States (Lechleitner et al. 1962, 1968; Collins et al. 1967; Fitzgerald 1970, 1978; Archibald and Kunitz 1971; Rayor 1985). In white-tailed and black-tailed prairie dogs (*C. ludovicianus*,) the disease can also result in significant decline of populations and in localized extinctions of colonies (Ecke and Johnson 1952; Clark 1977; Ubico et al. 1988). Following such decimation, prairie dogs may take years to recover or, in the case of Gunnison's prairie dog, suffer a significant retraction of the range (Fitzgerald 1970, 1978). Collier and Spillett (1975) did not believe that plague was an important influence on the distribution of the Utah prairie dog (*C. parvidens*) despite several isolations of plague from that species (Stark 1958; Centers for Disease Control records). Poisoning of rodents across the West obscured and perhaps caused underestimation of the effects of the disease on prairie dogs.

Plague in Colorado

In Colorado, the historic account by Ecke and Johnson (1952) indicates that large numbers of black-tailed and Gunnison's prairie dogs succumbed to epizootic plague or plague-like diseases during the 1940's. One such outbreak affected Gunnison's prairie dogs over much of South Park in Park County during 1945–47, spreading over a 96 km path and about 336,400 ha. At the start of the epizootic, prairie dogs were continuous over the entire park land. The prairie dog population declined to about 5% except animals on 116,830 ha where rodents were controlled. Where poisoning had been conducted, about 15% of the population remained unaffected by either poison or plague. Ecke and Johnson (1952) speculated poisoning had slowed the rate of progress of the disease and allowed some populations to escape the epizootic. Wyoming ground squirrel (*Spermophilus elegans*) numbers were also reduced by the disease during that period. Microtine and cricetid rodents (*Microtus* and *Peromyscus*) were thought to also have been reduced in numbers, but northern pocket gophers (*Thomomys talpoides*) did not seem to be affected.

In the late 1950's and 1960's, the late R. R. Lechleitner and his students at Colorado State University began a series of studies of the ecology,

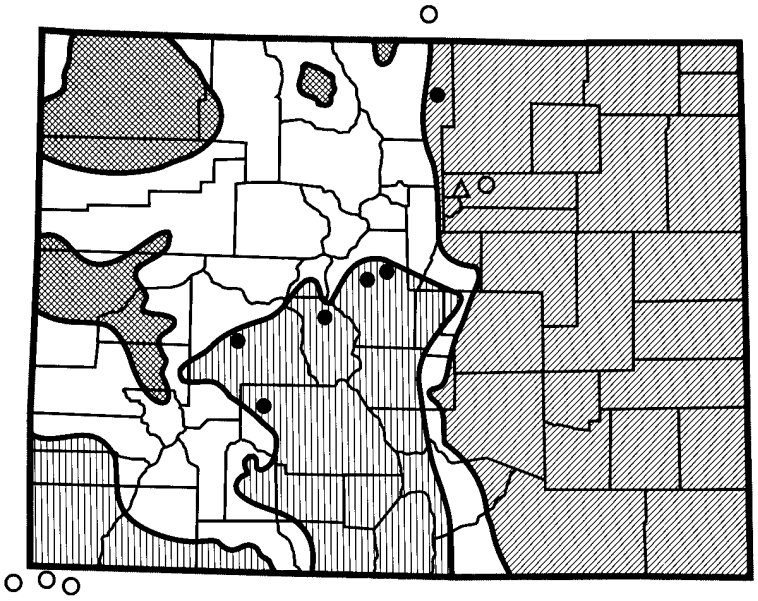

Fig. 3. Locations of plague isolations in Colorado discussed in this paper (*black circles*) and distributional ranges of the white-tailed (*vertical lines*), Gunnison's (*checkered fields*), and black-tailed prairie dogs (*diagonal*). *Circles* represent plague in prairie dogs in Colorado or nearby in Wyoming (Clark 1977) and New Mexico (Collins et al. 1967). *Triangles* are isolations from other species.

distribution, and behavior of prairie dogs in Colorado (Tileston and Lechleitner 1966; Waring 1970; Fitzgerald and Lechleitner 1974). During those studies, many outbreaks of plague were observed in Gunnison's prairie dogs (Kartman et al. 1962; Lechleitner et al. 1962, 1968; Fitzgerald 1970, 1978). The studies by Ecke and Johnson (1952) in South Park, by Kartman et al. (1962) and Lechleitner et al. (1962) in Chubbs Park, Chaffee County, and by Lechleitner et al. (1968) in Cochetopa Park, Saguache County, involved large areas with infection and die-off of isolated colonies or subpopulations in similar conditions as those observed by Ubico et al. (1988) near Meeteetse, Wyoming (Fig. 3).

In contrast, Rayor (1985) near the Blue Mesa Reservoir in Gunnison County worked in a smaller, but more densely populated prairie dog town. The work by Fitzgerald (1970) on the Neukirch Ranch in South Park, Park County, focused on a small, isolated prairie dog town farther than 13 km from any other prairie dogs. Individuals in that colony died from plague in 1966 despite efforts to control the epizootic with Malathion insecticide. Two reintroductions of prairie dogs in 1971–73 (Neukirch 2) and 1975–77 (Neukirch 3) also were unsuccessful because of plague. When studies of plague ended in 1977, no other prairie dog colonies were known to exist in South Park. Despite Kartman's (1960) suggestion that mechanisms observed in epizootics cannot be generalized, the studies in Colorado, which included studies of plague in both large complexes and in small isolated colonies, allow for general observations.

Mammalian Associations in Prairie Dog Colonies

Plague epizootics in prairie dog colonies in Colorado primarily involve the prairie dogs and their normal host fleas but no related small mammals. In all cases, prairie dog populations under study were totally eliminated (Table 2).

Because prairie dogs are highly vulnerable to plague, they should not be long-term reservoirs of the disease. However, factors such as persistence of plague in fleas or in the soil (Goldenberg and Kartman 1966; Christie 1982), density and degree of coloniality of the species, or winter torpor in some species of prairie dogs may cause the disease to persist for several seasons (Lechleitner et al. 1968; Fitzgerald 1970). Seasonally, the increased density at the emergence of new litters in spring and early summer and later the dispersal of young prairie dogs may enhance the spread of plague in or between colonies (Rayor 1985; Ubico et al. 1988).

Several authors (Kartman et al. 1958; Marchette et al. 1962; Goldenberg et al. 1964) suggested that microtine and cricetid mice or more resistant sciurids (*Spermophilus* in general) are responsible for maintaining low levels of infection leading to periodic epizootic outbreaks in susceptible mammals like prairie dogs in sylvan areas.

Table 2. *Characteristics of plague-infected colonies of Gunnison's prairie dogs in Colorado and white-tailed prairie dogs in Meeteetse, Wyoming.*

Study area	Total area (ha)	Density[a] (ha)	Effect of plague	Duration	Confounding variables
Chubbs Park	647	1.1	Die-off	1959	poison — 1958
Cochetopa Park	11,655	1.1	Die-off	1964–65	poison — 1964
Neukirch	5.7	2.0	Die-off	1965–66	Insecticide
Neukirch 2	5.7	0.9	Die-off	1972–73	
Neukirch 3	5.7	1.6	Die-off	1976–77	Insecticide
South Park	24	"high"	Die-off	1949	poison — 1948
		100	Die-off	1949	poison — 1948
Blue Mesa[b]	60	17–25	Die-off	1981	
Meeteetse	3,000	3.8	Decline	1984–85?	Insecticide

[a] Maximum density in concentrated areas.
[b] Density at Blue Mesa is highest reported in this species and one of the highest of prairie dogs in general.

Other workers (Lechleitner et al. 1968) suggested that mobile carnivores transport infected fleas from one area to another. Despite the plausibility of both theories, they have not been demonstrated in prairie dogs in Colorado.

Lechleitner et al. (1968) and Fitzgerald (1970) obtained serologic positives for plague antibodies from Wyoming ground squirrels, northern pocket gophers, deer mice (*Peromyscus maniculatus*), porcupines (*Erethizon dorsatum*), and badgers (*Taxidea taxus*). However, the number of animals with plague titers, with the exception of badgers, was extremely low. Of 234 sera in the deer mouse during ongoing epizootics, only 4 (<2%) were positive for plague antibody. Less than 1% of 120 Wyoming ground squirrels were serum positive during the Neukirch epizootic. The extensive surveys of the 1940's (Ecke and Johnson 1952, South Park) also revealed few Wyoming ground squirrels with plague-positive fleas (4 positive pools of 134, 3%).

Screening of fleas for plague has not been productive for species other than prairie dogs (Ecke and Johnson 1952; Kartman et al. 1962; Lechleitner et al. 1968; Fitzgerald 1970). Only 13 pools of fleas were plague positive from over 300 flea pools collected from 18 mammals in the studies in Colorado. A more detailed study of pocket gophers in a known focal area for plague would be of interest because one positive flea pool and one serum positive were isolated from 55 sampled animals. Holdenried and Quan (1956) found *Thomomys* sp. moderately resistant to plague infection, and pocket gophers typically share habitats with *Cynomys*. The data suggest that serological or flea investigations of most small mammals are not time- or cost-effective for routine surveys in prairie dog colonies contemplated as potential black-footed ferret release sites.

Time spent in collecting fleas from burrows or live prairie dogs during ongoing epizootics in Chubbs Park, Cochetopa Park, and the Neukirch site resulted in plague isolation from 57 of 352 (16%) flea pools from prairie dog burrows and 16 of 84 flea pools (19%) from live prairie dogs (Kartman et al. 1962; Lechleitner et al. 1968; Fitzgerald 1970; J. P. Fitzgerald, University of Northern Colorado, unpublished data). At Meeteetse, 13 of 86 flea pools from burrows were positive (14%) and 31% of flea pools (37) from prairie dogs were positive (Ubico et al. 1988). The periodic collection of fleas from these sources is necessary to better understand the dynamics of flea populations and monitor prairie dog colonies considered as possible release sites for black-footed ferrets. Preferably, such surveys should be initiated at least 1 to 2 years prior to release of ferrets to gain an understanding of flea dynamics and the general condition of prairie dogs.

The survey by Clark et al. (1982) and the summarized data in this paper suggest the vast number of potential interactions between hosts, fleas, and their community dynamics that could lead to interspecific passage of plague between other mammals (30 species minimum) or their fleas and prairie dog species and their fleas. Differences in the susceptibility to plague by conspecific mammals may influence the ecology of plague in a particular region (Marchette et al. 1962). Infections of humans and epizootics in urban settings caused by species previously thought to be unimportant, such as bobcats (*Felis rufus*), cottontails

Table 3. *Sex, age, and reciprocal of plague antibody titers of badgers captured in the Keukirch study area, 1967–74.*[a]

Animal	Sex	Age	Year and reciprocal of titer[b]							
			1967	1968	1969	1970	1971	1972	1973	1974
408	F	A	512							
409	M	J	8							
415	M	J	32							
416	M	J	16							
420	F	A	512	128						
426	M	J		0						
481	F	J		0			256	16		
500	M	J		16						
531	M	A		8,0[c]		64				
537	M	A		32		512				
538	F	J		64						
562	F	J		0						
563	F	A		32						
570	F	J		0	32					
608	M	A			32					
609	F	A			16					
625	M	J				64				
626	M	J				256				
631	M	J			16					
632	M	A			64					
634	M	A			0					
925	M	J					32			
926	M	A					128[d]			
987	M	J					256			
991	F	J							0	
1010	M	J							16	
1011	F	A							0	
1020	M	A							64	
1190	F	A								64

[a] Plague in prairie dogs was documented in 1965–66 and in 1973.
[b] A reciprocal titer of 32 or higher is considered conclusive evidence of plague antibody.
[c] Captured in June and October.
[d] Animal also had a tularemia titer of 1:32.

(*Sylvilagus* spp.), and fox squirrels (*Sciurus niger*), demonstrate the varied ways in which the disease can survive and be passed on in nature (Kartman 1960; Hudson et al. 1971; Poland et al. 1973).

A common denominator of all prairie dog species is the presence of hunting badgers in their towns (Fitzgerald 1970, 1978; Clark et al. 1982; Rayor 1985). Badgers and their diggings are highly visible and individuals are easy to trap or snare. Studies at the Neukirch site demonstrate that blood antibody titers of badgers fluctuate in response to plague (Table 3).

Data from adult female and juvenile badgers suggest that family groups are infected from common sources because the young animals hunt with their mothers. Because of their close association with prairie dogs and other ground-dwelling sciurids, badgers should be used in monitoring plague at any sites considered for the release of black-footed ferrets.

Flea Associations in Prairie Dog Colonies

Because bites by infected fleas are the prime passage of plague, the ecology of fleas must be considered (Kartman et al. 1958). Fleas are host-

Table 4. *Most common flea species collected during plague epizootics in prairie dogs in Colorado, 1960–73, and at Meeteetse, Wyoming, 1985.*

Study and host	Number examined	Number with fleas	Flea species[a]							
			OTC	OL	OH	OI	MW	RF	F	NI
Neukirch										
Burrows	1,717	242	294	87	16	146	6	5		
Cynomys gunnisoni	87	41	136	16	21	3	0	1		
Peromyscus maniculatus	144	82				3	60			
Spermophilus elegans	126	63		28		61				
Thomomys talpoides	22	15							38	
Neukirch 2										
Burrows	23	10	58	48		56				
Chubbs Park										
Burrows	157	64	521	234		76				
P. maniculatus	139						63			
S. elegans	4					5				
Cochetopa Park										
Burrows	2,700	587	11,033	445	1	85	1			
C. gunnisoni	59	43	54	19		15				
P. maniculatus	109	66					55			
S. lateralis	33	8			4	5				
T. talpoides	24	14							30	
Meeteetse, Wyoming										
Burrows	165	86	248	314		24		3		43
C. leucurus	32	32	85	54		8		4		15
P. maniculatus	53	24		2			40			
S. armatus	2	1	1	4						
Totals										
Burrows	4,762	925	12,154	1,128	17	404	7	8		43
Cynomys	178	116	275	89	21	26		4		15
Peromyscus	466	172		2		3	218			
Spermophilus	165	72		32	4	71				
Thomomys	46	29							68	

[a] Flea species: OTC = *Opisocrostis tuberculatus cynomuris*; OL = *O. labis*; OH = *O. hirsutus*; O = *Opisocrostis* sp.; OI = *Oropsylla idahoensis*; MW = *Monopsyllus wagneri*; RF = *Rhadinopsylla fraterna*; F = *Foxella ignota*; NI = *Neopsylla inopina*.

specific at least at the family and genera levels (Hubbard 1947; Stark 1958). The most important fleas during an epizootic are those most common or most prone to mechanical blockage and regurgitation of the plague bacillus into the host (Table 4). Although many fleas may be infected with plague, not all of them are necessarily infective. Probability and chance play important roles in maintaining plague under natural conditions. Fleas implicated in plague in Colorado (Ecke and Johnson 1952; Kartman et al. 1962; Lechleitner et al. 1968; Fitzgerald 1970; Barnes et al. 1972) are generally common on members of the genus *Cynomys*. Transfer of plague from small rodents to prairie dogs could be accomplished by interspecific exchange of infected fleas as demon-

strated in laboratory experiments (Hartwell et al. 1958). However, exchange of fleas has not been demonstrated in the studies in Colorado, and only a few fleas that are not common to prairie dogs have been taken from prairie dog burrows.

