IMPACTS OF URBAN PRAIRIE DOGS ON SOILS IN BOULDER, COLORADO

By Matthew R. Olivier University of Colorado at Boulder

A thesis submitted to the University of Colorado at Boulder in partial fulfillment of the requirements to receive Honors designation in Environmental Studies May 2013

Thesis Advisors:

Dale Miller, Environmental Studies Nichole Barger, Ecology & Evolutionary Biology Timothy Seastedt, Ecology & Evolutionary Biology, Committee Chair

> © 2013 by Matthew R. Olivier All rights reserve

Table of Contents

Abstract	ii
Acknowledgments	iii
Introduction	1
Background	4
Climate Change in Arid ecosystems	4
Black-Tailed Prairie Dogs (Cynomys ludovicianus)	5
The Importance of Soil	9
Soil Erosion	10
Literature Review	13
Prairie Dogs Effects on Net Primary Productivity	13
The relationship between ungulate grazers and prairie dogs	16
Prairie Dogs as Keystone species	21
Plague (Yersinia pestis) and Prairie Dogs	23
Climate Change in Colorado	28
Desertification and shrubland encroachment of grasslands	30
Wind Erosion	32
Materials and Methods	39
Prairie Dogs in Boulder County	39
Sampling Sites	40
Methods	41
Data Analysis	43
Results	45
Soil Samples Results	45
Soil Samples	51
Are Urban Prairie Dogs Still Keystone Species and Ecosystem Engineers?	55
Bare Soil Data:	58
Desertification on Boulder prairie dog colonies	61
Implications and Recommendation	65
Bibliography	71

Abstract

The Colorado Front Range has experienced a significant increase in urbanization and habitat fragmentation over the past half century. This increase in urbanization has created a highly fragmented landscape with areas of green space surrounded by urban and suburban environments. Along the Front Range of Colorado, the intense foraging and grazing habits of native black-tailed prairie dogs (Cynomys ludovicianus) on fragmented Open Space Mountain Park lands is interacting with erosional forces, nonnative plant invasions, and global climate change resulting in what could be considered novel shrubland communities. In this honors thesis I examine the questions: could prairie dog interactions with different elements of global climate change, such as increased soil erosion, increased temperature, and increased variability in precipitation, potentially transform the mixed-grass prairie ecosystems found on Boulder County Open Space into shrublands? What do these potential interactions imply for prairie dog and land management practices on Boulder County Open Space? Surface soil samples were collected from eleven prairie dog colonies located throughout Boulder County and one colony from Broomfield County. Results were then compared to bare soil cover data obtained by city managers to examine how vulnerable these colonies are to events such as minor dust storms For all 12 colonies sampled the mean percentage TOC and TN contained in the surface soils increased as you moved from on colony to colony edge to off colony. These results and the comparison of these results to the bare soil cover data comparisons indicate that desertification may be occurring on prairie dog colonies in Boulder County. This has significant implications for land managers in Boulder if they aim to preserve the native grassland ecosystems on Boulder County Open Space and Mountain Parks' lands.

Acknowledgments

I would like to thank Stower Beals for helping me obtain the bare soil cover data that was compared to the results of my surface soil samples. I would also like to thank the undergraduate students working in Timothy Seastedt's lab for prepping my surface soil samples so they could be analyzed by the CHN Analyzer. Finally I would like to thank my Honors Committee, Timothy Seastedt, Nichole Barger, and Dale Miller.

Introduction

Anthropocentric changes to the earth's climate and atmospheric chemistry caused by human activities, such as the burning of fossil fuels and rainforest deforestation, are altering the unique ecosystems of the Colorado Front Range. This region where the mixed-grass and short-grass prairies transition into the dry pine forests of the foothills of the Southern Rocky Mountains has experienced a significant increase in urbanization and habitat fragmentation over the past half century. This increase in urbanization has created a highly fragmented landscape with areas of green space surrounded by urban and suburban environments. Along the Front Range of Colorado, the intense foraging and grazing habits of native black-tailed prairie dogs (*Cynomys ludovicianus*) on fragmented Open Space Mountain Park lands is interacting with erosional forces, nonnative plant invasions, and global climate change resulting in what could be considered novel shrubland communities.

Prairie dogs have traditionally been considered to function as both keystone species and ecosystem engineers that maintain grasslands. There have also been discussions in recent decades among conservationists for their potential listing as a threatened or endangered species. Despite these attributes, black-tailed prairie dogs in recent years have facilitated minor winter dust storms at several sites along the Colorado Front Range.



Figure 1.1. Jan. 7, 2009: dust storm from prairie dog colony west of HWY 93 Boulder

In this honors thesis I examine the questions: could prairie dog interactions with different elements of global climate change, such as increased soil erosion, increased temperature, and increased variability in precipitation, potentially transform the mixed-grass prairie ecosystems found on Boulder County Open Space into shrublands? What do these potential interactions imply for prairie dog and land management practices on Boulder County Open Space? To examine these questions I collected surface soil samples from eleven prairie dog colonies located throughout Boulder County and one colony from Broomfield County. Results were then compared to bare soil cover data obtained by city managers and recently analyzed by Beals (2012) on colonies that I collected surface soil samples from to examine how vulnerable these colonies are to events such as minor dust storms. My hypothesis is that Prairie dog foraging habits in conjunction with erosional forces and global climate change could potentially transform the mixed-grass prairie

ecosystems of Boulder County Open Space into shrublands. This transformation might occur due to increased erosion and the subsequent loss of soil organic matter on colonies resulting in a change in dominant plant species composition from mixed-grasses to forbs and small woody shrubs.

Background

Climate Change in Arid ecosystems

Arid grassland and dryland ecosystems of the western United States are uniquely vulnerable to global climate change due to the fact the plants and terrestrial organisms in this region experience both water and temperature stresses near or at their physical tolerances for survival. Thus minor changes in the region's average yearly temperature and precipitation or changes in the magnitude and frequency of large scale climatic disturbances could significantly change the abundance, distribution, and composition of species in arid regions. These minor changes could also alter the ecosystem services that these arid regions provide (Archer & Predick, 2008). Current prediction models for climate change's impacts on the arid Southwest consist of warmer temperatures, a smaller number of frost events, an increased frequency of large scale climatic disturbances such as droughts, heat waves, and floods, and an increased demand for water by animals, vegetation, and humans (Archer & Predick, 2008). Additionally, below average snow packs coinciding with snow melting unseasonable early, will lower water supplies, create drought conditions, promote insect outbreaks, and increase the amount of wildfires that occur (Archer & Predick, 2008).

Precipitation predictions that take into account climate change for the arid Southwest boast a larger amount of uncertainty compared to the predictions for temperature. These climate predictions are based on very coarse and basic circulation models on a continental-scale that generally do not consider how land use or how changes in the type of vegetation cover affects climate. Also these precipitation prediction models tend to ignore important regional factors, such as the factors that influence monsoonal rainfall (Archer & Predick, 2008). Rainfall events are expected to increase in intensity, but their frequency is expected to decrease. Thus, soil erosion caused by runoff will increase in the arid Southwest after significant precipitation events. Also, wind erosion will likely increase during winter and spring due to the fact that there is less moisture in the surface soils of arid regions (Archer & Predick, 2008). Rain events and wind erosion typically remove nitrogen and other soil organic matter from soils. Thus increased water and wind erosion will result in increased losses of nitrogen and other soil organic matter from soils.

Black-Tailed Prairie Dogs (Cynomys ludovicianus)

Prairie dogs are large, herbivorous rodents that weigh approximately 1 kilogram when they reach adulthood. Prairie dogs live in burrows and they live colonially (Whicker & Detling, 1988). In the past, the black-tailed prairie dogs (Cynomys ludovicianus) were the most extensively distributed and the most abundant prairie dog species. They lived throughout both the mixed-grass and short-grass prairies of the Great Plains. Estimates of the average density and size of prairie dog colonies in the Great Plains prior to European settlement tend to vary, but Whicker and Detling (1988) estimate that they covered about forty million hectares in 1919. This area represents over twenty percent of the pristine mixed-grass and short-grass prairies available to prairie dogs prior to European settlement (Whicker & Detling, 1988). Prairie dogs have been historically viewed as agricultural and rangeland pests due to the fact that they compete with livestock for rangeland vegetation. Extensive and successful eradication efforts reduced their populations to less than two percent of those that existed a century ago (Whicker & Detling, 1988).

Prairie dogs live in family groups which are called coteries, and coteries tend to be very territorial. A prairie dog colony is typically composed of several coteries. Coteries can consist of just two individuals but can range up to twenty six prairie dogs. Studies have shown that the average coteries in South Dakota grasslands occupied areas of about 1 acre and ranged between 0.12 acres to 2.5 acres. These studies also showed that average coteries dug about 69 burrows, but the number of burrows created by single coteries ranged from just 5 burrows to 214 burrows (OSMP, 2010). Coteries construct multiple burrows to avoid being eaten by local predators, for sleeping, and for birthing their young. Due to the fact that Coteries are very territorial, the underground tunnel networks of one coterie do not connect with the tunnel networks of neighboring coteries. Aboveground coteries establish boundaries for their occupied territories through territorial disputes (OSMP, 2010). A coterie usually is made up of one adult male and several females, juveniles, and yearlings. The adult females and the male and female yearlings in a coterie are the young of females and the adult male from that coterie. However, in coteries the breeding males are the progeny of females from other coteries (OSMP, 2010).



Figure 2.1. Two black-tailed prairie dogs in a burrow.

Despite the fact that Prairie dogs have been historically viewed as agricultural and rangeland pests, they have also been labeled as both ecosystem engineers and keystone species. This is based on the belief that prairie dogs have a distinct effect on the biological diversity of grassland ecosystems. Keystone species include species that directly affect other species in their ecosystem. For example the direct affects of a keystone species might include predation and competition. Or the effects of a keystone species might be indirect because they act as ecosystem engineers, altering plant succession regimes and influencing the abundance and distribution of species in native ecosystems. There are some keystone species that influence other species and their abiotic environments both directly and indirectly (Lomolino & Smith, 2003). Prairie dog burrows provide shelter and nesting sites for small vertebrates and invertebrates such as

burrowing owls and tiger salamanders (Kotliar et al. 1999). Also, prairie dogs are an important source of prey for several predators such as the endangered black-footed ferret and the prairie rattlesnake (Kotliar et al. 1999). For conservation biologists the concepts of keystone species and ecosystem engineers are extremely important because when such species are extirpated from their native ecosystems the effects might spill over several trophic levels. This spill over could result in the collapse of local communities. However, more often than not these communities are replaced by communities of exotic generalist species that are adapted to the ever increasing human dominated landscape (Lomolino & Smith, 2003).



Figure 2.2. A black-tailed prairie dog

Historically, prairie dogs lived on extensive grasslands with very few restrictions to their movement and coexisted with large ungallant herbivors, such as bison (*Bison*

bison). Their populations were naturally controlled by predators such as black footed ferrets, raptors, and coyotes (*Canis latrans*). Prairie dogs that inhabit areas with very little anthropogenic land use changes, such as the Wind Cave National Park and parts of northern Mexico, retain their beneficial ecosystem effects, such as increased vegetation richness, diversity, and evenness. This is due to the fact that these pristine conditions are not as restrictive to prairie dog movements and colony expansions (Beals, 2012, & Coppock et al. 1983). In comparison, Boulder County is an extremely fragmented landscape with a great deal of urban and suburban development in the past half century. The densities of prairie dogs on colonies located in Boulder County are higher than colonies that are not surrounded by suburban and urban environments (Johnson and Collinge 2004), which might lead to changes in the local vegetation community composition and alter the competition for resources on colonies. When examining the effects of prairie dogs on vegetation in a similarly urban site outside Denver, Colorado, Magle and Crooks (2008) observed an increase in bare soil and forb cover on colonies.

