

White-tailed Prairie Dog (*Cynomys leucurus*): A Technical Conservation Assessment



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COVER PHOTO CREDIT

White-tailed prairie dog (*Cynomys leucurus*). Photograph by the Wyoming Game and Fish Department. Used with permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE WHITE-TAILED PRAIRIE DOG

The white-tailed prairie dog (*Cynomys leucurus*), a colonial sciurid of North America, historically occurred across 17-20 million ha (43-51 million acres) of high altitude (2,100 – 2,500 m; 6980 – 8,200 ft) grasslands, ranging from southern Montana to west-central Colorado and from eastern Utah to eastern Wyoming. Current estimates suggest the species occupies roughly 340,000 ha (840,000 ac), representing a range contraction exceeding 98 percent. Because of this substantial rangewide decline, the U.S. Fish and Wildlife Service (USFWS) was petitioned to list the white-tailed prairie dog under the Endangered Species Act. Following two years of review, in 2004, the USFWS concluded that the petition lacked substantial scientific information warranting the listing of the species. Thus, management of the white-tailed prairie dog remains primarily the responsibility of state wildlife agencies. Because white-tailed prairie dogs are found in four states, they are subject to a range of classifications and management.

The proximal factors behind the white-tailed prairie dog's historic, rangewide decline appear to include the conversion of native grasslands to agriculture and urban development, poisoning campaigns, and the arrival of an exotic and virulent disease, plague. Many of the factors that contributed to the historic decline in prairie dog distribution and abundance persist today; grasslands continue to be altered for human use, prairie dog colonies are still poisoned on both private and public lands, and plague epizootics continue to induce high mortality rates throughout the species' range. Additional anthropogenic factors, including recreational shooting and oil, gas, and mineral development have increased in recent decades and have unknown consequences for prairie dog distribution and abundance.

Although numerous factors constrain the distribution of white-tailed prairie dogs, plague appears to be the single most important factor currently influencing the distribution and abundance of the species. Plague is present throughout the range of the white-tailed prairie dog and is capable of inducing 85 to 100 percent mortality in exposed colonies. In addition to directly reducing colony size and prairie dog abundance, plague increases interannual variation of population size and increases distances between colonies, which may ultimately reduce the viability of entire complexes of colonies. Besides its direct effects on prairie dog population biology, little is known about sylvatic plague epizootics; we currently lack the ability to predict plague outbreaks and have not identified methods to prevent outbreaks or to ameliorate the effects of an outbreak once it has begun. Thus, management of the white-tailed prairie dog needs to consider the stochastic effects of plague on prairie dog population biology.

The distribution of white-tailed prairie dogs within the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS) has been intermittently mapped since 1987. From available data, it appears that three small complexes occur on National Forest System (NFS) lands within Region 2, encompassing approximately 253 ha (624 acres), or less than 0.1 percent of the species' current distribution. However, recently developed habitat models predict that the national forests within Region 2 have roughly 90,181 ha (222,846 acres) of suitable habitat for white-tailed prairie dog colonies. Thus, maximizing prairie dog occupancy on NFS lands in Region 2 could add substantially to the current occupied land base of white-tailed prairie dogs. In addition to expanding the distribution of white-tailed prairie dogs within their native range, increasing their distribution on NFS lands could also influence the viability of neighboring colonies on other land ownerships. Establishment of relatively protected colonies on Region 2 NFS lands could serve as refugia and sources of augmentation to colonies that have experienced population declines resulting from poisoning, recreational shooting, habitat loss, or plague. Thus, although the current distribution of white-tailed prairie dogs within Region 2 is quite limited, NFS lands could significantly influence the distribution and persistence of this species over large areas of its range.

To promote the persistence and growth of white-tailed prairie dog populations on lands in Region 2, we recommend:

- ❖ rigorously surveying NFS lands for white-tailed prairie dog colonies
- ❖ documenting the distribution and abundance of white-tailed prairie dogs over multiple years to better understand their population trends

- ❖ managing habitat for prairie dogs by limiting grazing and initiating controlled burns around colonies to control shrub growth
- ❖ prohibiting recreational shooting and poisoning on NFS lands
- ❖ reintroducing white-tailed prairie dogs to previously occupied and suitable sites on USFS lands that are too distant from existing colonies to be naturally recolonized.

Management and restoration of white-tailed prairie dog colonies within national forests will not only benefit the species, but will also be advantageous to the many species that preferentially use and depend on prairie dog colonies, including the obligate prairie dog predator, the critically endangered black-footed ferret (*Mustela nigripes*).

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INTRODUCTION

This conservation assessment is one of many being produced for the USDA Forest Service (USFS) Rocky Mountain Region (Region 2) Species Conservation Project. The white-tailed prairie dog is the focus of an assessment because Region 2 lists it as a sensitive species. The USFS defines a sensitive species as a plant or animal species whose population viability is identified as a concern by a regional forester because of significant current or predicted downward trends in abundance and/or in habitat capability that would reduce its distribution (USDA Forest Service 2005). A sensitive species may require special management, so knowledge of its biology and ecology is critical.

This assessment addresses the biology, ecology, conservation status, and management of the white-tailed prairie dog throughout its range, with emphasis on Region 2. The nature of the assessment leads to some constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced for the Species Conservation Project are designed to provide land managers, biologists, and the public with a thorough discussion of the biology, ecology, and conservation of certain species based on current scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of implications of that knowledge, and outlines of information needs. The assessment does not seek to prescribe management. Instead, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). The assessment also discusses management recommendations proposed elsewhere or being implemented across the range of the species.

Scope

This conservation assessment examines the biology, ecology, conservation status, and management of the white-tailed prairie dog with specific reference to the geographic and ecological characteristics of the Rocky Mountain Region. It is concerned with characteristics of white-tailed prairie dogs in the context of the current environment. The evolutionary

environment of the species is considered in conducting the synthesis, but placed in a current context.

In producing the assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on white-tailed prairie dogs are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were regarded with greater skepticism, but we chose to use some of this material when refereed information was unavailable. Unpublished data (e.g., Natural Heritage Program records) were important in estimating the geographic distribution of this species.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and observations limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, strong inference, as described by Platt, suggests that experiments will produce clean results (Hillborn and Mangel 1997), as may be observed in certain physical sciences. The geologist, T. C. Chamberlain (1897), suggested an alternative approach to science where multiple competing hypotheses are confronted with observation and data. Sorting among alternatives may be accomplished using a variety of scientific tools (e.g., experiments, modeling, logical inference). Ecological science is, in some ways, more similar to geology than physics because of the difficulty in conducting critical experiments and the reliance on observation, inference, good thinking, and models to guide our understanding of the natural world (Hillborn and Mangel 1997).

Confronting uncertainty then is not prescriptive. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. More specifically, when dealing with uncertainty in this assessment, we always noted when inferences were

made, and when the strength of evidence for particular ideas was not certain, we used phrases such as ‘...is likely to...’, ‘...is probable that...’, ‘...might be...’.

Application and Interpretation Limits of This Assessment

Most of the data presented in this assessment are from site-specific studies. An important limitation of this assessment is its applicability to areas beyond locations where the data were collected. While some characteristics remain similar throughout the range of the white-tailed prairie dog, community assemblages become increasingly different as the distance increases between sites. Therefore, the ability to predict the response of white-tailed prairie dogs to various factors becomes more difficult and uncertain as the distance between inference communities increases. Thus, the information should be interpreted and applied generally where conservation plans are developed by inference.

Publication of Assessment on the World Wide Web

To facilitate their use, species conservation assessments are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, Web publication will facilitate the revision of the assessments, which will be accomplished based on protocols established by Region 2.

Peer Review

In keeping with the standards of scientific publication, assessments developed for the Species Conservation Project have been externally peer reviewed prior to their release on the Web. This assessment was reviewed through a process administered by the Society for Conservation Biology, which chose two recognized experts (on this or related taxa) to provide critical input to the manuscript.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

In July 2002, the U.S. Fish and Wildlife Service (USFWS) was petitioned (Center for Native Ecosystems et al. 2002) to list the white-tailed prairie dog under the Federal Endangered Species Act of 1973 (16 U.S.C. 1531-1544, as amended) (ESA). Following two years of review, the USFWS concluded in November 2004 that the petition lacked substantial scientific information warranting the listing of the species (U.S. Fish and Wildlife Service 2004). Thus, management of white-tailed prairie dogs remains primarily the responsibility of state wildlife agencies. Because each state has established different strategies to manage prairie dogs within their jurisdiction, the classification of the white-tailed prairie dog (**Table 1**) ranges from a “nongame wildlife species in need of management” (Montana; Montana Prairie Dog Working Group 2002) to simply a “nongame mammal” (Utah and Wyoming; Seglund et al. 2004). Currently, USFS Region 2 lists the white-tailed prairie dog as a sensitive species (USDA Forest Service 2005). The Nature Conservancy classifies the rangewide status of the white-tailed prairie dog as G4, indicating that the species is apparently secure from extinction globally (NatureServe 2005). At the state level, The Nature Conservancy classifies the white-tailed prairie dog as apparently secure (S4) in Colorado, vulnerable to extirpation (S3) in Wyoming, likely imperiled in Utah (S2?), and critically imperiled in Montana (S1) (**Table 1**; NatureServe 2005).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The white-tailed prairie dog is distributed across four states (principally Colorado, Wyoming, and Utah, with a limited area of occupancy in south-central Montana), and so is subjected to four different state-level regulatory mechanisms and management plans.

Table 1. Natural Heritage Program state ranks (NatureServe 2005) and state agency classifications (Seglund et al. 2004) of the white-tailed prairie dog throughout its range. Region 2 states are in bold.

State	Natural Heritage Program state rank	Classification by state wildlife management agencies
Colorado	S4 – apparently secure	small game species
Montana	S1 – critically imperiled	nongame species in need of management
Utah	S2? – imperiled?	nongame
Wyoming	S3 - vulnerable	nongame wildlife in need of management^a

^aListed as a “Species of Special Concern” (not a statutory category)

The State of Colorado classifies the white-tailed prairie dog as a small game species. A small game license is required to shoot white-tailed prairie dogs, but private landowners and their immediate family members are exempt from license requirements. The statewide season for this species is year-round with no bag or possession limits. Participants in recreational shooting contests cannot kill more than five prairie dogs during each event. In Colorado, toxicants can be used to control prairie dog colonies, but only by a licensed applicator (Seglund et al. 2004). Colorado has not developed a management or conservation plan for the white-tailed prairie dog.

In Wyoming, the white-tailed prairie dog is classified as a nongame wildlife species, but recreational shooting is allowed. Of the states with white-tailed prairie dogs, regulations limiting shooting are weakest in Wyoming. This species can be hunted year-round on public and private lands without a license, and there is no bag or possession limit. The Wyoming Game and Fish Department has recently listed the white-tailed prairie dog as a species of special concern, but this designation carries no statutory implications. Wyoming has not developed a management or conservation plan for the white-tailed prairie dog (Grenier personal communication 2006).

In Utah the white-tailed prairie dog is designated a nongame mammal. However, as in Wyoming, recreational shooting is allowed, licenses are not required, and there are no bag or possession limits. Presumably to prevent hunting from inflicting high levels of mortality on prairie dog pups, recreational shooting is illegal on public land from 1 April to 15 June. No such regulation exists for private lands, where prairie dogs can be shot year-round. However, recreational shooting of white-tailed prairie dogs is prohibited in the reintroduction zone for black-footed ferrets (*Mustela nigripes*) in eastern Uintah County (Seglund et al. 2004). In 2003, the Utah Division of Wildlife Resources added the white-tailed prairie dog to its sensitive species list. Addition to the list was intended to stimulate development of a state management plan to preclude federal listing of the species under the ESA; however, at this time, Utah has not developed a management or conservation plan.

The white-tailed prairie dog is classified as nongame wildlife in need of management in Montana. It is illegal to shoot white-tailed prairie dogs on public lands other than state school trust lands. Poisoning, however, is allowed on both public and private lands, so long as it adheres to Environmental Protection Agency

(EPA) regulations. In addition, the Montana Department of Agriculture offers technical assistance to private landowners for poisoning prairie dogs on private lands. In 2002, the Montana Prairie Dog Working Group released the Montana Prairie Dog Conservation Plan (Montana Prairie Dog Working Group 2002). The plan designated the white-tailed prairie dog as a nongame wildlife species in need of management and instituted a year-round closure of white-tailed prairie dog shooting on public land. The plan stipulates that the management regulations for prairie dogs will be reviewed and subject to change annually. The current shooting closure on public lands is effective until the next review on 28 February 2008. The prairie dog plan was collectively approved by the Montana Fish, Wildlife, and Parks, the Montana Department of Agriculture, and the Montana Department of Natural Resources and Conservation. Various federal agencies, including the USFS, also pledged cooperation to the state plan (Seglund et al. 2004). Montana does not list the white-tailed prairie dog on its endangered or threatened species list, but the state has designated it as a species of special concern. Although this listing does not change the legal status of the species, it does influence the Montana Fish, Wildlife, and Parks priority list for research and management among nongame animals. In addition, Montana Fish, Wildlife, and Parks and the Bureau of Land Management have recently prepared a draft environmental assessment proposing to reintroduce white-tailed prairie dogs into formerly occupied areas. The current plan outlines the translocation of between 60 and 350 animals from active colonies in Wyoming or Montana to up to five vacant sites in Montana (Seglund et al. 2004).

In 1998, the Interstate Prairie Dog Conservation Team (IPDCT; originally known as the Interstate Black-Tailed Prairie Dog Conservation Team) was established to provide a coordinated effort to manage information and data associated with the status, distribution, and abundance of prairie dogs throughout western North America. In 2001, the White-Tailed Prairie Dog Working Group (WTPDWG) emerged from the IPDCT as a focus group specifically concerned with the interstate management of the white-tailed prairie dog. In 2004, the WTPDWG completed a conservation assessment of the species in response to the 2002 petition to list the white-tailed prairie dog under the ESA. The assessment reviewed the status of white-tailed prairie dog distribution and documented threats to the persistence of the species. Similar to the USFWS finding, the WTPDWG concluded that listing the white-tailed prairie dog as federally threatened was currently unjustified (Seglund et al. 2004).