Once plague has invaded a prairie dog colony, the fleas responsible for infection and transmittance are well know. In Colorado, the species *Opisocrostis tuberculatus cynomuris*, *O. labis*, *O. hirsutus*, and *Oropsylla idahoensis* were identified from plague-positive flea pools. At the Neukirch site (Fitzgerald 1970), *Opisocrostis tuberculatus*, *O. labis*, and *O. hirsutus* were present in positive flea pools in 1965 and 1966. In the second die-off in 1973 (J. P. Fitzgerald, University of Northern Colorado, unpublished data), *O. tuberculatus*, *O. labis*, *Oropsylla idahoensis*, three *Thrassis bacchi*, and a single *Epitedia* were in plague-positive flea pools. *Thrassis bacchi*, a flea of prairie dogs and ground squirrels, was listed by Pollitzer (1954) as an important plague vector. The genus *Epitedia* is associated with a variety of mice, woodrats, and chipmunks. In the study in the Cochetopa Park (Lechleitner et al. 1968), the two *Opisocrostis* species and *Oropsylla idahoensis* were considered the important plague vectors, and infected *O. tuberculatus* were recovered 1 year after the last prairie dogs had died. In the study in the Chubbs Park (Kartman et al. 1962; Lechleitner et al. 1962), up to 13 months after an epizootic, both *O. tuberculatus* and *O. labis* were positive for plague. Rayor (1985) at Blue Mesa, where the density of prairie dogs was very high, reported plague isolation from *O. tuberculatus* and *O. hirsutus* and extremely high numbers of fleas and infected fleas. Plague at Meeteetse primarily involved the fleas *O. tuberculatus* and *O. labis*, although two other species, *Neopsylla inopina* and *Rhadinopsylla fraterna*, were infected (Ubico et al. 1988). Of the last two species, the former is common on *Spermophilus armatus*, whereas the latter occurs on *Spermophilus*, *Neotoma*, and other cricetids (Stark 1958). The authors attributed the lack of *O. hirsutus* to the climatic conditions at the site and the fact that it is a warmer weather species.

Based on findings in a laboratory, none of the species of *Opisocrostis* common in prairie dog epizootics is considered a highly efficient vector. Their importance is believed to depend on mass transmission of the bacillus and large numbers of infected and infective fleas (Kartman et al. 1962; H. E. Stark, Centers for Disease Control, unpublished report).

Few fleas common to other mammals show up with regularity on swabs from prairie dog burrows. For example, deer mice regularly live in prairie dog burrows, but few of its fleas (*Monopsyllus wagneri)* are taken from burrows (Table 4). *Rhadinopsylla fraterna* does not seem to be a very common flea, and its presence in study areas in Colorado and Wyoming is probably associated with *Spermophilus elegans* and *S. armatus,* suggesting that plague could be cross-transmitted between prairie dogs and ground squirrels by this species. *Oropsylla idahoensis* is another species that frequents both ground squirrels and prairie dogs (Table 4).

Control With Insecticide

Fitzgerald (1970) used 1% malathion dust during the epizootic of 1965–66. Although numbers of fleas were reduced in the treated areas, the epizootic eliminated all prairie dogs in treated and untreated areas. In 1976 and 1977, during the second reintroduction of prairie dogs, Fitzgerald (1978) applied 5% carbaryl dust to burrow entrances, but this did not prevent plague from eliminating prairie dogs. Barnes et al. (1972) reported control of *Opisocrostis hirsutus* with 2% carbaryl dust in black-tailed prairie dogs in eastern Colorado. Barnes (1993) further discusses control of fleas. Further research into the use of insecticides for the control of fleas in prairie dog colonies is needed.

Implications of Plague for the Management of Black-footed Ferrets

Management of the black-footed ferret (*Mustela nigripes*) calls for the maintenance of prairie dog habitat and populations. The studies of plague in Colorado and the presence of plague over much of the range of prairie dogs suggest that maintenance or reestablishment of prairie dogs may be difficult and costly. What can be learned from research into plague to date is perhaps where not to try introductions of black-footed ferrets and environmental conditions that minimize losses of prairie dogs from plague.

The historical records and lack of contradictory findings suggest that black-tailed prairie dog colonies in eastern Montana and the Dakotas are prob-

ably prime areas for reintroductions of ferrets if plague is a concern. Surveys (with badger serologies) and studies of fleas should be conducted in selected sites in these three states in advance of any contemplated releases of ferrets. Black-tailed prairie dogs in Colorado are periodically affected by plague, especially along the Front Range. Colonies in Boulder, Fort Collins, and most recently on the Rocky Mountain Arsenal have had plague epizootics in the last several years (Centers for Disease Control records); Ecke and Johnson (1952) documented the widespread presence of the disease in the 1940's. Colorado does not have sufficient large-sized, plague-free black-tailed prairie dog towns for the introductions of ferrets.

The ecology of plague in white-tailed prairie dogs needs to be studied in more detail. My own observations of all of the species of prairie dogs in the United States and information from surveys of black-footed ferret in central Wyoming in 1981 and from my visit to Meeteetse in 1985 during the plague epizootic suggest that the diffuse, loose colonies of white-tailed prairie dogs over thousands of hectares of central and western Wyoming and along the Utah and Colorado border are suitable habitat for black-footed ferrets. White-tailed prairie dogs have increased in numbers over much of that area since the mass poisoning campaigns that were discontinued in the 1970's and 1980's. Although plague occurs over much of that area, few data exist to suggest that white-tailed prairie dogs are severely affected by the disease. Perhaps that is simply because of a lack of detailed study of the ecology of plague in the region.

Information from studies in Colorado (Kartman et al. 1962; Lechleitner et al. 1962, 1968; Fitzgerald 1970, 1978), from Collins' et al. (1967) summary of epizootic plague in New Mexico, and from Cully (1993) clearly indicate that Gunnison's prairie dog colonies in New Mexico, Arizona, and Colorado should be avoided for introductions of ferrets. Gunnison's prairie dogs do not seem to be increasing in numbers over much of their range despite reduced poisoning. Size, shape, density, and other factors of prairie dog towns may have little bearing on plague outbreaks if enzootic conditions exist and if host and vector numbers are sufficiently high for transmission. In Colorado, extremely small and dense large towns were similarly affected. Poisoning of prairie dogs frequently confounded research (Table 1). In general, I have no confidence in the reduction of the spread of plague. In fact, in South Park, Park County, Colorado, prairie dogs were eliminated from the entire area as a result of mass poisoning and periodic plague. Range retraction is also significant in Chaffee and Lake counties.

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Techniques for the Transplant of Utah Prairie Dogs

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Abstract. Since 1972, the Utah Division of Wildlife Resources (UDWR) transplanted more than 13,000 Utah prairie dogs (*Cynomys parvidens*) to 41 sites. Techniques for transplants were refined after studies in 1979 and 1986. The 1986 study furthered refinement of techniques by UDWR and greatly improved the transplant. The study revealed that weight, sex, age of the moved animals, date of the transplant, and control of badgers (*Taxidea taxus*) were critical to the success of transplants. Transplants were improved when sites were monitored closely for badgers and badgers were removed during the first 2 years. Juvenile prairie dogs could not be successfully moved until they reached a minimum weight of 500 g. Transplanting adult females was not successful until they had completed lactation and had recovered their body weight to approximately 750 g. Adult males could be moved with minimal losses at any time during the field season. In Utah, transplants begin in late March and end in late August.

Key words: *Cynomys parvidens*, Utah prairie dog, transplant survival, predation, habitat quality.

The Utah prairie dog (*Cynomys parvidens*) used to inhabit nine Utah counties (Hardy 1937) but now is in only five in southwest Utah. The population declined from 95,000 in 1920 (Collier and Spillett 1974) to 3,300 individuals in 1973 when the species was listed as endangered. Following partial recovery and stabilization of the population at 5,000–6,000 animals in 1983, the U.S. Fish and Wildlife Service reclassified the Utah prairie dog as threatened and instituted a program to control prairie dogs on private lands in Iron County, Utah. This control, done by the Utah Division of Wildlife Resources (UDWR), began in 1972, and allows the taking of 500–1,500 prairie dogs / year when damage to private agricultural lands is serious. Removed animals are used for recolonizing sites formerly occupied by Utah prairie dogs and other suitable habitat. This paper describes the transplant program in Utah, including early transplants and current transplant methods of UDWR.

Transplant Techniques, 1972–83

Beginning in 1972, the regional game manager of UDWR in Cedar City began moving Utah prairie dogs from private agricultural lands to a series of Bureau of Land Management (BLM) sites and later to U.S. Forest Service lands. The prairie dogs were live-trapped by a water method. Water is first flushed down the hole with a large diameter hose and then a fan of water is sprayed across the hole. When the prairie dog tries to exit the hole, it raises its head through the fan of water and was noosed. As many as 25 animals were placed in large holding cages and hauled to a transplant site. The prairie dogs were released on the ground at the transplant site. The water method worked well on established, dense colonies in agricultural sites where the tank truck did not have to move often. About 100 prairie dogs could be moved in a day, and all could be removed from a site with this method. Because of

aggressive interaction in the holding cages, group-holding cages were discarded and prairie dogs were captured and held in individual live traps (Tomahawk and Havabait traps).

By 1979, water trapping had been eliminated because of concern that some prairie dogs might not be able to emerge and would drown. Labor-intensive removal with spring-loaded traps was used exclusively. Also by this time, holes for the prairie dogs at the transplant sites were made with an auger (0.5–1.0 m deep × 15 cm in diameter). When the prairie dogs did not stay in the area, 46 cm chicken wire fence was installed on the perimeter of the site. Perimeter fences also were not successful in retaining prairie dogs. Finally, welded wire baskets (1.2 m × 1.8 m × 0.3 m) were used to contain prairie dogs in a small area, and this method continues to be used. With an auger and a 7.6 cm bit and then a 15.2 cm bit, two holes are made for each basket. The 7.6 cm bit was discarded because the freshly transplanted prairie dogs could not turn around in the bottom of the hole and had to back out. The 15.2 cm bit was eventually replaced with a 12.7 cm bit because the 15.2 cm hole did not require additional digging by the badgers and there was high predation. In the fall of 1982, the regional nongame manager documented a 100% loss of transplanted prairie dogs at two sites. Evidence indicated badgers were excavating the burrows and killing the prairie dogs.

In 1982 and 1983, a pilot study was conducted and 75 adult prairie dogs were transplanted for the first time during spring. The preliminary results of this study revealed that transplants of adults in spring may be successful. Because of the high predation rates and apparent success of releases in spring, a 2-year study was initiated by UDWR and Brigham Young University to determine the causes of mortality, survival, behavior, dispersal, and habitat interactions of transplanted Utah prairie dogs. The results of this study and the refinements of techniques were incorporated into current techniques.

Current Transplant Techniques

Site Selection and Preparation

Guidelines for selecting a site (Table 1) for the transplanted Utah prairie dogs were prepared by Crocker–Bedford and Spillett (1981) and were modified by UDWR. Prairie dogs at higher elevations need sites with distinct characteristics (Table 2) because of the need to finish life history stages in a shorter amount of time. A site must be well-drained and must have at least a 1 m soil layer between the surface and the water table. A site with visible, old mound systems rates higher because the prairie dogs can reestablish burrow systems where they previously existed. A site

Table 1. *Guidelines for selecting transplant sites for Utah prairie dogs.*

- The area must be well-drained. A prairie dog must be able to inhabit a burrow system 1 m underground at any time without becoming wet.
- The soil in the burrow area must not easily cave in. The soil must not be sand or loamy sand. A caliche layer must be below the 1.2 m level.
- Elevation does not seem to be a limiting function in transplants. Prairie dogs from the Cedar Valley (1,675 m) were moved to Tidwell Slopes (2,800 m) as successfully as prairie dogs from Loa (2,440 m).
- A site is best suited for transplant if it has evidence of a former mound system.
- Vegetation of a site should not be so dense or so high that it prohibits the prairie dogs from seeing through it or over it. Vegetation that is taller than 30 cm should be chopped off mounds.
- Moist swale vegetation in the form of grasses, forbs, and shrubs must be available throughout the period that Utah prairie dogs are active above ground. Moist vegetation is particularly essential in drought years and in the dry months of June through August and should be within 180 m of the home burrow area throughout summer.
- The transplant sites should be 1,600 m from private land. Suitable barriers such as trees, rock outcrops, and ledges should be between transplant sites and private land if the sites are closer to private land.

Table 2. *Desirable variables of vegetation in transplant sites above 2,100 m.*[a]

Canopy cover	Range (%)	Recommended
Total	35–45	42%
Grasses	10–45	35%
Cool season	10–40	30%
Warm seasons	1–20	5%
Forbs	1–10	5%
Shrubs	1–40	2%

[a] Crocker–Bedford 1976.

Table 3. *Recommended variables of vegetation of sites for transplanted Utah prairie dogs.*[a]

Canopy cover	Recommended range (%)	Minimum	Maximum
Total	25–45	20	85
Cool season grasses[b]	20–40	0[c]	70[c]
		1–5[d]	70[d]
		5–15[e]	70[e]
Warm season grasses	5–10	0	40
Forbs	5–15	0[f]	40
Shrubs (other than rabbitbrush)	0–0	0[f]	15
Rabbitbrush	1–3	0[f]	15

[a] Adapted and modified from Crocker-Bedford and Spillett (1984).
[b] The minimum requirements for cool season grasses vary with different elevations.
[c] 0–1,800 m.
[d] 1,991–2,590 m.
[e] 2,591–above m.
[f] Some flowers and seeds of dicots must be available from mid-June to September, but it does not take many flowers to feed a population of prairie dogs.

should not have large stands of shrubs or old mounds covered with vegetation more than 30 cm in height. The vegetation reduces visibility for the prairie dogs and should be chopped lower especially on old mounds. We found that because altitude does not seem to be a limiting factor, prairie dogs from lower elevations can be moved to much higher elevations. In Utah, prairie dogs have been captured at 1,645 m and moved to 2,650 m without difference in survival from prairie dogs that were moved from one high elevation site to another (Utah Department of Wildlife Resources files).