The Importance of Soil

Earth's surface soils and the nutrients that they hold are in danger. This is evinced by events such the desertification of grasslands in central Mongolia, the dust-bowl events in northwest China, and the massive dust storms across north and central Africa that have occurred in the past ten years. Surface soil losses in some arid regions of the planet are greater than fifty tons per hectare in a single year this is almost a hundred times faster than the rate of soil formation, and this means that the Earth is losing approximately 0.5cm of surface soil per year in some regions (Banwart, 2011). Surface soils are at the center of Earth's critical zone, which is the thin veneer extending from the canopies of forests down to our aquifers (Banwart, 2011). Soils are formed when rocks break up and dissolve. This is helped along by soil organisms that create tiny particles that bind with decaying biomass and living microbes to form larger soil particles. Greater than 60% of fertile soil particles range from 0.25 mm to 10 mm (Banwart, 2011). These soil particles have a great deal of organic nutrients and minerals, which are processed by microbes into forms that are useful for plants. The pores spaces between soil particles retain enough moisture for biological growth, drainage of excess water, and to allow oxygen to reach plant roots (Banwart, 2011).

Soil Erosion

Soil erosion can have undesirable impacts on the landscapes and on the plants and animals that inhabitant those landscapes. Soil erosion, which is the loss or redistribution of soil by wind and water from the earth's surface, can radically change soil nutrient content, primary productivity, and even alter the landscape's topography. Severe soil erosion could also lead to health issues for the general public due to long-distance transport of contaminants contained in soils such as agricultural pesticides, herbicides, and radionuclides (Breshears et al. 2003). Erosion issues are particularly prominent in semi-arid and arid regions due to the rather sparse vegetation cover, which allows more wind and water to directly erode and redistribute the surface soils. The different functions of both wind erosion and water erosion for a specific ecosystem or landscape are critical. Both types of erosion are believed to serve as important factors that influence the size and structure of vegetation communities, and both processes help to moderate the desertification process transforming grasslands into shrublands. Scientists have also hypothesized that both wind and water erosion could be influenced by climate change (Breshears et al. 2003).

Even thought soil redistribution through both wind and water erosion are controlled by completely different physical forces, overall these processes share three important stages. The first stage of soil erosion involves the separation of surface soil particles from the substrate by the energy of water or wind. The second stage involves the physical transport or redistribution of the previously detached soil particles as runoff due to water erosion or dust emissions, due to wind erosion. The third and final stage is the deposition or settling of surface soil particles when the velocities of wind or water decrease below the point at which they can transport soil particles. (Breshears et al. 2003). Despite the fact that both wind and water soil erosion events share the same three stages, there are distinct differences between the two processes. One example of these differences is the fact that the separation from the substrate and transport of soil particles by wind and water occur over differing temporal scales (Breshears et al. 2003). The transport of surface soil particles by water tends to occur as an intermittent, event-based phenomenon associated with infrequent, high intensity precipitation events. In the same way, the large-scale transport of surface soil particles by wind occurs during extremely intense wind events, specifically periods of high winds lasting for several hours to a couple of days. Conversely, powerful short lived gusts of wind on generally tranquil days can result in the transport of soil particles, and depending on the region theses short lived

wind gusts might be expected to occur with greater frequency than intense precipitation events (Breshears et al. 2003).

The redistribution of surface soil by water erosion and wind erosion also differ in the general directions they are able to transport the detached soil particles. The transport of soil particles by water is generally more of one-way redistribution process with the principal direction of soil transport being downhill. The redistribution of soil by water is for the most part irreversible meaning that soil particles that are eroded in rain events are unlikely to be transported back up hill in a subsequent rain event (Breshears et al. 2003). However, the redistribution of soil particles by wind can occur in any direction the wind blows but it typically follows the prevailing weather or circulation patterns of the region. Also, wind transport is somewhat reversible meaning that soil particles that are redistributed downwind could be returned close to their location of origin by an opposing wind of equal strength and duration (Breshears et al. 2003). Also in a crude sense, the redistribution of surface soils by wind can be conceptualized as having two-directional components. The first component is vertical transport of soils (e.g. height >1 m above the soil surface) which usually involves smaller soil particles being transported over long distances either into an area nearby its original position or to an entirely new location tens or hundreds of miles away. The second component of wind transport is the horizontal transport of surface soils which typically involves larger soil particles being redistributed horizontally just above the surface of the ground (e.g. height <1 m above the soil surface) (Breshears et al. 2003).

Literature Review

Prairie Dogs Effects on Net Primary Productivity

Several studies have been conducted to examine the effects of prairie dogs on aboveground net primary productivity. Net primary productivity is the quantity of new plant material produced annually and includes new biomass, root exudates, transfers to mycorrhize, and hydrocarbon emissions (Chapin et al. 2011). Prairie dogs do not hibernate like some other rodents. Thus, they forage and graze on aboveground vegetation all year round. Also prairie dogs tend to clip and completely remove vegetation on their colonies without consuming it to assist in predator detection. Prairie dogs foraging habits create distinct patches within grasslands, and the ecosystem processes that occur on prairie dog colonies might occur at different rates than those outside the colonies (Whicker & Detling, 1988). Grasslands worldwide can typically support high herbivore loads. Cattle and native ungulate herbivores generally consume between 30-40% of the aboveground net primary production on grasslands. In addition insects, such as grasshoppers, can consume 5-15% of aboveground net primary production. In comparison, grassland areas colonized by prairie dogs typically lose 60-80% of above ground net primary productivity to wastage and consumption by prairie dogs and other herbivores (Whicker & Detling, 1988).

The average prairie dog burrow system has two separate entrances, an average depth below the ground surface of approximately 1-3 m, an average total length between burrow entrances of 15 m, and an average diameter of 10-13 cm. From these dimensions it has been estimated prairie dogs mix approximately 200-225 kg of soil per burrow system. Typically there are several burrow systems on a single prairie dog colony

(Whicker & Detling, 1988). Most of excavated soil from prairie dog burrow systems is deposited around the burrow entrances, creating soil mounds 1-2 m in diameter. The number of burrow entrances for a single colony could range from 50-300 burrow entrances per hectare (Whicker & Detling, 1988).

In 1984 Whicker and Detling (1988) conducted a study during which they collected blue grama samples from heavily grazed prairie dog colonies and from lightly grazed uncolonized prairie sites in Wind Cave National Park, South Dakota. Their objectives were to determine how grazing affected primary production, nitrogen uptake, and biomass and nitrogen allocation after prairie dog foraging. They also sought to determine how prairie dogs and other herbivores respond to changes in the grazing regime of grasslands (Whicker & Detling, 1988). Whicker and Detling (1988) found that off-colony plants produced 121% more biomass and their nitrogen content was 203% greater than on-colony plants. On-colony plants allocated a higher percentage of nitrogen and biomass to their roots compared to off-colony plants, while the Off-colony vegitation allocated a greater percentage of their resources to reproductive structures and leaf sheaths. They also found in response to defoliation by prairie dogs, on-colony plants increased their nitrogen uptake per root biomass by 122% and they also increased total leaf-blade nitrogen content by 141%. Despite these marked increase in nitrogen content, several factors associated with grazing may add to increased concentrations of nitrogen in foliage and aboveground nitrogen content on prairie dog colonies. For example, these colonies may receive more nitrogen in the form of nitrate ions and ammonium from excretion products of large herbivores such as cattle and bison that graze alongside prairie dogs on colonies (Whicker & Detling, 1988).

Coppock et al. (1983) also conducted a study in the northern mixed-grass prairie at Wind Cave National Park, South Dakota. They set out to determine the effects of the black-tailed prairie dogs on North American grasslands specifically the effects on plant species diversity, nutrient dynamics, and seasonal aboveground plant biomass following colonization for different periods of time. At that time, multiple studies had shown that on the short-grass prairie plant species diversity is greater on prairie dog colonies compared to the nearby uncolonized sites. However changes in plant species diversity as a function of time since colonization had not been considered (Coppock et al. 1983). Their study found that peak live plant biomass was greatest on the portion of the study area that was uncolonized by prairie dogs with an average biomass density of 190 g/m², and live plant biomass was lowest on a section of the study area that had colonized for three to eight years with an average biomass density of 95 g/m² (Coppock et al. 1983). The oldest portion of the prairie dog colony they studied had been colonized for over twenty six years had a peak live biomass density of 170 g/m², which was not significantly different from that of the uncolonized prairie. On prairie dog colonies the amount plant litter and standing dead vegetation decreased significantly as the time since colonization increased. They also found that greatest plant species diversity occurred on the young prairie dog colonies that have only been colonized for three to eight years (Coppock et al. 1983). Coppock et al. (1983) also found that nitrogen concentrations in plant shoots varied considerably as the time since colonization increased. Shoot-nitrogen was lowest in plants from the uncolonized site and greatest in plants collected from the longestcolonized areas of the prairie dog colony.

The relationship between ungulate grazers and prairie dogs

The vast majority of North America's historic grasslands were developed and maintained by the grazing of large ungulate herbivores. Ungulate herbivores increase ammonia volatilization, rates of denitrification, rates of nutrient redistribution through urine and fecal deposition, and net nitrogen mineralization on the grasslands they inhabit (Fahnestock & Detling 2002). Historically, the most common of these large ungulate herbivores was the bison (*Bison bison*) of the Great Plains. Their numbers before the nineteenth century were estimated to range between 30 million and 60 million bison (Fahnestock & Detling 2002). The realization of the United States' manifest destiny and the subsequent westward exploration of North America in the 1800s lead to the extensive slaughter of bison across the Great Plains. The expansion of the United States reduced the bison populations of the Great Plains to just a few thousand bison by the beginning of the twentieth century. As a result of the unmitigated slaughter of bison, the ecological role of bison in grassland ecosystems is poorly understood and greatly underappreciated (Fahnestock & Detling 2002).

At approximately the same time that bison populations were at their lowest point, populations of black-tailed prairie dogs (*Cynomys ludovicianus*), which much like the bison is also widely considered to be a keystone species, were being significantly reduced in the grasslands of North America (Fahnestock & Detling 2002). Bison and other large herbivores such as pronghorn (*Antilocapra americana*) and elk (*Cervus elaphus*) tend to utilize prairie dog colonies for grazing and resting a great deal more than one would expect based on the proportion of habitat colonized by black-tailed prairie dogs that is

available to these ungulate herbivores. This use of prairie dog colonies by ungulates is chiefly due to the changes in vegetation quality and the modifications of nutrient cycling processes caused by prairie dog foraging and burrowing habits (Fahnestock & Detling 2002).

In 1994 Fahnestock and Detling (2002) began conducting a long-term study in Badlands National Park, South Dakota in order to determine the ecological consequences of the presence and exclusion of bison and prairie dogs upon multiple aspects of grassland community dynamics. Through experimental field treatments they aimed to determine the impacts of prairie dogs and bison on nitrogen dynamics and aboveground biomass of different plant functional groups, on grassland species diversity and composition, on soil nitrogen availability, and on nitrogen mineralization trends (Fahnestock & Detling 2002). Their hypothesis was that on colonies where both prairie dogs and bison occur, prairie dogs would have much more pronounced influence on the mixed-grass prairie than that of the bison. Fahnestock and Detling (2002) also hypothesized that on grassland ecosystems where both prairie dog and bison occur their total influence on that ecosystem is greater than the sum of their individual impacts.

