A REVIEW OF PRAIRIE DOG POPULATION DEMOGRAPHICS AND IMPLICATIONS FOR MANAGEMENT IN MONTANA

MONTANA DEPARTMENT OF FISH, WILDLIFE AND PARKS

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EXECUTIVE SUMMARY

Black-tailed (*Cynomys ludovicianus*) and white-tailed (*Cynomys leucurus*) prairie dogs are classified by the Montana Department of Fish, Wildlife and Parks as species of concern due to sharp population declines throughout their range over the past 200 years. Prairie dog reductions have been attributed to disease, poisoning and elimination of habitat. A keystone species, which supports species such as the endangered black-footed ferret, burrowing owl and mountain plover, black-tailed prairie dogs are in need of management throughout the state, but many factors affecting prairie dog populations are still unknown.

The following paper reviews potential threats to prairie dog sustainability (disease, population control and recreational shooting), tools currently available to manage prairie dogs (translocation, habitat manipulation and monitoring methodologies) and identifies weaknesses in the available scientific literature, in order to make useful recommendations for future prairie dog research and management in Montana.

INTRODUCTION

Two species of prairie dogs (Family Sciuridae) inhabit Montana; the black-tailed prairie dog (*Cynomys ludovicianus*) and the white-tailed prairie dog (*Cynomys leucuris*). The range of the white-tailed prairie dog is limited to one county in south central Montana (see Figure 1), while black-tailed prairie dogs inhabit colonies located throughout much of the lower elevation sagebrush-grassland complexes east of the continental divide (see Figure 2).

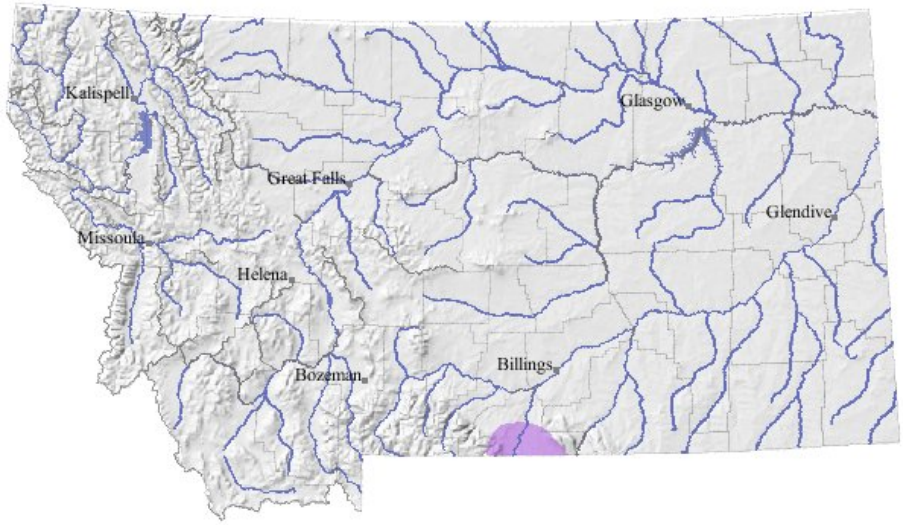

Figure 1. Distribution of the white-tailed prairie dog in Montana.

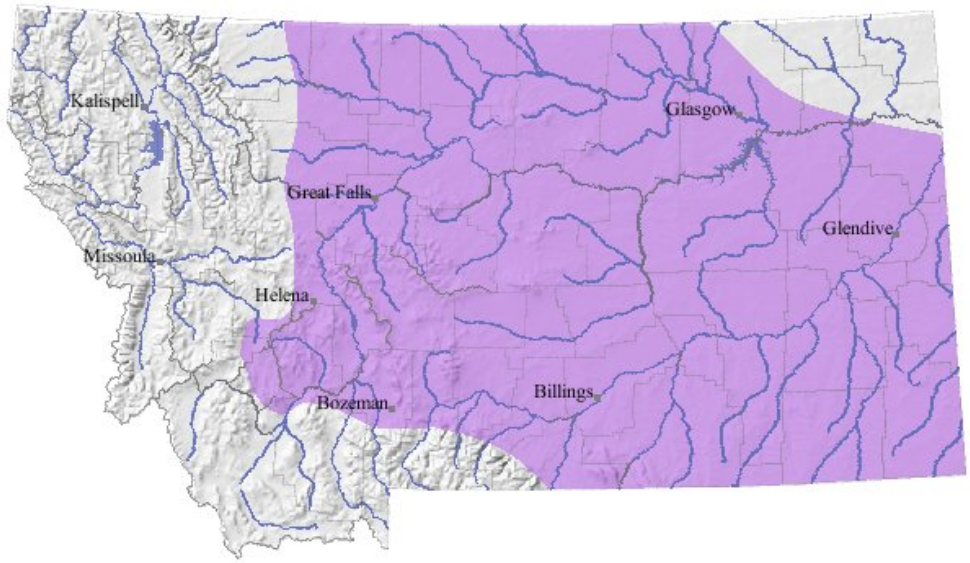

Figure 2. Distribution of the black-tailed prairie dog in Montana.

Prairie dogs are herbivorous, diurnal, colonial, burrowing ground squirrels. Adult prairie dogs average 14-16 inches in length, and can weigh over 3 pounds. Color of fur can vary from yellowish to reddish to dark brown, but often resembles the color of local soil because dirt is often mixed into fur. Physically, black-tailed prairie dogs can be distinguished from white-tailed prairie dogs by a longer, black-tipped tail (Hoogland 2003).

The black-tailed prairie dog is considered a keystone species of the Great Plains (Miller et al. 1994). The areas it occupies provides habitat for a myriad of plant and animal species via prairie dog grazing, clipping and burrowing activities (Fahnestock et al. 2003, Detling 1998). Prairie dogs also serve as a prey base for a number of vertebrate carnivores, most notably the endangered black-footed ferret (*Mustela nigripes*), which is the only prairie dog obligate in Montana and is completely dependent upon prairie dogs for survival (Kotliar et al. 1999). Other species such as burrowing owls (*Athene cunicularia*) and mountain plovers (*Charadrius montanus*) are near-obligates of prairie dog colonies and are often associated with prairie dog colonies (Dinsmore et al. 2001, Kotliar et al. 1999, Knopf and Rupert 1996, Smith and Lomolino 2004).

Historic abundance of prairie dogs is unknown, although multiple efforts have been made to estimate the historical range of the black-tailed prairie dog (Virchow and Hygnstrom 2002, Knowles et al. 2002). These estimates vary between 80 and 110 million acres from Canada to Mexico (USFWS 2008), and 1.4—6 million acres in Montana (Knowles 1998, Flath and Clark 1986). Previously accepted estimates include 90, 000 occupied acres in Montana (Van Pelt 2007). A recent survey conducted by

Montana Fish, Wildlife and Parks (2009) suggests that prairie dogs may occupy more than 190,000 acres statewide, indicating a secure population.

For more than 100 years, prairie dogs have persisted despite tremendous obstacles limiting their abundance. Sodbusters converted sagebrush/grasslands complexes to cropland. Prairie dog eradication programs were initiated in response to perceived threats to grazing competition (Whicker and Detling 1988, Summers and Linder 1978). Failed cropland conversion and overgrazing by livestock often enhanced prairie dog habitat, especially in sagebrush areas that dominated much of central and eastern Montana (Vermiere et al. 2004, Virchow and Hygnstrom 2002). In addition, sport shooting of prairie dogs is a popular recreational activity (Pauli and Buskirk 2007a, Vosburgh and Irby 1998), although it is unknown whether or not shooting actually limits populations. The most dramatic population reduction to occur in the past 50 years, however, was the result of plague spreading from the west coast to reach prairie dog populations in the Great Plains. (Cully and Williams 2001).

Because of the prairie dog's tenacity, it has been the subject of multiple conservation and grassland sustainability topics. Federal and state guidelines for management of prairie dogs are not always congruent-and change with the shifting legal status of the prairie dog. In 1998, the black-tailed prairie dog was petitioned for immediate protection under the Endangered Species Act. In 2000, the prairie dog received "candidate species" status, indicating the protection was warranted, but precluded by other priorities of the United States Fish and Wildlife Service (USFWS). After a thorough review was conducted by the USFWS, the black-tailed prairie dog was removed from the candidate list in 2004. In 2007, the listing removal was challenged

and at the time of this review, the USFWS was seeking comments and conducting an additional status review of the species.

Prairie dogs are often affected by density-related factors such as crowding, food availability, disease and dispersal (Koford 1958). A density-dependant factor is defined as a factor that acts in proportion to the density of animals (Robinson and Bolin 1989). Some diseases, for example, are density-dependant because a higher percentage of the population becomes infected as density increases. Natality and mortality are often density-dependant factors. The maximum reproductive capacity of a species under optimal conditions is referred to as biotic potential. Biotic potential is often density-dependant, and may change as conditions change. Many wildlife populations exhibit density-dependant growth in response to various risks. Prey species often display higher survival and reproduction rates associated with mortality (Fowler 1987). In the case of prairie dogs, density-related constraints are demonstrated by demographic differences between old, stable colonies and young, expanding colonies, which are more able to approach their biotic potential (Hoogland 2006). Black-tailed prairie dog colonies can rebound relatively quickly after natural or unnatural crashes because the remaining individuals can grow faster, survive better, are more likely to breed as yearlings and have larger litters in the absence of density-dependant factors (Hoogland 2006). This phenomenon is particularly pronounced when excess habitat is available (i.e., after a plague epidemic or following chemical control). When some members of a population are taken, the remaining individuals compensate with increased survival or reproduction. Many of these population attributes may be applied to population

response following plague, control, or recreational shooting and will be discussed throughout this review.

The following contains a review of current issues land and wildlife managers face when making critical decisions regarding prairie dogs, their habitat and the grassland ecosystem. The focus is generally on black-tailed prairie dogs because of their abundance in Montana, but management considerations for white-tailed prairie dogs have been included as well. Unless otherwise indicated, all references to “prairie dogs” refer to black-tailed prairie dogs. Any manufacturer names are included for informational purposes only. No endorsement is implied by product mention.

This review begins with a summary of disease-related issues pertinent to the prairie dog, with an emphasis on Sylvatic plague—given that plague is likely the most pervasive threat to the prairie dog throughout its range. The next section includes effects and costs of parasite and prairie dog control, impacts of recreational shooting and methods to aid colony expansion, including prairie dog translocation. The concluding portion reviews methods to estimate prairie dog abundance and distribution, followed by management recommendations and future research needs identified by the completion of this literature review. A glossary of wildlife management terms is located in the appendix.

CHAPTER 1

EFFECTS OF DISEASE, INCLUDING PLAGUE

Prairie dogs are highly social and strictly colonial,and are therefore more likely to transmit disease than other rodents (Hoogland 2003, Bai et al. 2008). Many of these diseases are caused by bacterium carried by the ectoparasites (fleas, ticks and lice), which prairie dogs host. Black-tailed prairie dogs are especially susceptible to intra-specific disease transmission due to allogrooming (colony individuals grooming each other) and dense aggregation that occurs between conspecifics (individuals of the same species) and within colonies (King 1955, Trevino-Villareal 1990, Cully and Williams

2001). This activity is not often observed in white-tailed prairie dogs (Tileston and Lechleitner 1996, Hoogland 2003) and may help explain why large, colony-wide die-offs are less commonly observed within that species. Hoogland (1981) further investigated possible explanations for differences in coloniality between the two species. Black-tailed prairie dogs are able to detect predators more quickly, even though they spend less time scanning for predators, than white-tailed prairie dogs-due to their dense colonial nature. White-tailed prairie dogs are forced to spend more time being alert, but can rely on protective cover if a predator is nearby (Hoogland 1981).

In addition to ectoparasites, prairie dogs can host a variety of endoparasites including protozoans, tapeworms (cestoda) and roundworms (nematoda). The effects of these parasites are largely unknown (Hoogland 2003). Nematoda (*Calodium hepaticum*) have been documented in a zoo colony of black-tailed prairie dogs (Landolfi et al. 2003) but it remains unknown what prevalence, if any, this roundworm has in wild populations.