Climate exerts a controlling factor on transplant success at higher elevations. In mild winters with little snow pack, prairie dog colonies can grow by 25% annually; severe, long winters with deep snow pack can cause a 90% mortality in transplanted and native colonies. Thus, population fluctuations in colonies are probably greater at higher than at lower elevation. Reintroduction in sites without prairie dogs should start at lower elevations and proceed to higher elevations.

Soil in the burrow area must not be subject to cave-ins. Sand or loamy-sand are poor soil types for prairie dogs. The soil must be at least 1 m deep over a caliche layer to allow the prairie dogs to establish hibernacula below the frostline but above the caliche layer. During the first year, transplanted prairie dogs probably experience high mortality if there is not sufficient time to establish deep burrows. Therefore, survival rates are higher of animals that were transplanted in spring than of animals that were transplanted in summer.

Moist swale vegetation (including grasses, forbs, and some shrubs) has to be available throughout the activity period of prairie dogs. Presence of moist vegetation is especially important in drought years and in the dry months of June through August. This vegetation should be within the normal foraging range of the prairie dog or within 180 m of the home burrow. A list of vegetative parameters has been prepared for the Utah prairie dog (Table 3).

Seasonal Field Schedule

We begin field work with the spring adult census in late February. Populations in colonies at lower elevations are sampled until their numbers stabilize and most animals emerge from hibernation. Formal counts then proceed from lower to higher elevations until completed at the end of May. The best counts are made on clear, calm, sunny days, and every effort is made to elicit alarm calls from individuals so that most prairie dogs stand up or come to the top of the mounds. The Utah Department of Wildlife Resources has had great success with a canine tease (coyote mimic) to alarm the prairie dogs. If the alarm call is handled correctly, prairie dogs stand up for an extended period, facilitating counts. Colonies that have been subjected to shooting or have recently had predators pass through are more difficult to

count because the distance from the observer at which prairie dogs withdraw into burrows increases. Each colony is counted twice. Investigators use binoculars when prairie dogs are easy to observe or spotting scopes when the animals are wary. The highest count is recorded and mapped on USGS quad maps if the difference is small. If the difference exceeds three, a third count is made.

In Utah, trapping of adults begins in late March when there is vehicle access to the transplant site and the ground is sufficiently dry for digging by the prairie dogs. Adult males and females are transplanted until the end of April. Thereafter, females are not transplanted because they are stressed easily because of pregnancy. Traps are inspected every 2 h to remove and release females at the trap site. Only adult males are moved from May until the last week of June when Utah prairie dog juveniles reach 500 g and females have recovered their weight to approximately 750 g. Throughout July and August, all trapped animals are moved to the transplant sites. In late August or early September, the animals must be moved to sites with existing burrows or they will have little chance of surviving winter.

Transplant Equipment

Utah prairie dogs are live-trapped with 15 cm × 15 cm × 61 cm, double-door Tomahawk traps. Trap release tension should be fine-tuned with needle nose pliers to improve trap success. Traps are placed at occupied burrows in the morning before sunrise and before the prairie dogs emerge. Traps must be placed carefully so that they will not move when the prairie dog enters. Traps can be placed on flat or leveled ground anywhere around the mound. Better success can sometimes be obtained by placing the trap on the ramp of dirt leading into the burrow with the bait pan facing away from the entrance. On windy days, the traps can be placed upwind of the occupied burrows so that the odor of the bait blows across the burrow entrance. Traps should be checked every 4 h in the spring and every 2 h in the summer. During the summer, the activity pattern of the Utah prairie dogs becomes bimodal, and traps can be closed in the middle of the day and reset in the late afternoon. Prairie dogs become stressed from heat and some die if left too long in the summer sun. When trapping only adult males in May and June, traps are left open in the evening and even overnight. This can only be done during warm, dry nights or trapped animals become torpid and seriously stressed by morning. Better success in trapping only males can sometimes be obtained by setting most traps on the periphery of the colony where more of the young adult males seem to be. Animals can be successfully held overnight in live traps if placed in a protected area. We place prairie dogs in a shed overnight and cover the traps on three sides with tarps or cardboard. We place the traps on cardboard over concrete floors. Utah prairie dogs eat cavy pellets in the laboratory or other captive situations and should be fed in the morning before being released. During transport, truck beds should be lined to protect prairie dogs from muffler or catalytic converter hot spots. Live-trapped animals should be covered with a tarp on three sides in the truck bed to protect them from the sun and reduce stress. Successful transplants require a constant reduction of stress on the animals.

At the transplant site, we place prairie dogs in unoccupied burrows or in holes that we excavate and cover with baskets. At transplant sites, adult males usually dig several extra burrows that new transplants use. Social interactions are limited for the first 2 years at a transplant site, and the introduced animals encounter few, if any, aggressive interactions (Jacquart et al. 1986). Supplemental transplants to existing colonies to augment populations are done with caution. Animals are placed in unoccupied burrows around the periphery of the colony but are observed for aggressive encounters with earlier transplants. If aggression is excessive or there are no unoccupied burrows, the release site for supplemental transplants is moved 60–90 m away from the main colony. If unoccupied burrows are not available, the prairie dogs are kept in holding baskets to encourage them to dig burrows. These baskets are made from 2.5 cm × 5 cm welded wire and are 1.2 m × 1.8 m × 0.3 m rectangles with two doors in the top and a 0.6 m × 0.9 m hole in the bottom. They are placed over two holes that are made with a 12.7 cm × 1.8 m bit on a Little Beaver hydraulic auger. This 11 hp wheeled unit is the safest and most efficient for preparing transplant sites. Holes are drilled as close to a 45° angle as possible and face to the north to provide shade. The basket is placed over the holes, and dirt is placed over the wire edge of the basket hole to slow the escape of prairie dogs. In windy areas, the baskets are held down with rocks in the corners. The two doors on top are kept closed and functional so that prairie

dogs cannot climb through and badgers cannot enter. As many as 15–20 baskets can be used at a transplant site. Baskets must not be moved to new locations until the two to four animals in the basket have established a burrow in the basket or just outside. The animals usually leave the basket and establish burrows nearby, and more animals can be placed in some baskets without moving them. To prevent injuries, two large adult males are not placed in one basket. Adult males should not be placed side by side at any time during transplant or holding.

Baits

Bait for prairie dogs is a mixture of rolled oats and peanut butter and can be refined to raise trapping success. The bait is mixed fresh in the morning, carried to the trapping site, and put in the traps just before they are placed in the colony. Prebaiting traps before driving down dusty roads to the trap site can lower trapping success. Some brands of peanut butter, such as Jiff, stick to the bait pan better even when mixed with a large percentage of rolled oats. Oats do not seem to make a difference to trapping success. Livestock rolled oats should not be used in peanut butter bait because they do not mix properly and stick. When old bait is cleaned off the traps, it should be used as a prebait at the trap site to expose the prairie dogs to the bait. Cooking extracts such as almond, anise, and even peppermint have been used with some success. They should be added immediately after baiting because they evaporate rapidly. In alfalfa fields, cavy pellets can increase trapping success. Pellets must be kept fresh in a sealed container and added to the peanut butter-rolled oats mix just before baiting the trap. Extra pellets can be strewn around on the ground to further attract prairie dogs.

Predators

Badgers are the main predators of prairie dogs at transplant sites. Other predators include raptors, coyotes, foxes, skunks, and humans. Until they establish a burrow system that is sufficiently complex, prairie dogs at transplant sites are very vulnerable to predation by badgers. Established colonies usually suffer predation around the periphery where juvenile prairie dogs move. New transplant sites should be searched daily for signs of badgers such as excavated burrows, scat, tracks, and remains of prairie dogs.

We begin monitoring transplant sites for predators in March and continue until the site becomes inaccessible because of snow. If necessary, badgers are controlled at the site with either firearms or traps. Leghold traps are unsuitable for transplant sites because prairie dogs are too often caught in them and the public is very much against their use. At transplant sites of the Utah prairie dogs, #330 conibear kill traps are used. These are sufficiently strong to quickly kill a badger and large enough to prevent prairie dogs from tripping them. Conibear traps can be set among prairie dog burrows or in corridors at the periphery of the colony. The use of firearms can be effective. Where it is legal, badgers can be taken at night by spotlight or just at daylight and before sunrise. They are rarely observed during the day in the transplant sites.

Raptors can be a problem at transplant sites. The area around a proposed transplant site should be surveyed and moved if occupied nests of golden eagles, red-tailed hawks, or ferruginous hawks are nearby. Predation by golden eagles on five Utah prairie dogs with radio transmitters was documented. Where possible and with appropriate permits, raptors should be harassed with nonfatal explosives, either M-80 shotgun shells or firecrackers, to elicit their departure from transplant sites. Foxes, coyotes, and skunks do not exercise significant predation at transplant sites. However, if they opportunistically key in on a site, they have to be controlled.

Control of Disease

Plague (*Yersinia pestis*) is the only problematic disease in the management of prairie dog. Outbreaks of plague terminate transplants and eliminate entire populations of prairie dogs. Profound isolation is necessary to prevent the disease from spreading to other areas. All equipment (including truck beds and traps) at a contaminated site has to be steam cleaned. No domestic canines should be allowed around vehicles, equipment, or prairie dogs in a suspected disease area.

In Utah, a documented outbreak of plague in the Bryce Canyon National Park in 1983 was evidenced by weak, sick-appearing Utah prairie dogs that were unable to escape public handling and were brought to rangers. The animals died almost immediately and were sent to the state health laboratory where plague was diagnosed from the fleas and sera. Animals suspected of having plague at a transplant site should be

euthanized, placed immediately into zipper top plastic bags to contain the fleas, put on ice, and taken to the appropriate state health laboratory.

In 1983, staff of the Bryce Canyon National Park attempted to limit the outbreak of plague by dusting the entrances of all the prairie dog holes with Sevin. A similar procedure is routinely used during transplants of the Utah prairie dog. As the prairie dogs are removed from the trap site, they are dusted with a small amount of powdered Sevin and allowed to sit for 10–15 minutes before they are loaded into the truck.

Marking Transplanted Prairie Dogs

During 1984 and 1985, a graduate student (Jacquart et al. 1986) and, during 1986, the Utah Department of Wildlife Resources equipped Utah prairie dogs with Telonics implant transmitters (2.5 × 6.4 cm, 26 g). The transmitters were surgically implanted in the peritoneal cavity of adult prairie dogs. They had a transmitting life span of 10–11 months, and their signals could be received from more than 1,600 m line of sight when prairie dogs were above ground. Underground in the ferrous soil of the project area, the range was limited to as little as 4.6 m but was usually 380 m. During implantation and other procedures, Utah prairie dogs were anesthetized with ketamine hydrochloride (Vetalar, Ketaset) at the dosage of 0.3 mg/kg body weight. Prairie dogs tolerate high dosages; but, if the animal is overdosed, it should be kept overnight in a warm building to insure the recovery of its thermoregulatory ability. A mixture of Acepromazine (0.04 mg / kg) and ketamine hydrochloride (0.3 mg / kg) can also be used for reducing handling trauma and for anesthetizing the animals. After surgically implanting the radio transmitters, 0000 chromic sutures were used to hold the incision closed. Prior to release, the animals were given a 1.0 cc injection of Flocillin to prevent infection from the surgery. The radio transmitter and the surgical platform were also wiped first with alcohol and then with betadine. Removal of the transmitters was a simple procedure because all the radios had encapsulated in fibrous tissue and simply popped out. New transmitters were put in the existing capsule without complications. Several adult prairie dogs carried transmitters for 2 years without adverse effects. Operating on extremely fat animals can be difficult. When the peritoneal cavity is opened, much fat pushes out and makes closing the incision difficult.

Radio collars were placed on juvenile animals and were not successful. The prairie dogs chewed the antennas off their radios and off the radios of conspecifics. Smaller implant radios are available for juveniles but have a shorter operating life and must be replaced twice a year.

Color marking of Utah prairie dogs for individual identification has been a failure. Ear tags are torn off and hair dyes wear off very rapidly. Tattoos are more reliable external markers. A four-digit number is tattooed on the shaved thigh of anesthetized animals and is easily recorded on recapture.

Competition with Livestock

Prairie dogs transplanted to a site must have little chance of causing range problems. When prairie dogs consume 10% of the annual production of grasses and forbs, they reduce production of palatable perennials (Crocker–Bedford 1976). Such reduction occurs when the index of the abundance of prairie dogs reaches approximately 78. The expected abundance index should be below 78 for transplanting. When the abundance index is below 60, prairie dogs consume less than 3% of the yield of grasses and forbs in a colony (Crocker–Bedford 1976). Crocker–Bedford (1976) recommends an abundance index of prairie dogs for the site should be at least 36. A regression was developed that explained 79% of the variation between the abundance indices of 19 rangeland colonies:

$$\text{Abundance index} = 138.2 - 0.0144\,X1 + 2.16\,X2 - 0.01713\,X3 + 7.27\,X4$$

where

X_1 = elevation (m),
X_2 = % cool season grass-canopy cover as much as 20%,
X_3 = average distance (m) from home burrow to swale, and
X_4 = swale wetness (0 = brown herbaceous material; 1 = dry green herbaceous material; 2 = moist green herbaceous material; 3 = soggy ground).

Prairie dogs transplanted to a site could migrate to potential habitat not managed by the Bureau of Land Management or the U.S. Forest Service. The Utah Division of Wildlife Resources thinks that when removal of prairie dogs for translocation programs is extended to all private lands in the current range, controlling animals

that are moved from transplant sites to private lands will be easy.

Crocker–Bedford (1976) estimated that transplanted prairie dogs require 5 years to expand and migrate 3 km from a transplant site. Dispersal is greatly restricted by a river, cliff, forest, or dense stand of tall shrubs. Such barriers inhibit migration for a few years. Thus, distances of more than 3 km or a barrier should separate transplant sites.

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Mark–Recapture and Visual Counts for Estimating Population Size of White-tailed Prairie Dogs

by

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Abstract. Wildlife managers need a technique for estimating densities and changes in density of prairie dogs (*Cynomys* spp.) over time. Four commonly used techniques are plugging of burrows, counts of the total number of burrows, mark–recapture, and visual counts. The choice of methods depends on the investigator's goals and objectives. Mark–recapture provides accurate and precise data and allows managers to examine the population ecology (e.g., survival, production) of prairie dogs in selected towns in detail. Mark–recapture is, however, time-consuming, expensive (traps, baits), and labor-intensive, permitting assessment of population size and structure in only a small number of towns. Because of these limitations, mark–recapture may not be appropriate for situations requiring rapid evaluation or monitoring of prairie dog populations.