To test these hypotheses Fahnestock and Detling (2002) established five separate treatments at three different mixed-grass prairie sites in Badlands National Park for a total of fifteen treatments. The first treatments were on uncolonized mixed-grass prairies with bison excluded. The second treatments were also on uncolonized mixed-grass prairie, but bison were allowed to graze and utilize the treatment sites. The third treatments were on active black-tailed prairie dog colonies with bison excluded. The fourth treatments were also on active black-tailed prairie dog colonies that were being

utilized by both prairie dogs and bison. The fifth and final treatments were on prairie dog colonies with both prairie dogs and bison excluded (Fahnestock & Detling 2002). Three years after the fifteen treatments were established there were only a small amount of differences in their measured parameters between the uncolonized mixed-grass prairie treatments where bison were excluded and the uncolonized mixed-grass prairie treatments where bison were allowed to graze. Also there were no considerable differences between the treatments that were established on active prairie dog colonies. However, there were significant differences, in every parameter measured by Fahnestock and Detling (2002) between the uncolonized mixed-grass prairie treatments and oncolony treatments. On the uncolonized mixed-grass prairie treatments aboveground biomass was over two times greater than the on-colony treatments. This is chiefly due to the fact that prairie dogs remove almost all of grasses on their colonies. Also the uncolonized mixed grass prairie treatments had less plant diversity and thus were dominated by just a few grass species, while on-colony sites were dominated by multiple forb species (Fahnestock & Detling 2002). On active black-tailed prairie dog colony treatments net nitrogen mineralization was about four times greater early in the growing season than on the uncolonized mixed-grass prairie treatments, however all 15 treatments experienced net nitrogen immobilization near the end of the growing season (Fahnestock & Detling 2002). Fahnestock and Detling's (2002) results bring about three significant conclusions in regards to prairie dog and bison vegetation interactions in Badlands National Park. The first conclusion is that bison have a relatively insignificant effect on aboveground biomass and species diversity in the mixed-grass prairie ecosystem and have no discernible impact on plant or soil nitrogen dynamics. The second conclusion,

which supports their first hypotheses, is that prairie dogs have a significant impact on the vegetation and soil processes on the colonies regardless of whether or not ungulate herbivores are grazing on their colonies Their third and final conclusion is that the removal of prairie dogs from their colonies does not result in the rapid regrowth of mixed-grass prairie plant species that are similar to the surrounding uncolonized grasslands (Fahnestock & Detling 2002).

Prairie dogs not only have a comparatively high dietary overlap with native ungulate herbivores such as bison and pronghorns, but they also have a very similar diet to domesticated grazers such as cattle. Due to the fact that prairie dog have long been viewed by ranchers as competitors with cattle for forage, prairie dogs have been the target of extensive and extremely successful eradication campaigns for over a century (Derner et al. 2006). However, conservationists in recent decades have expressed an increased interest in conserving prairie dogs due to their understanding that prairie dog's foraging habits contributes to the maintenance of grassland species diversity and that prairie dogs are a critical food source for predators such as the endangered black-footed ferret (*Mustela nigripes*). Thus, an impassioned debate has arisen between conservationists and ranchers over whether or not there is any merit in allowing prairie dog populations to expand their range in the western United States (Derner et al. 2006). There is a very high probability that prairie dogs reduce the carrying capacity that rangelands can support by consuming their potential food source, by clipping grasses and forbs to enhance their ability detect predators, by piling soil into mounds around their burrows, and by changing plant species composition (Derner et al. 2006).

Starting in 1981 there was a significant increase in the abundance and area occupied by prairie dogs on the shortgrass steppe of Pawnee National Grasslands in northern Colorado. This increase in prairie dog populations has intensified conflicts with local ranchers and prairie dog conservationists (Derner et al. 2006). Starting in 1999 Derner et al. (2006) started a six year field experiment on Central Plains Experimental Range in northern Colorado measuring cattle weight gains on four pastures; two pastures that had active prairie dog colonies and two pastures where prairie dogs were excluded (2006). All four of the pastures that were compared in their experiment had four common traits. The first was that all yearling steers had an average initial weight of 263 kg plus or minus 37 kg per animal. The second trait was that each pasture was the same size 129.5 hectares. Also, each the four pastures had a moderate stocking density of 1 yearling cattle for every 6.5 hectares of pasture. The fourth and final commonality between the four pastures was a five month grazing season. Their objectives of their field experiment were to: measure how fast prairie dog colonies expanded on the Central Plains Experimental Range pastures, assess the effect of pastures that were recently colonized by prairie dogs on the weight gains of cattle, and finally to estimate the potential economic impact that prairie dogs may have on the profits of cattle grazing in shortgrass steppe (Derner et al. 2006).

The results of their six year field experiment indicate that cattle weight gains decreased linearly as the percentage of the Central Plains Experimental Range pastures that were colonized by prairie dogs increased, but this rate of decreasing weight gains was slower than the rate of colonization by black-tailed prairie dogs. The decrease in cattle gains resulted in lower economic profit for the ranchers (Derner et al. 2006). They

20

found that if twenty percent of the pastures were colonized by prairie dogs the estimated value of one animal was reduced by approximately \$14.95 which is a reduction from \$273.18 to \$258.23 per cattle. Also with twenty percent of the pastures colonized the value of the land was reduced by \$2.23 hectare from \$40.81 to \$38.58 hectares, which is a 5.5% reduction in the value of the land. Also, they found that if sixty percent of the pastures were colonized by prairie dogs the estimated value of single animal was reduced by about \$37.91 and \$5.58 per hectare or about 14% in the value of cattle from these pastures (Derner et al. 2006).

Prairie Dogs as Keystone species

Prairie dogs have been identified as an ecosystem engineer and a keystone species based on the belief that they have a definite effect on biological diversity in grassland ecosystems (Kotliar et al. 1999). Conservationists have argued that if we protect prairie dogs, we potentially save essential components of grassland ecosystems including multiple declining grassland vertebrate species that are believed to be dependent upon prairie dog for survival. Thus, prairie dogs have been targeted for conservation efforts in some regions (Kotliar et al. 1999). Kotliar et al. (1999) believed that the magnitude of the prairie dog's impacts on grassland ecosystems has been largely overstated by previous studies of prairie dogs and their affects on biodiversity. They used a meta-analysis to review the evidence supporting the assumption that prairie dogs do indeed serve as a keystone species. They examined the assumptions that prairie dogs regulate ecosystems; that predator and small mammal abundances are higher on colonies; that biodiversity and species richness are higher on colonies; and that over 200 vertebrate species are associated with prairie dog colonies. Kotliear et al. (1999) reviewed over two hundred studies on prairie dogs and the species associated with prairie dog colonies dating back to 1902. Their meta-analysis of both the strength of species occurrence along with prairie dogs and species richness patterns indicated that the prairie dog's influence on vertebrate species richness may not be as strong as frequently claimed. Despite this fact, prairie dogs do significantly add to biological diversity on their colonies due to the fact that prairie dog colonies support a different composition of species compared to uncolonized grasslands (Kotliar et al. 1999). They also found that species dependent on prairie dogs such as swift foxes, ferruginous hawk, burrowing owls, mountain plovers and the endangered blackfooted ferrets have suffered significant population declines, and many are under consideration for conservation under the Endangered Species Act. Thus the conservation and management of prairie dogs will clearly benefit these species that are dependent on prairie dogs and are at risk of becoming extinct (Kotliar et al. 1999).

Lomolino & Smith, (2003) utilized a large scale experiment based on the anthropogenic reduction of black-tailed prairie dog colonies across the Great Plains to test the hypothesis that decline of black-tailed prairie dogs has also led to declines in diversity of native grassland vertebrates. In their study they compared species composition and species richness of mammals, amphibians and reptiles at 36 prairie dog colonies and 36 uncolonized sites in the panhandle region of Oklahoma between 1997 and 1999. The comparisons between communities at prairie dog colonies and uncolonized prairie paired sites indicated that species richness was not significantly greater on the colonized sites, but significantly more imperiled and rare species occurred on prairie dog colonies. Species that were positively associated with prairie dog colonies included badgers (*Taxidea taxus*), eastern cottontails (*Sylvilagus floridanus*), coyotes (*Canis latrans*), grasshopper mice (*Onychomys leucogaster*), swift fox (*Vulpes velox*), pronghorn antelopes (*Antilocapra americana*), striped skunks (*Mephitis mephitis*), whitetailed deer (*Odocoileus virginianus*), cattle, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), black-tailed jackrabbits (*Lepus califonicus*), barred tiger salamanders (*Ambystoma tigrinum*), plains spadefoot toads (*Scaphiopus bombifrons*), Great Plains toad (*Bufo cognatus*), Woodhouse's toad (*Bufo woodhousii*), prairie rattlesnakes (*Crotalis viridis*), western plains garter snakes (*Thamnophis radix*), Texas horned lizards (*Phrynosoma cornutum*), and ornate box turtles (*Terrapene ornata*) (Lomolino & Smith, 2003).

Plague (Yersinia pestis) and Prairie Dogs

Introduced pathogens that cause significant amounts of mortality in ecosystem engineers and keystone species probably have indirect effects on other species through changes in ecosystem structure and function. Plague (*Yersinia pestis*) was introduced into the United States from Eurasia in the early 1900s, and the disease was first seen in prairie dogs in the late 1930s and early 1940s (Hartley et al 2009). *Yersinia pestis* is the same pathogen that caused the plague epidemic in Europe during the Middle Ages that killed millions of people. Plague is chiefly a disease that affects rodents, but it remains a significant human health concern in many regions of the world (Stapp et al. 2004). Once outbreak plague takes hold on a prairie dog colony it causes virtually 100% mortality within that prairie dog colony. The high mortality rate for prairie dog colonies that experience a plague outbreak might be due to the fact that they are highly sociable rodents, which increases transmission rates due to contact between individuals and the sharing of burrows. Also prairie dog burrows are ideal environments for the growth of large populations of fleas, which are the primary vector for plague (Stapp et al. 2004). Plague outbreaks have occurred on the western half of the black-tailed prairie dog's range, which extends from northern Mexico up into the southern Canada and includes the shortgrass steppe and mixed-grass prairie (Hartley et al 2009). Before plague was introduced into the United States, individual prairie dog colonies would occupy single locations for several decades. However, where plague outbreaks have occurred, prairie dog colonies sometimes experience episodic extinction events. Usually the extirpated colonies are eventually repopulated by individuals from nearby colonies (Hartley et al. 2009).

Hartley et al. (2009) investigated how the introduction of the plague to blacktailed prairie dogs of the central United States grasslands, has changed the age distribution of their colonies on the shortgrass steppe, and the role prairie dogs play in determining plant community composition. Hartley et al's. (2009) first objective was to determine the frequency of plague epizootics or outbreaks on individual prairie dogs colonies and typically how long a colony remains inactive after a plague epizootic. Their second objective was to evaluate how plant communities respond to the lack of prairie dog foraging pressures after plague epizootic, and to evaluate if the effects of prairie dogs on plant communities with increasing colony age. Hartely et al. (2009) hypothesized that plague epizootics would essentially reduce the overall impact of prairie dogs on plant communities based on the fact that the effects of prairie dogs on plant communities increases with the age of the colony and that plague reduces average colony age (Hartley et al. 2009).

Hartley et al. (2009) used 25 years of spatially explicit monitoring data collected between 1981 and 2005 by the US Forest Service. They used these data to estimate the percentage of colonies that: experienced a plague epizootic within 5, 10, 15, and 20 years of constant prairie dog use; the percentage of colonies that were recolonized 2, 5, and 10 years after an outbreak of plague; and the percentage of colonies returned to their preplague size 2, 5, and 10 years after an epizootic of plague. Hartley et al. (2009) also analyzed plant community characteristics of young colonies that were between 3–8 years old, old colonies that were approximately 20 years old, and colonies that were inactive due to plague for 7 to 12 years to determine how colonies age and whether or not their active or inactive status influences the effects of prairie dogs on plant communities. Hartley et al. (2009) found that of the 98% colonies that experienced a plague outbreak, approximately half of those colonies remained inactive for at least 5 years following the outbreak, and less than half of those colonies attained their pre-plague extent within 10 years of an epizootic. The prairie dog colonies in this study experienced a lower vegetation canopy height, changed vegetation community composition, and reduced plant biomass due to the foraging habits of prairie dogs. These effects were most significant on the oldest prairie dog colonies. The vegetation on colonies that experienced a plague outbreak was not significantly different from the surrounding off colony sites for most variables measured (Hartley et al. 2009).

More and more evidence is coming to light concerning the relationship between infectious disease outbreaks and changes in climate variables. These changes in climate variables due to global climate change may have disturbing consequences for human populations and natural communities in the future. This new evidence implies that climate variables that affect the reproduction and survival of both host and vector populations might be useful in predicting outbreaks of infectious diseases (Stapp et al. 2004). Stapp et al. (2004) utilized data from the long-term program established by the USDA Forest Service that monitors the size and status (active or inactive) of prairie dog colonies on shortgrass steppe on the Pawnee National Grasslands to examine patterns of extinction and re-colonization of prairie dog colonies in Colorado. They studied patterns through time of prairie dog colony inactivity to identify plague outbreaks and to understand their relation to regional climate patterns, specifically those associated with El Niño Southern Oscillation (ENSO) events (Stapp et al. 2004). They also tested two hypotheses that relate to the potential consequences of prairie dog meta-populations and plague outbreaks. A meta-population is a regional group of connected populations of a species. Meta-populations are constantly being modified by increases in the number of individuals by immigration and births and decreases in individuals by deaths and emigration. Meta-populations are also modified by the establishment of new populations and extinction of old populations contained within the meta-population. Stapp et al's. (2004) first hypothesis was that the likelihood of prairie dog colony experiencing extinction due to plague decreases as the population size increase. Their second hypothesis was that isolated colonies are more likely to survive during local outbreaks than colonies that are close to one another.