A variety of federal acts influence the management of wildlife, including white-tailed prairie dogs, on National Forest System (NFS) lands. Among them, the National Forest Management Act (NFMA) of 1976 requires the USFS to "...provide for diversity of plant and animal communities based on the suitability and capability of the specific land area in order to meet overall multiple-use objectives..." With respect to poisoning prairie dogs, the Federal Insecticide, Fungicide, and Rodenticide Act of 1947 requires that all pesticides used in the United States be registered by the EPA (U.S. Environmental Protection Agency 2005). Currently, four vertebrate toxicants and fumigants are registered for field use in the United States: zinc phosphide, aluminum phosphide, fumigant gas cartridges, and acrolein. With the exception of gas cartridges, all poisons are Restricted Use Products and can only be applied by trained and licensed applicators. In addition, the ESA requires that federal agencies consult with the USFWS whenever actions carried out, authorized, or funded by those agencies "may affect" federally listed species. The purpose of this requirement is to ensure that federal actions do not jeopardize the continued existence of federally listed species. Because of the potential for causing death or secondary poisoning of the federally endangered black-footed ferret, an obligate predator of prairie dogs, the EPA is required to consult with the USFWS, per section 7(a)(2) of the ESA, regarding the authorization for use of certain pesticides and toxicants in the control of prairie dogs. Following a national-level consultation between USFWS and EPA in the early 1990's, the USFWS issued a programmatic Biological Opinion (U.S. Fish and Wildlife Service 1993) on the effects of vertebrate control agents on federally listed species, including the black-footed ferret. In that opinion, USFWS determined that application 10 pesticides could jeopardize the continued existence of 6 listed species in USFWS Region 6, including the black-footed ferret. Among those pesticides were aluminum phosphide and zinc phosphide, agents regularly used in the control of prairie dogs. Included in the opinion's incidental take statement, were "reasonable and prudent alternatives" (RPA) to avoid jeopardizing the continued existence of the black-footed ferret. RPA number 6 stipulated that surveys be conducted for black-footed ferrets in white-tailed prairie dog colonies greater than 200 acres but less than 1000 acres in size to ensure that ferrets are not present prior to treatment. Complexes larger than 1000 acres were not to be treated until evaluated by state or federal agencies for its potential in ferret recovery or until it is "block-cleared" (areas determined by USFWS not to be unoccupied by black-footed ferrets). To implement these RPA's, EPA labeled

these rodenticides to require, with the exception of "block-cleared" areas, that the USFWS be contacted prior to the application of labeled toxicants to ensure that ferrets are not incidentally killed during prairie dog control activities. Because different state USFWS offices have different consultation requirements for application of rodenticides in prairie dog colonies, it is prudent to contact the appropriate USFWS office prior to undertaking lethal control of prairie dogs to ensure compliance with existing law.

Biology and Ecology

Systematics and description

Clark et al. (1971) reviewed the systematics of the white-tailed prairie dog, which is classified within the Order Rodentia, Family Sciuridae and genus *Cynomys*. The genus *Cynomys* is further divided into two subgenera, *Cynomys* and *Leucocrossuromys*, which contain two and three extant species, respectively. Members of the subgenus *Cynomys* are characterized by a black-tipped tail and include the Mexican prairie dog (*C. mexicanus*) and black-tailed prairie dog (*C. ludovicianus*). Members of the subgenus *Leucocrossuromys* are characterized by a white-tipped tail and include the Gunnison's (*C. gunnisoni*), Utah (*C. parvidens*), and white-tailed prairie dog (*C. leucurus*).

The general color of the upper body parts of white-tailed prairie dogs is yellowish buff streaked with black. A spot above the eye and a large area on the cheek are blackish-brown. The tip of the tail is white, with hairs of the proximal half having bands of black interspersed with pale cinnamon, whereas those of the distal half are clear white (Clark et al. 1971).

White-tailed prairie dogs are sexually dimorphic, with adult males being heavier and larger than adult females (Tileston and Lechleitner 1966, Hoogland and Engstrom 2003). Mean (\pm 95 percent CI) adult male body mass is $1,139 \pm 99$ g (range = 750 to 1,700 g), while mean adult female body mass is 925 ± 46 g (range = 675 to 1,200 g). Similarly, mean adult male total length is 371 ± 4 mm (range = 342 to 399 mm), whereas mean adult female total length is 353 ± 4 mm (range = 315 to 375 mm). Sexual dimorphism in body weight varies seasonally, with maximal differences in the breeding season when males can weigh up to 36 percent more than females (Hoogland and Engstrom 2003). Tail length is the same in both sexes (40 to 65 mm), but notably shorter than that of the similar-sized black-tailed prairie dog (82 to 110 mm).

Distribution and abundance

The white-tailed prairie dog occurs in grasslands and grass-shrublands, typically at elevations between about 1,700 and 2,600 m (5,600 and 8,500 ft.), but are known from elevations in excess of 3,030 m (10,000 ft.) in Colorado (Lechleitner 1969, Armstrong 1972, Lechleitner 1969). More specifically, this species ranges from the Bighorn Basin in southern Montana, south across central and southwestern Wyoming into western Colorado and northeastern Utah, east to the Laramie Mountains in Wyoming and into North Park, Colorado, south into the lower Gunnison Valley, west across the Bear River Divide into extreme northern

Utah, and farther south into the Green River Valley (**Figure 1**; Clark et al. 1971). The two largest extant colony complexes of white-tailed prairie dogs are in northeastern Utah/northwestern Colorado and in the Shirley Basin of central Wyoming; these colonies encompass approximately 61,917 ha (153,000 acres) and 57,465 ha (142,000 acres), respectively (Knowles 2002). Seglund et al. (2004) have summarized the existing data on the current area occupied by white-tailed prairie dogs.

Known active white-tailed prairie dog colonies in Colorado occupy approximately 77,648 ha (191,866 acres), and those with unknown activity status occupy



Figure 1. Current distribution of the white-tailed prairie dog in North America by county (Fitzgerald 1994, Knowles 2002, Seglund 2004, J. Carlson personal communication 2003, M. Canning personal communication 2003, Wyoming Natural Diversity Database 2005).

another 19,021 ha (47,001 acres). In Wyoming, white-tailed prairie dog colonies occupy an estimated 185,988 ha (459,576 acres), but the proportion of active vs. inactive colonies is unknown. White-tailed prairie dog colonies occupy an estimated 57,463 ha (141,808 acres) in Utah. In Montana, recent mapping efforts identified six colonies of white-tailed prairie dogs distributed across an area of only 48 ha (119 acres). Based on this information, there are roughly 340,168 ha (840,573 acres) of mapped white-tailed prairie dog colonies. However, because these occupancy data were collected using different methods and with varying intensities of effort in each state, they only provide a rough approximation of the current area occupied by this species. Furthermore, it is likely that some colonies were not detected and mapped during surveys (Knowles 2002).

Although it has been estimated that greater than 50 percent of white-tailed prairie dog occupied habitat is located on public land (Seglund et al. 2004), little is known about the distribution and abundance of this species within these areas. Indeed, detailed information exists only for the largest colony complexes, which have been mapped regularly to assess their suitability for black-footed ferrets. Irrespective of complex size, however, very little data on the spatial extent of white-tailed prairie dogs on National Forest System (NFS) lands are available. White-tailed prairie dog colonies on NFS lands were intermittently mapped between 1987 and 2002, and from the available data, it appears that white-tailed prairie dogs occupy approximately 762 ha (1869 acres) across four national forests (**Table 2**; Ernst personal communication 2005). The largest concentration of colonies on NFS lands occurs on the Ashley National Forest (Region 4) in northeastern Utah; this complex extends onto non-NFS land in southwestern Wyoming (**Table 2**). Within Region 2, white-tailed prairie dogs occur only within the Arapaho-Roosevelt, Grand Mesa-Uncompahgre-Gunnison, Medicine Bow-Routt national forests, where they encompass an estimated 253 ha (624 acres), or less than 0.1 percent of the current distribution of this species (**Figure 2**; **Table 2**).

Population trend

Historically, prairie dogs were distributed throughout North America's temperate grasslands, but poisoning and shooting campaigns, land conversion, and plague dramatically reduced the distribution and abundance of all five species within the last century (Miller and Cully 2001). Merriam (1902) estimated that in the late 1800's, prairie dogs occupied 283 million ha (699 million acres). More recently, the USFWS estimated that roughly 160 million ha (395 million acres) of potential habitat existed in North America, but only about 80 million ha (198 million acres) were occupied at any one time (Gober 2000). By 1971, it was estimated that prairie dog distribution had declined to less than 0.6 million ha (1 million acres; Fagerstone and Biggins 1986), representing a range contraction exceeding 99 percent. Using predictive habitat models, it has been estimated that the historical range of the white-tailed prairie dog was between 17 and 20 million ha (42 and 49 million acres; Center for Native Ecosystems et al. 2002, Seglund et al. 2004, U.S. Fish and Wildlife Service 2004). Even using this more conservative estimate of historic range occupation, the current occupied area would represent a range contraction of approximately 99 percent.

Data specific to current rangewide trends in white-tailed prairie dog distribution and abundance are severely lacking for two reasons. First, the historic distribution of the white-tailed prairie dog is based largely on anecdotal observations or predictive habitat use models; virtually no empirical data on the spatial distribution of white-tailed prairie dogs prior to the mid 1980's exist. Second, data on population trends have been collected from only a handful of colonies occurring on public land and, therefore, may not accurately represent rangewide distributional trends. Furthermore, the results of these mapping efforts are confounded by different sampling protocols, preventing straightforward comparisons across time and among colonies. Therefore, only rough inferences can be made from the existing data on the spatial distribution and abundance of a few colonies over a relatively short time period.

Table 2. Areal extent of white-tailed prairie dog colonies on USDA Forest Service land.

National Forest	Hectares	Acres
Ashley (Region 4)	509	1245
Grand Mesa-Uncompahgre-Gunnison (Region 2)	216	534
Medicine Bow-Routt (Region 2)	19	46
Arapaho-Roosevelt (Region 2)	18	44



Figure 2. Approximate distribution of the white-tailed prairie dog (dotted red line) and general locations of active white-tailed prairie dog colonies (red circles) within NFS Region 2 lands (green shading). White-tailed prairie dogs occupy 253 ha (624 acres) of land across three Region 2 national forests, (Medicine Bow-Routt, Arapaho-Roosevelt, and Grand Mesa-Uncompahgre-Gunnison National Forests).

In Wyoming, two colony complexes, Meeteetse and Shirley Basin, have been studied for the past few decades. In 1915, the U.S. Department of Agriculture estimated that white-tailed prairie dogs at the Meeteetse complex encompassed roughly 80,900 ha (200,000 acres) (Knowles 2002). The areal extent of the Meeteetse complex had declined to about 4,925 ha (12,170 acres) by the time black-footed ferrets were discovered there in 1981 (Knowles 2002). Since the initial documentation of plague in 1985, the amount of occupied land has fallen to 405 ha (1000 acres; Cully and Williams 2001), representing a 99.5 percent decline since 1915. Similarly, in the Shirley Basin complex, white-tailed prairie dogs have steadily declined since the detection of plague in 1987 (Cully and Williams 2001). The Shirley Basin complex enveloped an estimated 137,600 ha (340,000 acres) prior to plague,

but was reduced to approximately 57,465 ha (142,000 acres) following epizootics (Knowles 2002).

In Colorado, two colony complexes have been repeatedly mapped since the late 1980's. In 1992, these complexes combined to encompass 9,272 ha (22,912 acres) of active colonies. Seven years later, surveys revealed that the areal extent of active colonies had declined by 92 percent to 735 ha (1,816 acres). In 2002, both complexes were mapped again, but there appeared to be little change in their active area since 1999 (Seglund et al. 2004).

In Utah, nine colony complexes have been mapped since the mid-1980's. The time interval between surveys for each complex ranged from 8 to 17 years (earliest beginning in 1985 and most recent

surveys concluding in 2002). The percent change in colony area ranged from a decline of 11 percent to an increase of 31 percent. Of the nine complexes, five had increased in size while four had decreased (Seglund et al. 2004). The gross change in areal extent between the first survey and most recent survey was a decrease of about 4,100 ha (10,132 acres).

In Montana during the 1970's, white-tailed prairie dogs were present at 15 colonies encompassing 313 ha (773 acres) in Carbon County (Flath 1979). After re-examining 14 of 15 colonies in 1997, only two colonies totaling 39 ha (96 acres) were active (Montana Prairie Dog Working Group 2002). By 2003, the active area of colonization increased slightly to approximately 48 ha (119 acres). Thus, white-tailed prairie dog distribution in Montana has decreased by 83 percent since the 1970's (Seglund et al. 2004).

From the available data, decreases in the size of colony complexes give reason for concern that the long-term viability of this species could be threatened. Declines within the past two decades have been documented in 85 percent of the mapped white-tailed prairie dog colonies, including on the two largest remaining white-tailed prairie dog colony complexes in the Shirley Basin, Wyoming and in northwestern Colorado/northeastern Utah (Knowles 2002, Seglund et al. 2004). However, it is difficult to conclude unequivocally that these data reflect a continuing rangewide trend for the species (Luce personal communication 2003). As previously stated, these spatial data are limited because of small sample sizes, non-random selection of colonies, and a limited temporal scale.