Visual counts may provide a rapid, inexpensive approach for indexing the total (adult + juvenile) size of white-tailed prairie dog (*C. leucurus)* populations on a large number of grids. Visual counts may be appropriate for initial screening of populations in complexes that were selected as reintroduction sites for black-footed ferrets (*Mustela nigripes*) or complexes already inhabited by ferrets. However, because visual counts provide only an index of population size, they are not appropriate for the study of prairie dog population dynamics.

Key words: Black-footed ferret, burrows, *Mustela nigripes*, mark–recapture, population index, visual counts, white-tailed prairie dogs, *Cynomys leucurus*.

Black-footed ferrets (*Mustela nigripes*) depend on prairie dogs (*Cynomys* spp.) for food (Campbell et al. 1987) and cover (e.g., litter rearing sites, shelter). Successful management of ferrets and conservation of ferrets depend on management of prairie dogs. The estimation of densities of prairie dogs is essential to management.

Techniques of Estimating the Population Size of Prairie Dogs

Several techniques have been used to estimate population size and density of prairie dogs. The four most common techniques are (1) counts of

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plugged and reopened burrows (Tietjen and Matschke 1982), (2) counts of total number of burrows (Forrest et al. 1985; Houston et al. 1986), (3) capture–recapture of the animals (Otis et al. 1978; Menkens and Anderson 1989), and (4) visual counts of the animals (Fagerstone and Biggins 1986; Knowles 1986; Menkens et al. 1990).

Plugging burrows and counting the number of reopened burrows has been used most commonly to evaluate the efficacy of rodenticides (Tietjen and Matschke 1982). The number of burrows opened per prairie dog is assumed to be constant within and among sample plots. Monitoring yearly changes of density with this technique requires that these rates remain constant among years. Estimation with plugging of burrows is time and labor intensive and may not be efficient for the rapid evaluation of prairie dog population size and status in many towns or over large areas.

Counts of the total number of burrows in a town or grid have been used as an index of population size or density (Forrest et al. 1985; Houston et al. 1986). For this technique, the number of burrows in a town is assumed to change as rapidly as the density of the prairie dogs. For estimating the density of the animals by counting all burrows, change is assumed to be constant among and within sample plots and years. Burrows are, however, persistent, stable structures (Koford 1958), and short-term fluctuations in the number of prairie dogs probably do not reflect changes in the total number of burrows. The sum of burrows did not correlate with the densities of white-tailed prairie dogs (*C. leucurus*; Menkens et al. 1988) and thus is not a good index or estimate of population size or density of this species. The possibility of using the number of occupied burrows as an index of population size and density of white-tailed prairie dogs is currently under investigation (D. E. Biggins, G. E. Menkens, Jr., and S. H. Anderson, U.S. Fish and Wildlife Service, Fort Collins, Colorado, unpublished data).

Mark–recapture frequently has been used in studies of the ecology of prairie dogs (Tileston and Lechleitner 1966; Garrett et al. 1982; Rayor 1985; Cincotta et al. 1987; Cully 1989; Menkens and Anderson 1989). Mark–recapture involves trapping, uniquely marking, releasing, and recapturing prairie dogs on grids. This approach provides estimates of population size and other demographic parameters (e.g., survival, recruitment) that are accurate and precise (Seber 1982, 1986). In addition to detailed estimates of population size, mark–recapture allows investigators to gain detailed information on age and sex distributions and on general biology.

Counts of prairie dogs are a fourth alternative for estimating or indexing density. Visual counts have been used to study the ecology of black-tailed (*C. ludovicianus*) and white-tailed prairie dogs (Fagerstone and Biggins 1986; Knowles 1986; Menkens et al. 1990). For estimates by visual counts a linear relation is assumed between the number of counted prairie dogs and the density in an area; counts provide an index (high, medium, low) of density (Fagerstone and Biggins 1986; Menkens et al. 1990). Visual counts are for sampling a large number of populations in a short time (Fagerstone and Biggins 1986; Menkens et al. 1990).

Methods for Mark–Recapture

Mark–recapture involves systematic placement of live traps in a square or rectangular grid in a prairie dog colony and unique marking and release of all captured animals. The process of recording the number of tagged and recaptured animals is repeated for several days. The tag numbers of all captured animals that were previously marked are also recorded. Population size is estimated from these data with one of many different models, each of which requires specific assumptions about the data (Otis et al. 1978; Seber 1982, 1986; White et al. 1982). The first assumption that must be evaluated is that of demographic closure. Populations are demographically closed if gains (births, immigration) or losses (deaths, emigration) do not occur during the trapping session. If gains or losses do occur, the population is demographically open. Because complete closure is unrealistic, the definition of demographic closure is relaxed to mean that the initial population experiences no known gains or losses (e.g., trap deaths are eliminated; Otis et al. 1978; White et al. 1982). Demographic closure may be tested only under very specific conditions (Otis et al. 1978), and each data set must be subjectively evaluated with information from the species' ecology. For example, although populations of white-tailed prairie dogs change throughout the year, the rate of change is lowest between the emergence of juveniles from the natal burrows (early June) and the immergence of adult males into hibernation (mid-August; Tileston and Lechleitner 1966; Clark 1977). The population may be assumed to be closed if the study is conducted between these periods and

during a short period when immigration or emigration are unlikely.

For open populations, the Jolly–Seber model is used (Seber 1982). During trapping periods (e.g., 1 day) individuals are assumed to have equal probability of capture and that this probability may change between periods. Although the Jolly–Seber model provides unbiased and precise estimates of population size in some situations (Seber 1986), estimates have a high degree of bias and large standard errors under conditions encountered in studies of white-tailed prairie dogs (≤50 captured animals with low probability of capture; G. Menkens, unpublished data). Because of these factors, we do not recommend its use for studies of white-tailed prairie dogs except when the assumption of closure is violated.

Models for estimating population size in closed populations also require very specific assumptions about the probability of an animal's capture. Probability of capture may be influenced by time, behavior, and individual heterogeneity (Burnham and Overton 1969; Otis et al. 1978; Seber 1982; White et al. 1982). If time influences probability of capture, all animals have the same probability in a period, but this probability may change among periods. When behavior influences probability of capture, all animals initially have the same probability but, after the first capture, the probability changes. They may become trap happy (capture probability increases) or trap shy (capture probability decreases). Models for which the individual's probability of capture is assumed to be heterogeneous allow each animal to begin in a study with a unique probability of capture that does not change between periods. Heterogeneity may be caused by many factors including sex, age, and unequal access to traps. Combinations of these factors may also exist (e.g., probability of capture may vary because of both a behavioral response and individual heterogeneity).

The magnitude of variation in probability of capture greatly influences the accuracy and precision of an estimate (Burnham and Overton 1969; Otis et al. 1978; White et al. 1982; Menkens and Anderson 1988, 1989). As the variation in probability of capture decreases, the estimate's bias, standard error, and confidence interval decrease. Field studies can be designed (Otis et al. 1978) that minimize variation in probability of capture, thus yielding an estimate with low bias, reasonable standard error, and narrow confidence interval.

Field methods for reducing variation in probability of capture are numerous (Otis et al. 1978; White et al. 1982) and may be easily incorporated into a study. Behavioral responses may be reduced by recapture techniques that are different from the original capture techniques. For example, prairie dogs can be captured with live traps and marked and then recaptured visually with spotting scopes (Fagerstone and Biggins 1986). Use of traps that prairie dogs do not avoid and use of nonintrusive marking techniques (e.g., ear tags instead of toe clipping) may also reduce avoidance of traps. If the number of captured prairie dogs is large, heterogeneity in probability of capture may be reduced by stratifying the data by sex and age categories and by performing separate analysis of each group (Otis et al. 1978; White et al. 1982). In addition to reducing variation in probability of capture, individual probability of capture and sample sizes should be large. Baits that are identical to or closely approximate natural food items and traps that prairie dogs do not avoid may help increase individual probability of capture and sample size.

After the data are collected, the correct model for analysis has to be carefully selected. Failure to use the correct model will result in an estimate with an unknown degree of bias and unrealistically small or unacceptably large standard errors (Otis et al. 1978; White et al. 1982). The selection of the model depends on the type and pattern of variation in probability of capture. Program CAPTURE (Otis et al. 1978; White et al. 1982), a commonly used program for estimating population size, includes an objective technique for characterizing variation in probability of capture to select the most appropriate model for estimating population size. Users must be cautious when applying CAPTURE to analyze data about white-tailed prairie dogs because CAPTURE's model selection routine selects the wrong model a high percentage of the time under conditions frequently encountered in these studies (Menkens and Anderson 1988). CAPTURE selects the correct model consistently only when behavioral responses are extreme or when the degree of individual heterogeneity in probability of capture is large (Menkens and Anderson 1988).

When extreme behavioral responses (e.g., trap avoidance) or large degrees of heterogeneity do not exist in the data, the Lincoln–Petersen estimator (Seber 1982) should be evaluated for estimating population size. The Lincoln–Petersen estimator provides estimates that are more accurate and have narrower confidence intervals and smaller stand-

ard errors than those by CAPTURE (Menkens and Anderson 1988). Thus, when analyzing mark–recapture data of white-tailed prairie dogs, we recommend the Lincoln–Petersen estimator and CAPTURE. Details of this analytical approach are presented in Menkens and Anderson (1988, 1989).

Visual Counts

Visual counts are obtained from an observation station at the edge of a square or rectangular grid. The grids for visual counts are similar to those in mark–recapture studies and their shape depends on the size and shape of the prairie dog town. Determining the size of the grid requires balancing several requirements. The grid must be large enough to provide a representative sample of density. Grids that are too small may lead to indices that do not correlate with density (Fagerstone and Biggins 1986). Grids that are too large, however, preclude quick and efficient counts and lead to indices with low reliability. For white-tailed prairie dogs, Fagerstone and Biggins (1986) recommend that grids be at least 10 ha; Menkens et al. (1990) found a high correlation between density and visual counts on grids from 8.1 to 13 ha. We recommend that grids for visual counts be in this size range and be of consistent size in a prairie dog complex.

To ensure that prairie dogs off a grid are not included in the index, the outer boundaries of each grid have to be marked clearly and visibly. Subdividing the grid into several smaller units also guides counters through the grid and prevents individual prairie dogs from being counted twice in one counting session. Markers for delineating the subunits should be distinct from those on the grid's edge.

Visual counts should be obtained from an elevated platform (e.g., truck, hillside) with a view of the entire grid. The station must be marked clearly and permanently to ensure that daily and yearly counts are obtained from the same location. If visual counts are used to monitor population trends through time, the same station has to be used each year.

Significant differences may exist in the ability of observers to see and count prairie dogs (Fagerstone and Biggins 1986). If observers differ greatly in their abilities, the index of density is unreliable. To avoid these differences, observers must be trained and procedures standardized. We suggest that the same individual perform all counts on a grid. When the use of several grids requires more than one counter, the counters must have equal abilities to see and count prairie dogs. A precount session should be held to train potential observers and standardize procedures for counts, including counts among years.

Counts may be made with either binoculars or spotting scopes. However, all observers should use either binoculars or spotting scopes to further reduce variation. The same type of equipment should be used for all counts on all grids. To maximize observer efficiency and to avoid double counting prairie dogs, counts should be made by systematically scanning the grid for a fixed length of time. Marks to delineate the subunits in each grid aid in this effort. The length of each scan should be the same for all counts and on all grids.

The time of year at which counts are made is determined by the researcher's goals. However, all counts must be done when the population is demographically closed.

Daily counts should be conducted when the number of prairie dogs aboveground is highest. The time of the greatest aboveground activity depends on the species and time of year. For example, white-tailed prairie dogs have a bimodal aboveground activity pattern during the summer; the periods of greatest daily activity are between sunrise and approximately 1030 h and between 1500 h and 1800 h (Tileston and Lechleitner 1966; Clark 1977). High correlations between density and visual counts of white-tailed prairie dogs were obtained by Fagerstone and Biggins (1986) and Menkens et al. (1990) when counts were performed during the morning activity period.

Short-term biotic and abiotic factors may greatly affect the number of prairie dogs that are aboveground at any single time (Tileston and Lechleitner 1966; Clark 1977). To ensure that the maximum number of prairie dogs are counted, several counts should be made during the period of highest activity and averaged. Menkens et al. (1990) counted each of their grids for 20 minutes each half hour (a minimum of seven counts per day) and obtained high correlations between density and visual counts. Fagerstone and Biggins (1986) obtained high correlations between density and visual counts by counting three times (36 min / count) during a 2–3 h period. We recommend that at least 1 count / hour be made during the counting period. Higher counting rates would probably further reduce the effects of short-term environmental variation on counts. Because prairie dogs reduce aboveground activity during harsh weather (e.g., rain,

high winds), counts should be made during moderate weather.

The density of prairie dogs may be indexed by counting for only one day (Menkens et al. 1990); however, the same environmental factors that lead to variation in aboveground numbers within days also lead to variation among days. We recommend that counts are made during the same time for three consecutive days to reduce the effects of environmental variability on the estimated density (Menkens et al. 1990). Fagerstone and Biggins (1986) found that the maximum count on a grid resulted in a higher correlation ($r = 0.95$) with an estimate from mark–recapture than with an estimate from the average of several counts.

Obtaining an index of density in an entire complex requires counting prairie dogs in several colonies throughout the complex. The number of grids to sample in a complex depends on desired precision and the size of the complex. Because mark–recapture and visual counts are variable, we recommend that at least 18 grids in a complex be sampled when the number of colonies in a complex is large enough to support this intensity of sampling.

In addition to assuming that observers are equal in their ability to count prairie dogs, the visual count technique also requires the assumption that prairie dogs are equally visible on each grid (Menkens et al. 1990). Large differences in sighting probabilities among grids result in a biased index, and the degree of bias increases with the magnitude of the variation in sighting probabilities. Heterogeneous sighting probabilities may result from many habitat and other environmental factors. The magnitude of variation in sighting probability may be reduced by sampling only grids in similar habitat types and on sites with similar topography. This means that in complexes with two or more habitat types, variation in sighting probability can be reduced by stratifying habitat and developing indices of density in each stratum. When complexes are stratified in such a manner, a complex-wide density index may be obtained with appropriate statistics for stratified sampling.

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A Technique for Evaluating Black-footed Ferret Habitat

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Abstract. In this paper, we provide a model and step-by-step procedures for rating a prairie dog (*Cynomys* sp.) complex for the reintroduction of black-footed ferrets (*Mustela nigripes*). An important factor in the model is an estimate of the number of black-footed ferret families a prairie dog complex can support for a year; thus, the procedures prescribe how to estimate the size of a prairie dog complex and the density of prairie dogs. Other attributes of the model are qualitative: arrangement of colonies, potential for plague and canine distemper, potential for prairie dog expansion, abundance of predators, future resource conflicts and ownership stability, and public and landowner attitudes about prairie dogs and black-footed ferrets. Because of the qualitative attributes in the model, a team approach is recommended for ranking complexes of prairie dogs for black-footed ferret reintroduction.

