THESIS

POPULATION ASSESSMENT OF BURROWING OWLS NESTING ON BLACK-TAILED PRAIRIE DOG COLONIES IN COLORADO

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ABSTRACT

POPULATION ASSESSMENT OF BURROWING OWLS NESTING ON BLACK-TAILED PRAIRIE DOG COLONIES IN COLORADO

In North America, grassland birds have experienced steeper and more widespread declines than any other avian guild due to habitat loss resulting from grassland conversion to cropland, increasing urban and energy development, and climate change (Knopf 1994, Askins et al. 2007). The historical area of native grasslands has decreased by 62% since the 1800s and contributed to the loss of nearly 40% of grassland bird populations since 1966 (Wilsey et al. 2019). Heterogeneity in climate, grazing, and fire across the landscape have resulted in the existence of different grassland types that vary in structure and composition. The shortgrass prairie is the driest and warmest of the Great Plains grasslands and is dominated by low-growing perennial grasses, forbs, and shrubs. The shortgrass prairie provides vital nesting and foraging habitat for many grassland birds. In Colorado, approximately 50% of the historic shortgrass prairie has been converted to other land uses (Neely et al. 2006). The partial loss of shortgrass prairie habitat has ecological consequences including loss of native vegetation and decreases in populations of grassland species, including grassland birds.

Black-tailed prairie dogs (*Cynomys ludovicianus*) are important drivers of ecosystem function in the shortgrass prairie because their colonial social structure, burrowing and foraging behaviors alter the landscape and provide areas of shorter vegetation and burrow systems that support increased biodiversity of animals and plants (Cully et al. 2010). Black-tailed prairie dogs function as a keystone species in shortgrass prairie ecosystems and create important breeding and

foraging habitat for grassland birds including western burrowing owls (*Athene cunicularia hypugaea*: Smith and Lomolino 2004). The western burrowing owl is a small diurnal raptor that lives in grasslands, deserts, and other open habitats. It is a partially migratory species where populations in the southern parts of its range in the southwestern United States, Mexico, and portions of Central and South America are typically year-round residents. Migratory populations occur in the grasslands of North America, arriving in early spring to start breeding as far north as Canada and departing in late August to return to their wintering grounds in the southwestern United States and Mexico (Poulin et al. 2011).

Burrowing owls typically nest in burrows dug by rodents such as prairie dogs and ground squirrels. In eastern Colorado, burrowing owls almost exclusively nest on black-tailed prairie dog colonies. Benefits of nesting on prairie dog colonies include increased predator detection from alarm calls, decreased predation due to the dilution effect, and reduced vegetation height. Black-tailed prairie dog populations have experienced an estimated decline of 90-98% since 1900 due to sylvatic plague outbreaks and habitat loss and alteration by human development (Miller et al. 1994, Desmond et al. 2000). Since prairie dog colonies provide critical habitat for burrowing owls and other species, population decline contributes to decreased availability of burrowing owl nesting habitat.

Conservation status of the burrowing owl varies across its range. It is a species of conservation concern in the western United States, threatened in Mexico, and endangered in Canada (Sheffield 1997). The western burrowing owl is currently listed as a state-threatened species in Colorado and is designated as a Tier 1 Species of Greatest Conservation Need in Colorado's State Wildlife Action Plan (Colorado Parks and Wildlife 2015). The last burrowing owl population assessment in Colorado was conducted in 2005 (Tipton et al. 2008, 2009) and since then, only local surveys limited in spatial and temporal extent have been conducted. This has prompted the need for an updated population assessment of burrowing owls nesting in eastern Colorado, where the majority of Colorado's burrowing owls breed on black-tailed prairie dog colonies. In this study, we provide an updated status assessment for burrowing owls on Colorado's eastern plains and seek to expand the current understanding of which black-tailed prairie dog colony attributes have the highest value for burrowing owl occupancy, density, and productivity.

We specifically examined how colony size, activity status, and vegetation characteristics influence these population parameters on 175 survey plots throughout eastern Colorado. We surveyed some of the same plots using similar methodology as Tipton et al. (2008, 2009) in their 2005 study, facilitating comparisons of burrowing owl populations 17–18 years later. The first chapter describes the distribution of burrowing owls nesting on black-tailed prairie dog colonies in eastern Colorado and serves to examine which black-tailed prairie dog colony characteristics drive the use of a colony by burrowing owls and the probability of successful reproduction. The second chapter focuses on burrowing owl density, productivity, and abundance in eastern Colorado to determine how many burrowing owls are present on occupied colonies and how productive they are on colonies where they do reproduce. The value of describing these components of burrowing owl populations in separate chapters comes from estimating and identifying the drivers of burrowing owl occupancy in chapter 1, then shifting to the finer scale of density to determine if the drivers of burrowing owl distribution are also driving density, productivity, and abundance.

We used a black-tailed prairie dog colony shapefile prepared by the Colorado Natural Heritage Program for Colorado Parks and Wildlife in 2020 as our sampling frame. This shapefile includes polygons that represent black-tailed prairie dog colonies with digitized boundaries, created using imagery collected in 2019 by the National Agriculture Imagery Program (NAIP). We used a spatially balanced sampling design to select potential plots and selected new samples for each survey year (2022 and 2023) to maximize sample size and spatial coverage of the large study region. From early May through early August, we conducted four surveys on 175 plots in eastern Colorado, counting all burrowing owls seen, with two visits occurring prior to juvenile emergence and two occurring after.

We estimated occupancy using a static multistate occupancy estimation model with two states: 'occupied' and 'occupied with successful reproduction'. We estimated density and abundance using distance sampling methods. We estimated productivity using a zero-inflated beta generalized linear model. We used occupancy data from Tipton et al. (2008) and dynamic occupancy models to evaluate burrowing owl local colonization and local extinction between 2005 and 2022 - 2023.

Our analyses indicate that burrowing owl occupancy and density are highest in southern Colorado and lowest in northern Colorado. Colonies with higher prairie dog activity level had higher probability of reproduction and higher densities of adult burrowing owls. Vegetation height was the main driver of juvenile density such that colonies with taller vegetation supported lower densities of juvenile owls. We estimated burrowing owl occupancy to be 0.84 (95% CI [0.62, 0.95]) and probability of successful reproduction on occupied plots to be 0.86 (95% CI [0.70, 0.94]). We estimated an average density of 3.47 (95% CI [2.79, 4.15]) adult owls/km^2 prior to juvenile emergence, 8.20 (95% CI [6.39, 10.00]) adult owls/km^2 after juvenile emergence, and 18 juveniles/km^2 (95% CI [13.86-23.66]). We expanded our density estimates to our sampling frame and estimated that there were 4,913 (95% CI [3,948-5,875]) adult owls prior to juvenile emergence, 11,613 (95% CI [5,333-17,893]) adult owls after juvenile emergence, and 26,580 (95% CI [19,623-33,537]) juvenile burrowing owls on black-tailed prairie dog colonies in eastern Colorado.

We found that prairie dog activity had a positive effect on burrowing owl density, successful reproduction, and productivity regardless of prairie dog colony size. This indicates that burrowing owls are effectively utilizing and nesting on small prairie dog colonies in eastern Colorado, which could make them more resilient to breeding season habit loss, fragmentation, or degradation. In addition, we found that northern Colorado had lower burrowing owl occupancy and adult density, but had a similar probability of successful reproduction and juvenile density compared to south and central Colorado. If northern Colorado can sustain stable burrowing owl densities, burrowing owl populations may have enough successful reproduction to maintain stable populations. The covariates we investigated in this study did not adequately explain this spatial pattern. However, it is likely that differences in climate, prairie dog population dynamics, land use, or some other factor could cause differences in local habitat and breeding conditions across Colorado.

The previous burrowing owl population assessment in eastern Colorado estimated burrowing owl occupancy to be 0.80 (95% CI [0.66-0.89]), density to be 3.04 adult owls/km^2 (95% CI [2.15, 5.13]), and adult abundance to be 3,554 (95% CI [3,928-8,445]) owls in eastern Colorado. This suggests that overall, burrowing owl populations in eastern Colorado are relatively stable and are likely to remain stable if efforts continue to preserve the prairie dog colonies that are vital for burrowing owls during the breeding season.

The burrowing owl is a state-threatened species in Colorado at the time of this thesis and thus we recommend future burrowing owl surveys to track population changes through time.

Future monitoring efforts can help identify the drivers of burrowing owl population change and clarify the spatial patterns we found. These future efforts should occur more frequently than the ~17 year time period between this population assessment and the last assessment in 2005. We recommend conducting burrowing owl surveys every 5 years because it exceeds the time lag between black-tailed prairie dog colony local extinction and cessation of burrowing owl nesting. In addition, a 5 year time interval coincides with the timing of the Colorado Natural Heritage Program's black-tailed prairie dog mapping efforts in eastern Colorado, from which we constructed our sampling frame. Using updated mapping efforts is vital for monitoring efforts because it may decrease the probability that a plot selected from the sampling frame contains a prairie dog colony that has gone locally extinct. We recommend future efforts should select new plots to survey for burrowing owls in addition to resurveying a subset of the plots from this study. Revisiting sites from this study would be helpful in determining burrowing owl population trends through time, while selecting new plots can increase the spatial coverage of surveys. This 2-year study provides an updated status assessment of burrowing owl populations across the black-tailed prairie dog range in Colorado that will help calibrate burrowing owl population models incorporating prairie dog colony extent, inform future monitoring plans, and help guide conservation of keystone species and their communities.

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INTRODUCTION

Most avian guilds are at risk due to various threats including climate change, land use change, and habitat loss (Rosenberg et al. 2019). In North America, grassland birds have experienced steeper and more widespread declines than any other avian guild due to habitat loss resulting from grassland conversion to cropland, increasing urban and energy development, and climate change (Knopf 1994, Askins et al. 2007). Grassland conversion has resulted in a loss of 62% of historical grasslands since the 1800s, which contributes to the loss of nearly 40% of the grassland bird population since 1966 (Wilsey et al. 2019). The loss of grassland habitats has profound ecological consequences including loss of native vegetation and biodiversity of the species that rely on these ecosystems (Knopf 2004).

The shortgrass prairie is a designation of grassland that is characterized by low-growing perennial grasses, forbs, and shrubs. The shortgrass prairie provides vital nesting and foraging habitat for many grassland birds. Habitat loss, degradation, and fragmentation is increasing in this landscape due to development in the oil and gas, urban, and agricultural sectors (Neely et al. 2006). In Colorado, approximately 50% of the historic shortgrass prairie has been converted for a variety of uses (Neely et al. 2006). This has led to population declines in multiple grassland species including black-tailed prairie dogs (*Cynomys ludovicianus*: Desmond et al. 2000). Prairie dog species are important drivers of ecosystem function in the shortgrass prairie because their breeding and foraging behaviors alter the landscape and provide areas of shorter vegetation and burrow systems that support increased biodiversity of animals and plants (Cully et al. 2010).

Black-tailed prairie dogs function as a keystone species in shortgrass prairie ecosystems and create important breeding and foraging habitat for grassland birds including western burrowing owls (*Athene cunicularia hypugaea*: Smith and Lomolino 2004). Western burrowing owls are small diurnal raptors that live in grasslands, deserts, and other open habitats. It is a partially migratory species where populations in the southern parts of its range in the southwestern United States, Mexico, and portions of Central and South America are typically year-round residents (Poulin et al. 2011). Migratory populations occur in the grasslands of North America, arriving in early spring to start breeding and departing in late August to return to their wintering grounds (Poulin et al. 2011). The relationship between burrowing owl populations and prairie dog colonies is well documented (Klute et al. 2003). Burrowing owls typically nest in burrows dug by burrowing rodents such as prairie dogs and ground squirrels. They most commonly use black-tailed prairie dog and Wyoming ground squirrel colonies as nesting grounds, but they are also known to nest on white-tailed prairie dog and Gunnison's prairie dog colonies (Dechant et al. 2002, Klute et al. 2003). They may prefer black-tailed prairie dog colonies because their open nature and characteristically shorter vegetation increase predator detection (Dechant et al. 2002). Benefits from prairie dog presence include increased predator detection from alarm calls, decreased predation due to the dilution effect where prairie dogs are an abundant alternative prey source, and reduced vegetation height (Desmond et al. 2000). Plumpton and Lutz (1993) found that burrowing owls prefer to nest in black-tailed prairie dog colonies that have high burrow density, perch availability, and percentage of bare ground. Removal of burrowing mammals, including prairie dogs, and destruction of nesting habitat have been the main drivers of burrowing owl population decline (Klute et al. 2003, Sheffield 1997). Desmond et al. (2000) found that the number of nesting burrowing owl pairs declined as active prairie dog burrow density declined on 17 prairie dog colonies over a 7-year study. The absence of prairie dogs results in burrow deterioration and encroachment of dense vegetation, causing owls to eventually stop breeding at these sites (Dechant et al. 2002). Conrey (2010) found that burrowing owls occupied prairie dog colonies after a plague extinction event if there was enough connectivity with another colony such that the colony was eventually recolonized by prairie dogs.

Black-tailed prairie dog populations have declined by 90-98% since 1900 due to sylvatic plague outbreaks and habitat loss and alteration by development (Miller et al. 1994, Desmond et al. 2000). Since prairie dog colonies provide critical habitat for burrowing owls and other species, population decline contributes to decreased availability of burrowing owl nesting habitat (Jones 1998, VerCauteren et al. 2001). Other factors influencing burrowing owl decline include poisoning of prairie dogs, pesticide use, and alteration of wintering range habitat (Sheffield 1997, Macías-Duarte 2011). Varying levels of population decline have created variation in the conservation status of the burrowing owl across its range. It is a species of conservation concern in the western United States, threatened in Mexico, and endangered in Canada (Sheffield 1997). The burrowing owl is currently listed as a state-threatened species in Colorado and is considered a Tier 1 Species of Greatest Conservation Need in Colorado's State Wildlife Action Plan (Colorado Parks and Wildlife 2015). This indicated the need for updated research on burrowing owl distribution in Colorado. Most of the burrowing owls in the state nest in eastern Colorado on black-tailed prairie dog colonies, so our study focused on burrowing owl occupancy in this region of the state.

Occupancy models are effective tools for evaluating wildlife-habitat relationships and species distributions across landscapes. Previous studies have assessed burrowing owl occupancy and reproduction both in Colorado and throughout the species' range. In a large-scale study in north-central Montana, Alverson and Dinsmore (2014) assessed how prairie dog colony attributes affected burrowing owl occupancy over a 13-year period. They found that prairie dog colony size had a positive effect on owl occupancy while edge effects and plague epizootics had only weak effects. Other studies have shown positive relationships between burrowing owl habitat selection and prairie dog colony size (Hughes 1993, Desmond & Savidge 1996, Toombs 1997). However, there is ambiguity in the relationship between prairie dog colony size and burrowing owl use. Bayless and Beier (2011) found no effect of colony size on burrowing owl occupancy. Tipton et al. (2008) found that owl occupancy was higher on active colonies than inactive colonies, but occupancy declined with increasing cover of prairie dog colonies in the surrounding landscape.

Burrowing owls have also been known to have higher site fidelity on larger prairie dog colonies due to decreased nest predation and higher rates of nesting success compared to smaller colonies or those with lower densities of prairie dogs (Dechant et al. 2002). Burrowing owl reproductive success is likely influenced by breeding ground arrival date, nest initiation date, and the quantity and quality of available nesting and foraging habitat (Griebel & Savidge 2007). Earlier arrival and nest initiation date have been positively associated with burrowing owl reproductive success (Wellicome 2000, Griebel & Savidge 2007). Burrowing owl nest success has been shown to be higher on colonies with higher densities of active prairie dog burrows and larger distances between nest burrows (Bayless and Beier 2011). Previous research has shown that owls breeding on larger prairie dog colonies sometimes have greater nest success and less nest depredation (Desmond & Savidge 1996, Alverson & Dinsmore 2014). Larger colonies often have greater abundances of burrowing owls and nesting attempts (Griebel & Savidge 2007). However, there is some evidence of higher nest success on smaller colonies (Woodard 2002).