Activity pattern and movements

Circadian activity pattern

Clark et al. (1971) reviewed the daily and seasonal activity patterns of the white-tailed prairie dog. These animals are strictly diurnal, with aboveground activity ending before sunset and resuming after sunrise. Daily activity begins after sunrise, when prairie dogs emerge from underground and spend a short time sitting or standing, looking around the proximity of their burrows. After a few minutes, they begin to forage near their burrows, increasing the distance between burrows and feeding sites as the day progresses.

The activity patterns of white-tailed prairie dogs vary seasonally. During the hot summer months (June through August), prairie dogs return to their burrows

by mid-morning and generally remain under ground during the hottest parts of the day. Late in the afternoon, when high mid-day temperatures drop, aboveground activity, primarily foraging, resumes. This bimodal activity pattern contrasts with the unimodal activity pattern that characterizes the spring and fall months (from February to April and September to November), when aboveground activity peaks in the early afternoon. While above ground, prairie dogs spend most of their time feeding (36 percent) and sitting erect (34 percent). Other aboveground activities include laying down (16 percent), running (4 percent), vocalizing (4 percent), nose out of burrow (3.5 percent), kissing, digging, fighting (2 percent), and grooming (0.5 percent) (Orabona-Cerovski 1991).

Throughout the day, some level of activity is present in colonies, except when inclement weather conditions, such as heavy rain, hail, or extremely high temperatures, discourage individuals from leaving their burrows. Temperature is an important regulator of activity, with most activity occurring between -9 and 24 °C (16-75 °F) (Clark 1973). White-tailed prairie dogs are sensitive to heat, and in temperatures exceeding 24 °C (75 °F), they will salivate excessively to regulate body temperature. If temperatures do not fall, prairie dogs will die from hyperthermia (Clark 1973). Wind speed also influences prairie dog activity. Tileston and Lechleitner (1966) reported that daily activities were restricted when wind velocities approached 48 km per hr. Clark (1973), however, observed that activity was restricted only when wind velocities approached 90 km per hr. Even during favorable weather conditions, not all adults within a colony are above ground at the same time (Clark et al. 1971).

Seasonal activity pattern

White-tailed prairie dogs hibernate for 3.5 to 5 months in winter. First emergence of white-tailed prairie dogs appears to be independent of weather conditions and typically occurs between late February and mid-March (Bakko and Brown 1967, Clark 1973). Adult males become active about three weeks before adult females; juveniles emerge between late May and mid-June (Bakko and Brown 1967). By mid-July, adult males disappear below ground, followed by adult females several weeks later; by late August, all adults are inactive (Clark 1973). Juveniles enter hibernation between late October and early November (Clark 1973). For all age-classes, activity is completely terminated during the winter (Tileston and Lichleitner 1966). Unlike black-tailed prairie dogs, which only enter torpor in response to an exogenous stressor such

as food or water shortage, white-tailed prairie dogs are spontaneous hibernators and enter torpor in response to a persistent circadian rhythm, even if food and water are readily available (Harlow 1997).

The total amount of time that prairie dogs remain active during the year appears to be correlated to some extent with elevation. In Wyoming, at a colony located at 2,195 m (7,200 ft.), prairie dogs were active for a total of about 8.5 months (Clark 1968) while in northern Colorado, white-tailed prairie dogs living at higher elevations (2,500 m [8,200 ft.]) were active for only 7 months (Tileston and Lechleitner 1966).

Movements

Dispersal of white-tailed prairie dogs is not understood as well as their activity patterns. This is largely because marked individuals commonly disappear from colonies during studies, and the fate of those individuals is unknown. Despite this limitation, available information suggests that dispersal primarily occurs in early spring between March and April, and late summer between July and September (Clark 1973). Juvenile and yearling males are the predominant dispersers. Females tend to show greater fidelity to their natal areas (Michener 1983), but dispersal of juvenile females has also been reported (Orabona-Cerovski 1991).

Immigration appears to be common in populations of white-tailed prairie dogs. In southeastern Wyoming, 12 unmarked animals (seven males and five females) immigrated during the spring into a colony from which they were absent the previous summer (Clark 1973). In north-central Colorado, a relatively important population augmentation occurred when a colony gained 11 animals (five females and six males) by means of immigration (Tileston and Lechleitner 1966). Unfortunately, the authors reported no data on colony size before immigration. In northwestern and southeastern Wyoming, the immigration rate, defined as the percent of untagged adults appearing in a population of marked adults in a given year, averaged 24 percent over four years (Menkens 1987).

Information on emigration is scanty and mainly based on anecdotal observations. At one colony in Albany County, Wyoming, six (five males, one female) of 47 pups dispersed from their parturition burrows. The greatest distance a male moved from the colony boundary was about 300 m, to a series of abandoned burrows where it ultimately took up residence. The other five animals all moved less than 60 m and

reoccupied a series of old burrows. Mean distance moved by juvenile males was 82 ± 31 m ($n = 14$; range = 45 to 165 m) while mean distance moved by juvenile females was 127 ± 48 m ($n = 12$; range = 75 to 225 m) (Clark 1973). At the same colony, information on adult dispersal was provided for only two individuals. A one-year old male and an adult male of unknown age moved 0.4 and 2.7 km, respectively. Both individuals successfully settled at different colonies (Clark 1973). In north-central Colorado, Tileston and Lechleitner (1966) reported that only 25 percent of the known population at a white-tailed prairie dog colony was recaptured the following year. The fates of 75 percent of the missing individuals were undetermined, but one adult male moved approximately 400 m from its previous known location. In Shirley Basin, Wyoming, only 1 percent of males and 3 percent of females over a period of three years dispersed more than 200 m. Whether these low dispersal rates resulted from a small proportion of dispersing animals, a failure in recapturing dispersers, or dispersal distances being less than 200 m was unknown (Orabona-Cerovski 1991).

Habitat

Unlike other prairie dog species, white-tailed prairie dogs are capable of establishing colonies in a variety of habitat types including shrub-steppe, short-grass prairie, meadow, mountain valley, and transitional areas with mixed stands of shrubs and grasses (Tileston 1962, Baker et al. 1999, Seglund et al. 2004). Typically, colonies are located in plant communities with low vegetative height and in systems generally dominated by grasses, forbs, and low shrubs. The amount of low-lying vegetation within white-tailed prairie dog colonies can be highly variable; past authors have reported a range of 18 to 82% vegetative cover on colonies (Tileston and Lechleitner 1966, Menkens 1987, Orabona-Cerovski 1991). The topography of colonies also exhibits substantive variation; white-tailed prairie dog colonies occur on landscapes ranging from flat plains to rolling hills. In addition, larger colonies are often dissected by gullies and may contain small hills that rise 20 m (65 ft.) above the surrounding prairie (Orabona-Cerovski 1991).

Although no quantitative data have been published on habitat selection by white-tailed prairie dogs, several descriptions of habitat use have been reported. For instance, at six white-tailed prairie dog colonies in central Wyoming, total vegetative cover varied from 45 to 75 percent, with grasses and forbs representing over 70 percent of the total vegetation. Shrubs rarely covered more than 5 percent of a colony,

and densities ranged from a median of 0 to 3,100 shrubs per ha (0 to 1,250 shrubs per acre). Shrub height ranged from a median of 24 to 35 cm (0.8 to 1.1 ft.; Menkens 1987). Within a colony in southeastern Wyoming, short grasses and forbs were the dominant vegetation, constituting 88 percent of total vegetation. The most abundant plant species found were western wheatgrass (*Agropyron smithii*), and Indian ricegrass (*Oryzopsis hymenoides*) (Clark 1973). At colonies in the Shirley Basin of south-central Wyoming, average plant cover was 38 percent, with grasses and sedges composing the majority of vegetative cover (range = 6 to 41 percent of total cover). Species were primarily western wheatgrass, blue grama (*Bouteloua gracilis*), junegrass (*Loelera cristata*), Indian ricegrass, needle-and-thread (*Stipa comata*), broom snakeweed (*Gutierrezia sarothraei*), plains pricklypear cactus (*Opuntia polyacantha*), big sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), and rabbit brush (*Chrysothamnus nauseosus*). Bare ground was the predominant cover type (37 to 82 percent of the total cover throughout the colonies) (Orabona-Cerovski 1991). In north-central Colorado, three types of vegetation were characterized in white-tailed prairie dog colonies: sagebrush, dry meadow, and irrigated meadow. In the sagebrush type, big sagebrush was the dominant plant, followed by grasses and forbs. The average plant cover for this vegetation type was 10 percent (range = 3 to 15 percent). In the dry meadow type, herbs such as the mat muhly (*Muhlenbergia richardsoni*), sedges (*Carex* spp. and *Eleocharis pauciflora*), and tufted hairgrass (*Deschampsia caespitosa*) predominated; the average vegetative cover was a higher 60 percent. Similarly, the irrigated meadow type contained dense stands of sedges and tufted hairgrass, but, in contrast, contained other plant species including creeping bent (*Agrostis pelustris*), foxtail barley (*Hordeum jubatum*), timothy (*Phleum pratense*), aster (*Aster bigelovii*), knotweed (*Polygonum engelmanni*), and pussy toes (*Antennaria rosea*). Plant cover was highest in the irrigated meadow type, averaging 70 percent (Tileston and Lechleitner 1966).

White-tailed prairie dogs do not actively clip vegetation to suppress plant growth within the colony boundary. Therefore, habitat modification by this species is less pronounced than that resulting from the clipping habits of black-tailed prairie dogs. The absence of clipped vegetation in white-tailed prairie dog colonies makes the distinction between active colonies and adjacent uncolonized sites more difficult to detect than in black-tailed prairie dog colonies (Tileston and Lechleitner 1966, Menkens 1987). Baker et al. (1999) compared habitat characteristics between active white-

tailed prairie dog colonies and adjacent uncolonized sites and found that the vegetative cover was similar between the two, but they did detect that colonies had a higher percent of bare ground and a lower amount of standing plant biomass. In southeastern Wyoming, grazing activities of white-tailed prairie dogs appeared to favor graminoids and negatively affected forb abundance (Clark 1973).

Burrows are a key component of white-tailed prairie dog habitat. Prairie dogs use their burrows to avoid inclement weather, to avert high summer temperatures, to evade predators, and as hibernacula for several months in winter (Clark 1971). The burrow mound is usually a large, unconsolidated, semi-round structure composed of excavated subsoil (Clark 1971). One or more entrances can be found in each mound. Burrows contain one or more tunnels of variable length and are typically 1 to 2 m deep (Clark 1971). Use of an area by white-tailed prairie dogs appears to be correlated with soil characteristics. The soil in occupied areas is typically 30 to 50 percent sand and stone, which appears to provide greater structural stability for burrows compared with soils high in clay and low in sand (Menkens 1987).

Large variability in habitat features, such as topography and vegetation between colonies, suggests that white-tailed prairie dogs are able to persist over a wide range of environmental conditions (Menkens 1987). This observation suggests that large areas of suitable habitat for this species remain unoccupied. The factors that prevent white-tailed prairie dogs from colonizing these vacant habitats are unclear, but potential anthropogenic forces influencing white-tailed prairie dog distribution are discussed in detail in the Conservation section.

Food habits

Few researchers have investigated the diet of the white-tailed prairie dog. Tileston and Lechleitner (1966) found that the feeding habits of white-tailed prairie dogs in north-central Colorado varied seasonally. In the early spring, before plants became green, they primarily browsed on shrubs such as sagebrush (*Artemisia* spp.) and saltbush (*Atriplex* spp.). As spring progressed, green fleshy forbs, especially dandelion (*Taraxacum officinale*) and various species of the goosefoot family (Chenopodiaceae), became the major source of food. In summer (late June), seed heads developed by grasses, particularly western wheatgrass, and sedges constituted the bulk of their diet. During late September and early October, they most frequently ate the matured flowers

of rabbit brush. Consumption of roots was not observed, and only rarely were animals seen drinking water, suggesting that they primarily acquire their water from ingested foods.

Analysis of stomach ($n = 49$) contents from white-tailed prairie dogs inhabiting the Laramie Plains of Wyoming showed that animals fed almost exclusively on green plant material and seeds (Clark 1973). Arthropods, including adult insects and larvae, were seldom consumed. At the same site, direct observations of white-tailed prairie dogs showed that they mainly consumed graminoids (i.e., western wheatgrass, needle-and-thread, blue grama) and pricklypear cacti. Clark (1973) suggested that white-tailed prairie dog diet appeared to reflect plant availability rather than selection.

Breeding biology

Female white-tailed prairie dogs become sexually active at one year of age while males generally defer copulation until they are 2 years old (Hoogland 2003). Copulation occurs between late March and early April (Bakko and Brown 1967) and is preceded by a series of diagnostic behaviors including frequent sniffing of the estrous female's vulva and a distinctive mating call by breeding males, self-licking of the genitals by both sexes, and late final submergence at sunset by estrous females (Hoogland 2003). Vigorous male-directed female aggression has been also reported as a courtship behavior (Erpino 1968). Because approximately 75 percent of all copulations occur in underground burrows (Hoogland 2003), very little is known about copulation and the behavior immediately preceding it.

Gestation lasts about 30 days, with parturition occurring underground in late April or early May. The mean number of embryos per litter, estimated from counts of uterine scars, is 5.6 ± 0.7 (maximum = 10; Bakko and Brown 1967). White-tailed prairie dogs produce a single litter per year. Neonates are blind and hairless. Juveniles appear above ground in mid-June at an age of five to seven weeks old and approach adult size by late October.

Demography

Life history characteristics

White-tailed prairie dogs are short-lived rodents with high reproductive potential. Average litter size ranges from five to six pups per female per year

(Tileston 1962, Bakko and Brown 1967). However, high mortality rates for juveniles between parturition and first emergence from hibernation appear to offset this high reproductive rate. Forty percent of young have been reported to die before their first aboveground appearance in north-central Colorado (Tileston 1962). High mortality rates for juvenile white-tailed prairie dogs correspond with data reported for other prairie dog species (Hoogland 2001).