Key words: *Mustela nigripes*, *Cynomys*, habitat evaluation, prairie dogs, habitat model.

We are presenting a technique for evaluating habitat and potential reintroduction sites for the black-footed ferret (*Mustela nigripes*). We incorporated parts of existing models (Houston et al. 1986; Miller et al. 1988) into a new model. Our goal was the development of an easily understood and practical technique for evaluating the potential ability of prairie dog (*Cynomys* sp.) complexes (groups of prairie dog colonies in close proximity) to support black-footed ferrets with data that are easily and inexpensively collected. Our concern is simplicity. When choices of method or concept were available, we selected the simplest. Because ecological models are abstract constructs and simplifications of actual systems, they may approximate (but not duplicate) reality (Horton and Becak 1987). Thus, their value is in a capacity to contain conceptual information without complicating detail.

An evaluation should allow the ranking of habitat that is related to the number of breeding adult ferrets the habitat supports on a sustained basis. Furthermore, if a technique predicts the number of adult ferrets each site supports, progress in the recovery of the species (1,500 breeding adults in 10 or more populations, each with at least 30 adults; U.S. Fish and Wildlife Service 1988) can be rapidly estimated.

The following technique is based on two parts: (1) development of a numeric rating by energetics of ferrets, and (2) integration of the numeric rating with qualitative attributes into a comprehensive evaluation.

Quantitative Attributes

The Formula

We based quantitative evaluation of black-footed ferret habitat on abundance of prey because the prey base is fundamentally important to the ferret. Variables are combined as follows into a rating index:

$$R = \sum_{i=1}^{n} (A_i \times P_i) / 763 \text{ for } (A_i \times P_i) \geq 272.5$$

where

R = the number of ferret family groups that could be supported by the prairie dog complex (prairie dog complex is defined later),

A = the area of the colony with at least 3.63 prairie dogs per ha,

P = the density of prairie dogs in area A (prairie dogs per ha),

763 = the number of prairie dogs, under typical conditions, required to support one ferret family group for 1 year,

272.5 = the minimum number of prairie dogs needed to support one ferret family group for 1 year,

i = colony number, and

n = the number of colonies in the complex.

Individual ratings are calculated for each colony in the complex, and the overall rating is the sum of those individual ratings. The rating, R, for a complex is an estimate of the number of ferret family groups the complex can support. Colonies with fewer than 272.5 prairie dogs do not contribute to the rating of a complex. In South Dakota, ferrets frequently reproduced on small colonies in nonconsecutive years, presumably because of depletion of prairie dogs (Henderson et al. 1969; Hillman and Linder 1973). Colonies with ratings of less than 1.0 are not expected to support family groups of ferrets every year.

Evidence indicates black-footed ferrets are obligate associates of prairie dogs, relying on them for prey and using their burrows for shelter. Anderson et al. (1986) listed 310 museum specimens of black-footed ferrets, only 6 of which were located outside the range of prairie dogs. In the Meeteetse, Wyoming, complex, Biggins et al. (1985) found that 98% of the locations of all radio-tagged ferrets were in prairie dog colonies. Prairie dogs were about 90% of the black-footed ferret's diet in South Dakota and Wyoming (Sheets et al. 1972; Campbell et al. 1987).

Several researchers speculated about the effect resource availability has on spacing strategies and population density (Riebesell 1974; Schoener 1983; von Schantz 1984; Stamps and Buechner 1985; Carr and MacDonald 1986). To reduce factors of environmental variation on small populations prone to extinction, a reserve should be chosen for the availability of the target species' food resources (Goodman 1987). Morris (1987) reported population density of temperate small mammals depended on quality of habitat. In addition, raptor fledgling rates correlated positively with prey levels (Southern 1970; Smith et al. 1981; Janes 1984; Hansen 1987), as did population densities of gray wolves (*Canis lupus*; Messier 1985), lynxes (*Lynx canadensis*; Brand et al. 1976), bobcats (*Lynx rufus*; Litvaitis et al. 1986), weasels (*Mustela* spp.; Robina 1960; Erlinge 1974; Fitzgerald 1977), and coyotes (*Canis latrans*; Clark 1972). Prey availability influenced habitat selection by river otters (*Lutra canadensis*; Melquist and Hornocker 1983) and least weasels (*Mustela nivalis*; Erlinge 1974).

Our approach requires the assumption that prey base determines potential ferret density. Social behavior may dictate a maximum ferret density regardless of prey abundance, but evidence is conflicting. At the Meeteetse complex, more than one family group of ferrets occupying the same area at the same time was not uncommon (Paunovich and Forrest 1987), and density of feral domestic ferrets (*Mustela putorius furo*) increased as prey became more abundant (Moors and Lavers 1981).

Derivation of Rating Formula

Rationale

Recovery of the black-footed ferret depends on the number of breeding adult ferrets (U.S. Fish and Wildlife Service 1988). Thus, our formula is based on the prairie dog biomass that supports one family group of breeding adults and dependent young.

Higher densities of prairie dogs are needed for reproduction than for maintenance of individual ferrets. Erlinge (1974) suggested that in weasels a higher minimum rodent density was necessary for reproduction than for maintenance. Because of the litter, female weasels used a more restricted area when their food requirements were high (East and Lockie 1964). We assumed that female ferrets with litters would likewise restrict their movements during lactation and during the period from postweaning to dispersal. As a result, they must hunt in the immediate area more intensively and successfully.

Development of our formula may be summarized in five steps:

1. Calculate the prairie dog biomass that black-footed ferret family groups need during the year.
2. Convert prairie dog biomass to prairie dog numbers by estimating quantity of food that ferrets waste, and average weight of live prairie dogs.
3. Sum mortality of prairie dogs from predation by ferrets and other causes.
4. Estimate number of needed prairie dogs to support mortality in step 3, assuming typical prairie dog reproductive rates.
5. Estimate minimum density of prairie dogs necessary to provide sufficient prey in the largest home range of a female ferret with young.

In steps 3 and 4, we used two approaches that lead to the two numbers in the formula. First, we defined the lower limits of habitat that support reproduction in ferrets by assuming low mortality of prairie dogs from causes other than predation by ferrets and by assuming a high reproductive rate in prairie dogs. Using these optimum conditions assures that potential habitat is not overlooked. Second, we used moderate estimates of prairie dog mortality and reproduction to approximate the ability of prairie dog colonies to support reproducing ferrets under more typical conditions. Application of these two principles defining lower limits of habitat and estimating average carrying capacity are illustrated later.

Calculation of Prairie Dog Biomass

Data from captive black-footed ferrets and from published information on other *Mustela* species were used to estimate energetic needs of black-footed ferrets. A single captive ferret ate 50–70 g prairie dog meat / day (Joyce 1988). Similarly, captive Siberian polecats (*Mustela eversmanni*) ate 62 g prairie dog meat / day (Powell et al. 1985).

Although energetic costs of gestation are low, two captive black-footed ferret females increased their consumption two and three times during lactation, and weaned black-footed ferret young ate about 100 g prairie dog meat / day during a period of rapid growth (D. Kwiatkowski, personal communication). In comparison, lactating least weasels increased consumption by a factor of three (East and Lockie 1964) and lactating fishers (*Martes pennanti*), by two to three (Powell and Leonard 1983). Based on field observations, Paunovich and Forrest (1987) speculated that a female black-footed ferret with a weaned litter of five may have been killing 0.6 prairie dogs / day.

We therefore separated a female ferret's energetic requirements into five stages throughout the year and estimated her daily intake during each of those stages. We assumed gestation lasts 42 days, lactation lasts 42 days, postweaning demands on the female and her litter of 3.3 young (average litter size reported by Forrest et al. 1988) last 80 days, replenishing the drain of previous demands by the litter lasts 51 days, and maintenance lasts the remaining 150 days. Thus, annual consumption of prairie dog meat by the female and her young is

Female:

Maintenance	150 days × 60 g / day = 9,000 g
Gestation	42 days × 70 g / day = 2,940 g
Lactation	42 days × 180 g / day = 7,560 g
Postweaning	80 days × 75 g / day = 6,000 g
Post-dispersal replenishment	51 days × 70 g / day = 3,570 g

Young:

3.3 young × 80 days × 100 g/day/young
= 26,400 g

Because several home ranges of females are often overlapped by a male's activity area (Fagerstone and Biggins 1984; Richardson et al. 1987), we assumed 0.5 males inhabit the female's area for 1 year, adding the following biomass requirement:

Adult male: 0.5 male × 365 days × 60 g = 10,950 g

Total . . . . . 66,420 g

Conversion of Biomass to Prairie Dog Numbers

According to Hillman (cited personal communication in Stromberg et al. 1983), black-footed ferrets wasted 20% of the kill. In two studies, average weight of black-tailed prairie dogs (*Cynomys ludovicianus*) was 712 g (King 1955) and of white-tailed prairie dogs (*Cynomys leucurus*), 820 g (Clark 1977). We assumed the average prairie dog weighs 760 g, therefore, the number of prairie dogs needed to meet annual consumption by black-footed ferrets is

$$\frac{66{,}420\ \text{g}}{0.8 \times 760\ \text{g/prairiedog}} = 109\ \text{prairiedogs}$$

Mortality of Prairie Dogs

Ferrets are not the only cause of mortality in prairie dogs. Results from the Meeteetse complex indicated that biomass of badgers (*Taxidea taxus*) probably exceeded biomass of ferrets, and the badgers fed frequently on prairie dogs. More radio-tagged prairie dogs were killed by raptors and coyotes than by badgers and ferrets (D. E. Biggins, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data). Mortality also may result from disease, parasites, other predators, hunters, and so on. Thus, losses of prairie dogs from other causes are assumed to be at least 50% and more typically 250% of predation by ferrets. The low and moderate estimates of mortality in prairie dogs are

1. 109 × 1.5 = 163.5 prairie dogs / ferret family group / year and
2. 109 × 3.5 = 381.5 prairie dogs / ferret family group / year.

Required Population of Prairie Dogs

It was difficult to select low and typical rates of increase for prairie dogs; reported ratios of young to adults vary from nearly 0.0 to more than 3.0. In two longer-term studies, Hoogland et al. (1988) found an average ratio of 0.6 and Menkens (1987) reported an average ratio of 1.4. We use the midpoint (1.0) as the typical rate. Hoogland et al. (1988) showed an inverse relation between density of adults and production of young, leading to our choice of 1.5 at the lower limit of good habitat (where prairie dog density is only 3.6 / ha). Combining the low loss estimate (losses from other predators that equal 50% of predation by ferrets) with the high reproductive rate (1.5) and combining moderate loss (250%) with the moderate reproductive rate (1.0) provides estimates of required prairie dog populations. We assumed the population was stable from year to year. Because prairie dogs are routinely counted when population levels peak in summer, the annual production is added to the base population. Thus, the two estimates are

1. 163.5 / 1.5 + 163.5 = 272.5 prairie dogs (mid-July) and
2. 381.5 / 1.0 + 381.5 = 763 prairie dogs (mid-July)

Minimum Prairie Dog Density

For the purposes of defining and mapping all habitat capable of supporting reproducing ferrets, low prairie dog population requirements must be converted to a density value. Because a female ferret's moves are especially restricted during litter rearing, we assumed an area of activity no larger than 75 ha (an average of hectares of prairie dogs at the Meeteetse complex divided by number of ferrets during 1983 and 1984). If 272.5 prairie dogs must be present in 75 ha, the minimum density is

$$272.5/75 = 3.63 \text{ prairie dogs/ha.}$$

With an observability index of 0.495 (D. E. Biggins and G. E. Menkens, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data), a visual count of 1.8 white-tailed prairie dogs / ha represents an estimated density of 3.63 white-tailed prairie dogs / ha. With an index of 0.566 (D. E. Biggins and L. R. Hanebury, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data), a visual count of 2.06 black-tailed prairie dogs / ha represents an estimated density of 3.63 black-tailed prairie dogs / ha. On nine sites at the Meeteetse complex where black-footed ferrets raised litters, the lowest visual count was 2.59 prairie dogs / ha (D. E. Biggins, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data). The minimum visual count of 1.8 prairie dogs / ha based on energetics thus seems reasonable.

The rating formula is based on breeding habitat of ferrets, defined as having at least 3.63 prairie dogs / ha in mid-July. We recognized that many prairie dog colonies below this threshold value may support nonbreeding ferrets and, in fact, these buffer habitats may be critical to the persistence of ferrets. If two-thirds of the ferret population is lost each year (Forrest et al. 1985), a buffer of replacement animals could be instrumental in maintaining breeding populations for the long term. We initially planned to give buffer habitat some value in our calculations, but after considering the lower energetic demands of nonbreeding ferrets and the demography of the replacement process, we concluded that all complexes have an excess of buffer habitat and the attribute need not be included in the rating.

Data Collection and Evaluation

Ideally, the quantitative rating involves partitioning a prairie dog complex into the maximum number of ferret activity areas (≤75 ha) with at least 273 prairie dogs (with a few added constraints on shape of parcels). The concept is simple, but a map of a partitioned complex is impossible to construct because prairie dogs cannot be economically inventoried on large areas. Instead, sampling schemes that are a compromise between accuracy, precision, and practicality are employed.

Occupied Burrows as Indicators of Prey Abundance

Visual counts of white-tailed prairie dogs underestimate actual densities but correlate with estimated density from mark–recapture (Fagerstone and Biggins 1986; Menkens et al. 1991). Similarly, estimated densities from visual counts of radiotagged black-tailed prairie dogs are too low (D. E. Biggins and L. R. Hanebury, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data).

Visual counts of prairie dogs are more costly and time-consuming than counts of burrows; therefore, we propose counting burrows to assess quality of the prey (at least during initial screening). The correlation between estimates of prairie dog density and density of total burrows seems weak (King 1955; Menkens et al. 1988; D. E. Biggins and L. R. Hanebury, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data). The correlation is much stronger if only active burrows are used. D. E. Biggins and G. E. Menkens (U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data) found a high correlation ($r = +0.95$) between counts of active burrows of white-tailed prairie dogs and estimates of prairie dog density.