The last assessment of burrowing owl distribution in Colorado, by Tipton et al (2008), estimated that 80% (95% CI [66%, 89%]) of potential burrowing owl habitat was occupied in eastern Colorado. Since this study was conducted in 2005, there have been no broadscale updated assessments of burrowing owl occupancy in eastern Colorado. In this chapter, we provide an updated assessment of burrowing owl occupancy, investigate the rate of successful reproduction at occupied sites, and assess black-tailed prairie dog colony attributes that have the highest value for burrowing owl occupancy and successful reproduction in Colorado's eastern plains. Tipton et al.'s (2008) estimate was based on adult burrowing owls prior to juvenile emergence because the timeline of the surveys in their study was limited to the early part of the burrowing owl breeding season when mostly adult males are available for detection. During this time, females spend time below ground incubating and brooding and are thus mostly unavailable for detection. We extended the timeline of our surveys to include the period of the breeding season after juvenile emergence to obtain estimates of successful reproduction. Juvenile emergence refers to the first time that owl nestlings leave the nest burrow, which occurs 10-14 days after hatching (Zarn 1974a). Currently, no other study has assessed burrowing owl successful reproduction at a spatial scale incorporating all of eastern Colorado.

We specifically examined how colony size, activity status, activity level, and vegetation characteristics influence burrowing owl occupancy and successful reproduction on 175 survey plots throughout eastern Colorado. Previous studies have investigated the effect of prairie dog colony size and activity on burrowing owls at large spatial scales; however, few of these studies have included vegetation at those scales. The last burrowing owl population assessment in Colorado lacked vegetation covariates. Colonies that are active with prairie dogs and have higher prairie dog activity levels are predicted to positively influence owl occupancy and successful reproduction because higher prairie dog activity indicates that there are more well-maintained burrows that are suitable for burrowing owl nesting, shorter vegetation, and more alarm calling that makes it easier for owls to detect predators on the landscape. Larger colonies likely have a higher availability of nesting burrows, so colony size is predicted to have a positive effect on occupancy and successful reproduction. Though the literature has shown a positive effect of colony size, we are interested in looking at small prairie dog colonies (less than 10 ha) to determine if these colonies have suitable habitat characteristics to support burrowing owl presence and successful reproduction in eastern Colorado. A previous study in North Dakota found that burrowing owls may have a nesting ground requirement of 4-6 ha (Dechant et al. 2002), and burrowing owls have been known to nest on colonies as small as 1.9 ha (Klute et al. 2003). If burrowing owls can effectively nest and rear young on smaller prairie dog colonies, their populations may be more resilient to habitat loss, degradation, and fragmentation. We also expected that colonies with shorter vegetation and high cover of bare ground are more likely to be occupied by burrowing owls and have successful reproduction, because burrowing owls prefer to nest in colonies with shorter vegetation, presumably, so they can better detect predators and forage for insects. In addition, we hypothesized that vegetation cover within and surrounding the colony influences burrowing owl occupancy and reproductive success because burrowing owls are known to leave the prairie dog colony to forage in surrounding taller vegetation. We predicted that vegetation height and temperature would have a negative effect on the detection process because tall vegetation can make it difficult for observers to detect owls and on hotter days, owls may retreat below ground and be unavailable for detection.

We compared burrowing owl occupancy from the previous population assessment in 2005 (Tipton et al. 2008) to our assessment and investigated the effect of various prairie dog colony characteristics on burrowing owl local colonization and local extinction. We predicted that lower proportions of prairie dog colony in the landscape surrounding Tipton et al's (2008) survey plots may increase the probability of burrowing owl local extinction since prairie dog colonies may become inactive due to a plague or poisoning event and not get recolonized by prairie dogs. Since prairie dogs are vital to the creation and maintenance of nesting burrows for burrowing owls, their absence would drive owl local extinction. Plots that were unoccupied in 2005 by burrowing owls but were surrounded by larger proportions of prairie dog colony may be more likely to have burrowing owl local colonization. We hypothesized that a prairie dog colony that transitioned from active in 2005 to inactive in 2022/2023 would increase the probability of burrowing owl local extinction because prairie dogs are no longer maintaining burrows and owls are likely to stop breeding at these sites. If a prairie dog colony transitions from inactive in 2005 to active in 2022/2023, this might drive local colonization because prairie dogs have moved in and started creating and maintaining burrows, which supports burrowing owl breeding. Larger prairie dog colonies in 2019 may indicate that the colony has persisted through time and thus may have a positive effect on local colonization and a negative effect on local extinction.

This 2-year study serves to update our knowledge of burrowing owl occupancy and obtain estimates of successful reproduction in eastern Colorado. This will help calibrate burrowing owl population models incorporating prairie dog colony characteristics, inform future monitoring plans, and help guide conservation of keystone species and their communities.

FIELD METHODS

Study area

The study area encompasses the eastern plains of Colorado, corresponding to the overall range and distribution of the black-tailed prairie dog in Colorado at approximately 186,425 km^2 (Figure 1.1). Eastern Colorado is a matrix of habitats including urban, exurban, shortgrass prairie, and agricultural land. Native shortgrass prairie habitat is characterized by low growing perennial grasses, forbs, and shrubs. Buffalograss (*Bouteloua dactyloides*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Pascopyrum smithii*) are the most abundant grasses, but species composition varies across the state with differences in climate and soil. Dominant non-native species typically include cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola tragus)*, musk thistle (*Carduus nutans*), Canada thistle (*Cirsium canadensis*), wavyleaf thistle (*Cirsium undulatum*) and knapweed (*Centaurea* spp.) (Decker 2007). Dominant land uses in the study area include agriculture and cattle grazing. Oil, natural gas, and renewable energy have become increasingly prominent land uses over the past two decades (Jones & Pejchar 2013, Helmig 2020). Landscape heterogeneity in the shortgrass prairie is largely driven by grazing and fire. Historically, the American plains bison (*Bison bison bison*) was the dominant large grazer in the system. Today, cattle (*Bos taurus*) and pronghorn (*Antilocapra americana*) are the dominant large grazers and the black-tailed prairie dog is the dominant small grazer.

Due to residential development, burrowing owls have been extirpated from many urban areas along the Front Range of Colorado (Jones 1998). However, we included these areas in our sampling frame because there are still some existing black-tailed prairie dog colonies of varying size in urban and exurban areas (Colorado Parks and Wildlife 2020). Since burrowing owls almost exclusively nest on black-tailed prairie dog colonies in eastern Colorado (Tipton et al.

2008, 2009), our study sites occurred in areas with either active or recently active prairie dog colonies.

Plot selection

We used a black-tailed prairie dog colony shapefile prepared by Colorado Parks and Wildlife and the Colorado Natural Heritage Program in 2020 (Colorado Parks and Wildlife 2020) to construct our sampling frame in ArcGISPro 2.9.0. This shapefile includes polygons that represent black-tailed prairie dog colonies with digitized boundaries, created using imagery collected in 2019 by the National Agriculture Imagery Program (NAIP). This imagery was visually analyzed to identify potential black-tailed prairie dog colonies across eastern Colorado. In 2019, the total coverage of potential black-tailed prairie dog colonies in eastern Colorado was approximately 4,925 km^2. Of this total coverage, approximately 2,025 km^2 were identified as potential active colonies (Colorado Parks and Wildlife 2020). Only a small subset of the polygons in this 2020 black-tailed prairie dog colony shapefile were air- or ground-truthed, and there may be polygons that were falsely identified as prairie dog colonies, with a 26.3% estimated false positive rate in a similar 2016 effort (Howlin and Mitchell 2016). In addition, prairie dog colonies are extremely dynamic and boundaries may have changed since 2019 due to plague, poisoning, or environmental factors. Therefore, we overlaid our potential survey plots on recent NAIP imagery to increase the probability that there were still prairie dog burrows on the plot. We used 2021 NAIP imagery to assess our 2022 potential survey plots and 2022 imagery to assess our 2023 potential survey plots, arriving at our initial sampling frame. We originally aimed to use this updated NAIP imagery to draw polygons around the colony boundaries that were included in selected plots, to provide updated boundaries and colony size estimates. However, we did not proceed with this method because we would be biased toward colony expansion. There is no way to assess colony contraction from imagery since prairie dog mounds can be visible on imagery for a few years after they are abandoned. We also revisited a subset of Tipton's plots ($N = 32$), chosen by spatially balanced random sampling, to be able to compare occupancy between the two studies.

Across the 2022 and 2023 field seasons, we selected a total of 691 potential plots from the sampling frame in case there were access issues or the plot was not located on an actual prairie dog colony. We used a spatially balanced random sampling design using the SBS tool in ArcGISPro 2.9.0 (Stevens & Olsen 2004) to select potential plots. We selected 350 and 341 plots for 2022 and 2023 respectively. We overlaid our plots on the layer of potential prairie dog colonies and updated NAIP imagery to eliminate plots that lacked evidence of a prairie dog colony. From our initial sampling frames in 2022 and 2023, we dropped 132 and 61 plots respectively due to lack of evidence of prairie dog colonies from the NAIP imagery, arriving at our final sampling frame. We selected 1 km x 1 km plots (Figure 1.2) and placed a transect running through each plot such that observers were always 250 m away from the plot boundary to ensure that the entirety of the plot was adequately surveyed. We attempted to gain access to survey plots regardless of private or public land ownership. Plot size and transect placement were based on a 250 m detection distance for burrowing owls (Conway and Simon 2003).

We conducted this study over two field seasons that occurred May through August in 2022 and 2023. Burrowing owls have high breeding site fidelity to colonies and therefore, occupancy dynamics and successful reproduction estimates for a two-year study on the same plots would be less informative than doubling the sample size by selecting new sites in 2023. We ran simulations using single season occupancy models (MacKenzie et al. 2002) in Program MARK (White and Burnham 1999) to determine the number of plots and visits needed for this study (Table 1.1). The precision of occupancy estimates from 90 plots was not substantially different than 140 plots. Differences in precision between three and four visits were also not substantial. We based the probability of detection of burrowing owls on estimates from the occupancy and abundance study done by Tipton et al. (2008, 2009). If a plot needed to be moved due to access or location issues (i.e., plot fell outside the colony), we used a random bearing (in the direction of the colony) and a maximum distance of 250 m to select a new plot.

Black-tailed prairie dog colony size and activity level

We created three prairie dog colony size categories from the 2020 shapefile: small (≤ 10 ha), medium (11 - 299 ha), and large (≥300 ha). We originally allocated sampling effort equally between the size categories; however, landowner permission determined the final ratio of colony sizes. Small colonies in the shapefile had a mean size of 6.38 ha, which is close to the estimated 4-6 ha minimum size required for burrowing owls nesting in North Dakota (Dechant et al. 2002). Most colonies in the shapefile were categorized as small or medium. The large category contained fewer colonies but accounted for ~35% of the total area covered by black-tailed prairie dog colonies in Colorado. Within each very large colony (> 1000 ha), we placed two survey plots and pooled the data during analysis. Prairie dog colonies are heterogeneous because they are composed of patches of burrows interspersed by bare ground and vegetation; therefore very large colonies required two sample plots to get more precise parameter estimates. Since small colonies are less than 10 ha, our selection criteria for small plots required that the plot encompass the entirety of the prairie dog colony. For medium and large colonies, we required a minimum of 25% of the plot be covered by prairie dog colony to ensure that plots weren't dominated by non-colony grassland with only a small corner of a colony. We based this requirement on Tipton's (2008, 2009) plot requirements to allow for comparisons between our studies.

In our study, we defined the activity status of each prairie dog colony as either active or inactive. Inactive colonies were defined as colonies where prairie dogs were absent and no fresh sign was detected (scat and digging). On active colonies, we assigned prairie dog activity levels. In 2022, we used a qualitative approach to assess prairie dog activity level based on an assessment of burrow density and proportion of long inactive burrows (closed), recently inactive burrows (open but without scat or signs of digging), and active burrows (open with scat or signs of digging). The three activity level categories include low, medium, and high activity. We only surveyed recently inactive colonies if there were open burrows suitable for burrowing owl nesting. Colonies with low prairie dog activity had large patches of inactive burrows, including both long term and recently inactive burrows. Colonies with medium prairie dog activity had some patches of inactive burrows, but most of the burrows in the plot were open. Colonies with high prairie activity had a high density of active and open burrows with few or no patches of inactivity. In the 2023 field season, we added a quantitative method for assessing prairie dog colony activity level in addition to the method mentioned above. We assessed prairie dog activity level along the survey transect by recording whether there were long term inactive (closed), recently inactive (open), active burrows, or no burrows present within a 100 m radius of each vegetation point along the transect. We conducted this assessment during vegetation surveys on the third visit when observers collected vegetation and prairie dog activity data every 20 m along the survey transect.

Latitude

We investigated the effect of prairie dog colony latitude on burrowing owl occupancy and reproduction in three different structures: ordinal, categorical, and continuous latitude. Ordinal latitude splits eastern Colorado into three regions: south, central, and north. Categorical latitude also splits eastern Colorado into southern, central, and northern regions, but allows for a non-ordinal relationship. Continuous latitude was defined in the decimal degree format. We thought that ordinal and categorical latitude would be more interpretable for land managers because it is easier for a land manager to determine if their area of management is located within a region polygon than within a boundary of continuous latitude.

Vegetation

During the third of four visits each year, we conducted vegetation surveys to determine if vegetation height or cover influenced burrowing owl occupancy and successful reproduction. We assessed the vegetation structure of the colonies in terms of functional groups (grass, forb, shrub, and bare ground). Vegetation in the shortgrass prairie is best surveyed during peak biomass and green-up during June or early July (Dickinson and Dodd 1976). During the third visit to survey for owls, observers collected vegetation data using the line point intercept method (Herrick et al. 2021). Observers stopped every 20 m on the main transect line, walked 1 m off the transect, and dropped a pin flag from a ~0.5 m height (Robel pole), resulting in 100 points per transect. We collected mean height and functional group for plants that touched the vertical pin flag. Each vegetation point was characterized as being within 100 m of active, inactive, or no prairie dog burrows. Due to variability in the observers' pace, occasionally they ended up with 98 points at the end of the transect. If this was the case, observers walked 5 m toward the plot center from their last vegetation point and recorded another vegetation point. If they needed to do more than one, these vegetation points were located 20 m apart.

Precipitation

We used precipitation data to achieve two objectives. The first was to compare precipitation levels between years to evaluate if this influenced burrowing owl occupancy. The second was to create a proxy for vegetation height for each survey to assess the effects of vegetation on the detection process, because precipitation levels are positively correlated with vegetation height (Sala et al. 1988). We were only able to conduct comprehensive vegetation surveys on the third burrowing owl survey visit. However, 2023 was a wet year in the eastern plains of Colorado, with vegetation height increasing throughout the field season. Therefore, we used precipitation levels prior to surveys as a proxy for visit-specific vegetation in our detection process.

We obtained daily precipitation data for each of our survey plots from NOAA using the 'rnoaa' package in program R (Chamberlain & Hocking 2023). We identified the closest weather monitor within 30 km of each plot and extracted precipitation values for all days during the breeding season and the 7 days leading up to our survey day. For each plot, we summed the precipitation data from the whole breeding season to get a season-level precipitation sum that served as a proxy of vegetation height for the breeding season. We averaged the precipitation values for the week before surveys to obtain a visit-specific proxy for vegetation height.

Burrowing owl surveys

From the sampling frame of 691 potential survey plots, we obtained access and conducted one survey on 274 plots. Of these, 175 contained active or recently active prairie dog colonies and were thus suitable for subsequent burrowing owl surveys. We surveyed 85 plots in 2022 and 90 plots in 2023. We aimed to visit each plot four times, with two visits before owlet emergence and two after, between early May and August. However, logistical issues resulted in fewer than four visits to some plots. For each round of surveys, we began in the south and finished in northern Colorado since burrowing owl breeding is typically initiated earlier in southern Colorado. The first two visits (between May 1st and ~June 18th) provided an estimate of adult breeding distribution; we assumed that late arrivals were not likely after the first visit in May and that most nest failures occurred after this time period. Visits 3 and 4 occurred after owlet emergence (~ June 19th) and provided estimates of probability of successful reproduction.

Surveys took place during peak owl activity hours: morning (sunrise until ~11 am) and evening (~5:30 pm until sunset). At each plot, we determined the activity status of the colony as either active or inactive, with more detailed quantification of prairie dog activity occurring when vegetation was characterized. Observers recorded time and weather information for the survey start and end, using handheld weather meters to record temperature and wind speed. For each owl detection, observers recorded the time of detection, UTM coordinates of detection point, detection type (visual or auditory), distance and bearing to bird, age class (adult, juvenile, or unknown) of bird, number of adults and juveniles if more than one individual was seen close together (within ~3 m), and human disturbance within 100 m of bird. We defined human disturbance as fencing, roads, manmade structures and other objects, and trails.