Female white-tailed prairie dogs reach sexual maturity at one year of age (Tileston and Lechleitner 1966, Clark 1973), but the proportion of breeding yearlings is usually lower than that of adult females (≥ 2 years old; Menkens and Anderson 1989). At four colonies near Laramie and Meeteetse, Wyoming, the average percent of yearling and adult female white-tailed prairie dogs in breeding condition ranged from 13 to 87 percent and 30 to 100 percent, respectively (Menkens and Anderson 1989). Reproductive success, as measured by the proportion of adult females breeding, also exhibited significant interannual variation. In Wyoming, the proportion of adult females observed breeding during a three-year period varied from 92 percent to 30 percent to 100 percent (Menkens and Anderson 1989). It is unclear what factors influence reproductive activity and success in the white-tailed prairie dog.

Little information is available on adult prairie dog longevity. Prairie dogs have been documented to live up to eight years (Foster and Hygnstrom 1990), but four years is probably an old age for white-tailed prairie dogs in the wild. Age structure in white-tailed prairie dog populations changes seasonally. Colonies consist only of adults in May, but juveniles can comprise up to 77 percent of the total individuals within a colony from June to the following May (Clark 1973).

Juvenile sex ratios typically do not depart from 1:1 (Menkens and Anderson 1989, Orabona-Cerovski 1991). Conversely, adult sex ratios usually, but not always, favor a higher number of females. At two different colonies in Wyoming, sex ratios (M:F) were 0.45:1 (Menkens and Anderson 1989) and 0.57:1 (Orabona-Cerovski 1991). In contrast, Clark (1969) found that the sex composition for 121 prairie dogs near Laramie, Wyoming was relatively even (1:0.9). The skew observed in some populations of white-tailed prairie dogs may reflect male-biased dispersal of juveniles from their natal areas (Tileston and Lechleitner 1966, Clark 1973) or differential juvenile survival between sexes (Menkens and Anderson 1989).

In six different colonies near Laramie and Meeteetse, Wyoming, survival rates were slightly higher for adult (individuals ≥ 1 year old) than juvenile white-tailed prairie dogs. Similarly, survival rates tended to be higher for females than for males, regardless of age, but this difference was not statistically significant (Menkens and Anderson 1989). Survival rates of white-tailed prairie dogs also often exhibit considerable spatial and temporal variability. At three colonies near Laramie, survival rates of juvenile and adult cohorts varied from 9 percent (± 3 percent) to 50 percent (± 42 percent), and from 22 percent (± 14 percent) to 70 percent (± 27 percent) over a three-year period, respectively (Menkens and Anderson 1989). At three colonies near Meeteetse, survival rates of juvenile and adult cohorts varied from 7 percent (± 4 percent) to 44 percent (± 16 percent) and 9 percent (± 6 percent) to 23 percent (± 7 percent) over a two-year period, respectively (Menkens and Anderson 1989). The overall lower survival rates found at the Meeteetse colonies could have resulted from an outbreak of plague in the area (Forrest et al. 1988).

Density of adult white-tailed prairie dogs can be highly variable both between and within years. During the breeding season, average minimum population density was reported to be 3.5 individuals per ha (1.4 individuals per acre), but increased to 8.4 individuals per ha (3.4 individuals per acre) after the first appearance of juveniles above ground (Tileston and Lechleitner 1966). During three years of study at Shirley Basin, Wyoming, the mean population density ranged from 7.8 to 19.5 individuals per ha (3.1 to 7.7 individuals per acre), 8.0 to 28.8 individuals per ha (3.3 to 11.7 individuals per acre), and 0.1 to 23.0 individuals per ha (0.05 to 9.3 individuals per acre) in 1986, 1987, and 1988, respectively (Orabona-Cerovski 1991). Between consecutive years, the density of adult white-tailed prairie dogs dropped from 12.6 to 5.3 individuals per ha (5.1 to 2.2 individuals per acre) at one colony near Laramie, Wyoming (Menkens and Anderson 1989). Densities of white-tailed prairie dogs also vary between sites. Adult densities at six different colonies in Wyoming ranged from 0.8 to 12.6 individuals per ha (0.32 to 5.1 individuals per acre; Menkens and Anderson 1989).

Temporal-spatial differences in vegetation quality and quantity between sites might account for the fluctuations in population parameters reported for white-tailed prairie dogs (Menkens and Anderson 1989); however, empirical data supporting this speculation are lacking. Whatever the ultimate mechanism, drastic temporal and spatial variations in survival rates and

densities suggest that environmental heterogeneity greatly influences colonies of white-tailed prairie dogs (Menkens et al. 1988). As consequence, caution should be taken when making management decisions based on results between populations inhabiting different habitats, or similar habitats at different times.

To understand better how population demography and life history traits influence the population dynamics of the white-tailed prairie dog, we analyzed white-tailed prairie dog life history traits with an age-structured population model. This matrix-based analysis allows us to explore which vital rates (i.e., survival and birth rates of different age-classes) have a large impact on the population growth rate and population structure of white-tailed prairie dog colonies. Both our sensitivity analyses and stochastic population modeling revealed that juvenile survival was the most important population-level parameter influencing colony growth and viability. Thus, in order to maintain the viability of extant colonies or to promote the expansion of other colonies, managers should adopt policies to maintain high-rates of juvenile survival. In the **Appendix** to this assessment, we present a thorough description of methodological considerations and technical analysis for our matrix model.

Ecological influences on survival and reproduction

Little information is available on how different ecological factors influence the survival and reproduction of white-tailed prairie dogs. Winter severity appears to significantly affect prairie dog survival. A study in Wyoming reported that burrow mortality during winter accounted for 59 percent of losses in a white-tailed prairie dog population (Clark 1973). However, an index of winter severity was not reported, and other factors such as insufficient fat deposits, physiological malfunction, or disease were not measured and could have contributed to such mortalities. Similarly, drought probably reduces prairie dog survival and reproduction by decreasing the net primary productivity of plants, resulting in less food and energy available for prairie dogs to meet such necessary functions as lactation and hibernation. The amount of fat deposits before entering hibernation and reproduction also appears critical for white-tailed prairie dog survival; in fact, overwinter survivorship (Hoogland 2003) and reproductive output (Pauli 2005) for prairie dogs vary directly with body condition. Natural flooding of burrows can also negatively affect prairie dogs. For instance, Tileston and Lechleitner (1966) found that six marked prairie dogs inhabiting a burrow partially constructed under a ditch

drowned when the ditch was deepened and the burrow was subsequently flooded.

Differences in vegetation quality and quantity between sites and through time have been proposed as major factors driving the population dynamics of white-tailed prairie dogs (Menkens and Anderson 1989), but past research has failed in proving such relationships. Survival, percent of females breeding, and population density of white-tailed prairie dog populations in Wyoming were not correlated with spatial or temporal variations of several habitat attributes, including percent cover by grasses, forbs, shrubs, total vegetative cover, shrub density, shrub height, and topographic variability (Menkens 1987). Future research should evaluate whether other vegetation characteristics, such as nutritional value, along with changes in length of growing season could be responsible for the fluctuations observed in white-tailed prairie populations (Menkens and Anderson 1989).

Social pattern for spacing

The mean home range size for all age classes of white-tailed prairie dogs near Laramie, Wyoming ranged from 0.5 ± 0.1 to 1.9 ± 1.4 ha (1.29 ± 0.2 to 4.79 ± 3.4 acres; Clark 1973). Home ranges of juveniles were generally larger than those of adults were. Mean juvenile home range was 1.1 ha (2.8 acres) whereas mean adult home range was 0.9 ha (2.3 acres) (Clark 1969). For adult white-tailed prairie dogs, home range location and size tended to be constant between years. Juveniles, usually males, sometimes move to the periphery of the colony to establish their adult home range (Clark et al. 1971).

The social system of white-tailed prairie dogs is classified as a single-family female kin cluster, characterized by only one functional and transitory social unit that involves a lactating female and her dependent young (Clark et al. 1971, Michener 1983). These social units form moderately cohesive groups called clans that occupy a specific burrow system. However, territorial boundaries between clans are loose and, therefore, difficult to discern. Members of different clans can approach other burrow systems without being attacked, and clans forage in common feeding areas without displaying any kind of aggressive behavior (Tileston 1962). Juvenile females are philopatric, remaining in or next to their natal area, and ultimately inherit the site and resources from their mothers. Conversely, juvenile males disperse and establish their territories far from their natal areas (Michener 1983).

Spatial characteristics

Whether white-tailed prairie dog populations occur as metapopulations or exhibit source-sink population dynamics is unknown. Large populations, such as the colony complex in the Shirley Basin, Wyoming, might act as sources to small, peripheral populations. However, no study has yet investigated potential metapopulation or source-sink dynamics in the white-tailed prairie dog. Assuming that large populations are a source of displaced or dispersing individuals for smaller populations, reductions in source populations might have indirect, yet important consequences on smaller, seemingly independent populations. Further, extirpation or substantive reductions in the overall number of colonies may remove “stepping-stone” colonies, increase the distance between source and sink colonies and, therefore, reduce the probability of colony persistence.

While small, isolated colonies are generally more vulnerable to stochastic threats such as extreme weather events, shooting, or poisoning, they are more likely to avoid plague transmission and, therefore, less vulnerable to a plague-induced population collapse. Large colonies or dense complexes, on the other hand, are more resilient to environmental stochasticity and human threats, but appear to be more vulnerable to plague infection (Cully and Williams 2001).

Factors limiting population growth

Historically, mortalities from predation, hibernation, natural floods, and food shortages were probably the primary factors limiting the growth of white-tailed prairie dog colonies. However, anthropogenic factors (e.g., introduction of plague, habitat loss and degradation, and control campaigns) have largely supplanted natural regulating factors. We discuss these current threats to white-tailed prairie dogs in greater detail in the Conservation section of this assessment.

Community ecology

Prairie dogs are keystone species in North American grassland ecosystems (Miller et al. 1994), having large effects on community structure and function (Power et al. 1996). Prairie dog populations support predators, including the federally endangered black-footed ferret, which is an obligate prairie dog predator (Anderson et al. 1986). Prairie dog burrows also provide structural habitat for burrowing owls (*Athene*

cunicularia), prairie rattlesnakes (*Crotalus viridis*), and a variety of small mammals and herpetofauna (Miller et al. 1994). Through herbivory, prairie dogs alter vegetation and cycle nutrients (Holland and Detling 1990). Additionally, because of their strict coloniality, prairie dogs host a diverse assemblage of ecto- and endoparasites. Below we elaborate on the relationships of white-tailed prairie dogs with predators, competitors, parasites, and disease. We also developed a web of ecological relationships for white-tailed prairie dogs following Andrewartha and Birch (1984). The resulting envirogram (**Figure 3**) illustrates the proximal (centrum) and distal factors (web) thought to affect white-tailed prairie dog distribution and abundance.

Predators

Historically, black-footed ferrets were a primary predator of white-tailed prairie dogs, but the effects of ferret predation on prairie dog population dynamics are largely unknown (Campbell and Clark 1981). After the near extinction of the black-footed ferret because of prairie dog declines from eradication campaigns and plague outbreaks, the badger (*Taxidea taxus*) became the primary predator of white-tailed prairie dogs (Tileston and Lechleitner 1966, Campbell and Clark 1981), but only a few studies have quantified this predator-prey interaction. Campbell and Clark (1981) reported that badgers had reamed 27 percent (range = 10 to 62 percent) of the total burrows at white-tailed prairie dog colonies surveyed in Wyoming. Goodrich and Buskirk (1998) found that white-tailed prairie dogs occurred in 52 percent of stomach and fecal samples ($n = 44$) from badgers. In addition to badgers, aerial predators, including the golden eagle (*Aquila chrysaetos*) and the ferruginous hawk (*Buteo regalis*), regularly prey upon prairie dogs (Tileston and Lechleitner 1966, Campbell and Clark 1981). Numerous other mammalian and avian predators, such as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), long-tailed weasels (*Mustela frenata*), bobcats (*Lynx rufus*), and Swainson's hawks (*Buteo swainsoni*), have been observed at prairie dog colonies, but their impact on white-tailed prairie dog population processes is thought to be negligible (Campbell and Clark 1981).

Competitors

Cases of interspecific interference competition, including killing of potential competitors, have been reported between white-tailed prairie dogs and both Richardson's (*Spermophilus richardsonii*; Clark 1973) and Wyoming ground squirrels (*S. elegans*; Cooke

1990). Foraging areas and diets of these species often overlap, and white-tailed prairie dogs have been observed chasing ground squirrels feeding in their vicinity (Clark 1973, Cooke 1990). Three dead Wyoming ground squirrels, which had been bitten around the abdomen, were found within a few meters of active prairie dog burrows, presumably killed by the burrow occupant (Cooke 1990). The prairie dogs that chased Wyoming ground squirrels were lactating females and prehibernating juveniles (Cooke 1990). Agonistic interactions between prairie dogs and Richardson's ground squirrels occurred mainly during the joint prairie dog-Richardson's ground squirrel breeding-parturition season; otherwise, the species largely ignored each other (Clark 1973). Interference competition between prairie dogs and squirrels appears to be intensified during those seasons with high energetic needs (reproductive and prehibernating seasons) and is typically performed by age-sex groups (pregnant females and juveniles) with the highest energetic demands, those who would benefit the most from appropriating resources that otherwise would be consumed by ground squirrels.