During their study prairie dog colonies were considered extinct when Pawnee National Grasslands' records showed no activity in colonies that were formerly active and that there was evidence of plague on the colony (Stapp et al. 2004). To analyze how colony isolation and colony extent influences extinction, they analyzed surveys that took place during the two-years following five separate ENSO events. These ENSO events occurred during the winters of 1982-83, 1986-87, and 1997-98, including the lengthened ENSO period from 1991-1995 (Stapp et al. 2004). The relationship between colony extinctions caused by plague outbreaks and ENSO events suggests that abiotic factors such as soil moisture and air temperatures, which impact the survival of fleas, contribute considerably to plague outbreaks. Also the mild winters that are associated with ENSO events might increase the amount of forage available, and thus the survival of prairie dogs, allowing potentially vulnerable populations to reach the high densities that aid in the transmission of plague (Stapp et al. 2004). They also found that during plague outbreaks the rates of extinction for the largest colonies, greater than 16 hectares, were about as high as the smallest colonies, which were less than 3 hectares. Both the large and small colonies experienced extinction rates greater than 60% during plaque outbreaks. However, just one third of intermediate-sized colonies went extinct during local plague outbreaks (Stapp et al. 2004). The likelihood of a colony experiencing extinction during a local plague outbreak was influenced by the fate of surrounding colonies and colony size. There were no predictable patterns between the likelihood of extinction and the distance between colonies. This indicates that just because a colony is isolated doesn't mean that it is any less likely to extirpated by a plague outbreak (Stapp et al. 2004).

Climate Change in Colorado

Due to its complex topography, which includes plains, mountains, and plateaus, Colorado has an extremely variable climate. Colorado's Climate varies both temporally and spatially in temperature and precipitation. In Colorado from 1977 to 2006 temperatures have increased approximately 2°F (Ray et al. 2008). All regions of the state of Colorado that were examined by Ray et al. (2008) experienced warming during the period between 1977-2006 except for the southeast corner of the state, which experienced a slight cooling trend. General climate models for the Western United States show a 1°F increase in temperature over the last thirty years as a result of greenhouse gas emissions from human activities. Yet, no scientific studies have specifically investigated whether or not the observed warming trends in Colorado can be linked directly to anthropogenic greenhouse gas emissions (Ray et al. 2008).

The Climate prediction models that were examined by Ray et al. (2008) predict Colorado's temperatures will increase by approximately $2.5^{\circ}F$ [+1.5 to +3.5°F] by 2025, compared to the observed temperatures from 1950–1999. Also temperatures predicted increase by approximately $4^{\circ}F$ [+2.5 to +5.5°F] by 2050. These same climate prediction models for 2050 show an increase in summer temperatures by about 5°F [+3 to +7°F], and an increase in winter temperatures by approximately 3°F [+2 to +5°F] (Ray et al. 2008). Based on these predictive models the average summer temperatures will be at least as warm as or warmer than the hottest summers that were recorded between 1950 and 1999. Also, by 2050 summer temperatures typically of the Eastern Plains of Colorado are predicted to shift westward towards the Front Range and shift upward in elevation, bringing into the Front Range temperature regimes that occur today near the Colorado Kansas border (Ray et al. 2008).

For the entire state of Colorado there have been no reliable long-term climate prediction models for trends in annual precipitation. The variability between climate prediction models in relation to precipitation is high, which makes the prediction of precipitation trends difficult. The various climate prediction models examined by Ray et al. (2008) predict that annual mean precipitation will increase and decrease in Colorado by 2050. Based on models that show both an increase and decrease in annual precipitation, there will likely be an insignificant change in annual mean precipitation throughout Colorado, although a seasonal shift in precipitation did emerge in the climate prediction models (Ray et al. 2008). The seasonal shift in precipitation indicated by the models shows a state wide and large increase in the percentage of precipitation falling as rain rather than snow and reduction in snow water equivalent (SWE). The Snow Water Equivalent is a general measurement of the mountains' snowpack that is used to determine the amount of water the snowpack contains. SWE is basically the volume of water that would in theory be produced if you melted the whole snowpack at once. In Colorado, however, climate prediction models project that these changes in SWE will be smaller and not as significant as those experienced by other states in the Western United States due to the fact that most of Colorado's snowpack is above 8200 ft. 8200 ft is the elevation where winter temperatures remain well below freezing for most of the winter (Ray et al. 2008).

Desertification and shrubland encroachment of grasslands

Grasslands are encountering increasing threats from several anthropogenic activities, and thus they are becoming one of the most threatened ecosystems on the planet. The future of grasslands is extremely dependent on future grazing practice, future agriculture practices, and whether or not they change or intensify (Ceballos et al 2010). Humans utilize grassland ecosystems for global food production, which is expected to increase by greater than 75% over the next half century due to the fact that the human population is predicted to double. Around the world grasslands are being transformed by humans and ungulate herbivores into both croplands and desertified shrublands due to overgrazing by livestock. The desertification and fragmentation of grassland ecosystems is leading to the extinction of numerous local populations, changes in the composition and function of the ecosystems, the loss of ecosystem services, and the decline in human well-being (Ceballos et al 2010). Only 20% of the United States' central grasslands remain undeveloped, and the vast majority of these grassland are used for livestock grazing. Overgrazing by livestock leads to the eradication of perennial grasses and allows for the invasion of shrub vegetation, which results in grasslands being replaced by desert shrub communities (Ceballos et al 2010). These desert shrub communities can be dominated by shrubs that are unpalatable to livestock such as ephedra (long-leaf jointfir, *Ephedra trifurca*), and palatable ones such as mesquite (*Prosopis glandulosa*), which produces seeds that can be consumed by cattle. In some parts of the world, overgrazing by livestock has lead to the replacement of perennial grasses by forbs and annual grasses on a very large scale (Ceballos et al 2010). Grasslands that are dominated by perennial grass are distinguished by stable vegetation cover, uniform distribution of soil nutrients,

and surface soils that aren't particularly vulnerable to wind erosion. In comparison, desertified grasslands that are dominated by annual grasses have a great deal of variability temporally in vegetation cover and soil nutrients, and are extremely vulnerable to wind and water erosion (Ceballos et al. 2010).

Ceballos et al. (2010) conducted a study in the semi-arid grasslands of the Janos region of northern Chihuahua, Mexico. This region has experienced intense cattle grazing and these grasslands are home to one of the largest black-tailed prairie dog (Cynomys *ludovicianus*) complexes on the continent. This prairie dog complex has an extent of approximately 14,796 hectares, and it is the only significant colony persisting in the semi-arid grassland ecosystems of Southwestern North America (Ceballos et al. 2010). Ceballos et al. (2010) examined five questions during their study. Their first question was have there been landscape-scale changes in the area covered by native vegetation communities in relation to intensive livestock grazing and agriculture practices? The second question was if there were changes in native vegetation communities, have these changes affected the extent of the prairie dog complex? The next question they examined was do prairie dogs help maintain semi-arid grassland ecosystems and thus hinder the invasion of shrub communities? The fourth question was do shrublands and grasslands have differing vertebrate diversities, and if so, what is their total contribution to regional vertebrate diversity? The final question was have there been declines in vertebrate diversity that co-occur with the decline in prairie dog colonies (Ceballos et al. 2010)? Their results reveal that there were far reaching, very quick changes in the Janos grassland communities occurred, which lead to significant declines in vertebrate abundance of every taxonomic group. They also found that the 55,000 hectare prairie dog complex declined by 73% between 1988 and 2005 (Ceballos et al. 2010). The prairie dog complex they studied became increasingly fragmented over the seventeen years the study was conducted, and prairie dog densities experienced an abrupt decline, from an average density of 25 prairie dogs per hectare 1988 to 2 per hectare in 2004. Their results demonstrated that prairie dogs significantly hinder the invasion of woody plants, and that they also maintain and manage open grassland habitats by clearing woody vegetation. Once prairie dogs were removed from the grasslands there was a rapid invasion of shrub communities (Ceballos et al. 2010). Their comparison of shrublands and grasslands showed significant differences in the species compositions of both ecosystems. The species richness of the two ecosystems was greatest when both ecosystems were analyzed as one system. Shrublands had greater species diversity than grasslands for every vertebrate class, except large carnivores (Ceballos et al. 2010).

Wind Erosion

Dust is defined as fine particulate matter that can be detached from the surface of the earth by wind. These dust particles are small enough to be suspended and transported in the earth's atmosphere. Dust emissions fluctuate with climate, which is evinced by paleo-studies of ice cores. Dust productions also vary with human induced changes to the landscape (Field et al 2010). The Dust Bowl era of the 1930s across the Great Plains is possibly the most noteworthy example of how ecologically important dust can be. The Dust Bowl is considered by many environmentalists to be one of the most severe human caused environmental disasters in the history of the United States. The extensive
cultivation of the vast agriculture lands of the Great Planes, along with a severe drought that was affecting the region during the 1930s, caused significant increases in winderosion rates, resulting in the degradation of roughly 90 million hectares of arable land. In 1935 alone there was a loss of nearly 800 million metric tons of topsoil due to wind erosion (Field et al 2010). Atmospheric scientists are becoming more and more aware of the fact that dust is both a key climate driver and an element that contributes to uncertainty of climate models. Increased wind erosion and dust productions can cause considerable health problems for humans such as respiratory disease, and increased wind erosion also affects basic ecosystem functions at multiple scales ranging from individual plants up to global scales (Field et al 2010).

Wind erosion transports soil and dust particles through three different processes that are based on the diameter of the dust particles. The first process is called surface creep and typically transports soil particles with diameters greater than 500 micrometers, Saltation, the second process, transports soil particles with diameters ranging between 20 to 500micrometers. The final transport process, suspension, moves particles with diameters less than 20 micrometers (Field et al. 2010). These three processes transport and deposit soil, nutrients, and organic matter at different spatial scales. For example surface creep and saltating soil particles are only transported a few meters at a time and are the dominate processes transporting soil on a local scale. In comparison, suspended soil particles can be redistributed over long distances transporting dust particles on regional, continental, and even global scales (Field et al. 2010). The vast majority of the horizontal wind driven soil transport occurs close to the surface of the earth and the amount of soil being transported by wind decreasing drastically as height above the earth surface increases. Due to the fact that soil nutrients, such as phosphorus, carbon, nitrogen, and other organic matter often make up the smaller soil particles, soil fertility in dust producing areas decreases while areas where the dust particles are finally deposited have increased soil fertility (Field et al. 2010).

For a specific location dust emissions and wind erosion rates are influenced by multiple factors, such as small scale wind gradients and the relative humidity of the local atmosphere. Wind speed is analogous to how much energy the wind is able to exert on the soil surface to move soil particles. Most of the research done on wind erosion focuses on the threshold friction velocity, which is the wind speed at which particles of a given size under a given set of field conditions begin to detach from the soil surface (Field et al 2010). Soil moisture is one of the most important factors influencing erodibility of soil. The moisture content of surface soils is influenced by atmospheric relative humidity in semiarid and arid regions during periods of intermittent precipitation, due to the fact that soil moisture in between surface soil particles is generally at equilibrium with the moisture in the atmosphere. (Field et al 2010). At a specific location, erodibility of wind, soil type, topography, and vegetation cover are typically relatively stable. Soil moisture, on the other hand, is more variable and dynamic, and therefore soil moisture has a significant impact on erodibility of surface soil by wind (Chen et al. 1996). Chen et al. (1996) investigated the influence of soil moisture content on the erodibility of sandy loam soils using wind tunnel simulations. Their results demonstrate that as soil moisture increases the threshold velocity for the redistribution of surface soil particles by wind also increases (Chen et al. 1996). The fundamental factor that influences the increase in surface soil's resistance due to moisture content is the cohesive force between soil

particles and water. Cohesion or Cohesive forces are the property of soil particles sticking together or being mutually attracted to one another (Chen et al. 1996). They also found that there was a negative exponential relationship between the surface soil moisture content and the wind erosion rate. At the outset of their tests, with increased soil moisture the decrease in the wind erosion rate was very rapid. However, when the surface soil moisture content was increased above 4%, the decrease in the rate of wind erosion slowed and became almost constant with successive additions of moisture (Chen et al. 1996).