The bacterial fevers Bartonella and Rickettsia are infrequently transmitted by fleas (Reeves et al. 2007). In one Colorado study, Bartonella occurred in prairie dog populations at an average of 23.1%. This occurrence was documented particularly in juveniles, but did not persist in adult prairie dogs that were re-captured (Bai et al. 2008). Disease transmission to humans is possible, especially when residential areas are developed in close proximity to prairie dog colonies (Bai et al. 2008).

Most disease-related research has focused on Sylvatic plague (hereafter referred to as “plague”). Plague is caused by the bacterium *Yersina pestis*, is carried by more

than eighty flea species (Eisen and Gage 2009), and is found in more than two hundred mammal species (Parkhill et al. 2001, Poland and Barnes 1979). If untreated, plague is often lethal to humans (Levy and Gage 1999, Gailmand et al. 1997). Prairie dogs have evolved little immunity to plague, which can eliminate most or all animals within a colony in a matter of weeks from initial infection (Hoogland 2003). For these reasons, the remainder of this section will focus on plague dynamics, transmission, influences on prairie dog demography and prevention.

Plague dynamics

Plague is not endemic to North America and was introduced to the United States by 1900, probably via rats (*Rattus spp.)*, which arrived on Asian ships docking in San Francisco (Cully and Williams 2001, Link 1955). Plague had spread eastward to the Rocky Mountain States (Colorado, Kansas, Montana, New Mexico, Texas and Wyoming) by the late 1930's (Cully and Williams 2001). Curiously, plague has not spread eastward beyond the 102nd meridian (Cully and Williams 2001). Early impacts of plague in Montana are largely unknown, but research completed in the last 50 years indicates localized reduction or extinction of prairie dog colonies, and increased variance in colony size and distance between colonies. The population biology associated with plague outbreaks has broad implications for many grassland communities (Pauli et al. 2006).

When plague reduces or eliminates prairie dog populations, the effect on related plant and animal communities can be large. Carnivores, including the endangered black-footed ferret, ferruginous hawk and swift fox are immediately affected by a reduction in prey base (Cartron et al. 2004, Cook et al. 2003). This effect is most dire for black-footed ferrets, which depend on prairie dog colonies for survival (Miller et al. 1996). Other predators may not be as dependant on prairie dog colonies for survival, except in certain geographic areas (Nicholson 2004). Fleas displaced from prairie dog carcasses may transmit plague to other mammalian reservoirs such as coyotes and badgers that scavenge upon prairie dog carcasses (Boone et al. 2008). Furthermore, when plague eliminates a prairie dog population, prairie dog burrow systems eventually collapse, displacing burrowing owls, rattlesnakes and swift fox, which may not depend on prairie dogs for a food source, but certainly depend on prairie dogs for burrow excavation. Disappearance of prairie dog burrows also impacts smaller prey species, such as mice and cottontails, which utilize the burrows (Koford 1958), further complicating the issue of predator reliance on prairie dog colonies.

Indirect effects of prairie dog reduction or elimination are more subtle, and are poorly understood. Long-term absence of prairie dogs may result in an eventual shift in plant assemblage and associated habitat. It has been suggested that a return to pre-colonization vegetative communities may take ten to fifty years or longer (Johnson-Nistler et al. 2004, Cid et al. 1991). Short-term reductions in prairie dog numbers after human control (shooting/poisoning) typically result in a return to pre-treatment numbers within one to three years (Knowles 1986, Knowles 1987). Plant production, for example, showed no significant increases up to four years after prairie dog exclusion in

the Conata Basin, South Dakota (Uresk 1985). Detailed descriptions of long-term changes in vegetative communities after significant reductions in prairie dog numbers have not been documented. Furthermore, it is unknown whether population recovery mechanisms following a plague epidemic would depart from those following human control measures.

In humans, *Y. pestis* is extremely virulent, and mortality ranges from 50—100% if untreated (Levy and Gage 1999). About 3000 cases of plague are documented annually in humans worldwide (Lowell et al. 2005). Human infection is typically associated with periods of amplification that occur during wild plague epizootics (Levy and Gage 1999). Plague transmission is probably highest in high-density host populations, which causes further concern when prairie dog colonies are located near cities. These colonies typically have higher densities than those in rural areas due to geographic constraints (Johnson and Collinge 2004) and these locations are usually where human threat of plague is greatest (Bai et al. 2008).

Because of the potentially devastating outcomes of human plague outbreaks, it has recently come under scrutiny as a bioterrorism agent (Inglesby et al. 2000). Research is currently being conducted in an effort to distinguish between bioterrorism and naturally occurring strains (Lowell et al. 2005). DNA repeats have been identified in *Y. pestis* that can be used to identify plague mutations at small geographic scales. Epidemiologists are working with these isolates to “map” environmental sources at various locations. These results can then be combined with epidemiological data to obtain likely exposure sites and identify the infective source. In this way, plague cases

may be diagnosed and differentiated between a naturally occurring strain and an intentionally released strain (Lowell et al. 2005).

As previously mentioned, plague has profound impacts on prairie dog populations. It is estimated that between 1986 and 1998, plague reduced the cumulative area prairie dogs occupied in Montana by about 50% (Luce et al. 2006). Because the population distribution of prairie dogs resulting from plague epizootics can have broad implications for North American grassland communities, as evidenced above, much research has focused on attempts to identify plague transmission, persistence and biological effects.

Transmission

A variety of flea species serve as the primary vectors for plague transmission. *Y. pestis* grows in the gut of these fleas, forming a proventricular (foregut) blockage which stops the passage of a bloodmeal in the flea. The blood is then regurgitated, often infecting the flea's next host. Because the flea is still "hungry," it may spread inoculums to multiple hosts, as it loses host-specificity due to its starved condition (Cully and Williams 2001, Eskey 1938).

While proventricular blockage in fleas is the generally accepted method of plague transmission, several studies have focused on flea species that do not readily form proventricular blockages (Eisen and Gage 2009). This is because susceptible hosts

(starved fleas or prairie dogs) would typically die within two days, thus halting the rapid spread of plague. Short-term reservoirs must be necessary to drive epizootics. It has been suggested that transmission by blocked fleas may be important between epizootics, but unblocked fleas play a major role in epizootic outbreaks. It is these large epizootics that can nearly decimate, if not completely decimate, large prairie dog colonies (Rayor 1985, Menkins and Anderson 1991, Pauli et al. 2006).

Researchers have identified associations between plague epizootics and climate conditions (Snall et al. 2008), host abundance (Boone and Stapp 2008), and flea infestation rates (Eisen and Gage 2009). While it is evident that plague remains in the environment between outbreaks, one Montana study suggested that plague did not persist at prairie dog colonies two years after an epizootic (Holmes et al. 2006). Alternatively, plague may continually move across the landscape, or persist in permanent plague foci which consist of several host species occurring in an area.

Collinge et al. (2005a) evaluated a series of models based on plague data sets from Colorado and Montana, which included long-term climate data and instances of plague occurance. The models with the most support indicated a close association with precipitation in April—July of the previous year and “warm” days (days reaching 80 degrees Fahrenheit) during the year of the epizootic. These same models indicated a negative association with “hot” days (days exceeding 85 degrees Fahrenheit) of the current year. Many implications may be drawn from this research. Climate factors were associated with plague occurrence in Montana, so it may be possible to predict plague outbreaks based on climatic variables (Collinge et al. 2005a). Rodent densities may increase after periods of precipitation, only to decrease when temperatures favor plague

transmission. Perhaps most importantly, the best climatic predictors of plague in Montana correlated with the best climatic predictors of human plague in the southwestern United States (Collinge et al. 2005a). A separate analysis of the same data sets listed above suggested that roads, streams and lakes may serve as barriers to limit movement of prairie dogs, other hosts, or plague vectors/carriers (Collinge et al. 2005b). Clearly, more research is needed in this area but the combination of climate and topographical data associated with the spread of plague may help researchers better understand the dynamics of plague transmission.

Small rodents including grasshopper mice (*Onchomys leucogaster*), thirteen-lined ground squirrels (*Spermophilus tridecimlineatus*) and deer mice (*Peromyscus maniculatus*) are among species that can become infected by plague, or may possibly act as plague reservoirs during enzootic periods (Thiagarajan 2008). Grasshopper mice, in particular, could play a heightened role because they frequently scavenge upon rodent carcasses (Boone et al. 2008, Stapp et al. 2008). In addition, grasshopper mice were the only small rodent species that regularly tested seropositive during plague outbreaks in Wyoming (Stapp et al. 2008). While this may provide evidence that grasshopper mice act as a short term reservoir, it does not indicate that they serve as long-term, enzootic hosts of plague. A model developed by Colorado State University researchers suggests that a short-term reservoir is necessary for plague epizootic dynamics (Webb et al. 2006). If this is true, grasshopper mice may play an important, albeit indirect, role in plague transmission.

Infected fleas remain alive for about one day after the death of their prairie dog hosts (Boone et al. 2008). Thus the role of scavengers such as foxes, coyotes and

badgers may be important in the enzootic transmission of plague. In a Colorado study, 24% (15 of 61) live-trapped swift foxes (*Vulpes velox*) were seropositive for plague, although the fleas on these animals did not harbor *Y. pestis* (Salkeld et al. 2007). Seropositive foxes had been exposed to plague, but since these foxes were found in close proximity to plague infected prairie dog colonies, researchers could not determine whether foxes had become exposed at the infected colonies, or whether prairie dogs had become infected through exposure to swift foxes and their fleas (Salkeld et al. 1997). While these results do not infer that swift foxes act as plague reservoirs, they do support the assumption that mammalian carnivores may act as a source of infection to rodent communities (Boone et al. 2008, Salkeld et al. 2007). This research might also explain how plague may be transported between colonies.

Finally, it has also been suggested that plague may persist in the soil between outbreaks. If this is the case, it is unknown whether persistence occurs as a free-living, metabolically active and reproducing bacterium, with a host tissue such as a parasite of soil protozoa, or within a biofilm affecting nematode surfaces (Eisen et al. 2008).

Regardless of enzootic persistence, plague transmission during an epizootic is high within black-tailed prairie dog colonies (Cully and Williams 2001). Prairie dogs are highly susceptible to plague, either because they have been unable to evolve a defense or perhaps simply due to their colonial nature (Cully et al. 2006). Plague epizootics often result in local extirpation of colonies, reduced colony size or increased distances between colonies (Cully and Williams 2001). Interestingly, the resulting complexes of fragmented colonies may be one of the best protections from future plague epizootics.

Demography

The presence of plague can have a great impact on prairie dog demographics. In Wyoming, a plague epizootic reduced juvenile and adult prairie dog abundance by 95 and 96%, respectively (Pauli et al. 2006). Survivors of the epidemic apparently developed antibodies and either reorganized into functional coteries, or perhaps persisted as original coteries. This research demonstrated that outbreak survival was important for plague recovery. Historically, immigration into “plagued-out” colonies was thought to be the most important recovery mechanism. Further, this work implies immune response, rather than plague avoidance, allows for colony persistence.

Since nearly all prairie dog colonies have suffered dramatic size reductions, through control efforts such as shooting or poisoning or through disease, there is no control group from which to make population-based recommendations from (Daley 1992). As such, it is difficult to analyze prairie dog genetics objectively, especially as they relate to plague. Typically, small isolated wildlife populations are vulnerable to loss of genetic diversity through genetic drift. This was not the case, however, in Phillips County, Montana where gene flow was responsible for maintaining genetic diversity following a plague epizootic (Trudeau et al. 2004). It was suggested that geographic isolation actually protected colonies and allowed them to retain genetic variability. Over time it is thought that gene flow will compensate for the effects of plague. It remains unclear whether this is an adaptive strategy, or coincidence. Some wildlife populations

have simply evolved to withstand large size fluctuations without a major loss of genetic variability (Daley 1992).