We used two observers per visit to increase the overall detection probability of owls. We pooled detections between the two observers, who communicated with each other during surveys. During the first two survey visits of the 2023 field season, we experimented with a dependent double observer approach where the primary observer conducted the survey while the secondary observer took notes and recorded any missed detections by the primary observer (Nichols et al. 2000). The double observer approach allows for estimation of observer-specific detection probabilities and more precise occupancy estimates (Nichols et al. 2000). We tested whether the dependent double observer method increased precision in the occupancy estimator.

STATISTICAL METHODS

Occupancy

We estimated occupancy using the static multistate occupancy estimation model (Nichols et al. 2007) in Program MARK (White and Burnham 1999) with two states: 'occupied' and 'occupied with successful reproduction'. We pooled detections from our two-observer occupancy surveys. If at least one burrowing owl was detected by either observer, owls were considered to be present; if at least one juvenile was detected by at least one observer, reproduction was considered to be successful at the site level. Parameters in this model include the probability that a plot is occupied by burrowing owls (ψ_1), the probability of successful burrowing owl reproduction on occupied sites (ψ_2), the probability of detecting at least one owl where there is no reproduction (p_1), the probability of detecting at least one owl when juveniles are present (p_2), and the probability of detecting at least one juvenile on occupied plots with successful reproduction (δ).

We investigated the effect of prairie dog colony characteristics including prairie dog colony size, activity status, activity level, proportion of the plot covered by prairie dog colony, and cover of plant functional groups (grass, forb, shrub, bare ground) on burrowing owl occupancy (ψ_1) and successful reproduction parameters (ψ_2). We assessed the influence of vegetation height, observer team, and various environmental covariates including temperature, wind speed, cloud cover, season precipitation sum, and sum of precipitation one week before the survey (proxy for visit-specific vegetation height) on the detection processes (p_1, p_2, and δ).

We ran covariate correlation tests and did not include moderately correlated covariates (r >0.5) in the same model (Appendix tables 1.3 & 1.4). We considered additive and interactive relationships among covariates listed in Table 1.1 using a build-up model selection method

(Morin et al. 2020). In the build-up model selection method, covariates are first investigated on each parameter in separate modeling stages. Then the top covariates are carried into subsequent modeling phases to determine the top models. We determined the top model using the small-sample Akaike's Information Criterion (AICc) (Hurvich & Tsai 1989), where the top model has the lowest AICc value and the highest weight in the model set. If models were within 2 AICc units of the top model, we compared parameter estimates and beta estimates (strength of covariate effects) to see if they were similar.

Comparison to Tipton et al. (2008)

An objective of this study was to compare results from our study to a previous burrowing owl study in 2005 (Tipton et al. 2008) to determine how burrowing owl populations have changed since the last large scale population study in eastern Colorado. We surveyed some of the same plots using similar methodology as Tipton et al. (2008, 2009) in their 2005 study, facilitating comparisons 17–18 years later. We used dynamic occupancy models (MacKenzie et al. 2003) in Program MARK (White and Burnham 1999) to compare occupancy between Tipton et al's (2008) study and our study and to estimate local colonization and extinction rates between 2005 and 2022/2023 on 32 survey plots. In this study, local colonization (γ) is defined as a plot transitioning from being unoccupied in 2005 to being occupied by burrowing owls in the 2022/2023 field seasons. Local extinction (ε) is defined as a plot transitioning from being occupied in 2005 to being unoccupied by burrowing owls in the 2022/2023 field seasons.

We investigated how local colonization and local extinction were influenced by the proportion of prairie dog colony in 2005, observed occupancy status in 2005, prairie dog colony activity status in 2005 and 2022/2023, overall prairie dog activity status, burrowing owl plot-level density in 2005 (Tipton et al. 2008), prairie dog colony size in 2019, colony latitude, and the transition of prairie dog colony from active in 2005 to inactive in 2022/2023 and vice versa. The overall prairie dog status describes if the colony ever had active prairie dogs, such that if it was active in 2005, but not in 2022/2023, the colony is considered active. We considered additive and interactive relationships among the covariates listed in Table 1.3, using the same model selection techniques described in the Occupancy section above. We ran covariate correlation tests and did not include moderately correlated covariates (r >0.5) in the same model (Appendix tables 1.5a and 1.5b). Our sample size of n=32 plots for this comparison, dictated the maximum number of covariates that could be considered in one model.

RESULTS

Rate of false positive and long inactive prairie dog colonies

Across the 2022 and 2023 field seasons, we visited a total of 274 potential prairie dog colonies. Of these colonies, 180 colonies had open burrows, making them suitable for repeat surveys. We dropped five of these colonies due to access issues. We found a total of 58 false positives and 32 long inactive colonies, accounting for 21.16% and 11.67% of colonies visited, respectively. False positive colonies were identified in the 2019 shapefile, but were determined by survey crews to not have any prairie dog burrows present. The main causes of false positives were anthills and small circular patches of bare ground that cannot be distinguished from prairie dog burrows on the aerial imagery. Our false positive rate was slightly lower than the 26.3% false positive rate assumed to occur in the colony shapefile we used (Howlin and Mitchell 2016).

Occupancy

Our occupancy analyses of the 2022 and 2023 field seasons indicated that prairie dog activity level and latitude influenced burrowing owl occupancy and reproductive success (Table 1.4). Across the two years, we surveyed 175 plots and observed burrowing owls on 72% of plots and juvenile owls on 52% of occupied plots. These percentages represent naive occupancy and reproduction.

Our top multistate burrowing owl occupancy model estimated that the probability that a plot was occupied by burrowing owls was 0.84 (95% CI [0.62, 0.95]) and the probability of successful burrowing owl reproduction on occupied plots was 0.86 (95% CI [0.70, 0.94]). As latitude increased, the probability that a plot was occupied by burrowing owls decreased, with southern and central Colorado having a higher probability of burrowing owl occupancy compared to northern Colorado (Table 1.5, Figure 1.3). We investigated the effect of latitude on burrowing owl occupancy using Tipton's data, but found only a weak, non-significant effect. Prairie dog activity level did not have a significant effect on burrowing owl occupancy, and the apparent effect was in the opposite direction as predicted, but it did have a significant positive effect on the probability of successful burrowing owl reproduction on occupied plots (Table 1.5). Prairie dog colonies with higher prairie dog activity levels had a greater probability of successful burrowing owl reproduction (Figure 1.4). The probability of successful reproduction of burrowing owls on occupied plots was similar across south, central, and northern Colorado. Prairie dog colony characteristics that did not have a significant effect on burrowing owl occupancy included colony size, colony activity status, vegetation height, and percent cover of grass, forb, shrub, and bare ground. Cattle grazing was present on almost all of our plots, so we didn't have enough data on ungrazed plots to assess the effect of grazing.

The probability of detecting at least one burrowing owl was much greater on plots with successful reproduction (p_2=0.91, 95% CI [0.87, 0.94]) compared to plots without successful reproduction (p_1=0.24, 95% CI [0.10, 0.48]). Survey year had a significant effect on the probability of seeing at least one owl on plots that had successful reproduction (Table 1.5).

Detection was higher in 2022 (p_2=0.94, 95% CI [0.89, 0.97]) than in 2023 (p_2=0.86, 95% CI [0.81, 0.91]). We only detected juvenile burrowing owls on the third and fourth visits to our plots because these occurred after juvenile emergence. The probability of detecting successful reproduction was 0.79 (95% CI [0.72, 0.85]) and 0.77 (95% CI [0.69, 0.83]) for visits 3 and 4 respectively. Temperature had a negative effect on juvenile detection probability. At higher temperatures (>32.2 °C), juveniles were more likely to be underground in a burrow and unavailable for detection.

The dependent double observer method did not yield a significant improvement in the precision of our occupancy estimator because all observers had a high probability of detection when they were in the primary observer role. The pooled double observer approach yielded an occupancy estimate of 0.72 (SE=0.050) whereas the occupancy estimate from the dependent double observer approach was 0.70 (SE=0.048). Increased precision from this approach would be more noticeable if probability of detection was lower.

Comparison to Tipton et al. (2008)

Across the two survey years (2022 and 2023), we surveyed 32 plots that had previously been surveyed for burrowing owls in 2005 (Tipton et al. 2008). Of these plots, 25% had observed local colonization, and 16% had observed local extinction. Our dynamic occupancy analysis suggested that latitude influences burrowing owl local colonization (Table 1.7 & 1.8). Plots in southern Colorado had the highest probability of local colonization (γ) compared to central and northern Colorado (Figure 1.5). The top model suggested that prairie dog activity status during the 2022/2023 field seasons was also a significant predictor of local colonization. However, the confidence interval on the beta estimate used to determine covariate effect size overlapped zero, indicating that prairie dog activity status during the 2022/2023 field season did not have a significant effect on local colonization probabilities (Table 1.8). It likely ended up in the top model due to its large but insignificant effect size.

The transition of prairie dog activity status from active in 2005 to inactive in 2022/2023 was a significant predictor of burrowing owl local extinction (Table 1.7 & 1.8). The probability of burrowing owl local extinction (ε) was higher on plots that had an active prairie dog colony in 2005 but transitioned to inactive prior to the start of the 2022 and 2023 field seasons. When a plot contained a colony that transitioned active to inactive, the probability of burrowing owl local extinction was 0.88 (95% CI [0.34, 0.99]). If the plot contained an active prairie dog colony that did not transition to being inactive, the probability of burrowing owl local extinction was 0.016 (95% CI [0.0083, 0.24]).

DISCUSSION

Burrowing owl populations have been declining across regions of the Great Plains due to nesting habitat loss from grassland conversion and declines in populations of burrowing rodents such as prairie dogs. This chapter provides an updated estimate of burrowing owl occupancy and a baseline estimate of successful reproduction on black-tailed prairie dog colonies in eastern Colorado, where the majority of burrowing owls in the state nest. Our results indicated that burrowing owl occupancy was lower in northern Colorado compared to central and southern Colorado, but that successful reproduction was similar across the different regions of eastern Colorado. Similar probabilities of successful reproduction between northern Colorado and other regions of eastern Colorado indicate that burrowing owl occupancy can remain stable through time in northern Colorado if nesting conditions continue to be adequate for burrowing owl juvenile survival. The probability of successful burrowing owl reproduction was higher on colonies with higher prairie dog activity level, suggesting that these colonies had better nesting conditions. Prairie dog colony size did not influence the probability of burrowing owl occupancy and successful reproduction, emphasizing the importance of conserving and managing for active prairie dog colonies regardless of size. Our occupancy estimate was similar to that of the last population assessment which suggests that burrowing owl occupancy has generally remained stable in eastern Colorado since 2005. However, lower occupancy in northern Colorado may suggest the need for conservation and management if there is evidence of population decline in the future.

Occupancy

This study used occupancy models to investigate how various prairie dog colony characteristics influenced burrowing owl presence and successful reproduction on black-tailed prairie dog colonies across eastern Colorado. Our results showed negative effects of latitude on burrowing owl occupancy and positive effects of prairie dog activity level on burrowing owl successful reproduction on occupied colonies. Plots in southern and central Colorado had a higher probability of being occupied by burrowing owls than northern Colorado, but they had similar probabilities of successful reproduction. None of our other covariates explained this spatial pattern. However, this pattern could be driven by differences in precipitation and temperature regimes across the state, prairie dog population dynamics, differences in land use, or some other factor. These factors could cause differences in local habitat and breeding conditions for burrowing owls across the regions of Colorado. We investigated whether higher latitude populations have lower occupancy across the burrowing owl's range. Generally, higher latitude habitats support lower avian population density (Santini et al. 2023). Burrowing owl literature indicates that there is some evidence of increased population decline at higher latitudes within the burrowing owl's range (Klute et al. 2003, Macías-Duarte & Conway 2015), but there is conflicting evidence (Conway 2018, Sidle et al. 2024). The trend of burrowing owl population decline from 1966-2001 was estimated to be -4% in Colorado, -23.7% in Wyoming, -11.4% in South Dakota, -14.8% in Montana, -15.8% in North Dakota, and -26% in Saskatchewan (Klute et al. 2003). Macías-Duarte & Conway (2015) suggested that the burrowing owl range is contracting along its northern, eastern, and western borders and expanding southward. However, Conway (2018) found non-linear variation in negative burrowing owl population trends across latitudes, but that populations in Canada have had clear long-term negative trends. Sidle et al's (2024) study using burrowing owl population data from 1998 suggested that burrowing occupancy generally did not significantly decline at higher latitude grasslands in the Great Plains within the border of the United States, though some southern grasslands such as the Buffalo Gap and Comanche National Grasslands had higher occupancy than other grasslands.

There is evidence that northern Colorado once supported a larger proportion of burrowing owls in the eastern half of the state. A previous study on burrowing owl distribution in Colorado found that Weld County in northern Colorado had the greatest proportions of locations that were occupied by burrowing owls compared to other counties in Colorado's eastern plains (VerCauteren et al. 2001). The previous population assessment conducted by Tipton et al. (2008) did not examine the effect of prairie dog colony latitude on burrowing owl occupancy, so we investigated the effect of latitude on burrowing owl occupancy using Tipton's data but found only a weak, non-significant effect. However, previous research in 1998 on burrowing owl occupancy in the Great Plains grasslands indicated that Pawnee National Grassland in northern Colorado had fewer prairie dog colonies occupied by burrowing owls compared to Comanche National Grassland in southern Colorado (Sidle et al. 2024). This spatial pattern should be investigated in future studies to determine what factors are driving this trend. The important takeaway is that there is evidence of lower burrowing owl occupancy in northern Colorado compared to other parts of the state, which suggests that this region may warrant conservation action if distribution, abundance, or productivity show future decline in this region of the state.

Although prairie dog activity level did not seem to affect the probability that a site was occupied, the probability of successful reproduction on occupied colonies was higher with higher activity level. Prairie dogs play a vital role in maintaining burrows that provide critical nesting habitat for burrowing owls. Their burrowing behaviors help keep burrows open and clear such that burrowing owls can nest inside and effectively rear young. Colonies with higher levels of prairie dog activity have better burrowing owl nesting conditions because there is a higher density of available nesting burrows that are well-maintained. In addition, colonies with higher prairie dog activity level are likely to have shorter vegetation and higher rates of prairie dog alarm calling which benefit burrowing owl detection of predators on the landscape. Therefore, colonies with higher prairie dog activity level might have higher probabilities of burrowing owl nesting and nest survival until juvenile emergence. These results support previous studies that have found positive effects of prairie dog activity level on burrowing owl occupancy (Bayless and Beier 2011) and nest site selection (Lantz et al. 2007). Overall, our occupancy analyses reaffirm the importance of active prairie dog colonies for burrowing owl nesting in regions where these owls are predominantly using prairie dog burrows during the breeding season.

Our results indicated that prairie dog colony size did not have a significant effect on burrowing owl occupancy or successful reproduction. Small, medium, and large colonies had similar occupancy and successful reproduction probabilities. Therefore, burrowing owls are effectively using prairie dog colonies for breeding, regardless of colony size.

Comparison to Tipton et al. (2008)

Analyzing burrowing owl local colonization and extinction provides a snapshot of how occupancy has changed in the years between these studies and what habitat characteristics have driven this change. We found that when a prairie dog colony transitioned from active in 2005 to inactive in 2022 or 2023, the probability of burrowing owl local extinction was ε= 0.88 (95% CI [0.34, 0.99]). Although based on a relatively small number of plots, the high rate of local extinction once a prairie dog colony becomes inactive is logical and highlights the importance of active prairie dog colonies for burrowing owl breeding. Prairie dogs create and maintain burrows and surrounding vegetation which provide suitable nesting habitat for burrowing owls. Once a prairie dog colony becomes inactive, burrow conditions deteriorate and vegetation encroachment occurs, causing burrowing owls to eventually stop breeding at these sites. Burrowing owls will still nest on recently inactive prairie dog colonies for a period of 1-3 years depending on local soil and precipitation conditions, but will stop breeding on colonies that have been inactive for longer periods of time (Desmond et al. 2000).

We found that latitude had a significant negative effect on the probability of burrowing owl local colonization. Plots in southern Colorado had higher probability of local colonization compared to northern Colorado. Based on the 32 plots from Tipton et al. (2008) that we surveyed, none of the prairie dog colony covariates that we investigated proved to be helpful predictors of burrowing owl local colonization. However, it is likely that there is another habitat characteristic that we did not assess that is driving this regional trend. We saw similar regional trends in our occupancy estimates with plots in southern and central Colorado having a higher probability of overall occupancy. This suggests that local colonization may be driven by the unmeasured conditions that are driving higher burrowing owl occupancy. These conditions are likely related to prairie dog colony characteristics that support burrowing owl presence and successful reproduction.