Surface soil's resistance to wind erosion events is also determined by the strength of the soil and the presence of surface protectors, such as plant litter, biological and physical soil crusts, and rocks. Plant litter and rocks are generally too large to be redistributed by wind events and offer the best soil protection (Field et al 2010). However, the type of vegetation, the percentage of bare soil patches, and the arrangement of vegetation have the most significant influence on the ability of the wind to reach the soil surface. The patchy nature of vegetation in semiarid and arid regions results in wind driven redistribution of surface soils that is extremely heterogeneous in time and space (Field et al 2010).. The amount of surface soil that is redistributed by wind depends on the extent of the bare soil patches that the wind can erode. These bare soil patches do not include gravely or rocky areas due to their lack of surface soil. Also the height and density of the vegetation controls the size of the protected area downwind of individual plants (Breshears *et al.* 2009).

In 2004 Li et al. (2007) began studying two central relationships on grassland plots where the amounts of grass cover were manipulated on the Jornada Experimental

35

Range, which is in the northern half of the Chihuahuan Desert in southern New Mexico. The Jornada Experimental Range (JER) is one of the 26 Long Term Ecological Research sites set up by National Science Foundation. The first relationship they examined was how wind erosion rates and dust emissions were influenced by different amounts vegetation cover. The second relationship they analyzed was the extent of nutrient loss due to wind erosion with different amounts of vegetative cover (Li et al. 2007) The winds that are capable of eroding the surface soils at JER are extremely consistent coming out of the southwest 79% of the time, and principal wind erosion events occurring during the windy season between early March through May. The surface soils on the JER are rather complex but sandy loams and sandy soils are in general widely distributed. In some sections of the site there is a significant amount of black grama (Bouteloua eriopoda), but the dominant grasses belong to the *Sporobulus* genus, There is also extensive yucca (Yucca elata) coverage on the site (Li et al. 2007). Five $25 \times 50 \text{ m}^2$ treatments were set up parallel to prevailing winds. 25m buffers were established between each treatment to minimize the interference between treatments. Different levels of vegetation cover reductions were imposed on each treatment. For example in the 100% cover reduction plot, all grasses, perennial forbs, and perennial shrubs were removed. Except for the control treatment, which experienced no vegetation removal, there were three other treatments on which the vegetation cover was reduced by 75%, 50%, and 25% respectively. There was very little shrub cover at the beginning of the experiment, and shrubs were not removed. Reduced cover on treatment plots were maintained throughout the duration of the experiment (Li et al. 2007). In each of the five treatments, two 5×10 m² subplots were established to install windblown surface soil collectors on and to collect surface soil samples from. In the subplots, surface soil samples were taken from the top 5 cm with 2.5 cm diameter coring tool before the vegetation reduction occurred of the grass cover, and surface soils were sampled again in July of each of the following years 2004, 2005, and 2006. To collect windblown surface soils, Big Spring Number Eight dust samplers were installed on every subplot (Li et al. 2007).

Li et al. (2008) results indicate that wind erosion rates and nutrient loss by surface soil emissions are strongly related to the amount of vegetation cover. However the effectiveness of grass and shrubs at reducing the redistribution of surface soil is probably not equal. The significant increase in wind erosion rates between the 75% vegetation cover reduction treatment and the 100% vegetation cover reduction treatment indicates that sparsely distributed mesquites are fairly unsuccessful in reducing wind erosion rates and nutrient loss compared to grasses (Li et al. 2007). Their comparisons between nutrients in windblown surface soil and bare soil patches indicate that wind erosion is a chief cause for the loss of nutrients in regions with susceptible surface soils. They found that increased wind erosion during three windy seasons from 2004 to 2006 removed up to 25% of total nitrogen (TN) and total organic carbon (TOC) from the top 5 cm of soil. Also they found that approximately 60% of TN and TOC loss occurred during the first windy season of their study (Li et al. 2007). The equilibrium between net loss of nutrients by wind erosion processes and the adding of nutrients by biotic processes changed from a net loss of nutrients to a net accumulation between the 50% vegetation cover reduction treatment and the 25% vegetation cover reduction treatment. They estimated expected lifetime of surface soil TN and TOC was about ten years for the plot with the 100%

vegetation cover reduction treatment. This indicates that effects of wind erosion on soil nutrient contents can occur over extremely short timescales (Li et al. 2007).

Materials and Methods

Prairie Dogs in Boulder County

Black-tailed prairie dogs inhabit numerous Boulder County Open Space Mountain Parks (OSMP) lands. There are very large networks of prairie dog colonies located on the grasslands in the northern half of the county that have been set aside as OSMP (OSMP, 2010). Black-tailed prairie dogs inhabited nearly 3,500 acres of OSMP lands in 2005. However, as of 2008 the number of acres that were inhabited by balck-tailed prairie dogs has been reduced to 2,000 acres due to epizootic of sylvatic plague (Yersinia pestis) (OSMP, 2010). Prairie dog colonies experience a great deal of diversity in the ecological conditions found on Open Space Mountain Park lands. According to OSMP (2010) There are some prairie dog colonies in Boulder County that maintain healthy native grassland communities and that increase the abundance of small animal species that are associated with prairie dogs and their role as keystone species. Others colonies experience very high burrow densities due the fact that they are bounded on all sides by urban and suburban landscapes that prevent them from dispersing to other grassland patches to forage. These high burrow densities leads to an decrease in native vegetation communizes, an increase in nonnative vegetation communities, an increase in soil loss due to wind and water erosion events, and a decline in the vertebrate species that are associated with prairie dogs and their role as a keystone species (OSMP, 2010). In highly fragmented urban areas, where emigration opportunities are rare or non-existent, population densities of prairie dog colonies increase and grasslands are subject to extended periods of unusually high grazing pressure (OSMP, 2010). Black-tailed prairie dogs tend to have a preference for short and mixed-grasslands with alluvial, unconsolidated soils that aren't rocky and

are fairly flat OSMP lands. However, due to the fact that several prairie dog colonies on OSMP lands are surrounded by areas of suburban and urban development, prairie dogs can't expand their colonies, and they are forced inhabit less suitable sites with rocky soils and steep slopes (OSMP, 2010).

On monitored OSMP lands, the number of prairie dog colonies increased from 55 colonies in 1997 to 410 colonies in 2010. During this seventeen year period, prairie dog colonies ranged in extent from less than 0.01 hectares to 214 hectares with an the average colony extent of 4.5 hectares. The landscapes in Boulder occupied by prairie dogs are located within the short and mixed-grass prairie ecosystems, but cattle ranching, agriculture, and urban development have continued to alter the landscape since the 1850s (OSMP, 2010).

Sampling Sites

The mixed grass communities on OSMP lands represent multiple vegetation communities that occur over an extensive portion of North America. OSMP lands include vegetation communities that are similar to those occurring in the northern, southern and central Great Plains, as well vegetation communities that occur in the southwestern and intermountain regions of the western United States (OSMP, 2010). The mixed-grasslands that border the foothills of Boulder County include prairie communities that form a large matrix ranging from large stands to small patches of mixed-grasslands that are intermingled with xeric tall grass prairie. Approximately 9,850 acres or 40% of Boulder's Grassland Planning Area are made up of mixed-grass prairies (OSMP, 2010). At the foot

of the Flatirons, geology, diverse topography, and soils combine with an arid climate to create grassland vegetation communities dominated by grasses of mid height. These mixed grass species include green needle grass, western wheatgrass, little bluestern, needle and thread grass, New Mexico feathergrass, sideoats grama, and Rocky Mountain bluegrass. The mixed-grass lands in Boulder County also include shortgrass species such as buffalograss and blue grama (OSMP, 2010). The chief ecological disturbances that influence the mixed-grass prairie are ungulate grazing, black-tailed prairie dog foraging and burrowing, and fire. These natural disturbance regimes have been significantly altered since the settlement of the western United States. Historically, fires set by humans and naturally occurring fires took place with greater frequency and affected larger areas than in today's landscapes where fuel loads are reduced by livestock grazing and human efforts to actively suppress wildfires (OSMP, 2010). These modified disturbance regimes are reflected in the current composition of vegetation. Native plant species diversity has decreased in a number of areas because of frequent livestock grazing and due to the lack of ungulate grazing and lack of fire. The mean elevation of the county is approximately 1645 m above sea level (OSMP, 2010).

Methods

In the first three weeks of July, 2012 surface soil samples were collected from eleven active prairie dog colonies throughout Boulder County and one active colony located in Broomfield County. At each colony three replicates of ten soil cores were taken randomly to a depth of ten centimeters from the center of the colony, from the edge

of the colony, and from areas surrounding the colony that were uncolonized by the prairie dogs or previously colonized areas that were not being utilized by the prairie dogs at the time of sampling. However, there were no off colony soil cores taken for the Galucci site due to the fact that the southern edge of the colony ran up against Highway 36, which is a major thoroughfare between the cities of Boulder and Denver. The majority of the surface soil samples were taken from sandy loam or clay loam soils, but there is a high degree of variability between surface soils in Boulder County ("California soil resource," 2005). The ten samples from each of these sections of the colonies were composited in a single plastic zip lock bag. Soil samples were taken from depths of 0-10 cm due to the facts 1) this depth historically contained the 'A' horizon of most soils on near-level surfaces around Boulder, and 2) that several studies of soil nitrogen cycling have indicated that this soil depth was where the majority of the net nitrogen mineralization occurred (Frank & Groffman 1998). After the soil cores were collected they were then sieved through a 2mm sieve and dried at room temperature for multiple days. Then sub samples weighing approximately 5 g were taken from the three sampling treatments on each colony and ground to a fine powder by a ball mill. These 5 g sub samples were then oven dried at a temperature of 105°F for multiple days. Soil samples were then prepped for and analyzed by a ThermoQuest ® Flash EA 1112 model CHN analyzer to determine the percentage of total organic carbon (TOC), the percentage of total nitrogen (TN) and the carbon to nitrogen ratio (C:N ratio) of the soils at the center, on the edge, and outside of the sampled prairie dog colonies.



Figure 4.1. An example of off colony sampling treatment from the Sam's Lane colony

Data Analysis

The CHN analyzer results for percentage of TOC, percentage of TN and C:N ratio were analyzed using an ANOVA with site and treatment as the fixed effects variables (McDonald, 2009). The data set consisted of 12 sites with three replicate measures of treatment (on-colony, edge of colony, and off colony, as noted above). I did not have sufficient replication to check on site-treatment interactions, but was able to do this in a qualitative way by comparing treatment patterns among the 12 sites. A post-hoc test to separate differences among sites and among treatments was then used to identify differences. In this analysis TOC, TN, and C:N ratios were the measurement variables and the sampling treatments, on colony, colony edge and off colony, and each individual colony were the main effect or nominal variables. The assumptions that go with an ANOVA are that each variable is normally distributed and have equal variances (McDonald, 2009). With this analysis I was able to test two hypotheses. First, that the TOC, TN, and C:N ratios were the same at all sites, and second, that the location of the samples with respect to the colonies was also similar. Once a significant difference is obtained in the main model, then the post-hoc tests (here, SNK test) identifies which among the sites or which among the treatments differ from the others.