White-tailed prairie dogs

While plague epidemics are most notable, and devastating, for black-tailed prairie dogs, white-tailed prairie dogs are similarly susceptible. Plague was first identified in fleas of white-tailed prairie dogs in 1936, in Wyoming (Cully and Williams 2001). Plague outbreaks have continued to be identified at various white-tailed prairie dog colonies in Wyoming (Anderson and Williams 1997, Clark 1977). Plague epizootics at white-tailed prairie dog colonies are generally characterized by slow, continuous population declines (Cully and Williams 1991) rather than colony-wide die-offs, as is often observed of black-tailed prairie dogs.

Colonies located on a white-tailed prairie dog complex near Meeteetse, Wyoming with burrow densities of less than 60 burrows/ha did not contain fleas yielding *Y. pestis* while others in the same complex, with burrow densities greater than 60 burrows/ha, did contain fleas (Anderson and Williams 1997). Most likely this represents some threshold at which plague is not easily transmitted. Because white-tailed prairie dogs are not as densely aggregated, and do not often participate in allogrooming and other colonial activities demonstrated by black-tailed prairie dogs (Tileston and Lechleitner 1996, Hoogland 2003), transmission between conspecifics is slow. Transmission is slow enough in white-tailed prairie dog colonies that, while some individuals die, some are left to reproduce, thus maintaining a viable host population, and a continuous cycle.

Prevention

Recent laboratory efforts to develop a plague vaccine show promise. One such effort offered a recombinant raccoon poxvirus, expressing the *Y. pestis* F1 antigen (RCN-F1), mixed with sweet potato feed, to captive black-tailed prairie dogs. Primary and booster "vaccinations" were fed. When exposed to plague, 56% of the prairie dogs who had consumed at least one vaccine-laden bait survived, compared to 12% in the control group ($p<0.01$) (Mencher et al. 2004). A similar but separate laboratory trial using RCN-F1 yielded similar results (Rocke et al. 2008). Another recombinant vaccine (F1-V fusion protein) was successfully used to protect captive black-footed ferrets from plague transmission (Rocke et al. 2004).

These vaccines have not been tested in free-ranging environments. Successful immunization of wild prairie dogs would likely reduce direct plague mortality and transmission (Mencher et al. 2004). Preliminary trials have been conducted to determine bait acceptance in free-ranging prairie dogs (Creekmore et al. 2002). Researchers are currently working to determine an appropriate delivery method for field applications and address regulatory issues so that field trials of RCN-F1 vaccination may begin (Rocke et al. 2008).

Plague eradication is not possible since the exact mechanisms of plague transmission and enzootic persistence are unknown. Reduction in plague occurrence and duration of epizootics, however, is achievable on prairie dog colonies. Because some family groups, or individuals, are capable of surviving plague epizootics, prairie

dogs do exhibit an unidentified form of resistance to plague. Additionally, it is not known why plague is not found east of the 102nd meridian (Cully and Williams 2001). Future research that aims to fill these gaps is greatly needed.

CHAPTER 2

PARASITE CONTROL

Prairie dog conservation efforts in areas of plague aim to reduce numbers of fleas known to carry *Y. pestis*. Of the several flea species known to transmit plague, *Oropsylla hirsutus*, *O. tuburculatus cynomuris* and *Pulex* spp. are among the most common (Cully and Williams 2001). See Table 1. In efforts to reduce flea numbers, thereby reducing the risk of plague transmission, land and wildlife managers often treat prairie dog burrows and colonies with insecticides. Following the federal ban of DDT in 1972 (EPA 1972), application of carbaryl dust (trade name Sevin, Bayer) was most

commonly used for flea control. Carbaryl effectively suppressed a plague epizootic on a prairie dog colony in 1969 and achieved 100% flea control in twenty four hours (Barnes et al. 1972). Carbaryl exhibited limited soil persistence and required repeated applications due to its short half-life (Beard et al. 1992). As such, carbaryl use has been discontinued or replaced by other insecticides. Insecticides used today are generally either pyrethroids (synthetic chemical compounds), or insect growth regulators.

Insecticides and modes of action

The pyrethroid family of insecticides are synthetic versions of pyrethrins, derived from chrysanthemum flower (*Chrysanthemum spp*.) compounds. Pyrethroids disrupt sodium and nerve channels, resulting in death of an insect (Brown 2006). Permethrin (trade name Pyraperm, Valent Biosciences Corporation) and deltamethrin (trade name DeltaDust, Bayer Environmental Science) are available as dusting powders and are usually applied directly to prairie dog burrows. Both dust formulations are effective, but deltamethrin may be more favorable for environmental use as it is moisture-resistant and may suppress fleas longer than pyrethrin (Seery et al. 2003). Pyraperm application immediately suppressed plague transmission at colonies showing initial signs of plague (Hoogland 2004). Evidence indicates that an experimental application of DeltaDust in Colorado effectively suppressed a plague epizootic during the summer of 2000 (Seery et al 2003).

Pyriproxyfen (multiple trade names and manufacturers) is an insect growth regulator available as a spray, powder and oral bait. Pyriproxyfen mimics a juvenile growth hormone, which keeps insects from metamorphosing into adult stages. Because insects cannot grow or reproduce, they eventually die (Brown 2006).

Table 1. Flea species collected from black-tailed (BT) and white-tailed (WT) prairie dog burrows and typical hosts .

Flea spp.	Prairie dog spp.	Typical Host	Source
Aetheca wagneri	BT, WT	Deer mouse	Salkeld and Stapp 2008, Holmes 2006, Seery 2003, Anderson and Williams 1997
Cediopsylla inequalis	WT	desert cottontail	Anderson and Williams 1997
Euhoplopsyllus glacialis	BT	cottontail	Salkeld and Stapp 2008
E. wenmanni	BT	Deer mouse	Seery et al. 2003
Foxella ignota	BT	pocket gopher	Salkeld and Stapp 2008, Seery et al. 2003
Hystrichopsylla dippiei	WT	Uinta ground squirrel	Anderson and Williams 1997, Ubico et al. 1988
Neopsylla inopina	WT	Richardson's ground squirrel	Anderson and Williams 1997, Ubico et al. 1988
Oropsylla hirsuta	BT	black-tailed prairie dog	Salkeld and Stapp 2008, Holmes 2006, Seery et al. 2003, Stevenson et al. 2003, Cully et al. 2000
O. idahoensis	WT	northern pocket gopher	Anderson and Williams 1997, Ubico et al. 2008
O. labis	BT, WT	cottontail	Salkeld and Stapp 2008, Ubico et al. 2008, Anderson and Williams 1997
O. tuberculata cynomuris	BT, WT	prairie dogs	Salkeld and Stapp 2008, Holmes 2006, Stevenson et al. 2003, Ubico et al. 2004, Anderson and Williams 1997
Pleochaetis exilis	BT	northern grasshopper mouse	Salkeld and Stapp 2008
Pulex spp.	BT, WT	coyote/fox	Salkeld and Stapp 2008, Seery et al. 2003, Stevenson et al. 2003, Cully et al. 2000, Anderson and Williams 1997
Rhadinopsylla fraterna	WT	Richardson's ground squirrel	Anderson and Williams 1997
Rhadinopsylla sectilis	WT	Deer mouse	Ubico et al. 1998
Thrassis fotus	BT	thirteen-lined ground squirrels	Salkeld and Stapp 2008, Holmes 2006, Stevenson et al. 2003, Cully et al. 2000
T. pandorae	WT	ground squirrels	Ubico et al. 1998

Non-target effects

At present, insecticide dusting powders may be among the best choices for controlling plague, especially in sensitive areas where black-footed ferrets are known to exist, or are planned for introduction. Unfortunately, these insecticides can also kill other arthropods located on prairie dog colonies, which are important in the diets of associated wildlife species. More than one-hundred and seventy vertebrate species are associated with prairie dog colonies (Miller et al. 1994). At least twenty-nine of these rely on arthropods for either all or part of their diets (Tyler and Shackford 2002, Agnew et al. 1986). These include mountain plovers, burrowing owls and horned larks. See Table 2.

Table 2. Vertebrate species associated with prairie dog colonies that rely on arthropods for all or part of diet, including type and season/life stage.

Species (common name)	Diet type	Season/life stage
Mammals		
deer mouse	moth/butterfly larvae	spring
N. grasshopper mouse	grasshoppers, spiders	year-round (as available)
Birds		
mountain plover	beetles, grasshoppers, crickets, ants	summering grounds
burrowing owl	beetles, spiders, grasshoppers, crickets	year-round (as available)
horned lark	wasps, ants. caterpillars, grasshoppers, spiders	mating season/fed to young
lark bunting	grasshoppers, ants, weevils, beetles	opportunistically, fed to young
killdeer	adult beetles, fly and beetle larvae	nestling
western meadowlark	caterpillars, grasshoppers	summer
Amphibians		
great plains toad	ants and other small arthropods	active periods
plains spadefoot toad	moths, caterpillars, beetle	active periods

In an attempt to identify any effects of Pyriproxyfen on non-target arthropods (fleas were targeted), Karhu and Anderson (2000) captured and classified arthropods before and after spray, powder and oral bait treatments. Many significant declines in arthropod abundance were noted but the authors suggest that these fluctuations were natural and not necessarily a result of the Pyriproxyfen treatments (with the exception of cicadas and aphids). Due to the various environmental factors associated with this effort, much more research is needed before the non-target effects of Pyriproxyfen are certain.

Limitations of insect control

Although a number of insect species can be affected by dusting powder intended for fleas, there have been no efforts to establish if, how, or to what extent this phenomenon affects insectivores that are commonly associated with prairie dog towns. They may themselves have compensatory mechanisms for finding food away from prairie dog towns, or exhibit “diet switching” to compensate for the lack of particular arthropods at prairie dog colonies. In addition, it is possible that a number of these species feed above ground on insects and arthropods that are not commonly found in prairie dog burrows, and dusting powder may not affect these species. Finally, even if dusting treatments are shown to have a major impact on non-target species, the secondary effect may be outweighed by the importance of maintaining healthy habitat for endangered species such as the black-footed ferret. This is likely a management decision that Montana wildlife managers will be faced with in the future.

CHAPTER 3

POPULATION CONTROL

Prairie dog population control is controversial in Montana and other western states for a variety of reasons. Land and wildlife managers are typically interested in conservation management of prairie dogs, which implies sustained use/take. In Montana, prairie dogs are currently classified as both a species of concern (Montana Fish, Wildlife and Parks) and a vertebrate pest species (Montana Department of Agriculture). As such, prairie dog control is unregulated, except in black-footed ferret recovery areas and chemical control treatment areas greater than 80 acres in size (Montana Department of Agriculture 2006).

Prairie dog management may include control for a number of reasons including maintaining rangeland production, perceived competition with cattle, human health issues, or landscape aesthetics. Because total eradication is not possible or reasonable in many circumstances, most prairie dog control efforts aim to either limit expansion or reduce colony size. Due to the biotic potential of prairie dogs, it is necessary to reduce populations by 90% to achieve long-term control (Montana Department of Agriculture 2006).

Some managers are concerned with localized prairie dog overpopulation. While "overpopulation" is a subjective term, and varies with land ownership and use, control of prairie dogs is desirable under certain conditions (Nash et al. 2007). High densities of prairie dogs can increase the rate and spread of disease-this is especially a concern in urban areas (Milne-Laux and Sweitzer 2006).

Integrated pest control

Various control techniques are available to reduce prairie dog numbers. These include cultural/biological control, shooting, traps, bait stations, burrow fumigants, toxicants, contraception and translocation (Foster-McDonald et al. 2006). Application of these control methods will vary depending on season, species and cost. An integrated control plan will generally include frequent crop rotation and soil tillage, as well as the encouragement of predators such as coyotes, fox, weasels and raptors (Montana Department of Agriculture, 2006). A deferred grazing program combined with predator attraction points, served to effectively reduce prairie dog acreage in Kansas (Snell and Hlavachick 1980). Shooting may reduce damage to crops where small, isolated populations exist but for effective control to occur a population must be kept under constant shooting pressure (Andelt and Hopper 1998) as explained in Chapter 4.