Our study yielded a slightly higher overall burrowing owl occupancy estimate of 0.84 (95% CI [0.62, 0.95]) compared to 0.80 (95% CI [0.66, 0.89]) in Tipton et al (2008). This suggests that burrowing owl occupancy in eastern Colorado has remained relatively stable in the period between these two studies. However, the average probability of occupancy in northern Colorado was 0.63 (95% CI [0.35, 0.83]), which is lower than the occupancy estimate from Tipton et al (2008). This suggests that overall occupancy of burrowing owls may have decreased in northern Colorado, though there is some overlap in the confidence intervals. None of our covariates that describe prairie dog colony characteristics explain this pattern, so there could be some other factor driving lower burrowing owl occupancy. Though these studies occurred 17 years apart, this comparison is useful in describing how burrowing owl occupancy has changed through time in eastern Colorado. Due to our small sample size of resurveyed plots for this comparison, inference is limited.

Conservation implications

We found that prairie dog colony size did not have a significant effect on burrowing owl occupancy and successful reproduction. This is important because if burrowing owls can successfully reproduce on smaller prairie dog colonies, they may be more resilient to breeding season habitat loss and fragmentation. Since our analysis showed that prairie dog colony activity level had a significant effect on occupancy probability, it would be important that these smaller colonies have active prairie dog populations with medium to high burrow maintenance activity. Our results support the idea proposed by Skagen et al. (2005) that the effect of habitat fragmentation on prairie bird species is often oversimplified and generalized. Their study found that daily survival of nests from two grassland birds, horned larks and lark buntings, decreased as patch size increased. This indicates that the traditional idea of viewing smaller patches as less suitable habitat may not be accurate for all species or regions.

It is difficult to manage prairie dog activity levels due to the dynamic nature of prairie dog colonies. Prairie dog colonies can exhibit boom and bust cycles due to the presence of sylvatic plague, with colonies experiencing local extinction over the course of a year. Colonies have been known to expand or contract due to interactions among plague, climate variation, and large herbivore grazing (Davidson et al. 2022). These dynamics create large variation in prairie dog colony activity level which makes it difficult to manage colonies to maintain higher levels of activity. However, Colorado Parks and Wildlife is actively managing landscapes in Colorado to maintain habitat for prairie dogs and other grassland wildlife. This includes plague management to ensure that at least a portion of a prairie dog colony remains active, to increase the likelihood of recolonization after a plague event (Tripp et al. 2017). Therefore, conserving active prairie dog colonies regardless of size should be prioritized to protect vital burrowing owl nesting grounds.

This study aimed to improve burrowing owl monitoring and thereby management in Colorado and other regions where burrowing owls are heavily relying on prairie dog colonies during the breeding season. Understanding which prairie dog colony characteristics support burrowing owl presence and successful reproduction can help Colorado Parks and Wildlife and other land managers, including federal and local agencies, target their conservation efforts. Our occupancy results suggest that northern Colorado may need more intensive conservation action if results from future burrowing owl abundance, density, and productivity studies indicate population decline compared to previous studies in eastern Colorado (Tipton et al. 2008, 2009).

The burrowing owl is a state-threatened species in Colorado at the time of this thesis and thus we recommend that future monitoring efforts should be conducted using a combination of new survey sites and revisits of a subset of the survey plots in our study. Our dynamic occupancy analysis to compare occupancy between this study and the last burrowing owl population assessment in eastern Colorado in 2005 worked well. Therefore, future revisits to our survey plots can provide more detail about changes to burrowing owl occupancy through time. We recommend a 5 year interval between future monitoring efforts because this exceeds the typical time lag between black-tailed prairie dog local extinction and cessation of burrowing owl nesting activity. Furthermore, a 5 year time interval provides the opportunity for future efforts to coincide with the Colorado Natural Heritage Program's black-tailed prairie dog mapping efforts, from which we created our sampling frame. Future monitoring efforts may also help to identify the drivers of the spatial trend that we found in this study and determine if that trend persists through time.

Future research

Shortgrass prairie ecosystems have been declining due to conversion to cropland and increased residential and oil and gas development (Neely et al. 2006, Helmig et al. 2020). Oil and gas development has increased in Colorado over the past two decades, with a large proportion of development occurring in northern Colorado in the Denver-Julesburg basin (Lupardus 2017, Helmig et al. 2020). Oil and gas development plays a role in habitat loss and fragmentation in Colorado (Jones and Pejchar 2013), but the effect of this development on biodiversity and wildlife populations has yet to be quantified. Future research should attempt to quantify habitat loss and fragmentation in the eastern plains of Colorado and relate it to burrowing owl occupancy. This would provide a landscape level context for our study and determine if habitat fragmentation and/or loss are driving the spatial patterns we observed.

Additional future work could focus on conducting smaller scale studies to determine the optimum combination of prairie dog activity level and colony size on working lands. The debate over the ecological importance of prairie dogs versus their perception as rangeland pests is an important component of burrowing owl conservation. The grazing behavior of black-tailed prairie dogs plays an important role in maintaining grassland heterogeneity and biodiversity (Augustine & Baker 2012). However, prairie dogs are sometimes considered rangeland pests because their foraging behavior can decrease forage production and availability for livestock, leading to reductions in livestock weight gains (Derner et al. 2006). Conservation of prairie dogs on working lands is a critical component of burrowing owl conservation, and future research should work more directly with private landowners to determine the best balance of human livelihood and prairie conservation.

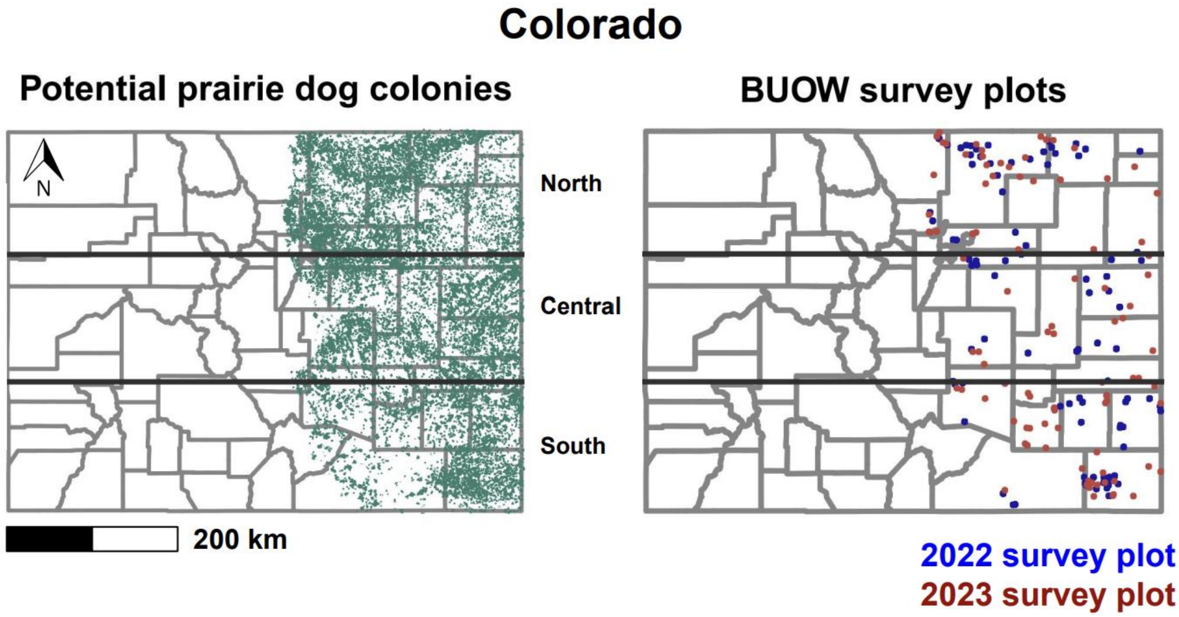

Figure 1.1: Maps of the study area with potential black-tailed prairie dog colonies (left) and burrowing owl survey plots (right). In the left map, the green area contains the potential black-tailed prairie dog colonies in eastern Colorado identified from 2019 NAIP imagery (Colorado Parks and Wildlife 2020). The map on the right shows survey plots from each year of the study, selected by spatially-balanced random sampling.

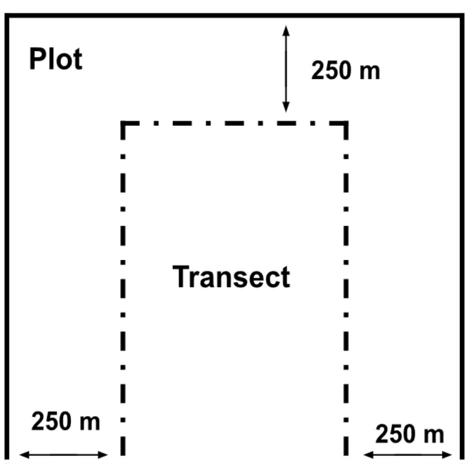

Figure 1.2: Diagram of the 1 km x 1 km plot and transect used for 2022 and 2023 burrowing owl surveys. The transect is represented by the dashed line within the plot. Vegetation data were collected ~1 m off the transect.

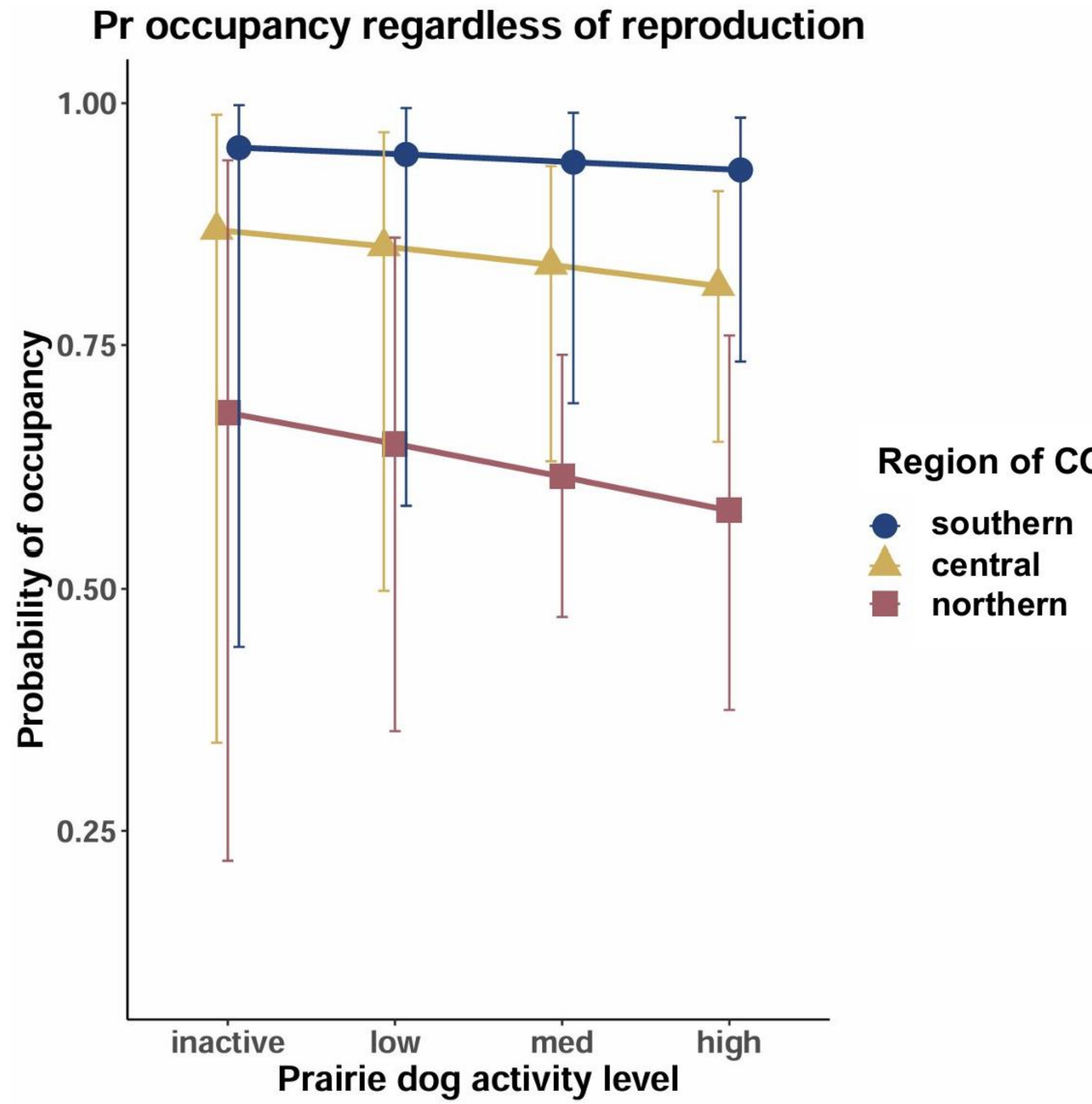

Figure 1.3: Probability of general burrowing owl occupancy (ψ_1) on prairie dog colonies in eastern Colorado, 2022/2023. The top multistate occupancy model included latitude and black-tailed prairie dog activity level; however, beta estimates (Table 1.5) indicate that prairie dog activity level does not have a significant effect on ψ_1.

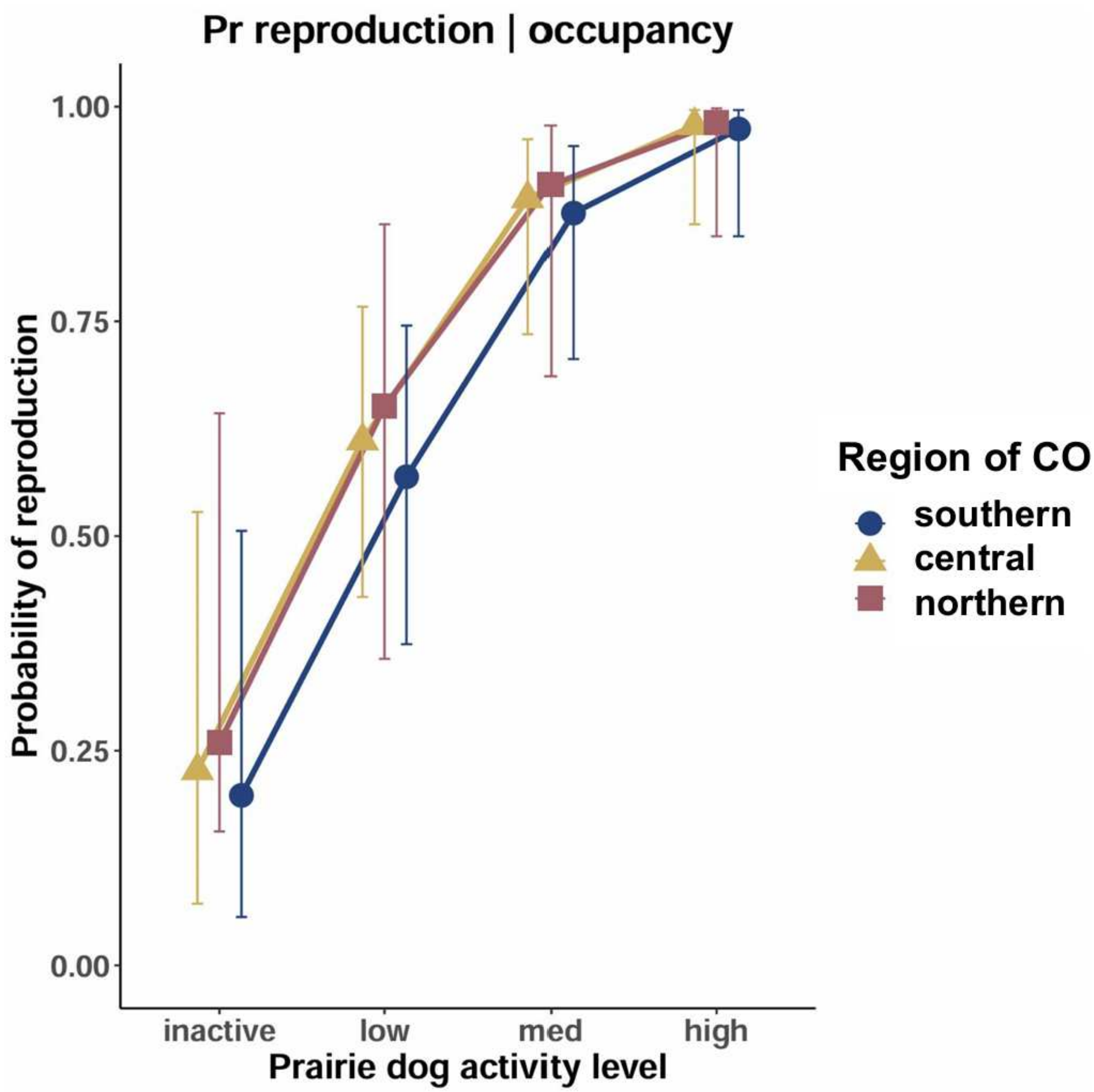

Figure 1.4: Probability of successful reproduction given burrowing owl occupancy (ψ_2) on prairie dog colonies in eastern Colorado, 2022/2023. The top multistate model included latitude and black-tailed prairie dog activity level; however, beta estimates (Table 1.5) indicate that latitude does not have a significant effect on ψ_2.