Results

Soil Samples Results

The surface soil samples from the twelve prairie dog colonies sampled show that some site effects existed for TOC contents in their surface soils (Table 1). Differences among the various sites for TOC are shown in Figure 5.1. Treatment effects for TOC were also noted (Table 1). The percentage of TOC generally increased as you moved from on colony to colony edge to off colony. The surface soil samples from the colonies samples also show that some site effects existed for TN contents in their surface soils (Table 1). Differences among the various sites for TN are shown in Figure 5.2. Treatment effects for TN were also noted (Table 1). Similar to the trend observed for TOC, the percentage of TN increased as you moved from on colony to colony edge to off colony. The surface soil samples from the colonies show that some site effects existed for the C:N ration in their surface soils (Table 1). However, The C:N ratio for each of the colonies sampled was not significantly different between each of the three sampling treatments (Table 1).The mean C:N ratio for the twelve prairie dog colonies sampled was 11.14.

Characteristic	Factor	Degrees of Freedom	F Value	P Value
тос	Colony	11	5.91	0.0002
	Treatment	2	4.52	0.0234
	Error	21		
TN	Colony	11	4.54	0.0011
	Treatment	2	3.59	0.0457
	Error	21		
C:N Ratio	Colony	11	7.30	<0.0001
	Treatment	2	0.62	0.5484
	Error	21		
Table 1. Significant statistics form a two way ANOVA for TOC, TN and C:N Ratio across all sampled colonies.				



Mean Percentage of TOC in Suface Soils Across Sampled Colonies

Figure 1.1: Means with the same letter are not significantly different.



Mean Percentage of TN in Surface Soils Across Sampled Colonies

Figure 5.2: Means with the same letter are not significantly different.



Mean C:N Ratio in Surface Soils Across Sampled Colonies

Figure 5.3: Means with the same letter are not significantly different.

The Sam's Lane and South Marshal colonies had significantly higher percentages of TOC in their surface soils than any of the other prairie dog colonies that were sampled with means of 4.2% and 3.6% respectively. Also, the Sam's Lane prairie dog colony had significantly higher TN in its surface soils with means of 0.35%. The South Marshal colony had a significantly higher C:N ratio than all the other colonies that were sampled with a mean C:N ratio of 15.08. On all the prairie dog colonies sampled TOC content was significantly greater on the off colony treatments compared to the on colony and colony edge treatments with a mean of 2.89%. Also on all the colonies sampled TN content was significantly greater on the off colony treatments compared to the other two treatments with a mean 0.25%. There was not a significant difference between the three treatments for C:N ratio on all the prairie dog colonies sampled.



Mean Percentage of TOC in Surface Soil Across Three Sampling Treatments

Figure 5.4: Means with the same letter are not significantly different .



Mean Percentage of TN in Surface Soils Across Three Sampling Treatments

Figure 5.5: Means with the same letter are not significantly different .

Discussion

Soil Samples

Based on the results of my statistical analysis of my surface soil samples, the foraging habits of prairie dogs along with wind erosion are the most likely cause of the decline in surface soil nutrients that was present on all sampled colonies. For all 12 colonies sampled the mean percentage TOC and TN contained in the surface soils increased as you moved from on colony to colony edge to off colony. This is probably due to the fact the prairie dogs in an urban setting, such as Boulder, Colorado, consume significant percentages of the vegetation that grows on their colonies. This loss of vegetation leaves a great deal of the colony's surface soil bare and vulnerable to erosion. Due to the semiarid nature of Boulder's climate, bare surface soils on prairie dog colonies probably contains very little soil moisture year round, which is a key factor in preventing surface soil erosion. Chen et al. (1996) investigated the influence of soil moisture content on the erodibility of sandy loam soils using wind tunnel simulations. Their results demonstrate that as soil moisture increases the threshold velocity for the redistribution of surface soil particles by wind also increases (Chen et al. 1996). Also, minor dust storms and dust emissions from prairie dog colonies in Boulder County were observed during the winters of 2008/2009, 2010/2011, and 2011/2012 (Seastedt et al. 2013). Surface soil erosion due to water or surface runoff on prairie dog colonies in Boulder County is probably not as significant as wind erosion due to semiarid nature of Boulder's climate and due to the fact that prairie dogs typically colonize relatively flat expanses of prairie (OSMP, 2010). However, for my study the soil samples were collected during the first three weeks of July, 2012 which was the onset of monsoon season in Colorado Monsoon

season brings moisture from the Pacific Ocean and Gulf of California to the Southwestern United States. This means that the mean percentages of TOC and TN in my surface soil samples could have been impacted by water erosion and surface runoff especially on the North Marshall, South Marshall, Galucci, and Broomfield colonies, which are located on or near a significantly sloped surfaces.

The Sam's Lane colony had the highest mean percentage of both TOC and TN compared to the 11 other prairie dog colonies from which soil samples were collected. This is most likely due to the fact that the surface soils on the Sam's Lane colony are extremely rocky. Rocky surface soils tend to collect and concentrate surface soils eroded by wind and water, which have high nutrient contents, in the interspaces of bare soil between rocks. The surface soils at Sam's Lane are so rocky that most if not all soil samples were taken from these interspaces between rocks due the fact that they were the only locations on the colony were a soil core could be taken to a depth of 10cm. Thus soil samples from all three sampling treatments (on colony, colony edge, and off colony) where high for both TOC and TN content with a mean percentage of 4.2% and 0.35% respectfully. Much like the Sam's Lane prairie dog colony, the South Marshall colony had a high mean percentage of TOC. The high TOC content of the surface soils of the South Marshall colony is likely caused by a poor quality coal seam that is close to the soil surface. The colony is located in a part of Boulder County that was an active coal minning district from the 1860s to the 1940s. Coal is composed primarily of carbon along with different quantities of various elements including sulfur nitrogen hydrogen, and oxygen (Sampson, 1995).



Figure 6.1. Dark soil as evidence of a coal seam on South Marshal colony

The surface soil samples from the colonies sampled show that each colony had different C:N ratios in their surface soils. This is most likely due to the somewhat unique geologic and land use histories of the individual sites. The South Marshall had the highest C:N ratio with a mean C:N ratio of 15.03. Much like the high percentage of TOC in South Marshall surface soils the high C:N ratio in these soils is probably caused by a poor quality coal seam that lies close to the soil surface (Sampson, 1995). Carbon and nitrogen inputs and outputs from ecosystems are typically small in comparison to the amounts of carbon and nitrogen that are cycled internally (Chapin et al. 2011) This phenomenon produces a fairly closed system and is most likely why there was not a significant difference between the three sampling treatments for C:N ratio on all the prairie dog colonies sampled. If surface soils contain more nitrogen in comparison to the carbon, then the soil has a low C:N ratio and microbes release nitrogen is into the soil from the decomposing organic material. On the other hand, if the soil contains more carbon compared to nitrogen, then the soil has a high C:N ratio and the microbes will utilize the soil nitrogen for further decomposition and the soil nitrogen will be immobilized and will not be available to plants (Chapin et al. 2011)

Components of soil organic mater such as TOC and TN are a critical part of surface soils. They provide both energy and carbon for heterotrophic organisms that live in soils, and these nutrients are essential for the growth of vegetation. Also the nutrients that make up soil organic matter strongly influences the rates of weathering and soil development, the soil structure, the water holding capacity of the soils, and the ability of soils to retain nutrients (Chapin et al. 2011). Due to the fact that soil organic matter is critical to multiple soil properties, the loss of these nutrients on prairie dog colonies in Boulder County could lead to the degradation of the native grassland ecosystems and the loss of biological its productivity. The loss of soil organic matter, including carbon and nitrogen, in surface soils on prairie dog colonies may also reduce the cation -exchange capacity of the colonies' soils and thus reduce their fertility. In soils the cation-exchange capacity is the capacity of soils to form electrostatic bonds between cations, which are positively charged, and negatively charged surfaces of soil minerals and organic matter. Cation-exchange capacity is used as a measure of the capacity of soils to retain nutrients and as a measure of soil fertility (Chapin et al. 2011). Soil organic matter has an extremely high cation-exchange capacity due to the fact that it contains -COOH and -OH groups. Organic molecule groups such as -COOH and -OH in soils increases the cationexchange capacity due to the fact that they increase the available negative charges in

soils. Thus, the build-up of organic matter in soils typically has positive impacts on soil fertility and the loss of soil organic matter typically has negative impacts on soil fertility (Chapin et al. 2011). Also in soils with a high pH, ammonium (NH₄) is converted to NH₃, which escapes into the atmosphere when the following reaction occurs: $NH_4^+ + OH^- \rightarrow NH_3 + H_2O$. This reaction occurs more often in alkaline soils, and the loss of NH₃ is magnified in in dry permeable soils with low cation-exchange capacity (Schlesinger et al. 1990). Since N and other soil organic matter are being lost on prairie dog colonies in Boulder County, which in turn is lowering the cation-exchange capacity, the loss of N in the form of NH₃ could be another source of nutrient loss for prairie dog colonies as the percentage of bare soil increase.

Are Urban Prairie Dogs Still Keystone Species and Ecosystem Engineers?

Prairie dogs have been labeled as both ecosystem engineers and keystone species based on the belief that they have a definite effect on the biological diversity in grassland ecosystems. Keystone species include those whose effects on other species in an ecosystem are direct for example through predation and competition, or the effects of species are indirect through their actions as ecosystem engineers, altering plant succession regimes and the species composition of native ecosystems (Lomolino & Smith, 2003). But in urban environments such as Boulder County do prairie dogs still continue to serve as ecosystem engineers and keystone species? My soil samples indicate that prairie dogs along with erosional forces are likely contributing to loss of soil organic matter on colonies in Boulder. Due to the fact that soil organic matter is very critical to multiple soil properties, the loss of these nutrients on prairie do colonies could lead to the degradation of the native grassland ecosystems and los of biological productivity (Chapin et al. 2011). It is clear that urban prairie dogs in Boulder are impacting or engineering the grassland ecosystems on which their colonies are located, but these impacts don't appear to be the positive impacts historically associated with prairie dogs being ecosystem engineers and keystone species.

Beals (2012) utilized vegetation surveys conducted by city mangers between 1997 and 2010 on Boulder County prairie dog colonies to determine if urban prairie dogs have positive impacts on the composition of plant species in urban environments. Beals (2012) results suggest that vegetation species diversity, richness and evenness were significantly lower on active prairie dog colonies (p < 0.01) compared to unoccupied areas. His analysis of plant functional groups showed a significant lower percentage of native perennial grasses (p < 0.01) and a significant increase in the abundance of introduced forbs on prairie dog colonies (p < 0.01) (Beals. 2012). Lomolino and Smith (2003) suggested that, unlike prairie dogs that live in natural and pristine grassland ecosystems, prairie dogs that are restricted to smaller habitat fragments probably don't act as a keystone species in those fragments. Lomolino and Smith (2003) studied prairie dogs colonies in fragmented landscapes in Oklahoma. They found that the effects of prairie dogs on aboveground terrestrial vertebrate communities varied significantly due to the landscape context of the colony rather than colony isolation. They concluded that if prairie dogs persist in isolated communities surrounded anthropogenic habitats they would no longer act as a keystone species Lomolino and Smith (2003).

However, prairie dogs living in areas that are devoid of anthropogenic habitats such as urban development still function as both ecosystem engineers and keystone species that maintain their grassland habitats. In a very recent interview with Public Radio International Gerardo Ceballos (2013) spoke about his efforts to bring back prairie dogs to Northern Mexico, and his efforts to help restore the native Mexican prairie. Ceballos has been an ecologist at the National Autonomous University of Mexico for the last twenty years. Much like prairie dogs in the United States, Mexican prairie dogs have been historically viewed as a rangeland pest, and thus the vast majority of prairie dog were eradicated from the Mexican prairies (Ceballos 2013). Without prairie dogs, the Mexican prairies transformed into shrublands due to a shrub called mesquite. Mesquite plants are able to push their roots deep into surface soils to suck up water, and the shrub attracts small organisms that consume the grasses surrounding the mesquite. The mesquite plants are unpalatable to the prairie dogs, and it hinders their ability to detect predators around their colonies. So prairie dogs do whatever they can to remove mesquite pants (Ceballos 2013). To remove the mesquite plants prairie dogs chew on the roots and they suck on their stems. Prairie dogs essentially do whatever they can to hinder the development of shrublands and to maintain their native grassland ecosystems. When prairie dogs are reintroduced into the Mexican shrublands it takes them approximately one year to remove misquite plants from their colonies (Ceballos 2013). Ceballos (2013) asserts that prairie dog are still keystone speices that grasslands depend on. He explained that on colonies that persisted despite eradication efforts and on grasslands where he reintroduced prairie dogs, badgers could be found. Badgers are extremely rare in Northern Mexico. Golden eagles are also extremely rare in Mexico, but Ceballos (2013)

observed more than twenty around a prairie dog colony in a single day. The fact that prairie dog serve as ecosystem engineers and keystone species in areas devoid of anthropocentric habitats, and the fact that their roles as keystone species appears to decline as prairie dog colonies become surrounded by anthropocentric habitats has important implications for land managers were prairie dogs still persist.