Lethal methods

Toxicants are often the most effective and economical method to control large populations of prairie dogs. Poison grain treated with zinc phosphide has shown a 65—

95% decrease in prairie dog populations when administered properly (Messmer et al. 1993, Knowles 1986). Even at these control rates, prairie dogs can return to post treatment levels within one to five years (Knowles 1986). While toxicant programs must continually be evaluated for cost effectiveness, this method of control has shown little impact on non-target song birds (Apa et al. 1991). Because zinc phosphide does not persist in animal tissue, it poses a very low risk of secondary poisoning to scavenging animals (Forrest and Luchsinger 2006). At present, zinc phosphide is the only treated grain-bait labeled for use on prairie dogs in Montana.

Burrow fumigants such as gas cartridges and aluminum phosphide tablets are an effective means of control. However, due to high labor and other costs associated with them, fumigants are generally restricted to small populations (Montana Department of Agriculture 2006). Hygnstrom (1994) compared efficacy of five burrow fumigants and concluded that all were an acceptable means of control. Nevertheless, not all burrow fumigants are labeled for use on prairie dogs. Fumigants currently labeled for use in Montana include aluminum phosphide and CO_2 ignitable gas cartridges (various trade names and manufacturers). Extreme care must be taken when employing fumigants to avoid non-target hazards.

Trapping may also be a viable option when small populations are present. Wire mesh cage traps can be set with bait such as rolled oats, peanut butter and fruit. Because heat stress may occur when live-trapped prairie dogs are exposed to the sun (Jacquart 1986), traps should be shaded and captured prairie dogs relocated or humanely killed. When green forage is available, it may be more difficult to attract prairie dogs to bait. In these cases, conibear body-gripping traps can be used

(Stockrahm and Seabloom 1998). These traps are set directly above the burrow opening and kill the prairie dog as it emerges.

Non-lethal methods

Where population control is desirable, but lethal techniques are not acceptable or legal, non-lethal management techniques may be utilized (Zinn and Andelt 1999). Non-lethal management includes contraception, visual barriers or translocation. All techniques are relatively new, and each may serve a unique purpose in the appropriate setting.

Contraception. Contraceptive control may be especially appropriate in urban areas where lethal methods are not socially acceptable. In rural settings, agriculture producers may be more tolerant of prairie dogs if colony expansion can be halted or slowed by contraceptives (Nash et al. 2007). DiazaCon (USDA APHIS) is a cholesterol-inhibiting contraceptive that shows promise for management of prairie dogs. In an experimental trial, DiazaCon was administered to prairie dogs as an oral bait applied to molasses coated oats (Nash et al. 2007). Treatment of DiazaCon (20, 25 Diazacholesterol), resulted in a 47% decrease in reproductive success of adult prairie dogs in northern Colorado (Nash et al. 2007). The results from this trial suggest that contraceptive control may have improved if prairie dogs were treated earlier in the spring. This type of cholesterol-inhibiting contraception may be favorable to other, hormonal-based contraceptives such as diethystilbestrone, but further work is needed to monitor long term behavioral effects (Nash et al. 2007). Additionally, chemosterilants

may not be labeled for use on prairie dogs, and are often not available to the public, making them impractical for public applications.

Visual barriers. Because prairie dogs tend to favor low-stature vegetation free from visual obstructions (enhancing detection and escape from predators), managers and researchers have been interested in erection of visual barriers to limit colony expansion. Barriers may be useful at land ownership boundaries or at the perimeter of cropland. Effectiveness of barriers depends on a number of factors, but generally seems limited by cost, durability, and maintenance. Visual barriers constructed of polyethylene mesh, galvanized roofing panels and silt fencing in Nebraska (Foster-McDonald et al. 2006, Hygnstrom 1996) and New Mexico (Merriman et al. 2004) were ineffective at reducing colony expansion. See Table 4. In contrast, pine tree and burlap visual barriers in South Dakota did effectively reduce prairie dog presence in experimental plots (Franklin and Garrett 1989). Terrall (2006) indicated depth of a vegetative barrier may be an important factor to consider when attempting to limit prairie dog expansion and depth of barrier may be more important than type of material used. Increasing depth of burlap barriers increased visual obstruction and decreased prairie dog breakthrough (digging under or climbing over) at South Dakota study sites (Terrall 2006). Effectiveness of visual barriers depends on site/location, materials used and maintenance required.

In an effort to understand why visual barriers had varying degrees of success, Foster-McDonald et al. (2006) examined behavior and movements of prairie dogs after construction of an SB Tensar® snow fence. SB Tensar® snow fence is constructed of black polyethylene plastic mesh, with see-through visibility of 60% (Foster-McDonald et

al. 2006). Results indicate that although the fence was durable (many visual barriers do not withstand environmental conditions such as high winds), it was not effective at controlling the movements and behavior of prairie dogs. Presumably, the 60% see-through visibility of the fence is not enough to effectively limit prairie dog visibility, and discourage use of the area. Foster-McDonald et al. (2006) suggest future research should be aimed at evaluation of fencing materials with high environmental durability and low see-through visibility.

Witmer et al. (2008) evaluated the effectiveness and durability of physical barriers in Boulder and Lamar Counties, Colorado that had been erected to restrict prairie dog expansion. These barriers were constructed with a variety of materials including vinyl, reinforced vinyl, chicken wire, woven nylon, and fiberglass and steel corrugated panels. Upon evaluation, it was noted that all barriers had been breached at least once, usually by prairie dogs digging under the barrier. High winds were responsible for most above-ground damage. The authors suggested fiberglass or steel panel barriers, regularly maintained and secured belowground, as the most effective physical and visual barrier, although these methods were most costly (Witmer et al. 2008). See Table 4.

Translocation. When a source population is identified, and a recipient site is located prairie dog translocation has proven to be an effective tool for prairie dog conservation. Translocation meets a number of management goals; to expand colonies on a preserve or in protected areas, re-establish populations that have been lost due to control or plague, limit expansion in areas that may cause conflict, relocate prairie dogs on land

that will be converted for development, and to manage outbreaks of sylvatic plague (Witmer and Fagerstone 2003, Witmer at al. 2003). Translocation will be discussed in further detail in Chapter 5.

Costs of control

Previously, cultural/biological, chemical, relocation, chemosterilization and barrier fencing were examined as means of prairie dog population control. The remainder of this section will compare costs (when available) and benefits associated with each of these methods.

Cultural/biological. While no data exist to compare financial loss/gains associated with cultural and biological control (including deferred grazing and predator attraction) these may be among the least costly available alternatives for prairie dog population management. It has been suggested that deferred livestock grazing at or near prairie dog colonies may result in additional production of aboveground forage (Cable and Timm 1987) although it is unclear whether this is attributed to the obvious state of rangeland improvement by practicing such rangeland management, or an indirect effect limiting prairie dog colony growth and expansion. Deferred livestock grazing (whether or not prairie dogs are present) often results in elevated forage production (Owensby et al. 1973). Because cattle/large ungulate grazing facilitates prairie dog colonization (Cable and Timm 1987), efforts to document grazing strategies and dietary preferences are often confounded.

Likewise, the costs associated with predator encouragement, including erecting raptor perches, or the cessation of predator control programs, have never been evaluated. Some research suggests that providing cover for predators does not significantly influence prairie dog populations (Snell and Hlavachick 1980), but the costs of such a management strategy are minimal when compared to other, more costly (in terms of time and dollars) control methods such as trapping or chemical treatments. On the other hand, certain segments of agriculture production, such as sheep operations, would likely suffer very negative consequences if a predator abatement program were to be halted, whereas a grain grower would not be as affected by a local increase in predator numbers.

Chemical control. Chemical control generally includes a toxicant placed on a grain bait, or burrow fumigation. Toxicants are often the most economical and effective form of control. In Montana, zinc phosphide is the only lethal toxicant labeled for use on prairie dogs (Montana Department of Agriculture). Efficacy can vary due to site, timing and location of bait placement, and environmental conditions. Generally, zinc phosphide treatment can achieve 85% efficacy (Hygnstrom and Virchow 1994). Cost and effectiveness of zinc phosphide control programs are outlined in Table 3.

Table 3. Comparison of chemical control costs.

Chemical family	Mode of application	Efficacy	Estimated cost ($/ha)	Year	Source
Aluminum phosphide	fumigant	97%	74.10	1990	Hygnstrom 1994
CO_2 Gas Cartridge	fumigant	95%	95.10	1990	Hygnstrom 1994
Methyl Bromide	fumigant	96%	37.67	1990	Hygnstrom 1994
Chloropcrin	fumigant	94%	40.14	1990	Hygnstrom 1994
M. Bromide/Chloropicrin	fumigant	96%	37.67	1990	Hygnstrom 1994
Zinc Phosphide	grain bait	n/a	14.09	1978-80	Collins et al. 1984
		95%	n/a	1986	Uresk et al. 1986
Zinc phosphide	grain bait	85%	n/a	1978	Knowles 1986
Zinc Phosphide	grain bait		94.84	2009	Current Market*
CO_2 Gas Cartridge	fumigant		281.32	2009	Current Market*

Because both cost and effectiveness associated with different treatments can vary so much, it is not surprising that cost-benefit ratios vary with nearly every treatment recorded in the available literature. Uresk et al. (1986) achieved a 95% reduction in prairie dog population, following treatment with zinc phosphide. Results suggested that because plants did not demonstrate an immediate recovery response, four years of continuous chemical control may be needed before range recovery could be realized.

A similar zinc phosphide treatment conducted in South Dakota provided an economic analysis of prairie dog control from both rancher and Forest Service viewpoints (Collins et al. 1984). Control was not deemed economically feasible from either perspective, as maintenance and control costs at an assumed annual prairie dog growth rate of 30% far exceeded the value of any AUM's (animal unit months) gained as

a result of this control. In fact, control was assumed unfeasible unless prairie dog annual growth rate was less than 10%; a figure that is highly unlikely since population growth is often density-dependant and highest after a population reduction (Cully 1997, Cully et al. 1997, Knowles 1987, Crosby and Graham 1986). In addition, the cost analysis was based largely on total forage production and did not take plant species into consideration, which may have a large impact on cattle forage preference (Provenza and Balph 1988). While recovery of previously occupied acreage alone was not deemed cost effective, cost analysis may have changed if the possible benefits gained from protecting uncolonized rangeland such as continued crop harvest/forage production could be quantified. This opportunity cost is largely ignored in scientific literature. Prevention or colony maintenance may be more cost-effective than outright control or population reduction once a colony has established in areas where prairie dog occupancy is not desired.

Use of barriers. Various types of physical and visual barriers have been evaluated as a mechanism to reduce prairie dog colony expansion as described earlier in this chapter. As effectiveness can vary with materials and application, cost varies with type and construction of fence (see Table 4 for comparison of barrier type and relative cost). Unfortunately, the barriers seemingly most effective at limiting prairie dog expansion (Franklin and Garrett 1989) do not include associated relative costs. Also, there is such variability in the estimated costs associated with each type of structure that some measure of standardization is needed to effectively compare costs, including labor associated with construction and maintenance of each structure. Witmer et al. (2008)

suggest that physical barriers may be best suited to slow colony expansion, rather than prevent expansion. More information is needed to evaluate the economic and biological trade-offs associated with slowing colony expansion.

Table 4. Cost and efficacy of physical/visual barriers constructed to limit prairie dog expansion

Barrier type	cost (100m)	Effective?	Reference
Galvanized roofing panel	$783	no	Merriman et al. 2004
Silt fencing	$214	no	Merriman et al. 2004
1m burlap, 3 rows	n/a	yes	Franklin and Garrett 1989
Ponderosa pine, 3 rows	n/a	yes	Franklin and Garrett 1989
Polyethylene mesh (Tensar)	$210	no	Hygnstrom 1995, Foster-McDonald et al. 1996
Vinyl	$3,000	no	Witmer et al. 2008
Corrugated steel/fiberglass	$6,000	yes	Witmer et al. 2008

Population control of prairie dogs is likely to remain controversial in Montana. Because total eradication of prairie dogs is rarely feasible, most population control efforts focus on limiting colony expansion or reducing colony size. Methods available to land managers in Montana include lethal control such as poisoning, burrow fumigation and trapping; and non lethal control such as contraception, visual barriers and translocation. Methods vary in cost and effectiveness and many costs associated with prairie dog control are unknown.