Parasites

One theorized cost of coloniality is enhanced parasite transmission and infection among colony members (Hoogland 1979). Thus, presumably because of their strict coloniality, white-tailed prairie dogs harbor a diverse assemblage of ecto- and endoparasites. Seville and Williams (1989) recovered eight species of endoparasites from white-tailed prairie dogs: four species of protozoa (*Eimeria cynomys*, *E. larimerenisi*, *E. ludoviciani*, and *Sarcocystis* sp.); two cestodes (*Hymenolepis cielli* and *Taenia mustelae*); and two nematode species (*Physaloptera* spp. and *Capillaria* spp.). In contrast, Shults et al. (1990) found that white-tailed prairie dogs occurring sympatrically with Wyoming ground squirrels harbored three different species of protozoa from the genus *Eimeria* (*E. beecheyi*, *E. morainensis*, and *E. bilamellata*). In Wyoming, white-tailed prairie dogs harbored 11 species of fleas (Siphonaptera) from seven different genera (Anderson and Williams 1997). However, the authors suggested that infestation by six of those species were accidental, while parasitism by four flea species (*Neopsylla inipina*, *Oropsylla tuberculata*, *O. idahoensis*, and *O. labis*) appeared more exclusive to the *Cynomys* genus. In addition, at least four species of ticks and mites (Acarina) have been documented parasitizing white-tailed prairie dogs (Pizzimenti 1975). Composition and abundance of the most common ectoparasites of

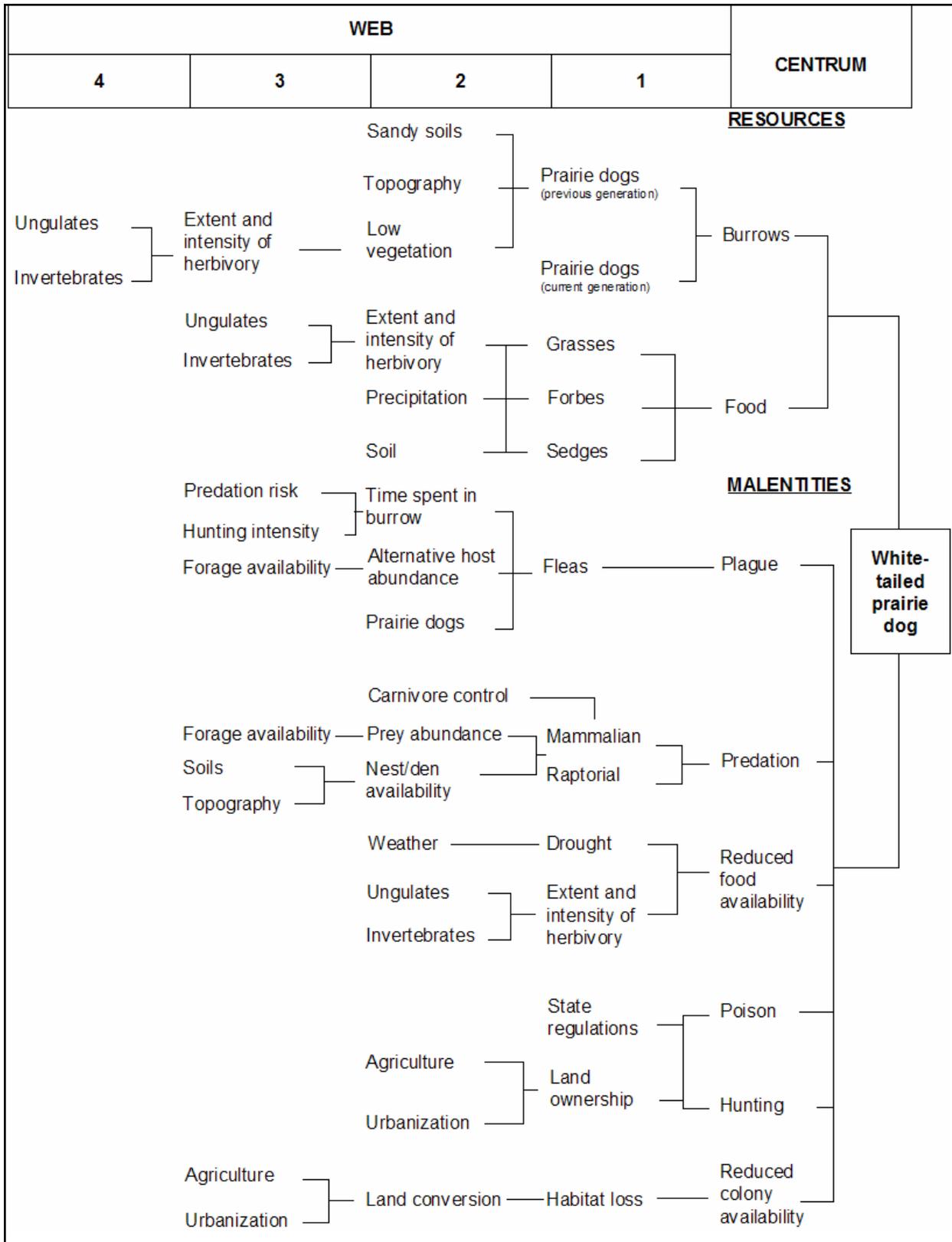


Figure 3. Envirogram representing the web of linkages between white-tailed prairie dogs and the ecosystem in which they occur.

prairie dogs appear to fluctuate seasonally (Anderson and Williams 1997) and following dramatic changes in prairie dog abundance (Pauli 2005).

Disease

By far, the most important disease for prairie dogs is now plague. Indeed, plague has been identified as one of the driving forces behind prairie dog population dynamics, persistence, and current distribution in the post-settlement era (Cully and Williams 2001). Plague is a flea-transmitted disease of rodents caused by the gram-negative coccobacillus bacterium, *Yersinia pestis*. Plague is exotic to the New World and appears to have arrived in North American Pacific shipping ports via ship-borne rats at the end of the 19th century (Biggins and Kosoy 2001). After its arrival, plague rapidly spread eastward across the United States and now occurs in all states west of the 100th meridian (Barnes 1993, Antolin et al. 2002), coinciding with the entire geographic distribution of the white-tailed prairie dog. Most sciurid species are vulnerable to plague, but prairie dogs appear to be particularly susceptible to infection, with epizootics causing up to 100 percent mortality in exposed colonies (Cully and Williams 2001). Although epizootics in prairie dog colonies have been documented for decades, the ultimate causes of plague outbreaks remain largely unknown.

Laboratory challenges have shown that all prairie dog species are extremely susceptible to small doses of *Yersinia pestis* (Cully and Williams 2001). White-tailed prairie dogs challenged with plague bacteria generally exhibited signs of illness within 3 to 4 days and were dead or moribund 2 to 3 days later. The mean lethal dose was 46 plague cells for white-tailed prairie dogs, but 25 percent of plague-challenged animals succumbed to infection after exposure to only two bacterial cells (Cully and Williams 2001). The first documentation of a plague-induced die-off among white-tailed prairie dogs was in 1936 from a colony in southeastern Wyoming (Eskey and Haas 1940). In a more comprehensive study, Clark (1977) found that within one year, an epizootic was capable of killing 85 percent of white-tailed prairie dogs in a colony from Wyoming. Years later, plague was diagnosed in a single juvenile from that same colony; however, no other individual exhibited sign of infection, and a population decline was not detected (Cully and Williams 2001). Menkens and Anderson (1991) documented a plague epizootic among three white-tailed prairie dog colonies within the Meeteetse, Wyoming complex. They found that infected colonies exhibited substantive declines in abundance and survival, but declines were transient,

with infected colonies rebounding within 1 and 2 years after exposure. Anderson and Williams (1997) determined that plague cycled through the Meeteetse complex each summer, with some colonies declining, some remaining unaffected, and others recovering from previous plague-induced declines. Although the effects of plague on specific colonies appear to vary, its overall impact on abundance and distribution is clearly negative; prairie dog abundance and colony size have been steadily declining on both Meeteetse and Shirley Basin complexes of Wyoming since the arrival of plague in the early 1980's (Cully and Williams 2001, Antolin et al. 2002).

Gradual population declines observed in white-tailed prairie dog colonies are contrary to the dramatic and punctuated population declines observed in other prairie dog species (Lechleitner et al. 1968, Rayor 1985, Barnes 1993). For example, plague can extirpate a colony of Gunnison's prairie dogs within a single year (Rayor 1985) and induce 95 percent mortality in a black-tailed prairie dog colony in a single summer (Pauli et al. 2006). Since white-tailed prairie dogs typically occur at lower densities and are less social than the other prairie dog species, plague transmission rates may be lower, resulting in slower, prolonged, and less punctuated die-offs from the epizootic (Gasper and Watson 2001).

Although the ultimate source of plague to prairie dogs remains unknown, it appears that plague is maintained in systems by plague-resistant species such as deer mice (*Peromyscus maniculatus*; Poland 1989), grasshopper mice (*Onychomys leucogaster*; Thomas et al. 1988), or kangaroo rats (*Dipodomys* spp.; Antolin et al. 2002), and it is episodically transmitted to prairie dogs via the exchange of infected fleas (Cully and Williams 2001, Antolin et al. 2002). Because of their abundance and ability to infest both white-tailed prairie dogs and plague-resilient small mammals, three flea species (*Opisocrostis tuberculata*, *Oropsylla idahoensis*, and *O. labis*) are likely the primary vectors of *Yersinia pestis* from small mammals to white-tailed prairie dogs (Anderson and Williams 1997). Carnivores, particularly canids, are also resistant to plague infection and therefore may function in the long-distance transmission and movement of plague to spatially-isolated prairie dog colonies. However, few studies have investigated the overlap of flea species between prairie dogs and local carnivores, and thus, the potential for transmission remains unclear. Finally, infected prairie dogs may also spread plague to neighboring colonies (Cully and Williams 2001, Pauli et al. 2006). After epizootics in the other prairie dog species, survivors appeared to

disperse long-distances to neighboring coterries (Pauli et al. 2006). If, following an outbreak, surviving white-tailed prairie dogs disperse to a neighboring, uninfected colony, then they may carry the disease or transplant infected fleas and, thereby, amplify the outbreak.

CONSERVATION

Threats

Historically, human eradication efforts have presented the greatest threat to the persistence of white-tailed prairie dog colony complexes. Although prairie dog control efforts have decreased in recent decades (Knowles 2002), they continue to occur on many private lands and some public lands. Both intentional and inadvertent anthropogenic forces significantly affect white-tailed prairie dogs, influencing their distribution, colony and complex size, and their very persistence. In addition, the arrival of an exotic disease (plague) has substantively altered white-tailed prairie dog population dynamics. We have identified the following four major factors that currently limit the abundance and distribution of the white-tailed prairie dog: (1) plague epizootics, (2) poisoning campaigns, (3) recreational shooting, and (4) habitat loss and degradation (**Table 3**). Although some persisting threats can be managed to minimize harm to white-tailed prairie dog populations, at this time plague is beyond effective management control, and its effects can only be monitored and potential management interventions sought through research (**Table 3**). Because of the ecologically pivotal role that white-tailed prairie dogs play in high-elevation grassland and grass-shrub systems, continuing threats to the viability and functioning of the species can have cascading and significant consequences for other grassland and grass-shrubland associates. Below we elaborate on the consequences of each identified threat.

Plague

Plague may now have the greatest persisting influence on white-tailed prairie dog population biology and colony persistence. Past authors have also implicated plague as one of the primary mechanisms behind the rangewide decline in abundance and distribution of all four prairie dog species in the United States (Antolin et al. 2002). Although plague did not enter the range of the white-tailed prairie dog until the 1930's and 1940's (Cully 1993), it now occurs throughout the entire distributional range of the species. Further, it has been suggested that plague has affected all white-tailed prairie dog populations to some extent (Knowles 2002). Outbreaks of plague result in extremely high mortality rates in white-tailed prairie dog colonies; indeed, past research has found up to an 85 to 100 percent mortality rate (Clark 1977, Cully and Williams 2001). Not surprisingly, then, plague affects the dynamics of white-tailed prairie dog colony complexes as well. Complexes repeatedly exposed to plague exhibit a cyclic pattern of plague-induced population declines followed by rapid repopulation and increased abundance (Antolin et al. 2002). However, it appears that these plague-induced boom-and-bust cycles ultimately result in successive population peaks that are progressively lower than the previous peak (Knowles 2002). Thus, plague appears to be causing a protracted decline in white-tailed prairie dog abundance.

In addition to reducing prairie dog abundance, plague has also influenced the spatial distribution and characteristics of prairie dog colonies in grassland landscapes. Since the arrival of plague, colony sizes have decreased and distances between colonies have increased as colonies have died out (Cully and Williams 2001, Lomolino and Smith 2001). Biogeographic theory contends that smaller populations have a higher

Table 3. Primary anthropogenic threats to the persistence of the white-tailed prairie dog.

Anthropogenic threat	Occurrence	Effects on prairie dog colony	Potential manageability	Research needs
Plague	Rangewide	Reduction or extirpation	Low	High
Poisoning	Rangewide	Reduction or extirpation	High	Low
Recreational shooting	Rangewide ^a	Unknown	High	High
<u>Habitat loss/degradation:</u>				
Agricultural land conversion	Localized	Fragmentation and isolation	Low	Low
Urban land conversion	Localized	Fragmentation and isolation	Low	Low
Gas, oil, mineral extraction	Localized ^b	Unknown	Moderate	High

^aExcluding 48 ha in Montana and the black-footed ferret reintroduction sites in eastern Uintah County, Utah

^b>55% of the species is distributed on BLM-managed lands, which have the potential for high levels of development; 77% of the species distribution in Wyoming, which has potential for future development

probability of extinction, and more isolated populations have a lower probability of recolonization following local population extinction (Lomolino and Smith 2001). Therefore, by reducing colony size and increasing distance between colonies, plague reduces the probability of colony persistence, lowers recolonization rates, and alters the viability of populations at a broad spatial scale.