Bare Soil Data:

Beals' (2012) study looked at the role of the prairie dogs in urban areas of Boulder County to assess whether or not the benefits to plant communities historically associated with prairie dogs being a keystone species are maintained. Beals (2012) used 50 meter line point intercept surveys with magnifying optical sight with a crosshairs superimposed on it. Data was collected at 100 different points along each of these transects. All vegetation and non-vegetation that was in the sight of the crosshairs was classified by species. Also, non-vegetation was categorized as bare soil, rock standing dead vegetation or litter (Beals, 2012). Some of Beals' (2012) point intercept vegetation surveys were conducted on five prairie dog colonies that I took surface soil samples from, and his percentage of bare soil data is relevant to my study due to the fact that these bare soil patches are where soil organic matter is likely to be lost due to erosion. These colonies include North Blip, Galucci, Klein, Sam's Lane, and Van Vleet. Point intercept vegetation surveys were conducted at each of the colonies by city managers once a year for different periods of time between 1997 and 2010. Also the Sam's Lane colony had two point intercept vegetation transects for each survey conducted between 1999 and 2009.



Figure 6.2. Beals (2012) percentage of bare soil for years after colonization

The North blip colony had 8 vegetation surveys conducted on it sporadically between 1997 and 2010. The mean percentage of bare soil cove on this colony was 57.25% with a max percentage of bare soil cove of 73% and a minimum percentage of bare soil cover of 44%. The Galucci colony had 4 vegetation surveys conducted from 1997 to 2001. The mean percentage of bare soil cover on the Galucci colony was 17.5% with a max percentage of bare soil cover of 29% and a minimum percentage of bare soil of 7%. The Klein colony had 4 vegetation surveys conducted between 1997 and 2001. The mean percentage of bare soil colony on this colony was 30% with a max percentage of bare soil cover of 45% and a minimum percentage of bare soil of 17%. The Sam's Lane colony had 20 vegetation surveys conducted on it. The mean percentage of bare soil on this colony was 28.7% with a max percentage of bare soil cover 69% and a minimum percentage of bare soil cover of 7%. The Van Veelt prairie dog colony had 3 vegetation surveys conducted from 1999 to 2001. The mean percentage of bare soil on this colony was 53% with a max percentage of bare soil cover of 58% and a minimum percentage of bare soil cover of 48%. The mean of the mean percentage of bare soil across all five colonies was 37.29%, and the mean maximum percentage of bare soil across these colonies was 54.8%.

These percentages of bare soil cover data indicate that significant portions of these prairie dog colonies are lacking in vegetation cover and are potentially vulnerable to erosional forces and the subsequent loss of soil organic matter. Due to the fact that my surface soil samples from these same colonies exhibit the trend that both TOC and TN increased as you moved from on colony to colony edge to off colony the loss of soil organic matter is likely occurring in these bare soil patches. The highest maximum percentage of bare soil cover on these five colonies was the North Blip colony with 73% of the colony being covered by bare soil. In 2010 prairie dogs occupied about 1,200 hectares of OSMP grasslands in Boulder County. Hypothetically, if all 1,200 hectares of prairie dog colonies had the same amount of bare soil as the North Blip colony, then 876 hectares of prairie dog colonies would be bare soil that is vulnerable to erosion, soil organic matter loss and desertification. Figure 6.2 from Beals (2012) shows that across all prairie dog colonies on which vegetation surveys were conducted that the percentage of bare soil cover generally increased with the number of years that the prairie dogs occupied the colonies. This general trend of decreasing vegetation cover and increasing

bare soil may also indicate that some desertification is occurring on prairie dog colonies in Boulder.

Desertification on Boulder prairie dog colonies

Both my surface soil samples, which show that both TOC and TN increased as you moved from on colony to colony edge to off colony, and Beals (2012) percentage of bare soil date seem to indicate that some desertification might be occurring on Boulder prairie dog colonies. When desertification of grasslands occur the distribution of water, N, and other soil nutrients that was somewhat uniform under grasslands is replaced by an increase in their spatial and temporal heterogeneity. The heterogeneity of soil nutrients can allow shrubs to invade grasslands. In these new shrub communities, soil resources are concentrated under shrubs, while wind and water erosion remove materials from interspaces between shrubs and redistributes surface soil to new locations on the landscape (Schlesinger et al. 1990). According to Schlesinger et al. (1990) the desertification of grasslands could potentially produce a negative feedback. As grasslands are replaced by shrublands and a higher percentage of the surface soils are bare, soil surface and air temperatures increase, despite the fact that the albedo of shrubland soils are greater than grasslands. Higher surface temperatures increase heat circulation in the atmosphere, and shrublands have low relative humidity and precipitation. Hot, dry soils slow down the buildup of organic N in the soil, and thus further increase the spread of shrublands that contain plants that are less closely linked to N turnover in the surface soils. Due to the fact that these abiotic factors constrain biotic factors, the balance tips

further in favor of the development of arid shrubland ecosystems (Schlesinger et al. 1990). This negative feedback of desertification could potentially threaten the undisturbed grassland surrounding prairie dog colonies in Boulder where colonies are not completely bounded by urban environments.

Despite the fact that it is commonly assumed that desertification results in a reduced amount of vegetation growth, the net primary productivity of a desertified shrub land is similar to the net primary production of native grasslands. However, the quality of the net primary production changes because shrublands lower the potential economic gains that could come from the land if it was utilized as rangeland for livestock (Schlesinger et al. 1990). Currently Boulder Open Space and Mountain Parks Department leases about 5,900 hectares of OSMP lands to ranchers and farmers for livestock grazing and agricultural production, and prairie dogs resided on approximately 1,200 hectares of OSMP grasslands in 2010 (OSMP 2010). On some of the colonies I took surface soil samples there was evidence of livestock grazing in the form of desiccating cow patties. The co grazing of both livestock and prairie dogs has land management implications in light of my surface soil samples.



Figure 6.3. Fall 2008: vegetation cover mostly an annual species, storksbill



Figure 6.4. March 2009 The storksbill has Vanished...along with topsoil!

Implications and Recommendation

Urban prairie dogs along with erosional forces in Boulder County are impacting the soil organic matter of surface soils on their colonies. My surface soils show that that both TOC and TN increase as you move from on colony to colony edge to off colony. The vegetation surveys on Boulder County prairie dog colonies utilized by Beals (2012) illustrate that the percentage of bare soil generally increased with the number of years that the prairie dogs occupied their colonies (Figure 6.2). These studies along with the fact that minor dust storms and dust emissions from prairie dog colonies in Boulder County were observed during the winters of 2008/2009, 2010/2011, and 2011/2012 (Seastedt et al. 2013) suggests that desertification maybe occurring. If desertification is occurring on prairie dog colonies located Boulder OSMP lands than this has important implications for the land managers of these grassland ecosystems. The prairie dog colonies on OSMP lands that are surrounded by urban environments could be considered novel ecosystems. Novel ecosystems tend to be composed of new combinations of species under new abiotic conditions (Seasted et al 2008). Beals (2012) analysis of plant functional groups showed a significantly lower amount of native perennial grasses and a significant increase in the abundance of introduced forbs on prairie dog colonies in Boulder, which may indicate that these prairie dog colonies represent novel ecosystems. The aboitic conditions in this case are the urban environments surrounding prairie dog colonies in Boulder. Adaptive ecosystem management plans for these colonies must clearly acknowledge their novel status and take into account the possible future conditions of these ecosystems (Seasted et al 2008).



Figure 7.1. Dust emissions from prairie dog colony south of Boulder, CO, 7 January 2009

The mission of Boulder's Open Space and Mountain Parks Department is protect and preserve the natural environment and land resources that exemplify Boulder. They aim to promote the appreciation and land use that sustains the natural values of the land (OSMP 2010). Beals (2012) analysis of vegetation surveys suggests that vegetation species diversity richness, and evenness, were all significantly lower on OSMP grasslands occupied by prairie dogs than on unoccupied grassland areas in Boulder County. These results along with my surface soil samples suggest that the mission of Boulder's Open Space and Mountain Parks Department is being accomplished on OSMP grasslands that are unoccupied prairie dogs but not on OSMP grasslands occupied by prairie dogs. This raises the question if the Open Space and Mountain Parks Department really aim protect and preserve the natural environment and land resources on OSMP grasslands how should they go about doing it?

Should they eradicate all of the prairie dogs that are living on OSMP grasslands with the hope that the native grasslands will return to their pre colonization states? Or should the Open Space and Mountain Parks Department seed the occupied grasslands with mixed and short-grasses to reduce the percentages of bare soil cover and reduce the loss of soil organic matter due to erosion? In a study conducted by Munson et al. (2012) on land that the Conservation Reserve Program (CRP) had converted to perennial grasslands they examined the potential of these grasslands to recover from large losses in soil organic carbon (SOC) and N caused by past agricultural land use. The study was conducted on the Central Plains Experimental Range (CPER) of Shortgrass Steppe Long Term Ecological Research site located 60 km northeast of Fort Collins, Colorado. They examined 18 years of N and SOC recovery in fields that were seeded by the CRP with both native and non-native perennial grasses. In the surface soils underneath these grasses the SOC and N content increased by as much as 200 g/m^2 for carbon and 14 g/m^2 N in just 9 years. After 9 more years of recovery time, Munson et al. (2012) found that the soils under grasslands that were seeded by CRP had recovered 60% of the total SOC and 67% of the total soil N when compared to the soils of untouched Shortgrass Steppe. This study suggests that seeding OSMP grasslands that are occupied by prairie dogs could recover the soil organic matter that was lost on prairie dog colonies, but it also raises more questions. Would prairie dogs have to be removed from the OSMP grasslands while the grasslands are seeded and if so how long would they have to be removed before the grasslands are considered recovered? Another question is how would the Open Space and Mountain Parks Department pay to reseed grasslands occupied by prairie dogs. Would they excise at tax increase on the citizens of Boulder, and would the citizens of Boulder be willing to pay such a tax? Also some of the colonies located on OSMP grasslands are co-grazed with local ranchers' livestock. Would livestock grazing on these prairie dog colonies have to be suspended while the grasslands are seeded and recovering, and if so would the Open Space and Mountain Parks Department or Boulder County recoup those ranchers for their potential economic losses from not having their livestock graze on OSMP grasslands?

Another land management option the Open Space and Mountain Parks Department could consider for prairie dogs on OSMP grasslands is to just let nature take its course and take a hands off approach to managing prairie dogs. This could potentially lead to the prairie dogs eventually consuming all the vegetation on their colonies, which could lead the prairie dogs to extirpate themselves. This is a very likely outcome to hands off management plan especially if these colonies are completely bounded by urban environments and prairie dogs can't disperse to find new food sources. The extirpation of prairie dog could potentially allow the colonies to become re-vegetated and recover some of the lost soil organic matter, but if enough soil organic matter has been lost then the desertification process is likely to continue on the extirpated colony and might spread to surrounding unoccupied grasslands. It is also quite possible that hands off approach could lead to extirpation of prairie dog colonies due to epizootic of plague. Epizootics of plague have been shown to be associated with El Nino events (Stapp et al. 2004), and as we are currently in a La Nina event. Thus, an El Nino event is likely to occur in the coming years ("El Niño theme," 2013). Again the extirpation of prairie dogs could potentially
allow the colonies to become re-vegetated and recover some of the lost soil organic matter, but if enough soil organic matter has been lost then the desertification process is likely to continue.