CHAPTER 4

RECREATIONAL SHOOTING

Recreational shooting of black-tailed prairie dogs occurs throughout the current range of prairie dogs in Montana, except on closed federal lands. Many sport shooters travel to Montana during the summer in pursuit of such opportunities. The precise economic impacts this activity has in areas of Montana are largely unknown. Graber et al. (1998) has identified recreational shooting as a population reduction mechanism which may threaten prairie dog population viability and sustainability. Hickman et al. (1999) also suggest recreational shooting has significant effects on prairie dog populations. Yet other research indicates overall impacts on prairie dog populations are minimal (Vosburgh and Irby 1998, Knowles 1987).

Although available literature demonstrates mixed results regarding effects of recreational shooting on prairie dog populations, shooting likely has important implications for non-target animals associated with prairie dog colonies, particularly those that scavenge upon prairie dog carcasses (Pauli and Buskirk 2007a, Kramer 1997).

Raptors and other scavengers such as foxes and coyotes feed on prairie dog carcasses after a colony has been shot but the risk of doing so may be greater than the benefit. Scientific evidence suggests negative non-target impacts associated with lead consumption from prairie dog carcasses containing lead or lead residue from bullets, particularly expanding bullets (Pauli and Buskirk 2007a, Stephens et al. 2008).

Effects of recreational shooting on prairie dog populations

Prairie dog shooting was examined as a means of population control on two small prairie dog colonies (14.6 and 3.5 acres in size) on the Charles M. Russell National Wildlife Refuge (CMRNWR), Montana in 1978 and 1979 (Knowles 1987). A concentrated shooting effort at these two colonies resulted in an average population reduction of 69% after two years. Shooting was effective at negating colony expansion during these years, nearly eliminating all prairie dogs in the smaller colony. Knowles (1987) hypothesized that reduction of prairie dogs beyond some threshold may have long-term negative effects. Within five years of the shooting study, however, the larger colony had expanded to 140% of its pre-study size, while the smaller colony had expanded to 90%. The Montana Department of Agriculture (2006) suggested that prairie dog populations need to be reduced by 95% to have an effective impact on populations.

Vosburgh and Irby (1998) similarly concluded that recreational shooting could be used as a tool to manage or limit colony expansion rather than eliminate populations. In 1994 and 1995, the authors monitored ten colonies open to shooting and eight colonies

closed to shooting in north-central Montana to determine the effects of recreational shooting on these colonies. Results indicated a 35% decline in overall prairie dog population size at shot colonies and 15% decline in control colonies during the shooting periods of each year (early to late summer). These numbers may be somewhat misleading, however, because prairie dog density was higher at shot colonies than control colonies during both spring and fall census periods (Vosburgh 1996). Presumably, 15% is the average annual mortality rate at these sites due to natural, non-human causes. It was hypothesized that the 35% reduction rate may have been offset by compensatory reproduction/survival in response to recreational shooting, especially because no statistical differences were detected between active burrow density or vegetation cover in shot and control colonies (Vosburgh 1996).

It is also possible that a relationship may exist between higher densities associated with shot colonies and survival associated with vigilant behavior. Prairie dogs subject to recreational shooting were more alert and were twice as likely to retreat into their burrows when humans approached than were prairie dogs on control colonies (Vosburgh 1996). This was likely a conditional response to avoid shooters. Vosburgh suggests that summer mortality may have been compensated for by decreased mortality or increased reproduction during other periods. The two year scope of the study, however, was not enough time to adequately evaluate compensatory responses (Vosburgh 1996).

In a more recent effort to quantify and qualify the effects of recreational shooting on prairie dog behavioral effects, Pauli and Buskirk (2007b) challenge the notion that prairie dogs can quickly rebound from hunting losses through compensatory

mechanisms. During the summers of 2003—2004, attributes of five paired shot/control prairie dog colonies were compared on the Thunder Basin National Grassland, Wyoming. Methods included above-ground scanning counts, live-trapped/marked individuals and fecal collection. Body condition was assessed by obtaining a ratio of weight to hind-foot length from live-trapped animals. Immediately following shooting, alertness increased in treatment colonies from 5% to 29% of aboveground activity. Shooting did not significantly affect juvenile body condition, but did reduce adult body condition. In contrast, while adults exhibited similar stress levels before and after shooting; juveniles displayed increased stress levels after shooting. The difference in stress level response between the age groups is likely because juveniles tended to stay aboveground during shooting periods, while adults sought refuge belowground. This observation also helps to explain why juveniles were disproportionately shot, when compared to adults. Higher stress levels, while not immediately apparent by reduced juvenile body conditions, may result in reduced future survival and recruitment (Pauli and Buskirk 2007b).

In addition to generally decreased body condition, flea loads increased by 30% in adult prairie dogs on colonies subjected to shooting (Pauli 2005). This was probably a result of a combination of related factors such as excess fleas displaced from shot prairie dogs transferring to survivors. Flea loads remained elevated in these survivors because shooting reduced the amount of time adult prairie dogs spent aboveground-socializing and allogrooming. While flea loads returned to pre-shooting levels within one year, the interim period may have significant implications for the transmission of

disease, especially plague, as higher flea loads increase the risk of plague transmission (Pauli 2005).

Both shot and control prairie dog colonies increased in areal size during the 2003—2004 study (Pauli 2005). Non-hunted colonies exhibited a greater increase, however, suggesting that recreational shooting mortality may not have been compensatory when shooting pressure reduces a prairie dog population by 25 to 30%. Male densities were able to rebound within one year of shooting pressure even though males were disproportionately shot more often (Pauli 2005). This may be because less males were forced to disperse, or because the “vacancies” left by the removed males provided room for male immigrants. Females rarely disperse from natal colonies (Hoogland 2006, Hoogland 1982, Garrett and Franklin 1981).

Some density dependant factors that tend to limit population growth are healthy for the colony as a whole; for example, dispersal of males discourages inbreeding (Hoogland 1982). If recreational shooting is affecting density dependant factors that typically serve to regulate population health, there may be profound implications for future reproductive capability, ultimately affecting long term survival and recruitment (Pauli and Buskirk 2007b). Age-sex groups also differed in response to shooting (Pauli and Buskirk 2007b). These differences may lead to a decrease in reproductive ability the year following shooting, indicating that risk-disturbance overwhelmed the density-dependant effects of shooting in prairie dogs.

Secondary effects of recreational shooting

Lead poisoning can occur in many vertebrate species and is especially prevalent in raptors, as a result of infesting bullet fragments containing lead while scavenging on rodent carcasses (Kramer 1997). In a brief demonstration of ten recovered prairie dog carcasses that had been shot, four contained metal fragments (Stephens et al. 2008). The majority of fragments were copper (used in cartridge jackets) but three of the four carcasses contained an average of 11.5 mg lead. The lead fragments are small enough to be ingested by a raptor, but probably not large enough to be avoided (Stephens et al. 2008).

In a more thorough analysis, Pauli and Buskirk (2007a) evaluated 59 prairie dog carcasses that had been shot with both jacketed and expanding .223 cartridges. Only 7% of prairie dogs shot with jacketed bullets contained metal fragments, but 87% of prairie dogs shot with expanding-type bullets contained metal fragments. Because jacketed bullets typically passed-through prairie dog carcasses, Pauli and Buskirk (2007a) recommended either usage of jacketed bullets, or lead free ammunition for recreational shooting of prairie dogs in order to lower the risk of lead poisoning to scavenging raptors and mammals.

CHAPTER 5

PRAIRIE DOG TRANSLOCATION

Prairie dog management can include both population reduction and expansion. As such, managers often relocate animals from healthy, high-density colonies, to either establish or supplement extinct, recently plagued or low-density colonies. This process is known as translocation. Translocation programs vary, but typically include live trapping prairie dogs in wire mesh cages (Truett et al. 2001). Translocation has been used recently to restore populations after plague induced declines (Dullum et al. 2005). If a colony does not die off completely, recolonization is slow. This occurs because in areas where plague is present, nearby colonies have also been affected. Otherwise, nearby colonies might have provided immigrants for recolonization (Knowles 1986).

Early translocation efforts, which included random trap and release of individual prairie dogs, were not very successful. Now, wildlife managers can assemble new coteries (family units) whose age and sex ratios resemble those under natural conditions. The success of a translocation program can depend on a variety of factors,

both controlled and environmental. These include time of year, predator control, source population selection, recipient site suitability, socialization and sex/age ratios at release.

Once prairie dogs are trapped an immediate application of a flea control agent is applied (Truett et al. 2001). This practice reduces flea and disease transmission between both conspecifics and human handlers. Other prairie dog collection methods may include capture after burrow flooding or use of a vacuum truck (Truett et al. 2001). Because livetrapping while females are lactating severely reduces survivability of juveniles, it is best to focus trapping efforts after juveniles are weaned, typically in June or July (Hoogland 2006). Acceptance of bait placed in traps may be greater later in summer as well, when less green forage is available (Henderson 1989). Care must be taken to check traps regularly as prairie dogs are particularly susceptible to heat stress.

To increase reproductive success at the recipient site, Hoogland (2006) suggests that sex ratios be skewed toward females. This more closely matches coterie assemblage under natural conditions. Alternatively, early translocation of males to sites without established burrow systems may aid in creating burrows for subsequent release of females and juveniles later in the summer (Jacquart 1986). A typical prairie dog coterie, or family unit, consists of one adult male, three to four adult females and their offspring (Hoogland 1995). Survivorship may increase when prairie dogs are translocated as a coterie (Shier 2006a,b). Other studies indicate that keeping family units intact may not be as important for survival (Long 2006, Bly-Honess 2004). Whether coterie relocation is important to long-term survival or not, live trapping prairie dogs from adjacent burrows is probably the most efficient method, and may often include family members.

Source populations

Ideal source populations are large, high-density and disease-free. Population reduction and removal may be warranted in areas where development is imminent, or control is desired due to human or agricultural concerns. Removal of less than 25% of a healthy prairie dog population does not affect long-term survival (Long et al. 2006). After capture and flea treatment, prairie dogs should be quarantined and observed for signs of sickness for fourteen days. It is suggested that autopsies be performed on any individuals that die during this time (Long et al. 2006). Quarantine facilities should be well-ventilated, climate-controlled, and provide food and water ad libitum (Mariani and Williams 1998). Individuals who successfully complete the quarantine process are ready for release at the new colony site.

Recipient site

In addition to locating a healthy source population, translocation success can be greatly enhanced by identifying a suitable recipient site. Roe and Roe (2003) developed habitat suitability guidelines for prairie dog translocation that include evaluation of soils, vegetation height, cover and slope (see also Reading and Matchett (1997) for attributes of Montana prairie dog colonies). Of course, historical records and pre-existing burrows likely provide the best indicators of habitat suitability. If prairie dogs were present at a site in the recent or historic past, suitability is high and relocation efforts will probably be more successful than attempting to establish a prairie dog population at a site that has never been occupied (Long et al. 2006).

Suitable release sites may fall under one of the following four categories:

1) Recently abandoned/controlled colonies

    a. Burrows still intact and visible

    b. Offers immediate protection from predators

    c. May need insecticide treatment pre-release, especially if plague has recently been present (Truett et al. 2001)

2) Historic locations with evidence of past occupancy

    a. May be located via photographs or chemical records

    b. Prairie dogs will readily find and excavate old burrows, even if they have become plugged/overgrown

3) Other existing suitable site

    a. May not have evidence of past occupancy

    b. Often identified via remote sensing, either satellite imagery or aerial photos

    c. Suitable vegetative and physical attributes present (Roe and Roe 2003, Reading and Matchett 1997)

4) Man-made site

    a. Typically includes habitat modification

b. Employs use of artificial burrows, nesting chambers and retention/acclimation cages

Unless recently occupied, the recipient site may need habitat alteration to achieve conditions favorable to prairie dog release. This is especially true if vegetation is greater than 12cm high (Truett et al. 2001). Shrubs, if present, should be removed or reduced in height to facilitate predator detection and escape. Mowing, grazing, burning, chaining and herbicide application are all acceptable methods, although livestock grazing and burning are probably the most easily achieved (Truett et al. 2001).