Currently, we lack the ability to predict the occurrence of future plague outbreaks and have not conclusively identified what species are responsible for maintaining plague in the system and transmitting plague to prairie dogs. Further, we are incapable of effectively controlling an outbreak once it has begun. Researchers have investigated a variety of methods to prevent outbreaks in prairie dog colonies, including the use of insecticides to kill fleas (Fitzgerald 1978), insect growth regulators to control flea populations (Karhu 1999), and oral plague vaccines to immunize prairie dogs (Creekmore et al. 2002). However, both flea control measures and oral vaccines for prairie dogs are, at present, rudimentary, costly, and impractical to apply (Creekmore et al. 2002). These methods may prove useful for colonies where black-footed ferrets have been reintroduced, but for the majority of white-tailed prairie dog colonies, such actions are simply too expensive.

Research has found that some individual prairie dogs are capable of naturally surviving plague infection in the field. Seroconversion, or the development of antibodies to plague, has been documented in surviving black-tailed (Pauli et al. 2006) and Gunnison's prairie dogs (Cully et al. 1997). Further, several white-tailed prairie dogs in Utah have recently been documented surviving and developing antibodies to plague following an epizootic (Stroh in Knowles 2002). If antibody development among survivors is a heritable trait among prairie dogs, as it is among other rodent species (Biggins and Kosoy 2001), survivors may be able to convey plague resistance to their offspring giving rise to a cohort that is more resilient to plague infection. It remains to be seen whether surviving, plague-resistant prairie dogs are capable of conveying plague resistance to their progeny.

Poisoning

Because of perceived conflicts with livestock (Merriam 1902, Bell 1921), prairie dog eradication campaigns have occurred for over a century. Initially, poisoning programs were small and locally implemented, but beginning in the early 1900's, property owners and state and federal agencies collaborated to poison prairie

dogs on millions of hectares of western grasslands (Bell 1921, Cottam and Caroline 1965). Although most poisoning activities targeted black-tailed prairie dogs, all prairie dog species were subject to early eradication efforts. Historical data specific to poisoning white-tailed prairie dog colonies are unavailable; therefore, the following historical accounts of poisoning campaigns apply to all four species of prairie dogs in the United States. In Colorado, approximately 18 million ha (44 million acres) of prairie dog and ground squirrel habitat were treated with poison grain bait from 1912 to 1923 alone (Clark 1989 in Knowles 2002). In Wyoming, intensive eradication efforts began around 1915 and persisted into the early 1970's (Martley in Campbell and Clark 1981). In fact, a 1923 Wyoming State law required that prairie dogs be exterminated, and by the end of that year, more than 1.1 million ha (2.7 million acres) had been poisoned and declared 95 to 100 percent cleared of prairie dogs. Between 1915 and 1927, more than 290,000 kg (638,000 lbs.) of strychnine grain was distributed over 2 million ha (5 million acres). Poisoning efforts in Wyoming continued to increase in the early 1930's, but exact poisoning rates are unavailable. In the early 1940's, poisoning in Wyoming began to decline; throughout the decade, about 60,000 ha (148,300 acres) were poisoned annually. In the 1950's, poisoning rates declined to roughly 50,000 ha per year (123,555 acres per year), while between 1966 and 1972 an average of 27,140 ha (67,070 acres) was treated annually (Clark 1973). Poisoning efforts further declined in the early 1970's, coinciding with an Executive Order (Number 11643) in 1973 that banned the use of compound 1080 and strychnine. Since the mid-1970's, prairie dogs have made modest recoveries in some previously poisoned areas (Cully and Williams 2001).

Although direct control measures on prairie dogs have declined since the 1970's and some of the most potent poisons have been prohibited, poisoning remains one of the major factors regulating prairie dog populations (Van Pelt 1999). Indeed, federal- and state-sponsored prairie dog poisoning campaigns on private and public land are relatively common (Roemer and Forrest 1996), and legal poisons are 90 percent effective in controlling prairie dog populations (Roemer and Forrest 1996, Van Pelt 1999). Four vertebrate toxicants are registered for use in the United States; zinc phosphide is applied as bait above ground, whereas aluminum phosphide, gas cartridges, and acrolein are used as in-burrow fumigants. For the 2003 fiscal year, Wildlife Services of the U.S. Department of Agriculture reported using 28,108 fumigant tablets and 20 pounds of zinc phosphide oats for the control of white-tailed prairie dogs. Further, Wildlife Services distributed or

sold 127,600 fumigant tablets, 1,849 gas cartridges, and 270 pounds of zinc phosphide for white-tailed prairie dog poisoning (USDA Wildlife Services 2005). Because it appears that much prairie dog poisoning, particularly on private lands, may go unreported, it is unclear the degree and extent that white-tailed prairie dog poisoning still occurs (Patton personal communication 2005).

Recreational shooting

Although it appears unlikely that recreational shooting represents a rangewide threat to the white-tailed prairie dog (Knowles 2002, U.S. Fish and Wildlife Service 2004), few studies have investigated the impact of recreational shooting on prairie dog population biology, and no studies have quantified the effects of shooting on white-tailed prairie dog populations or their status rangewide. Further, little information exists concerning recreational shooting intensity of white-tailed prairie dogs on either private or public land.

Nonetheless, one recent study found that intense recreational shooting dramatically alters both individual- and population-level attributes of black-tailed prairie dogs (Pauli 2005). After colonies were experimentally exposed to recreational shooting, surviving prairie dogs altered their behavior (increasing vigilance and decreasing foraging), which precipitated decreases in their body condition. Changes in the attributes of survivors and a concomitant shooting-induced shift in the population structure reduced prairie dog reproduction; after shooting, pregnancy rates declined by 50 percent and overall reproductive output fell by 76 percent. Pauli (2005) concluded that, because of the prairie dog's strict coloniality, they appeared to be inherently susceptible to hunting-induced mortality and hunting-associated disturbances.

However, caution should be exercised in extrapolating these findings to predict specific effects of shooting on white-tailed prairie dogs, which exhibit different life history strategies. White-tailed prairie dogs occur at lower densities and in colonies with greater vegetative cover (Tileston and Lechleitner 1966). Therefore, recreational shooting intensity appears to be lower for white-tailed prairie dog colonies than black-tailed prairie dog colonies (Campbell and Clark 1981). Further, because white-tailed prairie dogs are less socially organized (Tileston and Lechleitner 1966), negative effects associated with recreational shooting may not be as great.

Recreational shooting of white-tailed prairie dogs can be popular on particular colonies. Clark (1973) estimated that recreational shooting killed 75 percent of a white-tailed prairie dog population at a study site in southeastern Wyoming. However, the presence of plague might have confounded this observed decline. In Wyoming, four of 25 white-tailed colonies showed signs of shooting while 16 of 21 black-tailed colonies had been shot, poisoned, or both (Campbell and Clark 1981). Until more information is collected, documenting recreational shooting intensity and the effects of shooting on white-tailed prairie dog biology, both the local and rangewide consequences of shooting will remain unclear.

Habitat loss

Agriculture

Habitat loss due to agriculture has contributed to the dramatic decline of prairie dogs during the last century (Fagerstone and Biggins 1986). While poisoning efforts associated with agriculture eliminated many historic colonies, conversion of native grassland to agricultural use both directly eliminated colonies and reduced the likelihood of prairie dogs recolonizing such areas. However, the impacts of agricultural land conversion have been more widespread for the black-tailed prairie dog than the white-tailed prairie dog (Knowles 2002) because the latter typically inhabit more arid and often more rugged landscapes at higher elevations, which are less suitable for dryland agriculture (Tileston and Lechleitner 1966). Thus, when agricultural land conversions occurred in the 20th century, they were primarily restricted to areas where irrigation water was available (Knowles 2002).

The level of habitat loss due to agricultural development is unclear, particularly when some white-tailed prairie dog colonies have persisted for years in agricultural landscapes (Tileston and Lechleitner 1966). White-tailed prairie dog colony extirpation and fragmentation from agriculture have been reported in Montana (Fagerstone and Biggins 1986, Knowles 2002) and around the Bighorn Basin of Wyoming (Knowles 2002). Nonetheless, according to Seglund et al. (2004), active agricultural land only overlaps with less than 4.0 percent of the species' historic range. Therefore, although land conversion was historically important in shaping the distribution of white-tailed prairie dogs, it appears that present colony loss from agricultural conversion is locally important but represents only a minor rangewide threat to the species.

Oil, gas, and mineral development

Recently, concern has increased over the effects of mining and drilling on the white-tailed prairie dog biology and distribution (Center for Native Ecosystems et al. 2002, Seglund et al. 2004). It has been suggested that the construction of well pads, roads, and other equipment and facilities for oil, gas, and mineral exploration and extraction destroys and fragments white-tailed prairie dog habitat (Center for Native Ecosystems et al. 2002, Seglund et al. 2004). These developments may also degrade prairie dog habitat by compacting soil, altering surface water drainage, destroying vegetation, and providing additional perches for predatory raptors (U.S. Fish and Wildlife Service 1990). In addition, oil, gas, and mineral development indirectly causes greater road density, which may incidentally increase colony access by recreational shooters. Some contend that seismic exploration (vibroseis) may also affect prairie dogs by collapsing tunnel systems, causing auditory impairment, and disrupting their social structure (Seglund et al. 2004). However, no data have been collected on the effects of gas, oil, and mineral development on any prairie dog species, and at present, it is impossible to tell whether extractive industries significantly affect white-tailed prairie dogs. Because 77 percent of the white-tailed prairie dog range in Wyoming occurs on land that has the potential for oil and gas development and 55 percent of the entire range of the white-tailed prairie dog is on Bureau of Land Management land (Seglund et al. 2004), the effects of extractive industries on the species' population biology and distribution could be substantial.

Urbanization

Human population densities have increased in some areas within the white-tailed prairie dog's range. Urbanization associated with population growth has been particularly evident in certain areas of Colorado (especially the Grand Junction, Montrose, and Delta areas) and in the Uintah Basin of Utah (U.S. Fish and Wildlife Service 2004). Conversion of native grasslands and agricultural lands to urban development is particularly concerning because it permanently eliminates potentially suitable habitat. However, it is estimated that urbanization affects less than 1.0 percent of the white-tailed prairie dog's range (Seglund et al. 2004). Therefore, we believe that loss of habitat to urbanization is only significant at the local-scale and does not impose a rangewide threat to the white-tailed prairie dog in the near future.

Conservation Status of White-tailed Prairie Dogs in Region 2

Abundance and distribution trends

Insufficient data are available to critically evaluate the population trend of white-tailed prairie dogs in Region 2. Although an overall range decline has been well-documented for this species, recent efforts to determine current distribution and abundance trends have been limited by small sample sizes, non-random selection of study sites, and brief temporal scales (see Population Trend section). Different protocols and various mapping efforts have further complicated comparisons of population trends at mapped sites. The overall lack of scientifically defensible distribution and population trend data for the white-tailed prairie dog is particularly concerning because of the importance of this species to other native organisms. Indeed, the white-tailed prairie dog is recognized as a pivotal member of grassland systems, benefiting other native flora and fauna (Miller et al. 1994).

From the data that are available, however, decreases in colony size at several sites give some reason for concern that the long-term viability of this species could be threatened. Declines within the past two decades have been documented in 85 percent of the mapped white-tailed prairie dog colonies, including on the two largest remaining white-tailed prairie dog colony complexes in Shirley Basin, Wyoming and in northwestern Colorado/northeastern Utah (Knowles 2002, Seglund et al. 2004). Although the historic cause of the white-tailed prairie dog's range collapse appears to be a combination of poisoning campaigns and habitat conversion, plague has been implicated in many of the recent colony declines and appears to be the most influential factor currently limiting white-tailed prairie dog distribution and population growth (Cully and Williams 2001). Past authors have even suggested that plague has detrimentally impacted all remaining white-tailed prairie dog populations (Knowles 2002).

The most recent estimates of white-tailed prairie dog distribution are 185,988 ha (459,576 acres) in Wyoming, 77,648 ha (191,866 acres) in Colorado, 57,463 ha (141,808 acres) in Utah, and 48 ha (119 acres) in Montana (Seglund et al. 2004). Based on this information, there appears to be roughly 340,000 ha (840,000 acres) of white-tailed prairie dog colonies in North America. Two apparent conclusions emerge from these data: (1) similar to other prairie dog species, the white-tailed prairie dog has experienced a dramatic

range contraction (a decline >98 percent) since the 19th century and; (2) even after a dramatic range contraction, it appears that white-tailed prairie dogs still occupy an extensive amount of habitat and are probably not in danger of extinction in the foreseeable future.

Nonetheless, it appears that even a partial recovery by this species will depend on management actions aimed at ameliorating the effects of plague, reducing poisoning programs, and preventing additional loss and deterioration of habitat. White-tailed prairie dogs are a resilient species that, given protection from aforementioned threats, can persist and thrive under a wide range of environmental conditions (Menkens 1987). Past work has shown that natural habitat variability had little effect on population-level attributes such as prairie dog density, reproductive output, and adult survival (Menkens 1987). It appears, then, that with the removal or decrease in anthropogenic threats and plague-induced declines, prairie dog populations have the innate capacity to expand in a relatively heterogeneous environment.

Habitat trends

In general, habitat loss and degradation from agricultural and urban land conversion does not appear to constrain the distribution of the white-tailed prairie dog at a large scale. Currently, agricultural and urban land development affects less than 5 percent of the range of this species. However, the recent growth of extractive industries, such as oil, gas, and mineral exploration, poses a potential threat to prairie dog habitat and viability. It has been suggested that continued oil, gas, and mineral development could substantively fragment and degrade prairie dog habitat (Center for Native Ecosystems et al. 2002, Seglund et al. 2004). This is of particular concern for the white-tailed prairie dog because greater than 50 percent of the species' range has the potential for future gas, oil, or mineral development. Furthermore, fragmentation or habitat degradation could jeopardize the viability of colonies that have been previously affected by plague. Additional fragmentation could decrease recolonization rates, further isolate colonies, and therefore, reduce each colony's probability of persistence. Unfortunately, no data have been collected on the effects of gas, oil, and mineral development on prairie dog biology; future research should be geared towards characterizing and quantifying these effects.