A priori we knew that counts of prairie dogs are zero in the absence of occupied burrows and the relation between counts of active burrows and white-tailed prairie dogs was best described by a regression line through the origin ($r = +0.94$; Zar 1984):

$$\text{prairie dog count} = 0.073 \times \text{number of active burrows.}$$

If 3.63 prairie dogs / ha is the lower limit of good ferret habitat and a population density of 3.63 equals a visual count of 1.8 white-tailed prairie dogs, then good habitat should have at least 25 active burrows / ha (active burrows = 1.8 / 0.073).

The relation between counts of active burrows and black-tailed prairie dogs was best described by a regression line through the origin ($r = +0.65$; Zar

1984). We obtained the best fit for black-tailed prairie dog counts and active burrows with:

$$\text{prairie dog count} = 0.179 \times \text{number of active burrows.}$$

If 3.63 prairie dogs / ha is the lower limit of good ferret habitat and a population density of 3.63 equals a visual count of 2.06 black-tailed prairie dogs, then good habitat should have at least 12 active burrows / ha (active burrows = 2.06 / 0.179). A technique for sampling burrow density is described later, but colonies must first be mapped and the complex defined.

Mapping of Colonies

Inconsistencies in mapping can affect the rating. We attempted to solve this potential problem by (1) further standardizing mapping and (2) choosing a quantitative evaluation that is minimally sensitive to mapping. For the proposed technique, mapping can have a significant effect on defining the complex. Failure to map good habitat can affect calculations, but mapping marginal habitat does not increase the rating because areas of low prairie dog density are defined and excluded by the sampling of burrows. Forrest et al. (1985) defined a colony as a minimum of 10 burrow openings / ha. For our evaluation, a minimum of 20 burrows/ha is more appropriate. Resolution, the choice of the smallest parcel to be mapped, is equally important. We suggest viewing a colony as a group of 5-ha parcels, each of which must contain at least 100 burrows to be placed on the map. This implies that colonies smaller than 5 ha can be ignored.

Colonies of black-tailed prairie dogs have been mapped from black and white aerial photography (Cheatheam 1973; Tietjen et al. 1978) and from color infrared photography (Dalsted et al. 1981; Schenbeck and Myhre 1986). The scale of the photography was from 1:15,000 to 1:24,000. The primary characteristic that photo-interpreters used was the distinctive vegetative change caused by black-tailed prairie dogs; these vegetative ecotones were easily seen on color infrared photos. Costs of photo acquisition and interpretation ranged from \$0.10 to \$3.70/ha. Black and white aerial photography of the white-tailed prairie dog complex at the Meeteetse complex (ASCS, 1:20,000 and 1:40:000) was inadequate for accurate mapping of all colonies. Upland colonies were well defined because the tone of mounds contrasted with the background (the deeper soils were lighter colored than surface soil), but colonies on the alluvial bottomlands were poorly defined or could not be seen at all. Color infrared photography at a scale of 1:5,000 was acquired at a cost of about \$2.30 / ha and had adequate resolution for the detection of individual burrows and mounds on both soil types. Mapping of white-tailed prairie dog colonies must be based on the distribution of burrows because there seldom is a noticeable difference in vegetation. Aerial photography may not be suitable for the mapping of all complexes but is probably the most efficient aide for the mapping of many areas (especially of complexes of black-tailed prairie dogs. For comparisons of reintroduction sites and broad overviews of complexes (transfer to 1:100,000), the scales of original maps should be standardized (perhaps 1:24,000).

Definition of the Complex

Forrest et al. (1985) described a complex of prairie dog colonies as "a group of prairie dog colonies distributed so that individual black-footed ferrets (and thus genetic material) can migrate among them commonly and frequently." The expression "commonly and frequently" seems to refer to types of moves actually observed at the Meeteetse complex rather than long distance dispersal between widely separated colonies. The longest nightly moves observed in black-footed ferrets were about 7 km (Biggins and Fagerstone 1984; Richardson et al. 1987). We adopted that 7 km distance in the circumscription technique presented below. The process of circumscribing a prairie dog complex is analogous to describing the home range of an animal from a sample of locations. The following set of rules serves as a practical and biologically reasonable procedure for circumscribing a complex of prairie dog colonies (for a diagrammatic example of a simulated complex refer to Fig. 1):

1. Start at the northernmost point of the northernmost colony.
2. Pivot a 7 km-long line segment clockwise from due north until it touches a point on a colony. The line between the initial point and the second point forms the first segment of the polygon.
3. From the second point, superimpose the line over the first segment, then pivot the 7 km line clockwise until it touches a third point on a colony. This forms the second segment of the polygon.
4. If the 7-km line cannot be pivoted to another colony without bisecting the colony on which it is positioned, move clockwise around that col-

ony's perimeter until step 3 can be accomplished. The convex perimeter can thus become a segment of the boundary of the complex.

5. Continue until the polygon becomes closed.
6. In rare circumstances, a complex may have one or more large spaces without prairie dogs (diameter at least 7 km). Delete the space from the area of the complex, circumscribing it as follows:
   (a) start at the southernmost point of the northernmost colony in the empty space;
   (b) pivot a 7 km-long line counterclockwise from due south until it touches a point on a colony;
   (c) if the 7-km line cannot be pivoted to another point, move counterclockwise around that perimeter until (b) can be accomplished; and
   (d) repeat step (b) until the polygon becomes closed.
7. If an impassable barrier (to ferrets) splits the complex, the resulting parts must be redefined as two or more complexes with the method above.
8. Calculate the area with a polar planimeter.

Sampling of Burrow Density

We offer the following suggestions for sampling burrow densities on prairie dog colonies. A sample data sheet is provided (Fig. 2).

1. Use strip transects 1,000 m × 3 m and a Rolatape measuring wheel (for length) onto which a 3-m piece of electrical conduit is attached (for width) to establish length and width of these 0.3 ha transects. Wires hanging from ends of the conduit facilitated the occasional decision of whether to include borderline burrows. A burrow was included if more than half of the opening was within the transect swath.

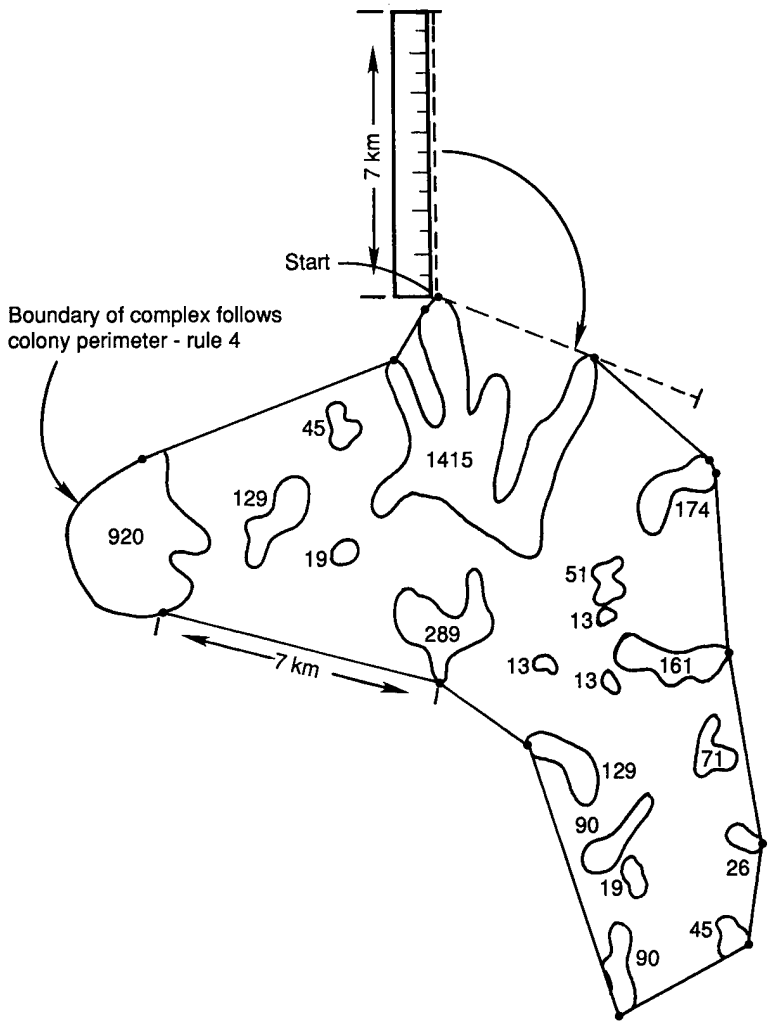


Fig. 1. Circumscribing a complex of prairie dog colonies. The *number* in or adjacent to a colony is its area in hectares.

Burrow Density and Activity Work Sheet

Area _____ PD Town _____

Observer _____ Date _____

Transect no.	Distance	No. burrows Active	Total	Transect no.	Distance	No. burrows Active	Total

Fig. 2. A work sheet to record burrow density and activity.

2. Keep separate counts of active and inactive burrows. Based on our observations of plague at the Meeteetse complex, the ratio between the two is a valuable index to health of the colony.
3. Count only burrows with openings with a diameter of at least 7 cm and so deep that the end is not visible. Large, badger-reamed burrows are counted because prairie dogs often keep using them after the badger departs.
4. Consider a burrow active if fresh prairie dog scat is in the opening or within 0.5 m of it. Fresh means droppings that are not dried hard and bleached white; fresh scat is greenish, black, or dark brown. This definition is conservative. Prairie dogs may even be seen entering burrows classified as inactive. However, criteria such as fresh digging, tracks, sightings, and so on were not used because of lack of consistency between observers; precision is more important than accuracy. A close, detailed inspection of each burrow is not necessary or desirable. A maximum of 10 s / burrow is sufficient, and active burrows are often obvious at a glance.
5. Sample sufficiently intensive to estimate the mean burrow density for the entire complex within 10% at the 95% confidence level. Accordingly, proportionately more transects are needed as complex size decreases or as variation in burrow density and activity rate increase. Presence of plague profoundly increases variation in the rate of burrow activity. On the 5,200-ha Meeteetse white-tailed prairie dog complex, counts on 796 transects provided 95% confidence intervals that were ± 6.5% of the estimated mean density. At 0.3 ha / transect, 4.6% of the complex was sampled ($0.3 \times 796 / 5200$). A 5% sample is usually sufficient.
6. Use systematic rather than random sampling. Sample size on individual colonies is proportionate to colony size and transects are evenly distributed in each colony. Transect spacing is used to determine the sample proportion (spacing = transect width / desired proportion). For a 5% sample, the transects are 60 m apart (3-m width / 0.05). Select a direction across the width of the colony and locate the start of a transect every 60 m. A gap equal to side-to-side spacing is left between the end of the last transect and the beginning of the next (e.g., 60 m). By preselecting the starting place and the direction of the transects, we attempt to avoid biasing the data.
7. Have the observers begin at one end of a colony and walk back and forth across it, reversing the course each time they reach the opposite side and working gradually toward the other end.

Orientation of the transects is determined by compass heading, but a straight line can be maintained by heading toward a distant point identified by a compass heading. The compass heading is important because it must be exactly reversed (after moving over to achieve proper spacing). If the colony border is reached in the middle of a transect, the transect may be continued during the spacing move and subsequently in the opposite direction; thus, some transects may be U-shaped. When approaching the colony boundary (do not let burrow density bias the choice of turning point), the observer must select a meter reading (on the Rolatape measuring wheel) and turn at that reading.

8. Avoid several pitfalls. Keep the transect as straight as possible. Above all, do not let distribution of burrows bias direction of travel. A straight course decreases the chance of divergent and overlapping transects on long, multitransect hikes. Sampling must be done only in mapped colonies. If Rolatape measuring wheels are used in colonies with very uneven topography or heavy shrub cover, they have to be tested under prevailing conditions and a correction factor has to be developed. Wheels measured distance with less than 1% error on most prairie dog colonies (D. E. Biggins and L. R. Hanebury, U.S. Fish and Wildlife, Fort Collins, Colorado, unpublished data).
9. Each person can be expected to complete 10–20 transects / day. At the Meeteetse complex, the average was 14 transects / person / day.
10. Sampling should be conducted during mid-June through August after young emerged.

Evaluation of Data

For an evaluation of habitat in each colony in the complex, counts of active burrows have to be available from a sample of 0.3-ha strip transects and colony size must be known. Proceed as follows:

1. Estimate the proportion of good habitat (equal to habitat capable of supporting ferret reproduction) as the number of transects with at least 25 active white-tailed prairie dog burrows / ha divided by the total number of transects or as the number of transects with at least 12 active black-tailed prairie dog burrows / ha divided by the total number of transects.
2. Estimate area of good habitat by multiplying proportion of good habitat by colony size.
3. Calculate average density of occupied burrows for only good habitat. Because each transect covers 0.3 ha, at least eight occupied burrows of white-tailed prairie dogs must have been counted along each transect (25 occupied burrows / ha multiplied by 0.3 ha) or four occupied burrows of black-tailed prairie dogs along each transect (12 occupied burrows / ha multiplied by 0.3 ha).
4. Convert the density of occupied burrows to density of white-tailed prairie dogs (PD DEN).

   $$\text{PD DEN} = (0.073 \times \text{active burrow density}) / 0.495$$

   Convert the density of occupied burrows to density of black-tailed prairie dogs (PD DEN).

   $$\text{PD DEN} = (0.179 \times \text{active burrow density}) / 0.566$$

5. Estimate the number of prairie dogs on good habitat by multiplying the result of calculation number 2 by the result of calculation number 4.
6. Estimate the number of ferret family groups that the colony supports by dividing the result from calculation number 5 by 763. If the result of calculation number 5 was less than 272.5, the colony receives a rating of zero (0).
7. The rating for the complex is the sum of all colony ratings.

Reintroduction sites for black-footed ferrets should be a minimum of about 400 ha (combined area of all colonies). A group of small complexes requires intensive management as habitat for a metapopulation of ferrets (Clark 1986; Brussard and Gilpin 1989; Harris et al. 1989). Complexes larger than 400 ha are desirable because the degree of human intervention is inversely related to complex size.

The quantitative model is a valuable aid in ranking reintroduction sites for black-footed ferrets, especially if its results are considered in combination with other qualitative criteria to be described later. The usefulness of estimating numbers of ferrets that can be supported in a complex has been emphasized, but the result must be viewed as only an approximation. The accuracies of the original estimated density of active burrows, the conversion from burrows to prairie dog counts, and counts to estimate density are uncertain. Many assumptions were made about energetics and demographic processes. In particular, natality and mortality of prairie dogs from other than predation have profound effects on the estimate, and both are expected to be highly variable.

Our evaluation of varying configurations of prairie dog complexes was hindered by lack of

data. Only two prairie dog complexes with ferrets (Mellette County, South Dakota, and Meeteetse, Wyoming) were studied. These complexes had extremely different configurations and were occupied by different species of prairie dogs. It should not be assumed that the South Dakota or Wyoming complexes were good habitat for ferrets just because ferrets persisted on them longer than elsewhere. The sequence of extinction of ferret populations may have been highly influenced by chance events when habitat became fragmented.