Prairie dogs may disperse upon release, in search of familiar surroundings or family members. A variety of methods have been employed to discourage dispersal at release sites. These include retention baskets and acclimation cages placed over a (man-made) burrow. These burrows may also be connected to a below ground nesting chamber (also man-made). Food and water may be provided at acclimation cages to decrease stress and lessen dispersal tendencies (Truett et al. 2001).

In addition to acclimating translocated prairie dogs to their new environment, aboveground cages offer temporary protection from predators. Recently translocated prairie dogs may become disoriented above ground, and are especially vulnerable to predation. In the absence of acclimation cages, it may be favorable to control mammalian predators such as badgers and coyotes at the release site before, during and after translocation (Truett et al. 2001).

Translocation efforts

Attempts to recover prairie dog populations reduced by plague were successful in north-central Montana (Dullum et al. 2005). Releases varied by group size and colony area. Researchers drilled holes to provide immediate shelter to prairie dogs at the release site, but did not provide retention baskets or acclimation cages. Sites with vegetation greater than 15 cm tall were mowed to accommodate prairie dog preference. Attempts were made to keep individuals from similar colony areas together, but animals were not marked to indicate kinship. Prairie dogs were dusted with commercial flea powder before release, but were not quarantined.

Survival rates were high; 5 of the 6 experimental colonies exhibited growth within 1 year of release and were considered “self-sustaining.” Prairie dogs were released in groups of 60 and 120, but group size had no significant effect on survivability. Prairie dogs released at large colonies experienced higher survival rates than those released at smaller colonies. This was probably because a sufficient prairie dog population was present to detect predators. Regardless of release size, most colonies exhibited growth within the first year post-release (Dullum et al. 2005).

A Colorado study that examined the effects of group size on survival after translocation found differences in release size. Researchers released groups of 10, 30 and 60 prairie dogs at colonies eradicated by plague. One year later, the only group size with more survivors than animals released were those with 60 prairie dogs (Robinette et al. 1995). The Montana results may have differed from the Colorado results because Dullum et al. (2005) only examined groups of 60 or more, while Robinette et al. (1995) examined groups of 60 or less. Release size of 60 individuals

may be approaching the minimum number for fast recovery and sustainability of prairie dog populations, although further work is needed to validate this assumption.

In recent years, the importance of social learning has been shown to play a role on survivorship of juvenile prairie dogs, and may have important implications on post-release survival (Shier and Owings 2006, 2007). Because predation poses the highest mortality risk after prairie dog translocation, efforts have been aimed at training juveniles to recognize and respond to predatory stimulus. In an experiment, juvenile prairie dogs were trained to recognize alarm calls at presentation of various predators. Later, these juveniles responded accordingly to the playback of alarm calls only (Shier and Owings 2006). In a similar trial, juveniles trained with experienced adults had higher success than those conditioned to playback calls only (Shier and Owings 2007). This type of social training, while time consuming, and likely costly, may increase post-release survival of juveniles, especially in areas of high conservation importance.

Table 5. Capture/release type, size and survivability of prairie dog translocations

Capture type	Release type	Av. # of dogs released	Av. size of colony one year post release	Source
Non-related individuals; mimic natural sex ratios	Hard release following plague epizootic	10	0.46	Robinette et al. 1995
		30	0.81	
		60	1.17	
Individuals retained from adjacent colony areas	Artificial burrows following plague epizootic	60	0.77	Dullum et al. 2005
		120	1.1	

Related individuals	n/a	70	0.4*	Long et al. 2006
Non-related individuals	n/a	70	0.5*	

*Long et al. (2006) calculated only surviving individuals-did not include colony growth

Translocation shows much promise for localized prairie dog conservation. Translocation may be a useful tool for prairie dog management in areas where population reduction is desired, such as in urban settings or areas planned for future development. Translocation may also serve to establish new colonies where prairie dog populations are desired, or supplement existing, low-density colonies following recent plague or control. No information is available, however, on relative economic costs of prairie dog translocation, but time-costs may vary depending on distance between donor and recipient sites, trapping and quarantine protocol and whether prairie dogs are translocated as functional coteries or existing family units.

CHAPTER 6

COLONY EXPANSION AND DISPERSAL

Prairie dog recovery may be assisted by facilitating colony expansion. The same habitat alteration methods used to ready a colony for successful translocation (burning, grazing, mowing, chemical control, etc.) may be implemented adjacent to active colonies to encourage colony expansion. Often, prairie dog colonies have become small and isolated as a result of human activities and/or plague. This phenomenon may be beneficial to reduce the exposure of plague and retain genetic variability in some areas but may not provide enough suitable habitat necessary for a fully functional grassland ecosystem at a large scale (Proctor et al. 2006, Trudeau et al. 2004). Furthermore, prairie dog management decisions are typically based on cumulative areas of occupancy, rather than actual prairie dog numbers (Proctor et al. 2006). For

these reasons, ecologists and land and wildlife managers are interested in facilitating restoration of prairie dogs through habitat modifications to encourage colony expansion.

Population Dynamics

Compared to some other rodents, prairie dogs reproduce slowly (Hoogland 2001). Small rodents such as voles or mice are capable of birthing multiple litters/year, ranging from two to nine young per litter (Pugh et al. 2003, Tamarin 1985, King 1968). Female black-tailed prairie dogs produce only one litter per year, and while females may give birth to up to eight offspring (Knowles 1987), infant mortality is high due to predation and infanticide (Hoogland 2001). Litter size averages three to four young at weaning (Hoogland 2003). Even so, prairie dogs are capable of exhibiting a high growth rate, especially when density within a colony is low (Crosby and Graham 1986, Knowles 1987). High growth rates are often exhibited following a plague outbreak, chemical control, or after initiation of a new colony (Cully 1997, Cully et al. 1997).

Prairie dog colonies can rebound quickly after a population crash, either natural or unnatural, because the remaining individuals grow faster, survive better, are more likely to breed as yearlings, and have larger litters (Hoogland 2006). This phenomenon is possible due to the absence of density-dependant factors such as food and space availability which would otherwise limit the population. When populations are not limited prairie dog colonies can demonstrate an annual growth rate as high as 2.19 (Crosby

and Graham 1986). Knowles (1985) observed dispersers traveling on roads and trails. These pathways may facilitate intercolony dispersal.

Dispersal and mortality factors

Parameters can be manipulated to achieve population growth or reduction. Under natural conditions (in the absence of plague or human-related population reduction), the three main causes of prairie dog mortality are predation, infanticide and inability to survive the winter (Hoogland 2006). Predation has been discussed elsewhere in this review (see Chapters 1 and 3). Infanticide can eliminate up to 39% of all litters born (Hoogland 2001) and may be a response to overcrowding (Fox 1975a, b). Winter survival depends on a number of environmental factors including precipitation, forage availability, body condition and length of season (Lehmer and Van Horne 2001).

When young-of-the-year emerge from burrows, competition for food and space occurs. Prairie dogs experience a limited amount of space in burrows and as food becomes limiting in the center of town, prairie dogs forage outward (Crosby and Graham 1986). As a colony ages, prairie dogs tend to focus feeding activities toward the outer edge of the colony, where they select for new vegetative growth, but return to the well-developed burrows in the interior area to sleep and breed (Garrett et al. 1982). This forces density-dependant dispersal of male yearlings, presumably to avoid

inbreeding (Hoogland 1982). Dispersing males were found with bite marks to the head and neck (Knowles 1985), likely obtained from a conflict over a limiting resource such as food or space. The combination of immigration and emigration of males to and from colonies encourages and maintains genetic variability, while discouraging inbreeding (Garrett and Franklin 1981). Females tend to stay at the natal colony. Dispersal of females does occur, although very rarely. The females that do disperse are typically older (Garrett and Franklin 1981) and usually travel long distances (Hoogland 2006). Long term field observations of prairie dogs revealed the genetic structure exhibited in most prairie dog colonies (female philopatry and polygymous mating) maintains a high rate of genetic diversity within individuals and coteries (Dobson et al. 2004). The dispersal patterns exhibited by prairie dogs (typically young males) help to explain why older colonies are more genetically similar than newer colonies, which may have been recently founded by dispersers (Roach et al. 2001).

Prairie dogs that disperse are more vulnerable to predation than those who remain in the home colony (Hoogland 2006). Dispersal may be hundreds of yards to several miles. If successful, dispersal results in colony expansion, repopulation of old prairie dog colonies and establishment of new colonies. Intracolony dispersal may occur between coteries, but highest mortality rates occur during intercolony dispersal, as yearling males move away from a colony (Garrett and Franklin 1981).

Habitat alteration to “direct” dispersal can reduce predation and improve survivability in two ways. First, removal of tall vegetation/shrubs can increase detection and facilitate escape from predators. Second, availability of adjacent habitat may cause dispersers to move from the colony edge rather than migrate to a different, or initiate a

new, colony. Prairie dogs may disperse from 2—10 km (Garrett and Franklin 1981, Knowles 1985, Crosby and Graham 1986). Predation on these intercolony dispersers is particularly high because calls cannot be heard to warn of danger, and predator hiding cover is often available away from a prairie dog colony. Colony expansion rather than long-range dispersal likely improves the colony growth rate and survivability as a whole.

Infanticide is a large cause of mortality among prairie dogs and can eliminate up to 39% of all litters born (Hoogland 2001). Three types of infanticide can occur, as described in Hoogland (1995 and 2006). The first, and most common, involves lactating females who kill and cannibalize offspring of close kin living in the same coterie (Type-I). The most likely explanation for this behavior is to gain nutrients essential for the lactating mother and her offspring. Type-II infanticide involves the killing and cannibalism of litters abandoned by mothers who do not show maternal behaviors (building a nest, defending nursery burrow, etc). Type-III infanticide is rare and occurs when invading males take over a territory and kill and cannibalize young juveniles that have recently emerged from the natal burrow (Hoogland 1995, 2006). Because infanticide plays such a large role in prairie dog survival, it has been hypothesized that prairie dog populations could be managed by stimulating/discouraging natural infanticide (Hoogland 2006), although it is not known how this may be achieved.

Winter Survival

Black-tailed prairie dogs do not hibernate and continually forage above ground throughout winter (except during periods of extreme cold or inclement weather). During

winter, any available above ground forage is typically of low nutritional value, so winter survival depends largely on fat accumulation. Inability to survive the winter often occurs with the youngest, or the oldest prairie dogs, as they are usually lightest, and have less fat stores than heavy, middle-aged prairie dogs (Hoogland 1995, 2006). Manipulation of above ground forage, such as applying fertilizer during summer and fall at prairie dog colonies, may ensure that enough nutrients are available in above ground forage to increase winter survival in areas where colony expansion is desired. In an effort to enhance vegetative growth with the hope of discouraging prairie dogs, 30 lbs of nitrogen per acre was applied at a prairie dog colony in Kansas (Snell and Hlavachick 1980). The resulting forage was consequently severely grazed by prairie dogs, which probably served to enhance their fitness rather than decrease it. Although in this case the manager's intended outcome was not achieved, this method may show promise where increased prairie dog survivability and fitness is desired.