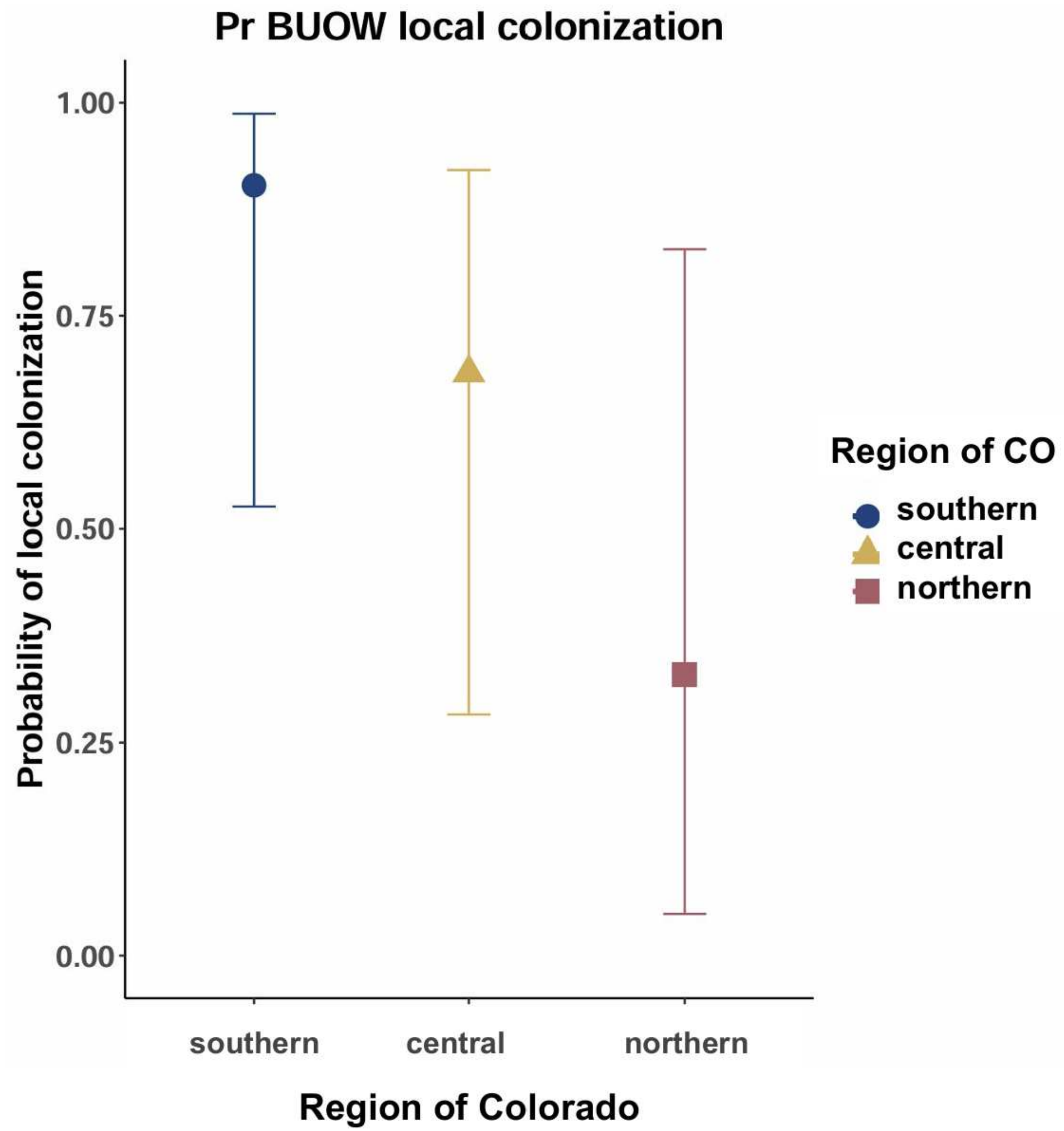

Figure 1.5: Probability of burrowing owl local colonization (γ) for the 32 plots sampled in 2005 (Tipton et al. 2008) and in 2022/2023 in eastern Colorado. The top dynamic occupancy model indicated that latitude had a significant negative effect on burrowing owl local colonization on prairie dog colonies in eastern Colorado.

Table 1.1: Results from simulations of a single-season occupancy study (MacKenzie et al. 2002) to determine the number of plots and revisits needed to get precise estimates of occupancy. The measure of precision included here is standard error (SE). The percentages in the SE column indicate the relationship of the standard error to the estimate of ψ (occupancy). For example: with 90 plots and 4 visits, the SE is 6.5% of the estimate of ψ.

# sites	# visits	ψ estimate	SE
90	2	0.81	0.085 (10%)
90	3	0.80	0.054 (6.8%)
90	4	0.80	0.052 (6.5%)
140	2	0.79	0.073 (9%)
140	3	0.80	0.055 (6.8%)
140	4	0.79	0.042 (5.3%)

Parameter and description:

ψ: burrowing owl occupancy

Table 1.2: Covariates considered in analysis of multistate burrowing owl occupancy on prairie dog colonies in eastern Colorado, 2022 - 2023.

Covariate	Parameter(s)	Covariate	Parameter(s)
Prairie dog colony activity status	ψ_1, ψ_2	% cover forb	ψ_1, ψ_2
Prairie dog colony activity level	ψ_1, ψ_2	% cover shrub	ψ_1, ψ_2
Grazing	ψ_1, ψ_2	% cover bare ground	ψ_1, ψ_2
Prairie dog colony size	ψ_1, ψ_2	Wind (mph)	p
Ordinal latitude	ψ_1, ψ_2	Temperature (°F)	p, δ
Categorical latitude	ψ_1, ψ_2	% cloud cover	p
Continuous latitude	ψ_1, ψ_2	Observer team	p
Survey year	ψ_1, ψ_2, p, δ	Precipitation season sum (mm)	p, δ
Vegetation height (cm)	ψ_1, ψ_2 p, δ	Average precipitation one week before survey (mm)	p, δ
% cover grass	ψ_1, ψ_2	Survey time	p, δ

Parameters and descriptions:

ψ_1: probability plot is occupied regardless of reproductive state
ψ_2: probability of successful reproduction on an occupied plot
p: probability of detecting at least one owl
δ: probability of detecting a juvenile owl (detecting successful reproduction)

Table 1.3: Covariates considered in analysis of dynamic burrowing owl occupancy analysis for eastern Colorado, comparing 2005 to 2022/2023. Occupancy and successful reproduction data were collected during the 2005 (Tipton et al. 2008),2022, and 2023 burrowing owl breeding seasons.

Covariate	Parameter(s)	Covariate	Parameter(s)
Overall prairie dog activity status	ψ	Proportion of prairie dog colony in 500 m buffer around 2005 plot	$\psi, \gamma, \varepsilon$
Activity status in 2005	γ, ε	Proportion of prairie dog colony in 1500 m buffer around 2005 plot	$\psi, \gamma, \varepsilon$
Activity status in 2022 or 2023	γ, ε	Proportion of prairie dog colony in 2250 m buffer around 2005 plot	$\psi, \gamma, \varepsilon$
Activity transition from active in 2005 to inactive in 2022 or 2023	ε	Prairie dog colony size in 2019	γ, ε
Activity transition from inactive in 2005 to active in 2022 or 2023	γ	Wind (mph)	p
Presence/absence in 2005	γ, ε	Temperature (F)	p
Plot level burrowing owl density in 2005	ε	% cloud cover	p
Latitude	$\psi, \gamma, \varepsilon$	Observer team	p

Parameters and descriptions:

ψ: probability that a plot is occupied by burrowing owls
γ: probability of burrowing owl local colonization
ε: probability of burrowing owl local extinction
p: probability of detection

Table 1.4: Multistate burrowing owl occupancy models with weight > 0.01. We ran 54 multistate occupancy models; see Appendix table 1.1 for full model selection table.

Model	ΔAICc	Model weight
ψ(state*ordinal latitude, state*activity level) *p*(state*year) *δ*(temp, year)	0	0.354
ψ(state*continuous latitude, state*activity level) *p*(state*year) *δ*(temp, year)	0.148	0.329
ψ(state*ordinal latitude, state*activity level) *p*(state*year) *δ*(temp, year, precipitation by visit)	2.16	0.12
ψ(state+ordinal latitude, state*activity level) *p*(state*year) *δ*(temp, year, season sum precipitation)	2.18	0.12
ψ(state*activity level, state*ordinal latitude) p(state*year) δ(year)	4.10	0.05
ψ(state*activity level, state* ordinal latitude) p(state*year) δ(temp)	5.33	0.02
ψ(state*activity level, state* ordinal latitude) p(state*year) δ(survey time)	8.37	0.01

Parameters and descriptions:

ψ: burrowing owl occupancy where the two states are ψ_1: probability plot is occupied regardless of reproductive state and ψ2: probability of successful reproduction on an occupied plot
p: probability of detection where the two states are *p*1: probability of detecting at least one owl and *p*2: probability of detecting at least one owl on a plot where juveniles are present
δ: probability of detecting a juvenile owl (detecting successful reproduction)

Table 1.5: Overall beta estimates from the top multistate burrowing owl occupancy model. β represents logit link function parameters that are used to determine effect sizes of covariates on real parameter estimates. * indicates statistical significance.

β	Estimate	SE and 95% CI
Effect of colony activity level on ψ_1	-0.15	0.44 [-1.01, 0.72]
Effect of colony activity level on ψ_2	1.67*	0.50 [0.69, 2.65]
Effect of latitude on ψ_1	-1.13*	0.48 [-2.09, -0.18]
Effect of latitude on ψ_2	0.17	0.36 [-0.54, 0.88]
Effect of survey year on p_1	-0.16	0.72 [-1.56, 1.23]
Effect of survey year on p_2	-0.92*	0.41 [-1.72, -0.12]
Effect of temp on δ	-0.046*	0.019 [-0.084, -0.008]
Effect of survey year on δ	-1.24*	0.39 [-2.01, -0.47]

Parameters and descriptions:

ψ_1: probability plot is occupied regardless of reproductive state
ψ_2: probability of successful reproduction on an occupied plot
p_1: probability of detecting at least one owl
p_2: probability of detecting at least one owl on a plot where juveniles are present
δ: probability of detecting a juvenile owl (detecting successful reproduction)

Table 1.6: Overall model estimates from the top multistate burrowing owl occupancy model.

Parameter	Estimate	SE and 95% CI
ψ_1	0.84	0.081 [0.62, 0.95]
ψ_2	0.86	0.058 [0.70, 0.94]
p_1	0.24	0.099 [0.10, 0.48]
p_2	0.91	0.017 [0.87, 0.94]
δ_3	0.79	0.035 [0.72, 0.85]
δ_4	0.77	0.035 [0.69, 0.83]

Parameters and descriptions:

ψ_1: probability plot is occupied regardless of reproductive state
ψ_2: probability of successful reproduction on an occupied plot
p_1: probability of detecting at least one owl
p_2: probability of detecting at least one owl on a plot where juveniles are present
δ: probability of detecting a juvenile owl (detecting successful reproduction)

Table 1.7: Dynamic burrowing owl occupancy models, comparing occupancy in 2005 (Tipton et al. 2008) to 2022/2023 on prairie dog colonies in eastern Colorado. All models with a model weight >0.01 are shown. We ran 35 dynamic occupancy models; see appendix table 2 for full model selection table.

Model	ΔAICc	Model weight
ψ(overall prairie dog activity status) γ(2022/2023 prairie dog activity status, latitude) ε(prairie dog colony transition from active to inactive) *p*(season, observer)	0	0.59
ψ(overall prairie dog activity status) γ(2022/2023 prairie dog activity status*latitude) ε(prairie dog colony transition from active to inactive) *p*(season, observer)	3.07	0.13
ψ(overall prairie dog activity status) γ(2022/2023 prairie dog activity status) ε(prairie dog colony transition from active to inactive) *p*(season, observer)	3.44	0.11
ψ(overall activity status) γ(ordinal latitude) ε(active to inactive transition) p(season+observer)	4.68	0.06
ψ(overall activity status) γ(.) ε(active to inactive transition) p(season+observer)	6.39	0.02
ψ(overall activity status) γ(inactive to active transition) ε(active to inactive transition) p(season+observer)	6.94	0.02
ψ(overall activity status) γ(.) ε(2022_2023 activity status) p(season+observer)	6.98	0.02
ψ(overall activity status) γ(proportion colony w/in2250m) ε(active to inactive transition) p(season+observer)	7.33	0.02
ψ(overall activity status) γ(proportion colony w/in1500m) ε(active to inactive transition) p(season+observer)	8.13	0.01

Parameters and descriptions:

ψ: probability that a plot is occupied by burrowing owls
γ: probability of burrowing owl local colonization
ε: probability of burrowing owl local extinction
p: probability of detection

Table 1.8: Overall beta estimates from the top dynamic burrowing owl occupancy model. β represents logit link function parameters that are used to determine effect sizes of covariates on real parameter estimates. * indicates statistical significance.

β	Estimate	SE and 95% CI
Effect of prairie dog colony activity status in 2022/2023 on γ	22.20	439.96 [-840.13, 884.52]
Effect of ordinal latitude on γ	-1.46*	0.71 [-2.86, -0.062]
Effect of prairie dog colony activity transition from active to inactive on ε	6.15*	2.79 [0.67, 11.62]

Parameters and descriptions:

ψ: probability that a plot is occupied by burrowing owls
γ: probability of burrowing owl local colonization
ε: probability of burrowing owl local extinction
p: probability of detection

REFERENCES

Alverson, K.M., and S.J. Dinsmore, 2014. Factors affecting Burrowing Owl occupancy of prairie dog colonies. *The Condor 116*(2): 242–250.

Askins, R. A., F. Chávez-Ramírez, B.C. Dale, C.A. Haas, J.R. Herkert, F.L. Knopf, P.D. Vickery 2007. Conservation of Grassland Birds in North America: Understanding Ecological Processes in Different Regions: "Report of the AOU Committee on Conservation." *Ornithological Monographs*, *64*, iii–46.

Augustine, D. J. and B. W. Baker. 2013. Associations of grassland bird communities with black-tailed prairie dogs in the North American Great Plains. *Conservation Biology* 27:324-334

Chamberlain S. and D. Hocking. 2023. _rnoaa: 'NOAA' Weather Data from R. R package version 1.4.0, <https://CRAN.R-project.org/package=rnoaa>.

Colorado Parks and Wildlife. 2015. State Wildlife Action Plan: a strategy for conservation of wildlife in Colorado. Denver, Colorado. https://cpw.state.co.us/aboutus/Pages/StateWildlifeActionPlan.aspx

Colorado Parks and Wildlife. 2020. Colorado Black-tailed Prairie Dog Range-wide Monitoring Report. Denver, Colorado.

Conrey, R. Y. 2010. Breeding success, prey use, and mark-resight estimation of burrowing owls nesting on black-tailed prairie dog towns: plague affects a non-susceptible raptor. Ph.D. dissertation, Colorado State University, Fort Collins, CO.

Conway, C. J., and J. C. Simon. 2003. Comparison of detection probability associated with burrowing owl survey methods. *Journal of Wildlife Management* 67: 501-511.

Conway, C.J. 2018. Spatial and Temporal Patterns In Population Trends and Burrow Usage of Burrowing Owls In North America. *Journal of Raptor Research*.52 (2): 129–142.