The Meeteetse Complex

Evaluation of the Meeteetse complex in 1988 (Table) illustrates the described computations. A computer spreadsheet (e.g., LOTUS, MULTIPLAN, QUATTRO) is convenient for manipulating data.

The described quantitative process seems reasonable when results are compared with data and conclusions from other studies. Forrest et al. (1985) predicted a need for 40–60 ha of habitat per adult ferret at a mean density of 54.5 ha / adult at the Meeteetse complex. The ratio of adult males to adult females was about 2:1 (Forrest et al. 1988), and male home ranges overlapped those of females (Fagerstone and Biggins 1984; Richardson et al. 1987). If 16.7 males are added to 33.4 females (Table) and the total of 50.1 is divided into 2727 (Table; hectares of good habitat), the result of 54.4 ha / adult ferret is within the predicted 40–60 ha / ferret. Assuming a high density of prairie dogs (30/ha) and using the minimum habitat requirements of our model (272.5 prairie dogs), a stable prairie dog population may support a female ferret's reproduction in a 9-ha area. Black-footed ferret families were raised on colonies as small as 10 ha in South Dakota (Hillman et al. 1979), and female European polecats, a similar species, used small home ranges (12.4 ha) when prey was abundant (Moors and Lavers 1981).

Integration of Quantitative and Qualitative Information for an Evaluation

Some important features of prairie dog complexes are not quantifiable. Miller et al. (1988) attempted to quantitatively incorporate two sociopolitical factors (landownership and

Table. *Attributes of the 1988 evaluation of the Meeteetse prairie dog complex that led to an estimate of black-footed ferret families each prairie dog town can support.*[a]

Town	Transects (No.)	Size (ha)	% good habitat	Ha	Burrows / ha	Prairie dogs / ha	Total prairie dogs[b]	R_i
Long Hollow	52	196.5	0.519	102.0	57.5	8.5	865.5	1.1
Lot 58	10	48.0	1.000	48.0	86.0	12.7	608.8	0.8
New Town	9	55.0	0.889	48.9	65.0	9.6	468.6	0.6
BLM 10	17	74.0	1.000	74.0	69.4	10.2	757.5	1.0
BLM 13	39	185.5	0.795	147.4	60.1	8.9	1,305.9	1.7
Rawhide	50	253.0	0.780	197.3	108.5	16.0	3,158.6	4.1
Spring Creek	71	459.5	0.944	433.6	89.2	13.2	5,706.0	7.5
Pickett / Grave	127	679.0	0.669	454.4	67.1	9.9	4,494.0	5.9
Core / Rose	268	1,901.5	0.373	709.5	38.6	5.7	4,034.3	5.3
91 Town	13	270.0	0.538	145.4	41.8	6.2	895.2	1.2
Thomas	23	51.5	0.696	35.8	52.3	7.7	276.3	0.4
Tonapah	11	61.0	0.000	0.0	0.0	0.0	0.0	0.0
Pump Station	68	363.0	0.574	208.2	56.5	8.3	1,735.5	2.3
Hogg	17	72.0	0.941	67.8	71.9	10.6	718.3	0.9
L Rawhide	7	191.0	0.286	54.6	58.3	8.6	469.5	0.6
Complex total	782	4,860.5		2,727.0			25,494.1	33.4

[a] R_i = number of prairie dogs / 763.

[b] Ha good habitat × (burrows / ha × 0.073) / 0.495).

development potential) into their model. In practice, it may be difficult to assign quantitative ratings to these categories and to some important biological categories. We therefore evaluate several biological and sociopolitical features qualitatively and integrate those rankings with the quantitative data.

Spatial Arrangement of Colonies

The spatial arrangement of colonies in a complex has important ramifications and should be considered in the evaluation (Minta and Clark 1989). Complexes of equal colony area can consist of few closely-spaced large colonies, many widely-separated small colonies, or various combinations thereof. As colonies become smaller and their spacing more distant, ferret populations may suffer the following consequences: (1) reduced gene flow, (2) decreased ability to recolonize prairie dog colonies vacated because of stochastic events, (3) decreased ability to disperse to new colonies after initial reintroduction or to colonize newly established prairie dog colonies, and (4) lowered mating success. Effects of each would probably become serious at different points on the size per distance scale; for example, lowered mating success may only occur at the lower extremes of size and density. Nevertheless, the same morphology of a prairie dog complex that promotes easy moves among colonies also facilitates spread of disease. Thus, an argument can be made for separation of subpopulations of ferrets and prairie dogs.

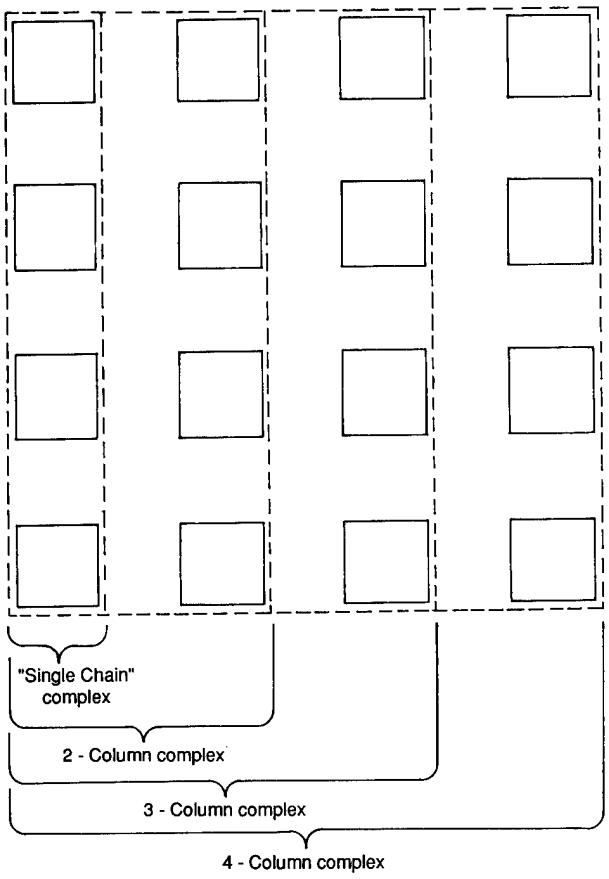
Houston et al. (1986) proposed two variables to characterize configuration of a complex-intercolony distance and frequency distribution of colony sizes. Intercolony distance is intuitively appealing because it seems to reflect the amount of nonhabitat a ferret might have to cross when moving from colony to colony; the attribute has been referred to elsewhere (Hillman et al. 1979; Forrest et al. 1985). Houston et al. (1986) and Miller et al. (1988) recommend interpretation of intercolony distance with a nearest-neighbor technique (a distance from each colony to its nearest neighbor with distances often used twice). This measurement is influenced by clumping of colonies in a complex; distances between clumps of colonies are ignored. The frequency distribution of colony sizes gives a disproportionately higher value to large colonies than to small colonies. Both frequency distribution and intercolony distance are sensitive to inconsistencies in mapping that can persist despite efforts to standardize (analogous to the taxonomic debates of lumpers and splitters).

We concur in principle with those who emphasize the potential importance of size, shape, and interspersion of colonies in a complex (Forrest et al. 1985; Houston et al. 1986; Miller et al. 1988; Minta and Clark 1989). However, we remain troubled by the mentioned quantitative difficulties. Consequently, spatial arrangement of colonies is not incorporated into the quantitative section of the model but is represented in a qualitative assessment of biological features.

To aid in the qualitative evaluation, we suggest calculation of the percent of complex area occupied by prairie dog colonies as a partial descriptor of size and juxtaposition of prairie dog colonies in a complex (Miller et al. 1988). We tested the attribute of percent occupancy on simulated and actual complexes representing many combinations of complex and colony shape, intercolony distance, and colony size and found it reflected our concept of suitable habitat in a prairie dog complex configuration for ferrets. The treatment of the percent occupancy concept by Miller et al. (1988) had two problems: (1) the procedure for circumscribing a complex to calculate its overall area was not well described and (2) long, narrow chains of colonies greatly inflated the percentage. The first problem addressed in the previously described procedure for circumscribing a group of colonies.

The second problem occurs when the complex (or part of it) consists of a long narrow chain of single colonies, causing opposite sides of the same colonies to form opposite boundaries of the complex. An example can be illustrated (Fig. 3) by calculating percent occupied for a single string of four colonies, adding a second column of four more colonies with the same intercolony spacing and recalculating percent-occupied, and so on. Our primary concern is with large percent-occupied values calculated from single chains of colonies; the change rapidly became inconsequential with adding the third and fourth columns of colonies. Thus, an additional rule (9) was added to the method of circumscribing a complex, to be used only when calculating the percent-occupied attribute. The following rule upwardly adjusts areas of complexes with single chains of colonies.

Rule 9. If opposite sides of two or more consecutive colonies define opposite sides of a complex or part thereof, add to total area of complex the amount of area determined by the following expression:



Number of Columns	"Percent Occupied"
1	57
2	38
3	34
4	33

Fig. 3. An example of the effect on percent-occupied caused by progressing from a single chain of colonies to a block of equally spaced colonies.

Adjustment = (average intercolony distance between colonies in the chain) × (curvilinear length of chain)

Curvilinear length of chain is the length of a line through the approximate center of each colony extending continuously from the beginning of the first colony to the end of the last colony.

Rule 9 is an approximation to avoid extreme overrating of percent-occupied because of single chains of colonies and ignores narrow complexes that are more than a single colony wide. The technique, however, is repeatable and should function well in practice.

In the Mellette County complex, only about 1% of the complex was occupied by prairie dog colonies, but the area supported ferrets. The configuration of the Mellette County complex seems far from optimum; perhaps this contributed to ultimate failure of that ferret population. Nevertheless, existence of black-footed ferrets on the Mellette County complex suggests that we limit the influence of percent-occupied on the rating. All actual complexes we examined to date were less than 40% occupied by prairie dog colonies; 22% of the Meeteetse complex was occupied (Houston et al. 1986).

Other Biological and Sociopolitical Factors

Quantification of the following biological and sociopolitical factors is also difficult (Fig. 4).

Plague

Factors of plague to consider are known occurrences of prairie dog die-offs and documentation of plague by the centers for disease control or others. Also consider the ratio of active to total burrows. If less than 50% of the burrows are active and no other significant causes of prairie dog mortality can be identified (e.g., poisoning), further investigate the possibility of plague (collect flea samples from prairie dog burrows, analyze blood samples from other carnivores such as badgers (Fitzgerald 1993), and look for prairie dog carcasses that can be examined.

Canine Distemper

Demonstration of canine distemper serum antibodies in other carnivores on or near potential reintroduction sites is cause for concern. An abundance of domestic or other wild carnivores may increase the probability of introduction and spread of canine distemper.

Potential for Expansion of Prairie Dog Populations

Assess the effects of other nearby prairie dog complexes and potential for prairie dog expansion inside and beyond present boundaries. Are other complexes sufficiently near to allow natural dispersal and consequent genetic exchange? Can other prairie dog colonies or small complexes between larger complexes serve as stepping stones for migration? Can prairie dog populations expand? Have prairie dog colony and complex size been controlled by poisoning or are limitations imposed by uncontrollable factors such as physiography? In short,

FACTOR	COMPARISON Complex 9 versus Complex 5	
Quantitative Biological:		
1. Result from model	+	0
Qualitative Biological:		
1. Arrangement of colonies	+	0
2. Plague potential	0	+
3. Canine distemper potential	+	0
4. Other nearby complexes	+	0
5. Potential for prairie dog expansion	+	0
6. Abundance of other predators	0	+
Sociopolitical:		
1. Future resource conflicts and ownership stability	+	0
2. Public and landowner attitudes and their potential to change	+	0
Overall rating and comments:		

Fig. 4. A sample checklist for comparing pairs of complexes.

consider the present situation and potential changes.

Barriers

Are partial barriers to moves by ferrets in the complex? Rivers may not be completely impassable barriers but may seasonally interrupt moves. Little is known of its swimming ability, but a ferret can cross ice-covered bodies of water. Lines of cliffs and congested highways can also impede free moves of ferrets.

Predators

Assess abundance and possible influences of other predators. Mammalian predators probably influence the dynamics of disease (Barnes 1993). Mammalian and avian predators prey on ferrets directly (Fagerstone and Biggins 1984) and compete for the same food. Presence of numerous great horned owls (*Bubo virginianus*), ferruginous hawks (*Buteo regalis*), golden eagles (*Aquila chrysaetos*), coyotes, badgers, and so on may make a site less appealing (than another site with fewer such animals) for reintroductions of ferrets, although control of predators during establishment of ferrets could partially compensate.

Integration

We found agreement on factors of quality of potential habitat for ferrets (models by Houston et al. 1986; Miller et al. 1988). The model presented here weights those factors differently than the other two models. To minimize disagreements in rating complexes and hence the weighting of each in the final evaluation, a democratic strategy by a team is probably the best solution. Team members can be nominated by the Interstate Coordinating Committee (ICC) and include (but not necessarily be limited to) present ICC participants. The only prerequisite should be familiarity with the ecology of black-footed ferrets and prairie dogs. We envision that (1) each team member independently rates all complexes (Fig. 4), (2) ratings are discussed in an open forum, (3) team members have the opportunity to change individual ratings, and (4) the individual ratings are combined. Individual ratings are made before collective discussions take place because some people have more aggressive, dynamic, and persuasive personalities than others; it seems preferable to have each evaluator's initial rating uninfluenced by the biases of others. On the other hand, diverse expertise and background may be represented on the team, and collective interchange of ideas would be beneficial.

A rating from all the variables without following some orderly process is difficult. Two formats for ranking complexes are offered.

1. Evaluate pairs of complexes by progressing down a checklist of factors (Fig. 4), again picking the best for each factor. Although we believe

biological attributes are the critical elements in identifying reintroduction sites, sociopolitical factors may be influential in the survival of ferrets. The final analysis must involve weighting of the individual factors according to relative importance and consideration of the margin of difference for each factor.

2. Evaluate all possible pairs of complexes, identifying the best of each pair. The complex with the most wins has the highest rating, and so on. A matrix can be helpful (Fig. 5).

Results from evaluation of a group of complexes may remain valid for a short time. Prairie dog ecosystems are dynamic. Irrespective of anthropogenic control of prairie dogs, numbers of prairie dogs can change rapidly. Plague can rapidly eliminate prairie dog colonies (Lechleitner et al. 1968), but the number of prairie dogs in a colony can double annually (Knowles 1986), and colony area can expand by more than 80% per year (Dalsted et al. 1981). Other biotic components of the ecosystem and the sociopolitical aspects may also undergo changes. Thus, periodic reevaluation of sites is necessary until black-footed ferrets are released. Subsequent to release, monitoring is essential.