Habitat modifications to encourage expansion

Prairie dog colony expansion primarily occurs when suitable habitat is located nearby (Garrett et al. 1982). Just as visual and physical barriers may halt expansion of prairie dog colonies (Witmer et al. 2008, Franklin and Garrett 1989), absence or removal of these barriers may direct colony expansion toward areas that are favorable and prairie dog colonization is desirable. Similarly, while deferred grazing may halt expansion or limit colony size (Snell and Hlavachick 1980), the reverse may aid in colony expansion. For example, heavy livestock grazing early and throughout the

growing season may provide optimal habitat for prairie dog expansion. This type of prescribed grazing should be used with caution, however, because it is likely to change plant species composition, increase erosion, and reduce productivity of palatable plant species after time, resulting in decreased range condition (Holochek et al. 1998, Pinchak et al. 1990, Pickford 1932). Furthermore, areas of shrub removal, especially sagebrush, should be limited to areas that are not of concern to greater sage-grouse and other sagebrush obligates (Frisina et al. 2001).

If prairie dog survivability can be increased by managing the top three natural mortality factors (predation, infanticide, winter survival), prairie dog densities will increase within a colony. When density-dependant factors become constrained, both intracolony and intercolony dispersal occurs. If nearby habitat is suitable for prairie dog colonization, intracolony dispersal is more likely, resulting in colony expansion rather than intercolony dispersal, and is accompanied by a decrease in dispersal-related predation. The following studies provide examples of how habitat may be altered to encourage prairie dog expansion.

In North Dakota, a combination of controlled burns and brush removal was used in an effort to increase prairie dog habitat and encourage colony expansion (Milne-Laux and Sweitzer 2006). Prairie dog colonies were chosen that had a recent history of expansion, which indicates the colonies are healthy, high-density and growing. Prairie dogs responded to the treatments by disproportionate expansion into the treated areas, when compared to the adjacent, untreated areas. In addition to the lack of cover at treatments, the expansion response was also related to weather, badger presence and colony density (Milne-Laux and Sweitzer 2006).

In Colorado, the influence of wild and prescribed burns was examined to determine the effects on colony expansion (Augustine et al. 2007). Results of this research indicate prairie dog expansion rate is marginally greater (P=0.066) in adjacent burned areas than unburned areas. In this effort, unburned colonies exhibited variable expansion rates, but all burned colonies had high expansion rates. Because this study was conducted during years of below-average rainfall, the authors hypothesize that colony expansion was probably higher than normal because of a limited food supply. The authors suggest that a similar effort completed in years of above-average precipitation may have resulted in more dramatic results, with prairie dogs having less of a tendency to expand unless ample habitat was available (Augustine et al. 2007).

These studies indicate that habitat manipulation can be used to aid the conservation of prairie dogs. Such methods also result in a dramatic landscape change, which may not be suitable for all species of concern, and should be limited to areas that are focal points of prairie dog conservation. Additional information is needed to determine how these landscape changes, and methods used, affect the surrounding prairie ecosystem.

White-tailed prairie dogs

Like black-tailed prairie dogs, female white-tailed prairie dogs tend to remain in natal areas, while juvenile and yearling males are the predominant dispersers (Michener 1983, Clark 1977). Unlike black-tailed prairie dogs, white-tailed prairie dogs rarely disperse farther than 200m (Pauli et al. 2006b). Also, because white-tailed prairie dogs

can colonize areas of varying habitat and topography, habitat manipulation to encourage or discourage colony expansion may be more difficult than for black-tailed prairie dogs. White-tailed prairie dogs do not actively clip vegetation, and display a higher tolerance for shrubs and tall vegetation than black-tailed prairie dogs (Menkens 1987) therefore, prescribed grazing or burning may not be as beneficial for that species.

Infanticide has not been documented as a major cause of death for white-tailed prairie dogs, but predation and habitat loss have been cited (Pauli et al. 2006b). Recent oil and gas drilling and exploration has limited white-tailed prairie dog habitat in Wyoming, and this may also be a threat in Montana. Because habitat and social dynamics differ from black-tailed prairie dogs, little is known about the role of drought, flooding and other environmental limiting factors for white-tailed prairie dogs. White-tailed prairie dogs are also true hibernators, unlike black-tailed prairie dogs, so their winter survival may depend on a different set of factors. More research is needed on survival, reproduction and dispersal characteristics of white-tailed prairie dogs so managers may better understand if and how these parameters can be managed to achieve desired conservation goals, including colony expansion.

CHAPTER 7

METHODS TO ESTIMATE OCCUPIED ACREAGE

Black-tailed prairie dogs have previously been assigned candidate species status under the USFWS Endangered Species Act. When prairie dogs were removed from the candidate species list in 2004 (USFWS 2004) the decision for removal was probably heavily influenced by recent survey efforts (Odell et al. 2007) which resulted in an increase of documented occupied acreage (from 676,000 acres to 1,842,000 acres, USFWS 2004). Prairie dog colonies had likely not expanded during this time period, but rather the candidate status prompted wildlife agencies and managers to increase efforts to document occupied acreage. The resulting figure, while about three times larger than was previously thought, was still less than 5 percent of estimated historical occupancy. Because the USFWS is currently conducting a range-wide status review of the black-tailed prairie dog (USFWS 2008), more methods of estimating prairie dog occupancy and abundance are being developed and refined. Current range-wide estimates of

prairie dog occupancy suggest 2,152,000 acres of occupied prairie dog habitat (USFWS 2008).

Methods to estimate abundance

Prairie dog abundance can be documented via visual counts (Powell et al. 1994, Menkens et al. 1990), live-trapping/marking for absolute counts, and population estimates can be obtained by mark-recapture or mark-resight (Severson and Plumb 1998). Burrow counts may reflect a measure of density, but are not usually suitable for population inferences. Attempts to quantify colony size and density have been made by plugging all burrows, then counting those that have been opened (Tietjan and Matschke 1982). Prairie dog densities vary between and within colonies, and burrow density varies as well, and may vary in relation to population densities (Powell et al. 1994). Burrow counts are often used to track population trends, but can be unreliable, especially when populations are declining (Facka et al. 2008). Colony size typically refers to total population, rather than areal size, and density estimates are useful in determining total colony size only at small scales due to variations in density.

In an evaluation of both white-tailed and black-tailed prairie dog habitat, above ground visual counts were highly correlated with mark-recapture estimates, and visual counts provide an acceptable index of prairie dog population size (Menkens et al. 1990, Severson and Plumb 1998). Yet, visual counts can underestimate prairie dog densities, thus counts should be conducted during periods of highest activity, when maximum numbers of prairie dogs are above ground (Powell et al 2004). This time period can

vary by season and latitude. Visual obstructions skewing results in aboveground counts are typically negligible for black-tailed prairie dogs (Severson and Plumb 1998), but may need to be taken into consideration for white-tailed prairie dogs (Menkens et al, 1990) due to differences in social, colony and vegetative structure, which occurs between the species.

Absolute population counts are best obtained by absolute marking, mark-recapture, visual counts or by a newer method, mark-resight. Maximum above-ground counts correlate with mark-recapture methods (Facka et al. 2008, Menkens et al. 1990, Fagerstone and Biggins 1986), but can be corrected using mark-resight (Facka et al. 2008, Magle et al. 2007). Mark-resight uses a double-sampling technique, where a sample of animals are marked, then total above-ground counts are made, including both marked and unmarked animals. This method was deemed superior to other population estimate methods due to a reduced effort needed, even though the average probability of re-sighting an animal was slightly lower than the recapture rate (Facka et al. 2008). It is important to note that this method was tested on relatively small towns, which may be troublesome because densities are often lower on small or newly initiated prairie dog colonies. This method requires validation of large, or older prairie dog colonies. See Facka et al. (2008) for a suggested approach to estimate prairie dog abundance at multiple scales.

Methods to estimate areal occupancy

Most importance is usually placed on area of occupied habitat, or suitable habitat and a variety of methods have been used to determine such areas. When areal extent of prairie dog occupancy is desired, remote sensing (aerial photos or satellite imagery) is usually employed (Assal and Lockwood 2007, Sidle et al. 2002, Dalsted et al. 1981), and boundary mapping is also used (Sidle et al. 2001). More recently, an aerial line-intercept method has been used (White et al. 2005, Sidle et al. 2001), although this method has drawn criticism (Assal and Lockwood 2007, Miller et al. 2005).

The aerial line-intercept method, similar to the line-intercept used in groundwork to estimate vegetative canopy cover, uses an aircraft flown along a series of pre-determined transect lines (Sidle et al. 2001). An aircraft passenger, and sometimes the pilot, enters a waypoint in a Global Positioning System (GPS) unit when the flown line intercepts a prairie dog colony boundary, and may include a distinction between active and inactive boundary points. Sidle et al. (2001) stratified a 4-state area (Nebraska, North Dakota, South Dakota and Wyoming) by colony density. Areas known to include prairie dog colonies were included in the high density strata, and areas not known to include prairie dog colonies made up the low density strata. In this way, unknown prairie dog colonies can be detected from the air. Similar methods have been used in Montana to estimate occupied acreage (Rauscher 2009, pers. comm.).

White et al. (2005a) followed methodology from Sidle et al. (2001) to estimate occupied acreage in Colorado, but estimated active colonies only, and did not provide a measure of inactive colonies. White (2005a) estimated 255,398 ha occupied throughout the survey area. This effort was criticized by Miller et al. (2005). In response to White (2005a), Miller (2005) conducted ground inspections of a non-random sample of

transects flown in the White study. Of the 1596 transects flown in 2003, eighteen classified as active were inspected from the ground and Miller (2005) suggested that White's data was prone to significant overestimation bias. Some areas previously classified as active either showed no signs of prairie dogs, were (or had become) inactive, or exhibited low densities due to a population reduction attributed to plague. Because this work was conducted two years after the initial aerial classification, it is possible that colony demographics (i.e.; active/inactive) may have changed, although it is unlikely that evidence of past activity could be overlooked. For example, if a colony had been subject to plague or control within the two years between surveys, sufficient evidence would still exist to suggest previous occupancy. One parameter used to indicate an inactive burrow-spider webbing-is probably not a meaningful measure of prairie dog activity because webs are typically spun overnight and presence does not necessarily indicate an inactive burrow. Also, Miller (2005) only inspected transects that may have been incorrectly classified as active, but did not inspect transects that may have missed areas of occupancy, or where new colonies may have formed.

White et al. (2005b) countered the assertions in Miller (2005) primarily because the ground inspections conducted by Miller (2005) could only have resulted in a negative bias, the same aerial tracks may not have been surveyed, and the surveys were conducted two years apart. The critiques of White (2005a) by Miller (2005) resulted in protocol changes that strengthened a future aerial line-transect survey effort for Colorado in 2006—2007 (Odell et al. 2008). These include an optimal allocation procedure to determine number of transects needed, entry of both active and non-active colony portions, and entry of exact flight line for future ground inspection efforts (Odell

et al. 2008, White et al. 2005b). Flight transects and ground-truthing were stratified by county, and included attempts to ground-truth 10% of all aerial transects. Ground-truthing suggested that aerial surveys accounted for 96% of true colony intercept lengths, but overestimated active colony area. Uncorrected estimates included 329, 529 active ha and 18, 292 inactive ha. This estimate indicated a 29% increase in active colony area when compared to the 2003 survey (White et al. 2005a). Furthermore, this estimate should be considered a minimum, because known colonies near urban areas were not included in the aerial surveys. Odell et al. (2008, p. 1315) further conclude that the ground-truthing conducted by Miller et al. (2005) was "meaningless because of the extremely long interval between surveys and the natural dynamics of prairie dog populations."

While no remote-sensing method is foolproof, aerial line-transects likely represent a time- and cost-effective method for gathering vast quantities of data over a large landscape scale. Future similar efforts will likely strengthen the protocol used for developing aerial line-transects to estimate areal extent of prairie dog colonies. It is also probable that the exchanges provided by Miller (2005), White (2005b) and Odell (2008) will greatly strengthen the science associated with prairie dog conservation.