Cully, J. F., S.K. Collinge, R.E. VanNimwegen, C. Ray, W.C. Johnson, B. Thiagarajan, D.B. Conlin, B.E. Holmes, 2010. Spatial variation in keystone effects: small mammal diversity associated with black-tailed prairie dog colonies. *Ecography 33*(4): 667–677.

Davidson, A. D., D.J. Augustine, H. Jacobsen, D. Pellatz, L.M. Porensky, G. McKee, C. Duchardt. 2022. Boom and bust cycles of black-tailed prairie dog populations in the Thunder Basin grassland ecosystem, *Journal of Mammalogy* 103(5): 1112–1126.

Dechant, J. A., M. L. Sondreal, D. H. Johnson, L. D. Igl, C. M. Goldade, P. A. Rabie, B. R. Euliss. 1999 (revised 2002). Effects of management practices on grassland birds: Burrowing Owl. Northern Prairie Wildlife Research Center, Jamestown, ND.

Decker, K. 2007. Central Shortgrass Prairie Ecological System: Ecological Integrity Assessment. Colorado Natural Heritage Program.

Derner, J., Detling, J., and Antolin, M. 2006. Are livestock weight gains affected by black-tailed prairie dogs? *Trends in Ecology & Evolution.* 4(9): 459–464.

Desmond, M.J. and J.A. Savidge. 1996. Factors influencing Burrowing Owl (*Speotyto cunicularia*) nest densities and numbers in western Nebraska. *American Midland Naturalist* 136:143- 148.

Desmond, M. J., J.A. Savidge, and K.M. Eskridge. 2000. Correlations between Burrowing Owl and Black-Tailed Prairie Dog Declines: A 7-Year Analysis. *The Journal of Wildlife Management 64*(4): 1067–1075.

Dickinson, C. E., and J.L. Dodd. 1976. Phenological Pattern in the Shortgrass Prairie. *The American Midland Naturalist 96*(2): 367–378.

Griebel, R.L. and J.A. Savidge. 2007. Factors influencing burrowing owl reproductive performance in contiguous shortgrass prairie. *Journal of Raptor Research* 41:212-221.

Helmig, D. 2020. Air quality impacts from oil and natural gas development in Colorado. *Elementa: Science of the Anthropocene*, 8(4).

Herrick, J.E., J.W. Van Zee, S.E. McCord, E.M. Courtright, J.W. Karl, L.M. Burkett. 2021. Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems. USDA-ARS Jornada Experimental Range.

Howlin, S. and J. Mitchell. 2016. Monitoring black-tailed prairie dogs in Colorado with the 2015 NAIP imagery. Western Ecosystems Technology, Laramie, WY.

Hughes, A. J. 1993. Breeding density and habitat preference of the burrowing owl in northeastern Colorado. Thesis, Colorado State University, Fort Collins, USA.

Hurvich, C.M., and Tsai, C.L. 1989. Regression and time series model selection in small samples, *Biometrika*, *76*(2):297–307.

Jones, S.R. 1998. Burrowing Owl. pp. 220-221 *in* Kingery, H.E., ed. Colorado Breeding Bird Atlas. Colorado Bird Atlas Partnership, Denver, Colorado. 636pp.

Jones, N. F. and L. Pejchar 2013. Comparing the ecological impacts of wind and oil & gas development: a landscape scale assessment. *PloS one*, *8*(11), e81391.

Klute, D. S., L. W. Ayers, M. T. Green, W. H. Howe, S. L. Jones, J. A. Shaffer, S. R. Sheffield, T. S. Zimmerman. 2003. Status Assessment and Conservation Plan for the Western Burrowing Owl in the United States. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication FWS/BTP-R6001-2003, Washington, D.C.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15:247–257.

Lupardus, R. C., "Potential Environmental Impacts of Oil and Natural Gas Production on a Shortgrass Steppe" (2017). University of Northern Colorado. PhD Dissertation.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. and Langtimm, C.A. 2002., Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83: 2248-2255.

MacKenzie, D., J. Nichols, J. Hines, M. Knutson, A. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology, 84*(8), 2200-2207.

Macias-Duarte, A. 2011. Change in migratory behavior as possible explanation for burrowing owl population declines in northern latitudes. Ph.D. Dissertation, University of Arizona, Tucson, AZ, USA.

Macías-Duarte, A. and Conway, C.J. 2015. Distributional Changes in the Western Burrowing Owl (*Athene cunicularia hypugaea*) in North America from 1967 to 2008. *Journal of Raptor Research.* 49(1), 75-83.

Morin, D. J., C.B. Yackulic, J.E. Diffendorfer, D.B. Lesmeister, C.K. Nielsen, J. Reid, E.M. Schauber. 2020. Is your ad hoc model selection strategy influencing your multimodal inference? *Ecosphere* 11(1): 1-16.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. *Conservation Biology* 8: 677-681.

Neely, B., S. Kettler, J. Horsman, C. Pague, R. Rondeau, R. Smith, L. Grunau, P. Comer, G. Belew, F. Pusateri, B. Rosenlund, D. Runner, K. Sochi, J. Sovell, D. Anderson, T. Jackson and M. Klavetter. 2006. Central Shortgrass Prairie Ecoregional Assessment and Partnership Initiative. The Nature Conservancy of Colorado and the Shortgrass Prairie Partnership. 124 pp. and Appendices

Nichols, J. D., J.E. Hines, J.R. Sauer, F.W. Fallon, J.E. Fallon, P.J. Heglund. (2000). A Double-Observer Approach for Estimating Detection Probability and Abundance From Point Counts, *The Auk* 117(2): 393–408.

Nichols, J. D., J. E. Hines, D. I. MacKenzie, M. E. Seamans, and R. J. Gutierrez. (2007). Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology* 88:1395-1400.

Plumpton, D.L. and R.S. Lutz. 1993. Nesting habitat use by burrowing owls in Colorado. *Journal of Raptor Research* 27(4): 299-304.

Poulin, R. & Todd, L.D., Haug, E.A., Millsap, B.A., Martell, M. 2011. Burrowing Owl (*Athene cunicularia*). The Birds of North America Online.

Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M., and Marra, P.P. 2019. Decline of the North American Avifauna. *Science*, *366*(6461), 120-124.

Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary Production of the Central Grassland Region of the United States. *Ecology, 69*(1), 40-45.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: Past, present, and future. *Wildlife Society Bulletin* 32:6–15.

Santini, L., Tobias, J. A., Callaghan, C., Gallego-Zamorano, J., Benítez-López, A. 2023. Global patterns and predictors of avian population density. *Global Ecology and Biogeography*, 32, 1189–1204.

Sheffield, S. 1997. Current Status, Distribution, and Conservation of the Burrowing Owl (Speotyto cunicularia) in Midwestern and North America. *2nd Owl Symposium*: 399-407.

Sidle, J.G., M. Ball, T. Byer, J.J. Chynoweth, G. Foli, R. Hodorff, G. Moravek, R. Peterson, D.N. Svingen. 2024. Occurrence of Burrowing Owls in Black-tailed Prairie Dog Colonies on Great Plains National Grasslands. *Journal of Raptor Research*, *35*(4): 316-321

Skagen, S. K, A.Y. Yackel Adams, and R.D. Adams. 2005. Nest survival relative to patch size in a highly fragmented shortgrass prairie landscape. *Wilson Bulletin 117*(1): 23-34.

Smith, G. A., and M.V. Lomolino. 2004. Black-Tailed Prairie Dogs and the Structure of Avian Communities on the Shortgrass Plains. *Oecologia 138*(4): 592–602.

Stevens, D. L., and Olsen, A. R. (2004). Spatially Balanced Sampling of Natural Resources. *Journal of the American Statistical Association*, *99*(465), 262–278.

Tipton, H.C, and P.F. Doherty, Jr. 2008. Occupancy of mountain plover and burrowing owl in Colorado. *Journal of Wildlife Management* 72:1001-1006

Tipton, H. C., P. F. Doherty Jr., and V. J. Dreitz. 2009. Abundance and density of mountain plover (*Charadrius montanus*) and burrowing owl (*Athene cunicularia*) in eastern Colorado. *The Auk* 126(3):493-499.

Toombs, T. 1997. Burrowing owl nest-site selection in relation to soil texture and prairie dog colony attributes. Thesis, Colorado State University, Fort Collins, USA.

Tripp D.W., Rocke T.E., Runge J.P., Abbott R.C., Miller M.W. 2017. Burrow dusting or oral vaccination prevents plague-associated prairie dog colony collapse. *EcoHealth* (14):451–462.

VerCauteren, T.L., S.W. Gillihan, and S.W. Hutchings. 2001. Distribution of burrowing owls on public and private lands in Colorado. *Journal of Raptor Research* 35(4): 357-361.

Wellicome, T.I. 2005. Hatching asynchrony in Burrowing Owls is influenced by clutch size and hatching success but not by food. *Oecologia* 142:326–334.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):S120–S138.

Wilsey, C.B., J. Grand, J. Wu, N. Michel, J. Grogan-Brown, B. Trusty, B. 2019. North American Grasslands. National Audubon Society, New York, New York, USA.

Woodard, J.D. 2002. The influence of diet, habitat, and recreational shooting of prairie dogs on burrowing owl demography. M.S. Thesis, Colorado State University, Fort Collins, Colorado.

Zarn, M. 1974a. Burrowing owl, *Speotyto cunicularia hypugaea*. U.S. Dep. Inter., Bur. Land Manage., Wash. DC. Tech. Note No. 250. 25pp.

CHAPTER 2: DENSITY, PRODUCTIVITY, AND ABUNDANCE OF BURROWING OWLS NESTING IN EASTERN COLORADO

INTRODUCTION

Grassland habitat loss, fragmentation, and degradation have facilitated major population declines of many grassland bird species (Knopf 1994). Grassland conversion to cropland and development in the residential and energy sectors has resulted in a loss of 62% of historical grasslands since the 1800s and a loss of nearly 40% of grassland bird populations since 1966 (Askins et al. 2007, Wilsey et al. 2019). The shortgrass prairie is the dominant grassland type in Colorado, characterized by low-growing perennial grasses, forbs, and shrubs. Nearly 50% of Colorado's shortgrass prairie has been converted to cropland or other land uses (Neely et al. 2006). This habitat loss has profound impacts on grassland species including the black-tailed prairie dog (*Cynomys ludovicianus*), a dominant native grazer in this system (Desmond et al. 2000). Black-tailed prairie dogs are considered a keystone species in the shortgrass prairie because they create vital nesting and foraging habitat for many species including western burrowing owls (*Athene cunicularia hypugaea*: Klute et al. 2003, Smith and Lomolino 2004).

The burrowing owl is a small diurnal raptor that nests in grasslands, deserts, and other open habitat, usually in burrows dug by fossorial mammals and sometimes reptiles such as tortoises. It is a partially migratory species where populations in the southern parts of its range in the southwestern United States, Mexico, and portions of Central and South America are typically year-round residents (Poulin et al. 2011). The migratory populations occur north of central California, central Arizona and New Mexico, and northern Texas. Migratory populations of western burrowing owls typically winter in the southwestern United States and Mexico, then migrate northward in the spring. The owls stay on their breeding grounds until late August, when they begin their migration to southern wintering grounds (Poulin et al. 2011).

In Colorado's eastern plains, burrowing owls almost exclusively nest on black-tailed prairie dog colonies (Tipton et al. 2008, 2009) because they are the main provider of nesting burrows and have grazing behaviors that keep vegetation height low, which increases the ability of owls to detect predators (Desmond et al. 2000, Dechant et al. 2002). Burrowing owls prefer to nest in black-tailed prairie dog colonies that have high density of burrows, perch availability, and bare ground cover (Plumpton & Lutz 1993). Colonies with higher densities of active prairie dog burrows have been known to support greater numbers of burrowing owl nesting pairs (Desmond et al. 2000). When prairie dogs are no longer present on a colony, burrow deterioration and vegetation encroachment eventually cause owls to stop breeding on the colony (Dechant et al. 2002). Since burrowing owls depend on black-tailed prairie dog colonies in eastern Colorado, black-tailed prairie dog decline results in a loss of burrowing owl breeding habitat, which can have negative impacts on burrowing owl populations (Jones 1998, VerCauteren et al. 2001). Prairie dog populations have experienced approximately 90 - 98% population decline since 1900 due to sylvatic plague and habitat loss (Miller et al. 1994, Desmond et al 2000). Factors that influence burrowing owl decline have included prairie dog population decline, pesticide use, and wintering habitat loss and alteration (Sheffield 1997, Macías-Duarte 2011). Burrowing owls are currently listed as a species of conservation concern in the western US, threatened in Mexico, and endangered in Canada (Sheffield 1997). In Colorado, burrowing owls are a state-threatened species and a Tier 1 Species of Greatest Conservation Need in Colorado's State Wildlife Action Plan (Colorado Parks and Wildlife 2015). The last population assessment in eastern Colorado was conducted in 2005; therefore, updated research on burrowing owl population parameters is crucial to monitoring this state-threatened species.

Population assessment is an important tool for assessing trends in species distribution and abundance through time. Studies that evaluate species density and abundance can reveal fine scale effects of habitat and other factors that influence populations that might not be apparent from simple presence/absence studies. Previous studies have estimated burrowing owl density, abundance, and productivity both in Colorado and throughout the species' range. Estimated burrowing owl density has varied across their range likely due to differences in habitat needs, analytical techniques, sample size, and timing (Ruiz et al. 2016). Estimates of burrowing owl density in North America range from 0.02-26.3 pairs/km^2 across all habitats and 1.5-26.3 pairs/km^2 in perennial grasslands (Crowe & Longshore 2010). Tipton et al. (2009) estimated adult burrowing owl density was 3.04 birds/km^2 (95% CI [2.82, 6.92]) and abundance was 3,554 birds (95% CI [3,298-8,445]) in eastern Colorado. The highest densities of burrowing owls in North America occur where burrows are concentrated, such as in prairie dog colonies in perennial grasslands (Crowe & Longshore 2010).

Previous studies that have evaluated burrowing owl productivity have assessed nest success. Lutz and Plumpton (1999) estimated that nesting pairs typically produce 3.62 $\pm$ 0.19 young that survive to fledge. Griebel & Savidge (2007) found that burrowing owls had a mean clutch size of 7.2 in contiguous shortgrass prairie. Larger prairie dog colonies have been known to support greater numbers of burrowing owl nests and fledglings (Savidge 2007, Ray 2016, Parker et al. 2019). Burrowing owl nest success is typically higher in grassland habitats compared to grassland remnants in urban areas and is linked to decreased competition from nearby nests (Griebel & Savidge 2007, Berardelli et al 2010).

In this chapter, we provide an updated assessment of burrowing owl density, abundance, and productivity in eastern Colorado. We investigated the effects of various prairie dog colony characteristics including colony size, activity status and level, proportion of prairie dog colony in the survey plot, and vegetation characteristics to determine the main drivers of these burrowing owl population parameters on 175 survey plots throughout eastern Colorado. We hypothesized that activity status and level, colony size, and bare ground cover would have a positive effect on burrowing owl density, abundance, and productivity because these conditions indicate prime nesting habitat. We expected that vegetation height and cover of different plant functional groups would affect these parameters because burrowing owls prefer to nest on colonies with short vegetation, but sometimes forage off the colony in surrounding taller vegetation. We surveyed some of the same plots using similar methodology as Tipton et al. (2008, 2009) in their 2005 study, facilitating comparisons 17–18 years later. This study will be used to inform burrowing owl conservation and management in Colorado by investigating what prairie dog colony characteristics are influential for burrowing owl density and productivity. However, our results are applicable to other regions where burrowing owls predominately nest on prairie dog colonies.

FIELD METHODS

The study area covers the eastern plains of Colorado, which incorporates the overall range and distribution of the black-tailed prairie dog in Colorado (Figure 2.1). The eastern plains of Colorado is comprised of shortgrass prairie, agricultural land, residential areas, and oil and gas development. Prominent plants in the shortgrass prairie ecosystem include buffalograss (*Bouteloua dactyloides*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Pascopyrum smithii*). Grazing is an important source of heterogeneity in this system, and is maintained by cattle (*Bos taurus*), pronghorn (*Antilocapra americana*), and black-tailed prairie dogs.

Historically, the American plains bison (*Bison bison bison*) was the dominant large grazer until hunting pressure caused major population declines in the 19th century.