Large portions of Wyoming and northern Colorado have experienced several years of drought, beginning sporadically in the late 1990's and

increasing in extent and severity (National Oceanic and Atmospheric Administration 2005). During the summers of 2000 through 2004, nearly every county in Wyoming experienced severe to extreme drought conditions. Such prolonged and severe drought conditions likely deleteriously affect the quantity and quality of forage for white-tailed prairie dogs, but monitoring efforts prior to and during this time are insufficient to corroborate this supposition. Recovery of quality white-tailed prairie dog habitat will likely be slow, even if precipitation increases and ameliorates drought conditions. Thus, drought could have long-lasting effects on white-tailed prairie dog biology, and certain management practices may exacerbate these effects. Research and monitoring are needed to quantify and understand the effects of drought on white-tailed prairie dog biology and distribution.

Management of White-tailed Prairie Dogs in Region 2

Implications and potential conservation elements

Although white-tailed prairie dogs only occur on a small portion of NFS lands in Region 2 (253 ha [624 acres]), their status and fate on those lands may have important implications for the rangewide viability of the species. Many white-tailed prairie dog populations currently occur on private lands and are subjected to unknown levels of poisoning and recreational shooting. In addition, plague outbreaks episodically and unpredictably induce substantive population declines or extirpate colonies across the species' range. Therefore, maintaining relatively protected, refugia populations on public lands may prove crucial to ensuring the long-term persistence of the species. Protected, refugia populations on public lands could serve as source populations that could augment declining or recently extirpated colonies with dispersing individuals. Establishing a system of such source populations that sustain surrounding colonies can only be successful, however, if viable growing colonies are distributed throughout the species' range. Although the current distribution of white-tailed prairie dogs on NFS lands is limited, existing colonies on lands administered by the Grand Mesa-Uncompahgre-Gunnison, Medicine Bow-Routt, and Arapaho-Roosevelt national forests could be encouraged to expand through habitat manipulation and the cessation of poisoning and recreational shooting.

Methods for translocating prairie dogs have been developed (Truett et al. 2001) and can be used to reintroduce white-tailed prairie dogs at locations

within national forests that were historically occupied or where suitable habitat exists. White-tailed prairie dogs likely exist or have existed on the White River National Forest, and it appears that large amounts of NFS lands within Region 2 are suitable for occupation by this species. Newly developed habitat models (Seglund et al. 2004) estimate that approximately 90,181 ha (222,846 acres) of potential white-tailed prairie dog habitat occur on USFS lands within Region 2. Thus, expansion of white-tailed prairie dog colonies on NFS lands within Region 2 alone has the potential to increase the overall distribution of the white-tailed prairie dog by as much as 27 percent. Through prairie dog reintroductions and proper habitat management, the USFS could considerably augment the rangewide distribution and abundance of the white-tailed prairie dog and, therefore, increase the long-term viability of the species.

Tools and practices

Mapping, surveying and monitoring

To document the distribution of white-tailed prairie dogs and to assess their population trends in Region 2, a variety of techniques will need to be employed, and interdisciplinary specialists (e.g., field ecologists, GIS specialists, plant ecologists) should be consulted. Although complex, such an assessment is feasible for the USFS, which is equipped with advanced GIS mapping and analysis tools.

Researchers have employed several, different techniques to map prairie dog colonies, including organized efforts of biologists to map occupied areas from personal observation (Knowles 2002), ground and aerial surveys (Forrest et al. 1988, Sidle et al. 2001), and high-resolution satellite or aerial images (Sidle et al. 2002). Using the personal knowledge of biologists to approximate the distribution of prairie dogs is economical and efficient, but it lacks rigorous quantification and, thus, prevents scientifically defensible data, and inherently underestimates the areas occupied. This obstacle is particularly significant for documenting white-tailed prairie dogs, which often occur in colonies that are difficult to detect and whose colony boundaries can be difficult to delineate. Further, having estimates from anecdotal observations could incorporate a bias in the data that differentially documents large, readily identifiable colonies compared to small, relatively inconspicuous colonies. Therefore, we recommend that observations be used only to generate preliminary data that will direct future, more

rigorous mapping efforts to regions that are believed to contain white-tailed prairie dog colonies.

Past research has used both aerial (Sidle et al. 2001) and ground (Forrest et al. 1988) surveys to more precisely quantify prairie dog presence and distribution. For ground-mapping efforts, surveyors walk through prairie dog colonies and map the colony. Although ground surveying can generate highly accurate, quantitative data, such efforts can be expensive and, particularly for white-tailed prairie dogs, may exhibit high variability based on the skill of surveyors. Each observer is likely to map colony boundaries differently due to the lack of well-defined boundaries at white-tailed prairie dog colonies (Seglund personal communication 2005). Therefore, prior to the initiation of surveys, clear definitions should be established to delineate colony boundaries. For areas that contain small acreages of colonies, ground surveys may be economically feasible and will provide the most precise data of white-tailed prairie dog distribution.

For areas with numerous or expansive prairie dog colonies, high quality aerial photographs, aerial surveys, or satellite images can be used to estimate prairie dog distribution. Although interpretation of aerial photographs and satellite images is generally less costly and time consuming than ground surveys are, colony delineation via aerial surveys has proven more difficult for white-tailed prairie dogs than black-tailed prairie dogs due to their more dispersed colony structure, lower densities, and use of shrubland habitats (Keinath 2004). Further, analyses using aerial surveys or satellite imagery may artificially inflate estimates of white-tailed prairie dog colony areal extent. Prairie dog burrows remain detectable in images for up to 20 years after they have been vacated. For this and other reasons, there has been recent debate over the validity of estimating even black-tailed prairie dog colony distribution with aerial line intercept over large areas (Miller et al. 2005, White et al. 2005a, White et al. 2005b). Because quantifying the distribution of colonies from images or aerial surveys can be difficult, GIS specialists and aerial photograph interpreters should be consulted prior to analyzing images, and population estimates derived from these methods should be validated with ground surveys.

Once the distribution of prairie dogs has been documented, managers should initiate monitoring programs to document changes in the abundance and distribution of prairie dogs on identified colonies. Various techniques have been employed to monitor

white-tailed prairie dog population trends as well, including counts of plugged and reopened burrows (Tietjen and Matschke 1982), counts of active and inactive burrows along belt transects (Biggins et al. 1993), mark-recapture techniques (Menkens and Anderson 1989), and visual counts (Fagerstone and Biggins 1986).

The technique of plugging burrows and counting the number reopened by prairie dogs is time-consuming and labor intensive, precluding its effectiveness for evaluating population sizes for more than a few small colonies or over large areas (Menkens et al. 1990). Further, this method only provides a rough index to prairie dog abundance.

Biggins et al. (1993) suggested that counting the number of burrows within a colony can be an economical and rapid method to index prairie dog abundance. During a four-year study, Menkens et al. (1988) noted that white-tailed prairie dog densities significantly changed on all but one study colony ($n = 6$), while burrow densities only changed on two of the colonies. They concluded that total burrow counts merely reflect prairie dog activity rather than prairie dog densities. However, Biggins et al. (1993) found that counts of only *active* burrows exhibited a strong correlation ($r^2 = 0.90$) with white-tailed densities and suggested that counting active burrows could be used as a monitoring tool. Unfortunately, differentiating active from inactive burrows can be difficult and requires training. Furthermore, prior to using active burrows as a surrogate of abundance, managers would have to approximate prairie dog abundance through mark-recapture or visual counts and construct a model that predicts abundance from burrow counts.

Mark-recapture techniques have been developed to estimate precisely the density and abundance of prairie dogs, but trapping also requires a considerable amount of equipment, personnel, and time. In addition, rigorous analyses of mark-recapture data require personnel with analytical and computational background. It is therefore impractical to estimate animal density over large areas (Fagerstone and Biggins 1986) or without sufficient personnel and funding. Nonetheless, this technique may be a useful method to determine the population size of smaller colonies and to collect attributes of colony members (e.g., body weight, reproductive status, age) as well.

Visual counts appear to be the most efficient and effective method for obtaining an index of white-tailed prairie dog density (Fagerstone and Biggins 1986,

Menkens et al. 1990). This is an effective method for estimating density due to the prairie dogs large size, diurnal activity patterns, and tendency to live in colonies. Studies that have compared population density estimates from mark-recapture data with visual observations have reported high correlations (Fagerstone and Biggins 1986, Menkens et al. 1990). Fagerstone and Biggins (1986) and Menkens et al. (1990) provide the assumptions and recommendations for doing visual surveys.

Species and habitat management

Unfortunately, the single most important determinant of prairie dog population dynamics, plague, is currently beyond management control. We recommend, therefore, that the USFS establish monitoring programs to document the pattern of plague epizootics on agency land. Colonies can be monitored and abundances determined effectively with seasonal visual counts (Fagerstone and Biggins 1986, Menkens et al. 1990). If prairie dog abundances exhibit a significant decrease between seasons, more intensive monitoring, using live-trapping, should be initiated. Following past methodologies (e.g., Cully et al. 1997, Pauli et al. 2006), managers can institute trapping and observations to determine whether or not an epizootic occurred. Live-trapped animals can be bled and samples analyzed for antibodies to plague. Extreme precaution should be used while live-capturing prairie dogs potentially infected with plague; the Center for Disease Control should be contacted before instituting any live-capturing procedures. If any of the surviving prairie dogs have developed plague antibodies, managers should protect those surviving individuals by terminating poisoning operations and closing colonies to recreational shooting. Plague-resilient individuals could be extraordinarily important to white-tailed prairie dog conservation; if plague antibody development is a heritable trait among prairie dogs, as it is in other rodent species (Biggins and Kosoy 2001), survivors could convey plague resistance to their offspring, giving rise to a population that is more resilient to outbreaks in the future. Thus, through rigorous monitoring, managers can document the pattern of plague on their land and protect surviving individuals on colonies following an epizootic.

Because plague cannot be controlled and because white-tailed prairie dogs currently occupy less than 0.1 percent of the potential habitat on NFS lands in Region 2, we recommend that all remaining colonies on national forests be managed to promote colony persistence and population growth. To advance viable

white-tailed prairie dog populations on national forests, we recommend that, first, poisoning be terminated and, secondly, that recreational shooting pressure is monitored to document the effects of shooting on those populations. If it appears that recreational shooting is deleteriously affecting white-tailed prairie dog colonies, those colonies may need to be closed to recreational shooters. Fortunately, the majority of colonies on NFS lands occur well within the boundary of public landownership, and potential conflict surrounding poisoning and shooting closures with private landowners should be minimal.

Habitat should also be managed to encourage white-tailed prairie dog persistence and growth on NFS land. Moderate levels of grazing, by livestock or free-ranging ungulates, benefit prairie dog populations by reducing vegetative height and increasing forage quality (Lauenroth et al. 1994). However, overgrazing negatively affects prairie dog populations by excessively removing vegetation and eliminating food resources. Similarly, controlled burns can be employed to reduce shrub abundance and height, and to improve forage quality (Hobbs and Schimel 1984, Cook et al. 1994). Previous work has found that low shrub height and density promote colony expansion (Osborn 1942) and increase the probability of success for prairie dog reintroductions (Player and Urness 1982).

For white-tailed prairie dogs to reoccupy much of the suitable habitat on NFS lands successfully, reintroductions may be necessary. If suitable habitat exists, managers may consider reintroducing prairie dogs at previously occupied sites or in suitable habitat where historic occupancy patterns are unknown. Numerous individuals have relocated prairie dogs successfully (e.g., Player and Urness 1982, Knowles and Waggenman 1998), and Truett et al. (2001) provide a rigorous review of methods to help ensure successful reintroductions.

Information Needs

Clearly, research is needed to better understand the distribution, abundance, and status of the white-tailed prairie dog across its range. In addition, future research needs to elucidate the effects of anthropogenic perturbations on the distribution, abundance, and population processes of this species. Therefore, we recommend that, first, annual mapping efforts are initialized to critically document the distribution of white-tailed prairie dogs and to better understand rangewide trends in prairie dog abundance and colony

size. Second, research needs to quantify the effects of anthropogenic disturbances on white-tailed prairie dogs; in particular, we need to better understand the consequences of plague, recreational shooting, and the extractive industries on prairie dog population viability. Finally, we need a better understanding of the white-tailed prairie dog population processes under a range of situations (i.e., highly disturbed to virtually undisturbed), particularly concerning survival, reproduction, and dispersal. Only after we accrue more information can we better manage and conserve this ecologically pivotal species. We outline the range of information needs for the white-tailed prairie dog below.

- 1) Develop and implement rigorous surveys to estimate the distribution and abundance of white-tailed prairie dogs in North America. In particular, document the current and historic distributions of this species on public lands.
- 2) Understand fundamental biological characteristics of the white-tailed prairie dog across its range. Specifically, research should attempt to:
 - a. Quantify life history characteristics, including survival, reproduction, and population growth rates.
 - b. Determine primary sources of prairie dog mortality in a range of habitats and the effects of different mortality sources on the demographic structure of colonies.
 - c. Measure variation in short- and long-distance dispersal rates of adult and juvenile white-tailed prairie dogs on relatively unperturbed colonies and those on colonies that have been substantively impacted by plague, poisoning, recreational shooting, or habitat fragmentation.
 - d. Determine habitat characteristics that alter prairie dog population dynamics and how habitat quality influences the aforementioned life history traits.
- 3) Determine how grazing intensity and timing alter habitat quality for the white-tailed prairie dog.
- 4) Quantify the abiotic habitat features (e.g., soil characteristics, topography etc.) that white-tailed prairie dogs select for when establishing or expanding a colony.