Informed land management decisions require a great deal of information concerning past, present, and future conditions of the parcel or section of landscape in question. My recommendation for the management of urban prairie dogs in Boulder County and other urban locations were prairie dogs persist is that we continue to study the prairie dogs and their impacts on the vegetation communities and the biogeochemical processes occurring on their colonies. My analysis of surface soil samples from 11 colonies in Boulder Colony and 1 colony in Broomfield County, and my analysis of a limited amount of Beals' (2012) percentage of bare soil cover data only provide a small piece of the urban prairie dog puzzle. I recommend that a multifaceted adaptive management approach be taken to better understand the urban prairie dogs. This adaptive management approach may included but is not limited to: continued surface soil sampling using a sampling treatments similar to the ones used in my study to better understand the loss of soil organic matter on colonies; vegetation surveys similar to those utilized by Beals (2012) to better understand changes in vegetation communities on urban colonies; daily or monthly soil moisture measurements on colonies to better understand how soil moisture changes along with climate change in Boulder County; the use dust collectors similar those utilized by Li et al. (2007) and Li et al. (2008) to better understand the severity of the loss of soil organic matter due to wind erosion; and finally analysis of climate prediction models specific to Boulder County or the Front Range to better understand how temperature and precipitation will change in the coming years due to

69

global climate change. I also think that the opinions of the general public should be taken into account when making land management decisions concerning urban prairie dog in Boulder and other urban areas where they still persist. This is due to the fact that some of the prairie dog colonies I collected surface soil samples from were adjacent to or part of recreational areas and suburban neighborhoods. Land management decisions would likely impact the aesthetic values of the recreational areas and neighborhoods, and land management decisions could affect the general public monetarily in the form of increased taxes and changes in their property values. Overall the more information that land managers like the Open Space and Mountain Parks Department have the more likely their decisions are to benefit the urban prairie dogs, the grassland ecosystems, and the anthropocentric communities that surround them.

Bibliography

- Anderson, D. W. (1985). They dynamics of organic-mater in grassland soils. *Journal of soil and water conservation*, 40(2), 211-216.
- Archer, S.R., & Predick, K.I. (2008) Climate Change and Ecosystems of the Southwestern United States. *Rangelands*, 30, 23–28.
- Banwart, S. (2011). Save our soils. Nature, 474, 151-152.
- Beals, S. C. (2012). Prairie dogs (cynomys ludovicianus) and vegetation dynamics in boulder, colorado: A retrospective analysis. (Master's thesis, University of Colorado).
- Breshears, D. D., Whicker, J. J., Johansen, M. P., & Pinder, J. E. (2003). Wind and water Erosion and transport in semi-arid shrubland, grassland and forest ecosystems: Quantifying dominance of horizontal wind-driven transport. *Earth surface processes and landforms*, 28, 1189-1209.
- Burke, I. C., Lauenroth, W. K., & Coffin, D. P. (1995). Soil organic matter recovery in semiarid grasslands: Implications for the conservation reserve program. *Ecological applications*, 5(3), 793-801.
- *California soil resource lab.* (2005, June 1). Retrieved from http://casoilresource.lawr.ucdavis.edu/drupal/
- Ceballos, G. (2012, January 25). Interview by A. D. Shapiro [Web Based Recording]. Can prairie dogs save mexico's prairie from the desert?. Public radio international: Living on earth, Retrieved from http://www.loe.org/shows/segments.html?programID=13-P13 00004&segmentID=8
- Ceballos, G., Davidson, A., Pacheco, J., List, R., Fischer, P. M., Barrera, G. S., & Cruzado, (2010). Rapid decline of a grassland system and its ecological and conservation implications. *PLOS one*, *5*(1), 1-12.
- Ceballos, G., Pacheco, J., & List, R. (1999). Influence of prairie dogs (cynomys ludovicianus) on habitat heterogeneity and mammalian diversity in mexico. *Journal of arid environments*, *41*, 161-172.
- Chapin, F., Matson, P., & Vitousek, P. (2011). *Principle of terrestrial ecosystem ecology*. (2nd ed.). New York, NY: Springer Science-Business Media.
- Chen, W., Zhibao, D., Zhenshan, L., & Zuotao, Y. (1996). Wind tunnel test of the influence of moisture on the erodibility of loessial sandy loam soils by wind. *Journal of arid environments*, *34*(4), 391-402.

- Cid, M. S., Detling, J. K., Whicker, A. D., & Brizuela, M. A. (1991). Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. *Journal of range management*, 44(2), 100-105.
- Coppock, D. L., Detling, J. K., Ellis, J. E., & Dyer, M. I. (1983). Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass. *Oecologia*, 56, 1-9.
- Derner, J. D., Detling, J. K., & Antolin, M. F. (2006). Are livestock weight gains affected by black-tailed prairie dogs?. *Frontiers in ecology and the environment*, 4(9), 459-464.
- Detting. J. K. (1988). Grassland and savanna: regulation of energy flow and nutrient cycling by herbivores. In L. R. Pomeroy and J. J. Gilbert, editors. *Concepts of ecosystem ecology* (pp. 131-148). New York. New York: Springer-Verlag.
- de Soyza, A. G., Whitford, W. G., Herrick, J. E., Van Zee, J. W., & Havstad, K. M. (1998). Early warning indicators of desertification: examples of tests in The chihuahuan desert . *Journal of arid environments*, *39*(2), 101-112.
- *El Niño theme page: Access to distributed information on El Niño*. (2013, March 21). Retrieved from http://www.pmel.noaa.gov/tao/elnino/1997.html
- Fahnestock, J. T., & Detling, J. K. (2002). Bison-prairie dog-plant interactions in a north american mixed-grass prairie. *Oecologia*, 132, 86-95.
- Field, J. P., Belnap, J., Breshears, D. D., Neff, J. C., Okin, G. S., Whicker, J. J., Painter, T. H., & Ravi, S. (2010). The ecology of dust. *Frontiers in ecology and the environment*, 8(8), 423-430.
- Frank, D. A., & Groffman, P. M. (1998). Ungulate vs. landscape control of soil c and n processes in grasslands of yellowstone national park. *Ecology*, 79(7), 2229-2241.
- Frank, D. A., & Groffman, P. M. (1998). Denitrification in a semi-arid grazing ecosystem. *Oecologia*, 117, 564-569.
- Hartley, L. M., Detling, J. K., & Savage, L. T. (2009). Introduced plague lessens the effects of an herbivorous rodent on grassland vegetation. *Journal of applied ecology*, 46, 861-869.
- Hook, P. B., Burke, I. C., & Lauenroth, W. K. (1991). Heterogeneity of soil and plant n and c associated with individual plants and openings in north american shortgrass steppe. *Plant and soil*, 138, 247-256.
- Jaramillo, V. J., & Detling, J. K. (1988). Grazing history, defoliation, and competition: Effects on shortgrass production and. *Ecology*, 69(5), 1599-1608.

- Johnson, W. C., & Collinge, S. K. (2004). Landscape effects on black-tailed prairie dog colonies. *Biological conservation*, 115, 487-497.
- Kotliar, N. B., Baker, B. W., Whicker, A. D., & Plumb, G. (1999). A critical review of assumptions about the prairie dog as a keystone species. *Environmental management*, 24(2), 177-192.
- Li, J., Okin G. S., Alvarez, L. J., & Epstein, H. E. (2008). Effects of wind erosion on the spatial heterogeneity of soil nutrients in a desert grassland of southern New Mexico. *Biogeochemistry*, 88, 73–88.
- Li, J., Okin, G. S., Hartman, L. J., & Epstein, H. E. 2007. Quantitative assessment of wind erosion and soil nutrient loss in desert grasslands of southern New Mexico, USA. *Biogeochemistry* 85, 317–32
- Lomolino, M. V., & Smith, G. A. (2003). Terrestrial vertebrate communities at black tailed prairie dog (cynomys ludovicianus) towns. *Biological conservation*, *115*, 89-100.
- Lomolino, M. V., & Smith, G. A. (2003). Prairie dog towns as islands: applications of island biogeography and landscape ecology for conserving nonvolant terrestrial vertebrates. *Global ecology and biogeography*, *12*, 275-286.
- Magle, S. B., & Crooks, K. R. (2008). Interactions between black-tailed prairie dogs (cynomys ludovicianus) and vegetation in habitat fragmented by urbanization. *Journal of arid environments*, 72, 238-246.
- Magle, S. B., Theobald, D. M., & Crooks, K. R. (2009). A comparison of metrics predicting landscape connectivityfor a highly interactive species along an urban gradient in colorado, usa . *Landscape ecology*, 24, 267-280.
- Montgomery, D. R. (2007). Soil erosion and agricultural sustainability. *PNAS*, 104(33), 13268-13272.
- Munson, S. M., Lauenroth, W. K., & Burke, I. C. (2012). Soil carbon and nitrogen recovery on semiarid Conservation Reserve Program lands. *Journal of Arid Environments*, 79, 25 – 31
- McDonald, J. (2009). *Handbook of biological statistics*. (2nd ed., pp. 182-190). Baltimore, Maryland: Sparky House Publishing.
- Okin, G. S., Gillette, D. A., & Herrick, J. E. (2006). Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. *Journal of arid environments*, 65(2), 253-275.

- OSMP (Open Space and Mountain Parks). 2010. *Grassland Ecosystem Management Plan*. City of Boulder Open Space and Mountain Parks, Boulder, CO.
- Ray, A.J., Barsugli, J.J., Averyt, K.B., Wolter, K., Hoerling, M., Doesken, N., Udall, B. and Webb, R.S. (2008) Climate change in Colorado. A report to the Colorado Water Conservation Board. 1-58.
- Rasmussen, P. E., & Collins, H. P. (1991). Long term impacts of tillage, fertilzer, and crop residue on soil organic-matter in temperate semiarid regions. *Advances in* agronomy, 45, 93-134.
- Samson, F., & Knopf, F. (1994). Prairie conservation in north america. *Bioscience*, 44(6), 418-421.
- Sampson, J. (1995). *Walking through history on marshal mesa*. Boulder, CO: City of Boulder Open Space and Mountain parks.
- Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in ecology and evolution*, 18(12), 648-656.
- Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A., & Whitford, W. G. (1990). Biological feedbacks in global desertification. *Science*, 247(4946), 1043-1048.
- Seastedt, T. R., Hobbs, R. J., & Suding, K. N. (2008). Management of novel ecosystems: Are novel approaches required. *Frontiers in ecology and the environment*, 6, 547-553.
- Seastedt, T. R., Hartley, L. M., & Nippert, J. B. (2013). Case study: Ecosystem transformations along the Colorado front range: Prairie dog interactions with multiple components of global environmental change. In R. J. Hobbs, E. S. Higgs, & C. M. Hall (Eds.), *Novel ecosystems: Intervening in the new ecological world order* (pp. 143-150). Hoboken, NJ: John Wiley & Sons, Ltd
- Stapp, P., Antolin, M. F., & Ball, M. (2004). Patterns of extinction in prairie dog metapopulations: Plague outbreaks follow el nino events. *Frontiers in ecology* and the environment, 2(5), 235-340.
- Uresk, D. W. (1985). Effects of controlling black-tailed prairie dogs on plant production. *Journal of Range Management*, 38(5), 466-468.
- Vermeire, L. T., Heitschmidt, R. K., Johnson, P. S., & Sowell, B. F. (2004). The prairie dog story: Do we have it right?. *Bioscience*, 54(7), 689-696.

- Wedin, D.A. 1996. Nutrient cycling in grasslands: An ecologist's perspective. p. 29-44
 In: R.E. Joost and C.A. Roberts (eds.) Nutrient cycling in forage systems. Proc.
 Sym. March 7-8, 1996 Columbia, MO. 'Potash and Phosphate Inst. and the Found.
 for Agron. Research, Manhattan, Kans
- Weltz, M. A., Kidwell, M. R., & Fox, H. D. (1998). Influence of abiotic and biotic factors in measuring and modeling soil erosion on rangelands: State of knowledge. *Journal of range management*, 51(5), 482-495.
- Whicker, A. D., & Detling, J. K. (1988). Ecological consequences of prairie dog disturbances. *BioScience*, 38(11), 778-775.