We conducted this study over two field seasons, which occurred during May-August in 2022 and 2023. We created our sampling frame in ArcGISPro 2.9.0 using a black-tailed prairie dog colony shapefile prepared by Colorado Parks and Wildlife and the Colorado Natural Heritage Program (Colorado Parks and Wildlife 2020). This shapefile was created by analyzing National Agriculture Imagery Program (NAIP) 2019 imagery to visually identify and draw boundaries around potential black-tailed prairie dog colonies in eastern Colorado. Using this shapefile, Colorado Parks and Wildlife estimated that the area of potential black-tailed prairie dog colonies in eastern Colorado in 2019 was ~4,925 km^2. Of this area, approximately 2,025 km^2 were identified as potential active prairie dog colonies (Colorado Parks and Wildlife 2020). Across the 2022 and 2023 field seasons, we used a spatially balanced random sampling design using the SBS tool in ArcGISPro 2.9.0 (Stevens & Olsen 2004) to select 691 potential survey plots from our sampling frame. Since our study area has a large extent and encompasses ~15,000 prairie dog colonies, we selected new survey plots in 2023 to double our sample size and improve our abundance inference to eastern Colorado. We selected 350 and 341 plots in 2022 and 2023 respectively and looked at updated imagery from 2021 and 2022 to eliminate plots that lacked evidence of a prairie dog colony.

After contacting private landowners and securing permits for access to survey plots, we ended up with 85 final plots in 2022 and 90 final plots in 2023. We determined the number of survey plots based on the desired precision level for occupancy estimates from Chapter 1. For each of our 1 km x 1 km plots (Figure 2.2), we placed a transect running through each plot such that observers were always 250 m away from the plot boundary to ensure that the entirety of the plot was adequately surveyed. We based our plot size and transect placement within the plot on the 250 m detection distance for burrowing owls (Conway and Simon 2003). Plots where access was problematic of the original placement was outside colony boundaries were moved by using a random bearing in the direction of the prairie dog colony and a maximum distance of 250 m. For a more detailed explanation of the field methods, see the relevant sections in Chapter 1.

We were interested in assessing the effects on density and productivity of various prairie dog colony attributes including prairie dog colony size, latitude, activity status and level, and vegetation characteristics including mean vegetation height and cover of different plant functional groups. Table 2.1 includes a full list of the covariates examined. From the shapefile of potential prairie dog colonies, we created three size categories: small (≤ 10 ha), medium (11 - 299 ha), and large (≥ 300 ha). Landowner permission determined the final number of plots in each size category. Since small prairie dog colonies were < 10 ha, we required that our survey plot covered the entirety of small colonies, while plots on medium and large colonies needed at least 25% of the plot to be covered by prairie dog colony. This was based on plot requirements from Tipton et al. (2008, 2009) to facilitate comparisons between these studies.

We defined prairie dog colony latitude in three distinct ways: ordinal, categorical, and continuous. Ordinal and categorical latitude both split eastern Colorado into southern, central, and northern regions. Continuous latitude was defined in decimal degree format. Ordinal and categorical latitude were expected to be more interpretable by land managers because they can more easily determine if their management area is located within a regional polygon rather than a continuous latitude. However, we decided to also look at the beta estimates from all three latitude designations to make sure the effect of latitude was similar across the designations.

Prairie dog activity status was defined as either active (prairie dogs present) or inactive (prairie dogs absent). On active prairie dog colonies, we determined prairie dog activity level which can be labeled as low, medium, or high activity. A colony was designated as low activity when there were large patches of inactive burrows, including both long term and recently inactive burrows. Colonies designated as having medium prairie dog activity had some patches of inactive burrows, but most of the burrows in the plot were open. High prairie dog activity colonies had a high density of active and open burrows with few or no patches of inactivity.

We conducted vegetation surveys on our third survey visit (mid June to early July), which roughly corresponds to peak plant biomass and green-up in the shortgrass prairie (Dickinson and Dodd 1976). During the third burrowing owl survey, observers collected vegetation data using the line point intercept method (Herrick et al. 2021). Observers collected a vegetation data point every 20 m along the main transect line for a total of 100 points per plot.

We aimed to visit each of our survey plots four times between May 1st and August 5th to conduct burrowing owl surveys, although in some cases we could not reach a plot on each occasion. The first two visits (between May 1st and ~June 18th) provided an estimate of density for the adult breeding population; we assumed that late arrivals are not likely after the first visit in May and that most nest failures will occur after this time period. Visits 3 and 4 (~June 19th) occurred after juvenile emergence and provided estimates of juvenile density and adult density later in the breeding season. Juvenile emergence refers to the first time that owl nestlings leave the nest burrow, which occurs 10 - 14 days after hatching (Zarn 1974a). Estimated adult density after juvenile emergence is likely to be higher than prior to emergence, since females are more likely to be above ground and available for detection later in the breeding season.

We used a double observer approach to increase the overall detection probability of owls, where detection probability was pooled between the two observers, who communicated with each other during surveys. During the first two survey visits of the 2023 field season, we experimented with the dependent double observer approach where the primary observer conducts the survey while the secondary observer takes notes and records any missed detections by the primary observer. The double observer approach allows for estimation of observer-specific detection probabilities and more precise abundance estimates (Nichols et al. 2000). We chose to try this approach to assess whether the dependent double observer method increased precision in the abundance estimator.

STATISTICAL METHODS

Density

We estimated density and abundance using distance sampling methods in the “unmarked” package (Fiske & Chandler 2011, Kellner et al. 2011) in R statistical software (v 4.2.2 R Core Team 2021). Distance sampling models in “unmarked” expand on traditional distance sampling analysis to provide a framework to investigate covariates on density and abundance (Royle et al. 2004, Chandler et al. 2011). We specifically used the generalized distance sampling model of Chandler et al. (2011). The addition of the availability parameter (ϕ) allows for the possibility that some individuals were unavailable for detection, based on repeated visits to each site. This parameter describes the subset of the population that is available for detection and is typically used to model temporary emigration. Since burrowing owls can be located on a survey plot but be underground and unavailable for detection, this parameter is suitable for our study. Covariates can be added to this parameter to investigate what factors influence the availability of burrowing owls for detection by observers.

We analyzed data from survey visits 1 and 2 separately from visits 3 and 4 because the first two visits occurred prior to juvenile emergence and the second two visits occurred after emergence. We analyzed these separately to account for differences in burrowing owl density early and late in the breeding season and to obtain estimates of adult density for each of these stages. Prior to juvenile emergence from the nest burrow, typically only male owls are available for detection since females are incubating eggs or brooding young. Male burrowing owls are usually above ground, perched near the nest burrow or foraging. Once the juveniles emerge, females are more likely to be available for detection. Therefore, we built separate detection and density models for each age class (adult and juvenile) and breeding season categories (pre- and post-juvenile emergence).

We used the 'gdistsamp' function (Chandler et al. 2011, Royle et al. 2004) in unmarked to build models that investigated covariate effects on the detection function, density/abundance, and availability. We first determined the detection function that best fit our data, then investigated covariates on detection, density, and availability (Table 1). We ran covariate correlation tests and did not include moderately correlated covariates ($r > 0.5$) in the same model (Appendix Tables 2.5 & 2.6). We used a build-up modeling approach where top model structures were carried into the next modeling phase (Morin et al. 2020), based on small sample AICc model selection methods (Hurvich & Tsai 1989) to determine the model with best fit.

Abundance

To obtain estimates of burrowing owl abundance in our entire study area, we expanded our estimates of adult and juvenile burrowing owl density from our distance sampling analysis to all potential prairie dog colonies in our study area. To make a robust expansion of abundance to our study area, we used a map correction factor to correct for colonies that were false positives.

False positives arose when the 2019 NAIP imagery of potential prairie dog colonies in eastern Colorado indicated the presence of a colony, but then they were determined by observers to have no prairie dog colony present during the initial survey. We did not correct for long inactive prairie dog colonies because these may have been active at the time the imagery was taken in 2019 but became inactive prior to our 2022 and 2023 field seasons. Long inactive colonies were defined as colonies that had an active prairie dog colony at one point, but have since become inactive and consist only of collapsed prairie dog holes. Burrowing owls cannot nest in completely collapsed holes, so these long inactive colonies do not provide suitable nesting habitat. We implemented four methods for the map correction factor: no area removed from original layer of potential prairie dog colonies, 21.16% of potential prairie dog colony removed to account for ground-truthed false positives from our surveys, 27.93% of potential prairie dog colony removed to account for plots identified in 2021 and 2022 NAIP imagery that were unlikely to contain prairie dog colony, and 49.09% of potential prairie dog colony removed to account for both ground-truthed false positives and NAIP eliminated plots. Plots that were eliminated by looking at updated NAIP imagery prior to the field seasons had the potential to be classified as false positive or long inactive. However, due to logistical constraints, we did not visit these plots to determine their status.

To calculate burrowing owl abundance, we used an expansion process (Equation 1). We started with the total area of potential prairie dog colonies in the south, central, and northern regions of Colorado (*C*) and adjusted the areas to incorporate the proportion of potential active prairie dog colonies (*AC*) (Colorado Parks and Wildlife 2020). Then, we corrected for the rate of false positive colonies and NAIP-eliminated colonies in four separate scenarios (*CF*). Finally, we multiplied this area by our distance-sampling density estimates ($\widehat{D}$) for adults and juveniles pre- and post-juvenile emergence to get an estimate of burrowing owl abundance in our study area.

Equation 1: $\widehat{N} = C{*}AC{*}CF{*}\widehat{D}$

Our density estimates included sites with no detections of burrowing owls and thus they implicitly accounted for burrowing owl occupancy. Since C, AC, and CF are constant, the variance of $\widehat{N}$ is described by Var($\widehat{N}$)=$(C * AC * CF)^2$* Var($\widehat{D}$). Confidence intervals were calculated from the variance of $\widehat{N}$. Note that C differed for each region of the state, CF differed for each correction scenario, and $\widehat{D}$ differed for adults and juveniles pre- and post-juvenile emergence.

Dependent double-observer abundance

We explored dependent double-observer methods to estimate abundance for the first two survey visits in 2023 to see if there was an increase in precision of the estimates compared to the distance sampling method. To apply the model in Nichols et al. (2000), we ran Huggins closed capture models in Mark (White and Burnham 1999) to estimate burrowing owl abundance (N) and probability of detection (p) (Huggins 1989). We investigated covariates on p including observer, wind speed, temperature, vegetation height, cloud cover, and survey time.

Productivity

In avian research, nest searching and monitoring is the primary method for assessing productivity in bird populations. Given the logistics of our large-scale study, this was not a viable method for our study. Previous studies have used productivity indices in lieu of nest searching and monitoring (Ralph and Long 1995, Kuletz and Piatt 1999, Flanders-Wanner et al. 2004). To assess burrowing owl productivity, we used a productivity index that incorporates both the ratio of juvenile to adult burrowing owls and the counts of each age class. This provides a more precise method for estimating productivity than just using the ratio, because it takes into account density of owls such that higher density plots will be more highly weighted in the overall productivity assessment. We calculated adult and juvenile burrowing owl density for each plot using the common abundance estimator $\widehat{N} = C/\hat{p}$ (Lancia et al. 1994, Pollock et al. 2002) where $\widehat{N}$ is abundance, C is count of individuals, and $\hat{p}$ is probability of detection. We used the density and probability of detection estimates from our distance sampling analysis to inform C and $\hat{p}$ respectively. We calculated the Productivity Index, $\hat{P} = \widehat{N}_{(juveniles)}/(\widehat{N}_{(adults)} + \widehat{N}_{(juveniles)})$ for each survey plot (Flanders-Wanner et al. 2004). Since we used estimates of adult and juvenile abundances based on distance sampling models rather than raw counts, we treat P as continuous, and therefore beta regression models are statistically suitable for our analysis (Douma & Weedon 2019). We used zero-inflated beta regression models in the glmMTB package (Brooks et al 2017) in R statistical software (v 4.2.2 R Core Team 2021) to investigate relationships between black-tailed prairie dog colony attributes and productivity. Colony attributes included prairie dog colony size, prairie dog activity level, mean vegetation height, percent cover of plant functional groups, and latitude. We used small sample AICc based model selection methods to determine the model that best fit the data. We had to remove the activity status covariate from analysis because there were only three inactive colonies, and the lack of data caused model convergence failure. We also had to remove these plots from our model with prairie dog activity level due to the same issue.

Comparison to Tipton et al. (2009)

One of the objectives of this study was to compare results from our study to the previous burrowing owl density and abundance assessment in 2005 (Tipton et al. 2009) to determine if these population parameters have changed in the time period between these two studies. We surveyed a subset of 32 of Tipton's plots using the same survey methodology (Tipton et al. 2009) to facilitate comparisons 17 - 18 years later. We used distance sampling methods to estimate burrowing owl density and then expand density estimates to calculate abundance in eastern Colorado. We then compared our density and abundance estimates to those of Tipton et al. (2009).

RESULTS

Density

Adult burrowing owls prior to juvenile emergence (visits 1 and 2)

The top model from the distance sampling analysis indicated that latitude, prairie dog colony activity level, and bare ground cover influenced adult burrowing owl density prior to juvenile emergence (Table 2.2). Plots that contained colonies with higher prairie dog activity level supported greater densities of adult burrowing owls (Figure 2.3). Latitude had a negative effect on burrowing owl density (Figure 2.3). Plots in southern Colorado had the highest adult burrowing owl densities while northern Colorado had the lowest densities. Bare ground cover had a positive effect on adult density prior to juvenile emergence such that prairie dog colonies with higher bare ground cover supported higher densities of adult owls (Figure 2.4A). The top model for adult burrowing owl density prior to juvenile emergence estimated that there were 4.85 owls/km^2 (95% CI [3.88, 5.81]) in southern, 3.31 owls/km^2 (95% CI [2.72, 3.90]) in central, and 2.25 owls/km^2 (95% CI [1.77, 2.74]) in northern Colorado (Table 2.3). The overall estimate for adult owl density in eastern Colorado prior to juvenile emergence was 3.47 adult owls/km^2 (95% CI [2.79, 4.15]).

Temperature and wind speed had a negative effect on the availability of burrowing owls for detection. The average probability of availability was 0.67 (95% CI [0.56, 0.78]). Wind speed and cloud cover had a negative effect on the probability of detecting adult burrowing owls. The average probability of detection for adult burrowing owls for visits 1 and 2 was 0.77 (95% CI [0.73, 0.81]).

Adult burrowing owls after juvenile emergence (visits 3 and 4)

Results for adult owl density after juvenile emergence mirrored those prior to juvenile emergence except for effects associated with bare ground (Table 2.4). Prairie dog colony activity level had a positive effect on adult burrowing owl density, such that colonies with higher activity levels supported greater densities of owls (Figure 2.5). Latitude had a negative effect on adult density after juvenile emergence where plots in southern Colorado supported the highest densities of adult owls and plots in northern Colorado supported the lowest densities (Figure 2.5). Average adult owl densities after juvenile emergence for each region of Colorado and prairie dog colony activity level are listed in Table 2.6. Bare ground cover had a negative effect on adult density after juvenile emergence such that prairie dog colonies with higher bare ground cover supported lower densities of adult owls (Figure 2.4B). The top model for adult burrowing owl density after juvenile emergence estimated that there were 9.42 owls/km^2 (95% CI [5.08, 13.77]) in southern, 8.73 owls/km^2 (95% CI [7.54, 8.73]) in central, and 7.03 owls/km^2 (95% CI [6.54, 7.51]) in northern Colorado (Table 2.5). Adult density was higher after juvenile emergence compared to adult density prior to juvenile emergence.

None of the covariates we examined influenced the probability of availability, which was 0.26 (95% CI [0.15, 0.38]). The availability of adult burrowing owls for detection was lower after juvenile emergence compared to prior to emergence. There was a positive effect of precipitation levels one week prior to the survey on the probability of detection. The average probability of detection for adults in visits 3 and 4 was 0.81 (95% CI [0.77, 0.85]). Detection probability for adult owls after juvenile emergence was higher than prior to emergence.

Juvenile burrowing owls

The top model (Table 2.6) from the juvenile burrowing owl distance sampling analysis indicated that vegetation height had a negative effect on juvenile burrowing owl density. Plots with higher vegetation height supported lower densities of juveniles. There were no significant covariate effects on availability (ϕ) or detection probability (p). The probability of availability was 0.29 (95% CI [0.21, 0.36]). The probability of detection for juvenile burrowing owls was 0.79 (95% CI [0.77, 0.81]). The top model estimated juvenile burrowing owl density to be 18 juveniles/km^2 (95% CI [13.86, 23.66]).