A \ B	1	2	3	4	5	6	7	8	9
1		+	+	+	+	0	0	0	0
2	0		+	0	0	0	0	0	0
3	0	0		0	0	0	0	0	0
4	0	+	+		+	0	0	0	0
5	0	+	+	0		0	0	0	0
6	+	+	+	+	+		+	+	+
7	+	+	+	+	+	0		+	+
8	+	+	+	+	+	0	0		0
9	+	+	+	+	+	0	0	+	
Total +'s	4	7	8	5	6	0	1	3	2

Fig. 5. Matrix for comparing complexes. If a complex identified in a column has a higher black-footed ferret rating than a complex in a row, place a plus sign (+) in the appropriate column and row block. Otherwise place a zero (0) in the block. When all pairs of complexes are rated, determine the number of plus sign (+) scores for each column. The column-complex with the most plus sign (+) scores has the best reintroduction potential based on black-footed ferret families it can support. In this example, nine complexes are compared. Column-complex 8 has a higher black-footed ferret rating than rows-complexes 6, 7, and 9; thus, it has a total score

Acknowledgments

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Workshop Summary

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As preparation for the conference, participants were provided with a draft of each paper and a list of questions about the biology and habitat of prairie dogs (*Cynomys* spp.). At the workshop, the participants prioritized the questions for management and research (Appendix).

Disease

Sylvatic plague (*Yersinia pestis*) is the greatest threat to the health of prairie dogs. The ecology of that disease was thoroughly reviewed by Barnes (1993), Culley (1993), and Fitzgerald (1993). No other diseases of prairie dogs have the potential to cause epizootics of high mortality to prairie dog populations.

Plague was first documented in North America around the turn of the century. Although there is general agreement that plague is exotic to North America, there is disagreement about when plague arrived on the continent. Regardless, plague has the potential to profoundly influence the spatial and temporal distribution of prairie dogs, particularly when coupled with control and rapid changes in land use.

All four species of prairie dogs are susceptible to plague, and Gunnison prairie dog (*Cynomys gunnisoni*) colonies are often totally eradicated by the epizootic. Although Clark (1977) and Ubico et al. (1988) documented plague in white-tailed prairie dogs (*Cynomys leucurus*), little is known about the spread and persistence of the disease. White-tailed prairie dog colonies are not always decimated, and the disease sometimes spreads slowly (Culley 1993).

The participants identified several important factors for regulating the occurrence and persistence of plague. The density of prairie dogs may influence the behavior of plague. Although Clark (1977) reported that plague moved through a white-tailed prairie dog town in Wyoming when density, activity, and social behavior were greatest, Fitzgerald (1993) listed prairie dog colonies of varying densities that all succumbed to plague. The absence of recorded plague in South Dakota, North Dakota, Nebraska, western Kansas, or in the state of Chihuahua in northern Mexico where the highly social and densely distributed black-tailed prairie dog (*Cynomys ludovicianus*) populations occur support the contention that density is not the sole regulating factor of plague. Confounding these data, however, is the influence of climatic and soil regimes that may limit distribution of the plague vector (fleas) itself in the black-tailed prairie dog ecosystem.

A complex of discrete colonies has an advantage in restricting the transmission of disease and re-

ducing the rate of spread. Widely dispersed colonies, however, reduce the likelihood of intercolony movement by black-footed ferrets and heighten the potential of genetic problems of small isolated populations. An explicit assessment of the benefits and risks of various distributions is worthwhile for long-term management of reintroduced black-footed ferrets.

Information on the ecological importance of other mammals during plague cycles is scarce. Some mammals may serve as a reservoir for the disease. California voles (*Microtis californicus*) are the only known enzootic host, but because of the similarities in host physiology, rock squirrels (*Spermophilus variegatus*), Richardson's ground squirrels (*Spermophilus richardsoni*), and grasshopper mice (*Onychomys* spp.) may harbor plague in the enzootic state. Raptors, burrowing owls (*Athene cunicularia*), and carnivores also carry rodent fleas and may be a source of plague. Because so little is known about the ecology of plague cycles and because of the potential importance of maintaining stable prairie dog populations for the recovery of the ferret, additional research into plague cycles is warranted.

Even if prairie dogs recolonize after an outbreak, the ubiquitous occurrence of plague makes future epizootics likely. The mechanism of population recovery from epizootics is unknown. Based on the work with the endangered Utah prairie dog (*Cynomys parvidens*), the participants felt that research into the translocation of prairie dogs, particularly sites with a recent plague epizootic, may reveal the feasibility of artificially stabilizing prairie dog numbers. For example, enhancing prairie dog survival may be better than removing black-footed ferrets from a plague site. Nonetheless, the participants recommended that black-footed ferrets be captured if the prairie dog population drops precipitously (about 70%). Furthermore, the group recognized the importance of site-specific contingency plans for dealing with plague and ferrets after reintroduction.

It was suggested that future research produce a bait for inoculating prairie dogs against plague. Bio-engineering of plague-resistant prairie dogs was discussed in light of Culley's (1993) observation that some rodents seemingly developed an immunity to plague.

Participants said monitoring the occurrence of plague in potential reintroduction sites was important. Blood serum from predators (particularly badgers, *Taxidea taxus*) collected in late winter–early spring was recognized as a useful tool for identifying the presence of plague in a prairie dog complex. Over time, monitoring of carnivores would provide important baseline information about the ebb and flow of plague in the region. Although surveillance of plague in carnivores is more effective, surveys of fleas also identify the presence of plague. Fleas should be collected from about 50 burrows / colony, pooled into one sample, and analyzed (about $25 / sample in 1989) for the presence of plague.

The participants noted that stopping outbreaks of plague by dusting burrows with insecticide immediately upon detection of the outbreak was impossible. Barnes (1993) recommended permetharin (more research into effects would be helpful) to treat the diseased colony in the complex and that adjacent colonies be watched closely. Other animal dens also should be dusted and dead prairie dogs removed. Equipment and supplies should be stored near each reintroduction site.

Control of predators may be a tactic to prevent other carnivores from spreading plague. More importantly, it may reduce competition for the dwindling food resource. As prairie dogs decline, there may be a lag before carnivores depart the colony. Their competition with ferrets for food will be accentuated because fewer prairie dogs are available and the probability of a ferret being taken by another predator increases. Problems with predators occurred after translocating Utah prairie dogs.

Habitat Management and Population Dynamics

Several aspects of habitat affect the population size of prairie dogs: water areas, salt licks, disturbances, livestock grazing, river bottoms, fires, drought, soil characteristics, slope, water table, bedrock, drainage pattern, soil depth, previous use by prairie dogs, physical barriers, winter temperature, and elevation.

The group noted habitat differs by species of prairie dog. White-tailed and Gunnison prairie dogs are more common in shortgrass–bunchgrass, dense sagebrush, steep slopes, and at higher elevations; but black-tailed prairie dogs seem to prefer shortgrass–midgrass, flat slopes, sparse brush, and a history of disturbance. Alteration of habitat can affect prairie dog populations. Light grazing by livestock reduces the number of black-tailed prairie dogs, and deferred grazing eliminated some

colonies entirely; conversely, overgrazing stimulated the expansion of prairie dog populations (Uresk et al. 1981).

As with other wildlife, prairie dogs and black-footed ferrets benefit from wise management of habitat. The Endangered Species Act of 1973 (87 Stat 884, as amended, 16 U.S.C. 1531 et seq.) specifies that incentives should be used to preserve or enhance habitat of threatened and endangered organisms. The many other species (e.g., mountain plovers, burrowing owls) that also depend on the prairie dog ecosystem would also benefit from management.

As discussed by Hanson (1993), the precipitous decline of prairie dog populations during the last century was largely due to control of prairie dogs. By 1960, control had reduced the original geographic distribution of prairie dogs by approximately 98% (Marsh 1984). Control still continues and is a factor of prairie dog population dynamics.

Controls were historically based on competition for forage (Merriam 1902). Recent research revealed that the level of competition between black-tailed prairie dogs and livestock is only 4% to 7% at prairie dog densities of 44 / ha (Uresk and Paulson 1989). Other research revealed that the existence of livestock grazing and prairie dogs are not mutually exclusive on the western grasslands; despite less biomass on prairie dog colonies, forage quality, digestibility, and productivity increase from activities by prairie dogs (Coppock et al. 1983; Whicker and Detling 1993).

Researchers in Montana are investigating the effects of sustainable sport hunting on prairie dog populations (J. Grinston, personal communication, U.S. Bureau of Land Management, Malta, Montana). They reported a colony that had 15% annual expansion rates when the prairie dogs were not hunted, but a 3% expansion rate when they were hunted. In addition, shooting of prairie dogs provided an estimated annual economic benefit of $3.2 million to the local economy around the Buffalo Gap National Grassland in South Dakota (Sharps 1988). Potential death of ferrets (albeit accidental) should be considered. More research into the hunting of prairie dogs would benefit management.

Public Relations

Developing support for the conservation of black-footed ferrets is critical for successful management of ferrets. The group emphasized the importance of one-on-one meetings with ranchers and of addressing grazing associations, town meetings, wildlife organizations, and local conservation organizations. These meetings are important for coordinating activities of agencies and interest groups, educating the community, and developing local trust. Speakers must define positions consistently and clearly and address local concerns.

The group agreed that a model to identify costs and benefits to the private rancher, to wildlife, and to the general public would be very beneficial. The model should be clear and analyze gains and losses under a variety of land uses and identify a situation that is beneficial for wildlife and agriculture.

The national public must be informed and educated. Even if the focus of management is local, conservation is a national issue. Knowledge of a conservation program in one area may benefit species in another region with similar difficulties and contribute to the general public's interest in conservation issues. Because federal tax dollars support endangered species programs, those species are a national issue.

National education may also increase awareness of the effects of habitat destruction on wildlife populations. The conservation of any species must be centered around the habitat or ecosystem on which it depends. Managing to maintain a ecosystem before species are threatened is an obvious proactive choice. In the case of black-footed ferrets, we are already faced with a species in a crisis situation, and crises leave no viable alternative to the rescue of individual species.

National education requires convincing evidence that prairie dog ecosystems are in need of conservation. National baseline data on existing and potential prairie dog distribution and determinations on a regional level of the occurrence of plague, control of prairie dogs, and other factors potentially limiting the distribution of prairie dogs are essential.

Perhaps, the plight of a species, such as the black-footed ferret, can direct attention to conservation issues. Indeed the black-footed ferret is only a symptom of the harm of habitat fragmentation and the decline of the prairie dog community. Because prairie dog communities support a greater diversity of wildlife than a prairie without prairie dogs, the co-dependent species of prairie dog communities also suffer greater risk to survival. With education and time, species like the black-footed ferret may help people become aware of the value

of ecosystems and ecological processes so that future crises may be averted.

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Appendix. Questions for management and research in priority order in each category of disease, habitat management, population dynamics, and public relations

Appendix Table 1. *Disease.*

- What is the influence of plague on population dynamics of the individual species of prairie dogs?
- What is the role of other species in the transmission of the disease?
- What is the optimum distribution of colonies to minimize the spread of plague?
- How is plague transmitted to prairie dogs and by prairie dogs, both within and between colonies?
- Why is plague not found in certain regions?
- What factors promote plague outbreak?
- What physical characteristics influence the species composition and distribution of fleas?
- What is the best method for testing for the presence of disease in prairie dog colonies?
- What are the mechanisms of prairie dog population recovery after an epizootic and can we enhance that process?
- Will areas without plague but located in a plague zone ever be hit with the disease?
- What contingency plans are necessary for an epizootic?
- Can we bait-inoculate prairie dogs against the disease or perhaps bio-engineer an immune prairie dog?
- Is there a mechanism to stop plague between colonies, and if so, what is it?
- Is plague density dependent?
- Will prairie dogs eventually develop resistance to plague?
- Is there a source of prairie dog diseases?
- Can we identify other diseases that cause population decreases?
- Can we protect biologists from the disease?

Appendix Table 2. *Habitat management.*

- What habitat characteristics (biotic and abiotic) affect expansion of prairie dog colonies?
- How can vegetation be managed to favor high or low density prairie dog colonies (e.g., livestock)?
- How do habitat characteristics differ between species?
- What are the trade-offs between prairie dogs and livestock?
- What are the effects of prairie dogs on vegetation density and forage quality?
- What kind of tools, regulations, and economic incentives are available?
- What habitat characteristics influence prairie dog population dynamics?
- How do prairie dogs select colony sites?
- Which agency has the lead for determining habitat management for prairie dogs?

Appendix Table 3. *Population dynamics.*

- How are prairie dog expansion dynamics determined and how are prairie dog numbers managed?
- What factors are important in starting, expanding, managing, and controlling a prairie dog colony?
- How do forage quality and quantity of vegetation affect population dynamics?
- How can density and life history characteristics be used as management tools?
- Can a model predict what will happen to prairie dog populations? If so, how and what should be modeled?
- What are the artificial effects (shooting, grazing, oil and gas, surface mining, artificial barriers, etc.) on prairie dog population dynamics?
- At what size and age does a prairie dog town become self-sustaining? Does the center die out leaving the population at the edge? What factors determine distribution and density in colonies?
- What are practical and economic methods for enumerating prairie dog abundance (number of plots, number of years, techniques, etc.)?
- What is the required level of accuracy for identifying reintroduction sites and monitoring density of prairie dogs before and after release of ferrets?
- What are the key factors that influence population size?
- How can managers determine when the prairie dog population is in trouble and when to apply proactive management?
- What is the influence of plague on prairie dog population dynamics?
- How can the use allocation of prairie dog colonies be determined (human, ferret, etc.)?
- How do managers handle population variations in a prairie dog complex?
- What are the effects of weather on prairie dogs?
- Do new colonies contribute to long-term stability on a complex?
- Is there an optimum time of year to engage in management activities?
- How should the level of interchange between black-tailed prairie dog colonies be managed?

Appendix Table 4. *Public relations.*

- What are the short- and long-term strategies to enhance public involvement and stimulate education for conservation of prairie dog ecosystems?
- What sections of the public need to be addressed?
- How are objectives defined for the public?
- What are the economics of livestock grazing, poisoning, and prairie dog conservation?
- How do we convert the idea of single species management into a systems approach?
- Who are the key players to help develop education programs and who should those programs address?
- What legislative means are available to set aside lands?
- What is the public's interest in public lands?
- Who can best start and conduct public relations programs?

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U.S. DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally-owned public lands and natural resources. This includes fostering the sound use of our lands and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.