- 5) Identify habitat features that are most important for successful white-tailed prairie dog reintroduction.
- 6) Better understand the dynamics of plague in prairie dog colonies. Specifically, research should attempt to:
 - a. Quantify mortality rates induced by plague and how colony shape and size change following an epizootic.
 - b. Document the rate and extent of colony recovery after an epizootic.
 - c. Determine the relative importance of survivors and immigrants to colony recovery.
 - d. Identify the vectors of plague to white-tailed prairie dogs.
 - e. Continue to develop methods to minimize the effects of plague outbreaks on prairie dogs (e.g., controlling populations of plague vectors, vaccinating prairie dogs).
 - f. Understand the mechanisms behind plague antibody development in prairie dogs and determine whether plague resistance is a heritable trait among prairie dogs that can be conveyed to offspring of the survivors.
- 7) Ascertain how much poisoning occurs on public and private lands and determine how quickly and to what extent colonies recover from previous applications of poison.
- 8) Better understand the consequences of recreational shooting on white-tailed prairie dogs. Specifically, research should attempt to:
 - a. Estimate recreational shooting pressure on public lands
 - b. Determine rates of shooting across the range of the species.
 - c. Quantify the effects of recreational shooting on white-tailed prairie dog population dynamics. In particular, learn how shooting alters reproduction, survival, and prairie dog abundance.
- 9) Evaluate the effects of oil, gas, and mineral development on white-tailed prairie dog biology. Specifically, research should attempt to:
 - a. Quantify the degree that development (e.g., construction of well pads, roads, and other equipment and facilities) destroys and fragments white-tailed prairie dog habitat.
 - b. Evaluate how extractive industries directly affect prairie dog habitat (e.g., degree of soil compaction, change in surface water drainage, change in vegetative cover).
 - c. Determine whether seismic exploration collapses prairie dog tunnels, causes auditory impairment, or disrupts prairie dog social structure.
- 10) Begin to explore the relationship of colonies across landscapes. Specifically, research should attempt to:
 - a. Determine how colony viability is related to surrounding colonies.
 - b. Identify the importance of dispersers in colony viability and recolonization.
 - c. Investigate whether anthropogenic forces significantly alter these interrelationships.

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APPENDIX

Stage-based Matrix Model

Life cycle graph and model development

The life history data compiled from numerous studies (Tileston 1962, Menkens 1987, Orabona-Cerovski 1991, Bakko and Brown 1967, Menkens and Anderson 1989) provided the basis for a life cycle graph (**Figure A1**) and a matrix population analysis with a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001) for the white-tailed prairie dog. We used data selected from studies that was obtained during enzootic periods of plague activity. The model has four kinds of input terms: P_{21} describing first-year survival rates, P_{32} describing second-year survival rates, P_{33} describing survival after the third year, and m describing number of pups per female (**Table A1**). **Figure A2a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure A2b** gives the corresponding numeric values. The

model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female. λ , the population growth rate, is based on the estimated vital rates used for the matrix. Initially, the model was run using numeric values obtained from studies of white-tailed prairie dogs cited above. The results from running the model from these data yielded a suspiciously low λ , equal to 0.800. A λ of 0.800 describes a population in a precipitous decline towards extinction. We felt that this was an inaccurate depiction of most white-tailed prairie dog populations and altered the survival rate of all age classes by 0.097. These alterations yielded a lambda of 1.002, representing a very nearly stationary population and presumably, a more realistic version of the average dynamics of prairie dog populations. Although this suggests an essentially stationary population, the value is subject to the many assumptions used to derive the transitions and should clearly not be interpreted as an indication of the general well-being and stability of the population. Other parts of the analysis provide a better guide for assessment.

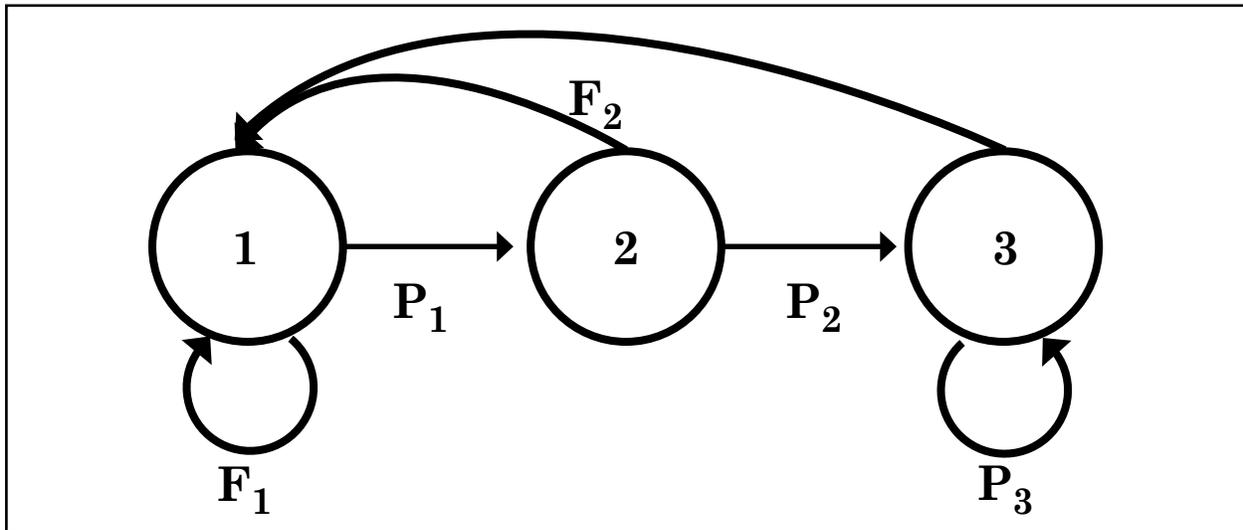


Figure A1. Life cycle graph for white-tailed prairie dogs. The first two stages are age-specific (first- and second-year individuals). The third stage represents a mixed stage of third-year and older individuals. Capital letters denote the survival rate (P_n) and fertility (F_n) of each stage class.

Table A1. Parameter values for the component terms (m_1 , m_2 , m_3 , P_{21} , and P_{32}) that make up the vital rates in the projection matrix for white-tailed prairie dogs.

Parameter	Numeric value	Interpretation
m_1	0.705	Number of female offspring produced by a female in Stage 1
$m_{2,3}$	1.50	Number of female offspring produced by a female in Stages 2 and 3
P_{21}	0.447	Survival through first year
P_{32}	0.507	Survival through second year

(A)

	1	2	3
1	P_1m	P_2m	P_3m
2	P_{21}		
3		P_{23}	P_{33}

(B)

	1	2	3
1	0.315	0.7605	0.7605
2	0.447		
3		0.507	0.507

Figure A2. The input matrix of vital rates, **A** (with cells a_{ij}) corresponding to the white-tailed prairie dog life cycle graph of **Figure A1**. (A) Symbolic values; (B) Numeric values.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on population growth rate (λ) of an absolute change in the vital rates (a_{ij} , the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, **A** [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 118-119). First, sensitivities show “how important” a given vital rate is to population growth rate (λ) or fitness. For example, one can use sensitivities to assess the relative importance of survival (P_i) and fertility transitions (F_i , which represent a compound of survival rates of the mothers and the number of pups produced). Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth (λ) of endangered species or

the “weak links” in the life cycle of a pest. **Figure A3** shows the “possible sensitivities only” matrix for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the sensitivity of λ to moving from an older reproductive stage back to an earlier pre-reproductive stage).

For this model, the results show that the sensitivity of λ to changes in first-year survival (32% of total sensitivity) and first-year reproduction (21% of total) and adult survival (15% of total) are the salient features. The major conclusion from the sensitivity analysis is that survival (especially of juveniles) is the key to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, a change of 0.5 in survival may be a big alteration (e.g. a change from a survival rate of 90% to 40%). On the other hand, a change of 0.5 in fertility may be a very small proportional alteration (e.g. a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to proportional changes in the

	1	2	3
1	0.419	0.187	0.191
2	0.644		
3		0.287	0.294

Figure A3. Sensitivity matrix, **S** (with cells s_{ij}) for the white-tailed prairie dog. The three transitions to which population growth rate is most sensitive are in bold. Only those sensitivities for which the corresponding a_{ij} is non-zero are shown.

vital rates (a_{ij}) and thus largely avoid the problem of differences in units of measurement. The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of fertility (F_i) and survival (P_i) for a given species.

Elasticities for white-tailed prairie dog are shown in **Figure A4**. The λ of white-tailed prairie dogs is most elastic to changes in the survival of first-year individuals (Stages 1 to 2, 29% of total), followed by “adult” survival (P_{33} , 15% of total elasticity). The transitions with the highest sensitivities and elasticities correspond fairly closely in relative magnitude. The survival rates, especially of juveniles, are therefore the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

	1	2	3
1	0.132	0.142	0.145
2	0.287		
3		0.145	0.149

Figure A4. Elasticity matrix, E (with cells e_{ij}) for the white-tailed prairie dog. The two transitions to which population growth rate is most elastic are in bold. Note that the elasticities sum to one.

Other demographic parameters

The stable (st)age distribution (SSD, **Table A2**) describes the proportion of each Stage (or Age-class) in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For white-tailed prairie dogs at the time of the post-breeding annual census (just after the end of the breeding season), first-year individuals represent 52.5% of the population, second-year individuals represent 23.4% of the population and third stage individuals (three year-olds and over) represent 24.0% of the population. Because the matrix contains information on time required for transitions, one can calculate the mean and variance of ages for stages that are heterogeneous for age (Cochran and Ellner, 1993). The means and standard deviations of the ages of the stages are shown in **Table A2**. Reproductive values (**Table A3**) can be thought of as describing the “value”

Table A2. Stable (St)age Distribution (SSD) and means and variances of ages of the stages for the white-tailed prairie dog model.

Stage	Description	Proportion in stage	Mean age (\pm SD)
1	First-year	0.525	0 \pm 0
2	Second-year	0.234	1 \pm 0
3	Third-year and older	0.240	3.03 \pm 1.44

Table A3. Reproductive values for females. Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, right at the census, egg) age class. The reproductive value of the first age class is always 1.0.

Stage	Description	Reproductive values
1	First-year	1.00
2	Second-year	1.54
3	Third-year and older	1.54

of a stage as a seed for population growth relative to that of the first stage. The reproductive value of the first stage is always 1.0. A female individual in Stage 2 is “worth” 1.5 first-year females, and so on (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The reproductive value result complements that of the sensitivities and elasticities. Only by increasing the survival through the first few years can one increase the number of older reproductive females that are the mainstay of the population. The cohort generation time for white-tailed prairie dogs is 2.4 years (SD = 1.5 years).

Stochastic model

We conducted a stochastic matrix analysis for white-tailed prairie dogs. The purpose of this stochastic modeling was not to assess the time to, or probability of, extinction. Instead, the purpose was 1) to assess the relative importance of different degrees of stochasticity – for example, does the level of environmental fluctuation have dramatic effects on population dynamics, or does the life history somewhat buffer the population against variation? 2) To assess whether variability would have dramatically different effects depending on the transitions it affected – for example, would variation in survival have much more impact than variation in fertility? We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (**Table**

A4). Under Variant 1 we altered the juvenile survival rates (P_{21}). Under Variant 2 we varied the fertilities, F_i . Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) under the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We varied the amount of fluctuation by changing the standard deviation of the random normal distribution from which the stochastic vital rates were selected. The default value was a standard deviation of one quarter of the “mean” (with this “mean” set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Variant 3 affected the same juvenile survival transitions as Variant 1, but was subjected to only half the variability (SD was 1/8 compared to 1/4 of the mean). We calculated the stochastic growth rate, $\log \lambda_s$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (**Table A4**) revealed that altering the juvenile survival rates had a detrimental effect on population trajectories. For example, the median ending size under the variable first-year survival rates of Variant 1 produced a median ending size (6,134 individuals) was smaller than the initial size of 10,000 and 55 of the 100 replicate populations declined, with 3 going extinct. In contrast, applying stochasticity to all the fertilities led to a median population size of 13,475 individuals, with 46 of the 100 replicates declining

Table A4. Results of four variants of stochastic projections for white-tailed prairie dogs. Stochastic fluctuations have the greatest effect when acting on “adult” survival rates (Variant 1).

	Variant 1	Variant 2	Variant 3
Input factors:			
Affected cells	P_{21}	F_i	P_{21}
S.D. of random normal distribution	1/4	1/4	1/8
Output values:			
Deterministic λ	1.0002	1.0002	1.0002
# Extinctions / 100 trials	3	0	0
Mean extinction time	1,638	n.a.	n.a.
# Declines / # surviving populations	52/97	46/100	6/100
Mean ending population size	87,429	341,862	315,743
Standard deviation	221,172	1.8×10^6	785,303
Median ending population size	6,135	13,475	99,912
Log λ_s	-0.0004	0.0001	0.001
λ_s	0.9996	1.0001	1.001
% reduction in λ	0.23	0.18	0.09

and none going extinct over the 2,000-year simulation (**Table A4**). This effect of stochastic variation is predictable from the sensitivities and elasticities. λ was most sensitive and elastic to variability in juvenile survival (**Figure A4**). It is also clear large-effect stochasticity has a negative effect on population dynamics. This negative effect occurs despite the fact that the average vital rates remain the same as under the deterministic model – the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001, pp. 390-392). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. For white-tailed prairie dogs under the reduced-variability stochasticity of Variant 3, none of 100 trials of stochastic projection went to extinction vs. 3 under the high-variability Variant 1. In addition, only six of the 100 runs led to declines in the low variability simulation vs. 55 in the high variability simulation (**Table A4**). These results suggest that populations of white-tailed prairie dogs are relatively tolerant to ‘mild’ stochastic fluctuations in first-year survival rates (due, for example, to annual climatic change or to human disturbance) but highly vulnerable to ‘high’ variability in juvenile survival. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity

or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously invariant vital rates (such as annual adult survival), with consequent detrimental effects on population dynamics.

Potential refinements of the models

Clearly, the better the data on survival rates the more accurate the resulting analysis. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of “stochastic” matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variation in vital rates. Using observed correlations would improve on this assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

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