Aerial photograph series may also be used to estimate occupied area. The USDA Farm Services Agency (FSA) routinely acquires aerial imagery available for government and civilian use. Created for agriculture-related inventory, National Agriculture Imagery Program (NAIP) has become a recent tool used to estimate prairie dog acreage. In 2006, South Dakota Department of Game, Fish and Parks obtained transects from NAIP imagery (2m resolution) and created a GIS layer stratified by areas

of high and low prairie dog density. Stratification was based on distribution of previously known prairie dog colonies (Kempema 2007). Transects were digitized and prairie dog colonies were identified. Later, the prairie dog colonies identified from NAIP imagery were evaluated from the ground. NAIP imagery adequately detected 93% of the colonies confirmed by ground-truthing, although it is unclear whether or not some NAIP "detected" areas were currently occupied. A major limitation of this methodology was that NAIP imagery, and ground-truthing was not sufficient in determining active status (Kempema 2007).

The Montana Natural Heritage Program has recently completed a pilot project to map a sample of prairie dog colonies in Montana using NAIP imagery (Bryce Maxell, pers. comm. 2009). Preliminary results indicate NAIP is useful to determine recent prairie dog activity, except in badlands areas typified by bare soil. NAIP imagery was particularly useful because it accurately detected previously unknown colonies. Ongoing efforts include continued mapping and digitizing of prairie dog colonization statewide, and will include ground-truthing of these areas (Bryce Maxell, pers. comm. 2009).

Although NAIP imagery may not always be adequate to determine active status of prairie dog colonies, it is a powerful tool that can likely be used to detect trends in prairie dog colonization, especially as colonies grow. Due to the ease of availability, scope of coverage and relative quality, NAIP can be used as a wide-range monitoring tool, and may become much more powerful if combined with other survey efforts.

In 2007, Assal and Lockwood evaluated raw and enhanced satellite imagery and aerial line-transect surveys to determine which remote-sensing method yielded most accurate results. Aerial surveys provided the highest rates of false positives (active colonies noted where no colony existed) and raw satellite imagery had the highest rate of false negatives (failure to detect an active colony). Based on this research, satellite imagery was recommended for determining areal extent of prairie dog colonies for a combination of cost efficiency and accuracy. Assal and Lockwood (2007) used Landsat 7 imagery, which provided up to $15m^2$ resolution. One limitation of this satellite imagery was the inability to distinguish between grazing by livestock or prairie dogs. This method achieved only 69% accuracy and does not adequately distinguish between active and inactive colonies. As such, Landsat 7 satellite imagery may not be rigorous enough for management considerations, but would be suitable for identifying potential habitat.

In contrast, high-resolution satellite panchromatic imagery (IKONOS satellite) has resolution up to 1m and is suitable for identifying prairie dog colonies, and delineating boundaries (Biggins et al. 2006). Sidle et al. (2002) successfully identified active colonies via IKONOS imagery and used the imagery to connect outermost burrows to establish a boundary perimeter. These colonies were verified by aerial flights, and the authors suggest using quarter-townships as monitoring units. Unfortunately, this high-resolution satellite imagery is too cost-prohibitive at present for large-scale use. These costs might decline if private companies launch satellites with similar imagery solution to compete with IKONOS (Biggins et al. 2006, Sidle et al. 2002).

Mapping prairie dog colony boundaries with GPS receivers yields accurate results, but is quite time consuming and expensive. One limitation to this method is that active colonies must have already been identified before they can be mapped. Remote sensing using aerial transects/photography or satellite imagery may provide a reliable means for identifying previously unknown prairie dog colonies (Sidle et al. 2001). Combining remote sensing with on-the-ground GPS mapping may be the strongest measure of prairie dog colonization. Because a variety of prairie dog mapping methodologies have been proven, standardization of these methods would be helpful, especially at a state-wide level. As estimates of occupancy are completed and compared, it may be possible to assign conversion factors to various data collection methods, so estimates can be meaningfully compared. Another alternative may be to evaluate various methods, and establish one as the preferred method for future surveys. This would eliminate the need for confusing conversions or comparisons in Montana.

SUMMARY AND MANAGEMENT RECOMMENDATIONS

As reviewed in this document, Montana land and wildlife managers are within reach of a number of resources that can be used to meet statewide prairie dog population objectives. Regardless of the level of protection (if any) that prairie dogs are afforded, prairie dog and grassland ecosystem conservation will continue to be an important focus throughout central and eastern Montana. Major recent advances have been made in prairie dog habitat and population detection, translocation procedures and understanding of plague dynamics but there remains much work to be done.

Plague will likely continue as the most pervasive threat to prairie dogs and associated colony dynamics. More information is needed on the exact mechanisms driving both enzootic and epizootic aspects of the disease. An effective plague vaccine, evidence of plague antibodies in surviving prairie dogs, successful dusting formulations and population recovery observed at some colonies show promise of plague recovery.

Future research that focuses on plague transmission and possible climate and landscape effects is needed. While plague eradication may not be possible at this time, or ever, a reduction in plague occurrence and duration of epizootics should be achievable, as evidenced at experimental sites.

Prairie dog population control will always be a controversial issue. Prairie dog colonization throughout the state will depend largely upon the land use patterns that exist statewide. It is important to remember that management can be achieved through a variety of means, and not all control measures are lethal in practice. It is known that control can be costly, and often outweighs any derived benefits. If for no other reason than economics, prairie dog control should not be pursued unless at a small, localized scale. Large-scale control programs are generally not cost-effective and should not be attempted until indirect costs and benefits can be quantified.

Prairie dog management will be greatly aided by a better understanding of impacts of recreational shooting on prairie dog genetic diversity, survivability, direct impacts on habitat and indirect impacts on associated species. It is likely the answers to these questions will depend largely on size and location of colony, distance to nearest colony and other anthropogenic effects such as prairie dog control and nearby land uses. Some level of recreational shooting may be tolerable, and even desirable, in areas demonstrating healthy prairie dog populations, while other vulnerable or isolated populations should be protected. Another important consideration for land managers may be the economic inputs and outputs associated with recreational shooting. The exact dependence (or independence) of local Montana economies on recreational shooters is largely unknown. Due to concerns regarding ingestion of lead by

scavengers and raptors, it has been suggested that ammunition be restricted to either lead-free or fully jacketed bullets only. Ballistics testing is recommended to validate this suggestion. Such testing by an expert would likely increase acceptance of recommendations to shooters prior to ammunition restrictions.

Translocation shows much promise for establishing new colonies, or supplementing low-density colonies. However, translocation can become very time-consuming, depending on methods used. Future research needs include information on size and kinship of successful translocations, as well as importance of social and predator training. Predator control may be desirable at some sites, but the direct and indirect ecosystem effects of predator control should be examined. Alternatively, diets of predators and scavengers that depend on prairie dogs as a main dietary component could be used to determine the amount of prey-switching that occurs when prairie dogs are removed from or integrated into a local system.

The easiest method to encourage or discourage prairie dog colonization is probably through direct habitat manipulation. Research has shown that it is possible to "guide" prairie dog expansion in areas where expansion is desired. On the other hand, preventing colonization is much less costly than attempting to eradicate an established population. Natural prairie dog dynamics can be exploited to control growth rates and achieve desired prairie dog densities, especially in areas of plague or past control. More research is needed on the role of infanticide and the mechanisms driving intra- and intercolony dispersal. Much caution should be taken when a prairie dog habitat conversion project is considered. Pilot projects should be small and controlled, and management implications (including land-use, plant community and associated species)

should be estimated before any conversion project is attempted.

It is likely that prairie dog populations, and associated occupied and suitable habitat, will continue to fluctuate within some range throughout Montana. Standardization of measurements should be a goal so complete statewide counts, or documentation of occupied acres can be made. New methodologies, such as aerial transect flights and other remote-sensing technologies have made it possible to achieve relatively inexpensive estimates of prairie dog occupancy. However, the importance of ground-truthing and careful monitoring cannot be overstated.

Finally, more important than amount of occupied acreage or methodologies used to estimate acreage, it is imperative that Montana land and wildlife managers further develop guidelines that establish focal areas for prairie dog conservation-large enough to support prairie dog obligates, but also juxtaposed to allow gene flow. Proctor et al. (2006) has identified 5 focal areas for prairie dogs in Montana, each at least 4000 hectares in size. Management and conservation of prairie dogs at these focal areas may provide the habitat necessary for long-term sustainability of the prairie dog and related grassland ecosystems. If adequate habitat is provided, prairie dogs will continue to affect the landscape in their unique way-just as they have for thousands of years.

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GLOSSARY OF SELECTED TERMS

ad libitum: Provided unlimited access to food and water.

aerial: From the air; aerial photos are taken from aircraft.

allogrooming: Grooming of others within a species.

anthropogenic: Human-caused.

areal: Description of an area or piece of ground. Generally refers to size.

conspecific: Within the same species. All black-tailed prairie dogs are conspecifics.

coterie: Prairie dog family group, usually containing one adult male, two to three adult females and their young. Large coteries may contain two adult males.

deferred grazing: Postponement of livestock grazing until vegetation has reached some critical stage, such as flowering.

demography: Issues related to survival and reproduction of a species.

diet switching: Changing of food types in response to availability.

emigration: The movement away from an area.

infanticide: Killing offspring of one's own species. May or may not be related individuals.

immigration: Movement into an area.

intercolony dispersal: Dispersal between colonies.

intracolony dispersal: Dispersal within a colony, but to a different area/coterie.

philopatry: Remaining in the natal territory. Most female prairie dogs exhibit philopatry.

polygamous: Mating behavior in which an individual has more than one mate at a time.

sex ratio: The ratio of males to females in an animal population.

LITERATURE REVIEW INFORMATION SOURCES

Over 180 sources of information were evaluated for inclusion in this review. The vast majority is referred journal articles, but conference proceedings, graduate theses, book chapters and various technical reports are included as well. The following figure represents the publication types included in this review.

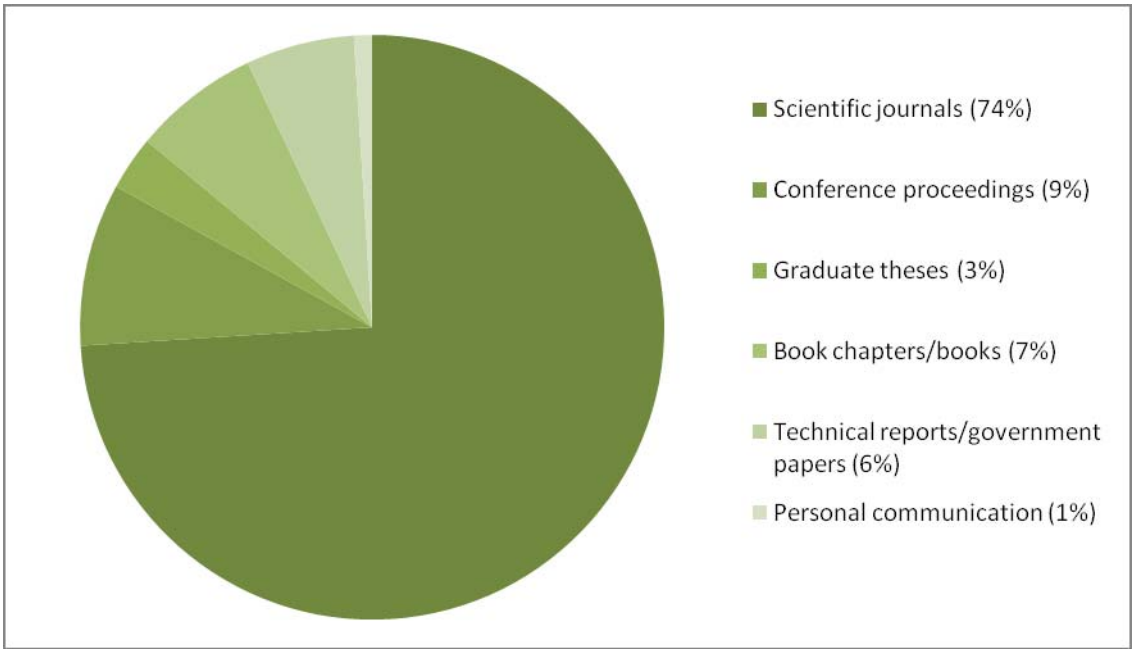

Figure 3. Information sources included in this literature review.