Abundance

We expanded the estimates of burrowing owl density from the distance sampling analysis to estimate burrowing owl abundance in our study area, which encompassed all potential black-tailed prairie dog colonies in eastern Colorado. We calculated abundance estimates under four scenarios that correct for the issue of prairie dog colony false positives in our study area (Table 2.7). The abundance estimates corrected for false positives based on ground truthing are likely the most robust estimates out of the four correction scenarios, because the false positive rate is based on ground truthing efforts during burrowing owl surveys rather than being based only on examination of imagery. In this scenario, we adjusted for the proportion of active prairie dog colonies, then removed 21% of potential prairie dog colonies to account for our false positive rate. We estimated that there were 4,913 (95% CI [3,948-5,875]) adult owls prior to juvenile emergence, 11,613 (95% CI [5,333-17,893]) adult owls after juvenile emergence, and 26,580

(95% CI [19,623-33,537]) juvenile burrowing owls on black-tailed prairie dog colonies in eastern Colorado.

When we split the estimates of adult abundance by region of Colorado, we estimated that there were 2,221 (95% CI [1,179-2,663]) adult owls prior to juvenile emergence in southern, 1,665 (95% CI [1,069-2,261]) in central, and 1,025 (95% CI [563-1,486]) in northern Colorado. We estimated that there were 4,314 (95% CI [2,325-6,304]) adult owls after juvenile emergence in southern, 4,095 (95% CI [826-7,364]) in central, and 3,203 (95% CI [658-5,748]) in northern Colorado. Since latitude did not influence juvenile density, we did not estimate juvenile abundance by region of Colorado.

Dependent double observer abundance

For the pre-emergence period in 2023, we ran models using Huggins closed capture models to estimate burrowing owl abundance and probability of detection (Huggins 1989). This method was not performing well and models were consistently underestimating probability of detection and overestimating abundance compared to our distance sampling results. For example, the model estimated the probability of detection to be 0.043 (95% CI [0.0012, 0.62]), abundance of burrowing owls prior to juvenile emergence to be 6,246 (95% CI [868 - 5,6293]), and abundance of burrowing owls after juvenile emergence to be 17,066 (95% CI [2,134 - 150,845]). Comparing these results to those of our distance sampling analysis gave cause for concern for interpretation coming from these models, so we did not investigate them further.

Productivity

Our zero-inflated beta regression analysis indicated an interactive effect of prairie dog colony activity level and colony latitude on burrowing owl productivity (Table 2.8). For plots with low prairie dog activity, plots in central Colorado had higher proportions of juvenile burrowing owls. Plots with medium prairie dog activity had similar proportions of juveniles across the different regions of Colorado. For plots with high prairie dog activity level, plots in southern Colorado had higher proportions of burrowing owls that were juveniles compared to central and northern latitudes. Productivity was highest for colonies with high prairie dog activity in southern Colorado (Figure 2.6). Prairie dog colony size and proportion of prairie dog colony in the survey plot were not significant predictors of burrowing owl productivity. Vegetation characteristics including vegetation height and percent cover of different plant functional groups were also not significant predictors.

Comparison to Tipton et al. (2009)

We expanded our estimates of burrowing owl densities on survey plots to our sampling frame and estimated that there were 4,913 (95% CI [3,948-5,875]) adult owls prior to juvenile emergence, 11,613 (95% CI [5,333-17,893]) adult owls after juvenile emergence, and 26,580 (95% CI [19,623-33,537]) juvenile burrowing owls on black-tailed prairie dog colonies in eastern Colorado. Tipton et al. (2009) reported a pre-juvenile emergence estimate of 3,554 (95% CI [3,298-8,445]) adult burrowing owls in eastern Colorado.

DISCUSSION

Across regions of the Great Plains, burrowing owl populations have been declining due to nesting habitat loss from grassland conversion and prairie dog decline. Compared to occupancy, which we examined in the first chapter, assessing density and productivity provide finer scale analysis of what prairie dog colony attributes have the highest value for supporting burrowing owl populations. Our results suggested that plots in northern Colorado supported lower adult burrowing owl densities compared to central and southern Colorado, but that juvenile density was comparable between the different regions of eastern Colorado. This indicates that the northern region of eastern Colorado contains nesting grounds capable of supporting high productivity, despite lower densities of adult burrowing owls. Prairie dog colonies with higher prairie dog activity level supported higher densities of adult burrowing owls, highlighting the importance of prairie dog behaviors that maintain burrows and surrounding vegetation during the burrowing owl breeding season. Our estimates of adult burrowing owl density and abundance were similar to the estimates from the previous population assessment by Tipton et al. (2009), indicating that the burrowing owl population in eastern Colorado has remained relatively stable since 2005. The regional differences that we found suggest that conservation and management actions may be needed in northern Colorado if future declines in burrowing owl density, abundance, and productivity occur.

Adult burrowing owl density

Our distance sampling analysis indicated regional differences in adult burrowing owl density, which was highest in southern Colorado and lowest in northern Colorado. None of the covariates we tested explained this spatial pattern. It is likely that differences in climate, prairie dog population dynamics, land use, or some other factor could cause differences in local habitat and breeding conditions across Colorado. The previous population assessment did not find that latitude had a significant effect on burrowing owl density or abundance (Tipton et al. 2009), indicating that this could be a novel spatial pattern. Results from the first chapter of this study showed that burrowing owl occupancy was lower in northern Colorado (Chapter 1). This was also supported by previous research that found that Pawnee National Grassland in northern Colorado had lower burrowing owl occupancy compared to Comanche National Grassland in southern Colorado in 1998 (Sidle et al. 2024). It is possible that the latitude effect we found in this study could be part of a larger pattern across the burrowing owl range, because higher latitude habitats generally support lower population densities of avifauna (Santini et al. 2023). The literature provides some evidence of more severe burrowing owl population decline at higher latitudes, particularly in Wyoming, Montana, North and South Dakota, and Canada (Klute et al. 2003). In addition, Macías-Duarte & Conway (2015) suggested that the burrowing owl range is contracting along its northern, eastern, and western borders and expanding southward. Conway (2018) confirmed higher burrowing owl population decline in Canada but did not find linear variation in population trends across latitudes. However, Sidle et al. (2024) found that while many of the United States National Grasslands in the Great Plains had similar burrowing owl occupancy in 1998, there were some grasslands with higher occupancy such as Buffalo Gap and Comanche National Grasslands. Colorado is not at the border of the burrowing owl breeding range in any of the cardinal directions and thus the latitude trend that we saw in this study may not fully be explained by previous literature.

We also found that prairie dog colonies with higher activity levels supported larger densities of adult burrowing owls during the breeding season. Although overall occupancy from Chapter 1 did not show this same pattern, we did find a higher probability of burrowing owl successful reproduction on colonies with higher prairie dog activity level. This is not a surprising result given that prairie dogs create and maintain burrows that owls rely on during the breeding season. Colonies with higher prairie dog activity level likely support greater burrowing owl densities because there is a higher availability of well maintained nesting burrows. The importance of active prairie dog colonies for supporting greater numbers of burrowing owls is supported by the literature. Desmond et al. (2000) found that the number of nesting burrowing owl pairs declined as active prairie dog burrow density declined over a seven year study. Plumpton and Lutz (1993) found that burrowing owls prefer to nest in black-tailed prairie dog colonies that have high burrow density and perch availability. In addition, colonies with higher prairie dog activity level are likely to have shorter vegetation and higher rates of prairie dog alarm calling which benefit burrowing owls' detection of predators on the landscape. Therefore, colonies with higher prairie dog activity levels might have higher numbers of burrowing owls because good nesting conditions are present.

We split our adult burrowing owl density analysis into adults pre- and post- juvenile emergence because males were typically available for detection in the early part of the breeding season, while females were typically below ground, incubating eggs or brooding young (though they occasionally emerged). Once the juveniles emerged, we were likely to see both males and females above ground. As predicted, we estimated higher densities of adult owls after juvenile emergence than earlier in the breeding season. Adult burrowing owl densities prior to and after juvenile emergence were both driven by latitude, prairie dog activity level, and bare ground cover, indicating that these factors were influencing adult densities across the breeding season. Juvenile burrowing owls and adult burrowing owls after juvenile emergence had a lower probability of being available for detection compared to adults prior to juvenile emergence. This may be due to variation in juvenile numbers on our survey plots between surveys 3 and 4. Not all burrowing owl nests will hatch at the same time, and thus some juveniles are likely to emerge in the 2 - 3 week period between surveys 3 and 4 and therefore not become available for detection until survey 4. In addition, juveniles may also move around more, hide more, or spend more time underground than adults. This likely drives down the probability that juveniles are available for detection, because the availability parameter is being estimated across these two surveys. Alternatively, it could be driven by changes in vegetation where vegetation grows taller and denser later in the breeding season. We are not sure why the model of adult density after juvenile emergence produced a lower estimate of availability for adult owls compared to prior to juvenile emergence. It could be due to a confounding effect between the detection and availability processes, increased foraging time off the plot, or that two repeat surveys is not enough to reliably estimate the availability parameter.

Interestingly bare ground cover had a positive effect on adult burrowing owl density prior to juvenile emergence but a negative effect on adult density after juvenile emergence. This is likely explained by the change in habitat conditions across the breeding season. In eastern Colorado, burrowing owls select nest sites and begin the breeding season in mid to late spring, prior to green up of vegetation that accompanies late spring and summer precipitation events. As the breeding season progresses and vegetation green up occurs, the height and cover of grasses and forbs increase. Therefore, later in the breeding season, there might be taller vegetation on prairie dog colonies and less bare ground cover. This indicates that landscape heterogeneity may be important for burrowing owls as they prefer to nest on prairie dog colonies that contain a mix of colony, bare ground, and vegetation in eastern Colorado. Plumpton and Lutz (1993) also found that increased bare ground cover supported higher densities of burrowing owls during the breeding season. Bare ground cover may also be an important driver of burrowing owl density because it indicates good ground conditions for burrow presence and foraging habitat. Burrowing owls typically hunt small insects, rodents, and songbirds, and thus greater bare ground cover can make it easier to run around and catch smaller prey items. This is especially important for juvenile owls after they emerge from the nest burrow since they mostly run to catch insect prey.

Tipton et al (2009) estimated that prior to juvenile emergence, adult burrowing owl density in 2005 was 3.04 adult owls/km^2 (95% CI [2.15, 5.13]). Our overall estimate for adult owl density in eastern Colorado prior to juvenile emergence was 3.47 adult owls/km^2 (95% CI

[2.79, 4.15]), indicating that burrowing owl density on black-tailed prairie dog colonies has remained relatively stable in eastern Colorado during the time period between these two studies.

Juvenile burrowing owl density

Our distance sampling analysis indicated that vegetation height was the main driver of juvenile burrowing owl density on black-tailed prairie dog colonies in eastern Colorado. We estimated an average of 18 juveniles/km^2 (95% CI [13.86-23.66]). We found that colonies with taller vegetation supported lower densities of juvenile owls. This is likely driven by burrowing owl nesting preferences towards colonies with short vegetation. Therefore, burrowing owl nest site selection might drive the density of juveniles because adult owls may not be nesting in colonies with tall vegetation. Burrowing owls prefer to nest on colonies with shorter vegetation so they can better detect and hunt prey and detect predators on the landscape. Ray (2016) hypothesized that vegetation height would negatively affect burrowing owl productivity; however, all of their sites had low vegetation that did not result in statistically significant differences between sites. We investigated the possibility that vegetation height was driving the detection process; however, this did not emerge in our top density model. We thought that vegetation height would drive the detection process more than the density process because owls are selecting nest sites prior to vegetation green up in the shortgrass prairie and taller vegetation makes it difficult to detect young owls.

Burrowing owl abundance

We estimated that there are 4,913 (95% CI [3,948-5,875]) adult owls prior to juvenile emergence, 11,613 (95% CI [5,333-17,893]) adult owls after juvenile emergence, and 26,580 (95% CI [19,623-33,537]) juvenile burrowing owls on black-tailed prairie dog colonies in eastern Colorado. The previous population assessment reported a pre-juvenile emergence estimate of 3,554 (95% CI [3,298-8,445]) burrowing owls in eastern Colorado (Tipton et al. 2009). Our abundance estimate shows a slight increase compared to that of Tipton et al. (2009), though there is overlap in the 95% confidence intervals of our estimates, indicating that burrowing owl abundance has remained relatively stable in eastern Colorado over the time period of 2005-2023. This chapter provides an updated adult burrowing owl population abundance in eastern Colorado for adults and sets a baseline for juvenile abundance during the breeding season, which can be used by future studies to track population changes through time. In contrast to the previous assessment, our abundance estimates include adults prior to and after juvenile emergence and juvenile abundances.

Burrowing owl productivity

Plots in southern Colorado had the highest productivity in colonies with high prairie dog activity levels. Productivity level between southern, central, and northern Colorado was comparable on colonies with moderate prairie dog activity level. Prairie dog activity level is driving higher burrowing owl productivity, but only on plots with high activity in southern Colorado. In Chapter 1, we found an effect of latitude on burrowing owl occupancy but not the probability of reproductive success at the plot level. However, our productivity results indicated that latitude was associated with the burrowing owl per capita productivity rate on prairie dog colonies. Our analysis of burrowing owl reproduction in Chapter 1 required that at least one juvenile owl was detected for a plot to have been identified as having successful reproduction, and thus represents a coarse scale of reproduction. Our productivity analysis was based on the proportions of owls that were juveniles on our survey plots and represents a finer-scale assessment of burrowing owl reproduction than Chapter 1. Colony size was not a significant predictor of productivity, which contrasts with other studies that have reported higher burrowing owl productivity on larger colonies (Savidge 2007, Ray 2016).

Conservation Implications

Density, abundance, and productivity are essential components of population assessments because they can help identify the fine-scale drivers of population trends through time. This chapter has shown that burrowing owl density and abundance have remained relatively stable since the last population assessment in 2005 (Tipton et al. 2009). We found in Chapter 1 that burrowing owl occupancy has also remained stable between these two studies. Burrowing owl populations are likely to remain stable if efforts continue to preserve the prairie dog colonies that are vital for burrowing owls during the breeding season. However, we did find evidence of lower adult burrowing owl occupancy and density in northern Colorado, indicating that this region of the state may need further investigation if there is a future downward population trend. Despite lower adult occupancy and density of burrowing owls, plots in northern Colorado still had high probability of successful reproduction and juvenile densities that were comparable to other regions of the state. This suggests that if adult densities remain stable through time, burrowing owl populations may have enough successful reproduction in northern Colorado to maintain population sizes.

Contrary to previous studies that have shown that large colonies support higher burrowing owl occupancy and density (Griebel & Savidge 2007), we did not find a difference in these population parameters between small (≤ 10 ha), medium (11-299 ha), and large (≥ 300 ha) colonies. This supports a previous study that found that colony size was not a good predictor of burrowing owl nest success and nest density (Conrey 2010). Woodard (2002) also found evidence of high nesting success on small prairie dog colonies. Essentially, burrowing owls are effectively utilizing and successfully reproducing on smaller prairie dog colonies during the breeding season. This may make burrowing owl populations in eastern Colorado more resilient to nesting habitat loss, degradation, or fragmentation, which are all potential drivers of burrowing owl population decline (Samson et al. 2004, Skagen et al. 2005). We also found that prairie dog activity level had a positive effect on burrowing owl density and abundance; however, it is difficult to manage for prairie dog activity level since this can vary dramatically among years. Rapid prairie dog colony expansion and contraction is driven by interactions among climate, plague, prairie dog population dynamics, active control of prairie dog populations, and grazing by large herbivores (Davidson et al. 2022). Therefore, burrowing owl conservation and management practices should not discount the value of small prairie dog colonies and should focus on preserving active prairie dog colonies regardless of size.

Future research

We could not identify the drivers of the spatial pattern in burrowing owl density and productivity with the covariates that we investigated in this study. Future research should focus on identifying the drivers of this regional trend by assessing differences in climate, prairie dog population dynamics, and land use across Colorado. Shortgrass prairie is declining due to cropland conversion and increased development in the energy sectors, including oil, gas, solar, and wind (Neely et al. 2006, Helmig et al. 2020). This could have profound impacts on prairie dog populations, and by association, burrowing owl populations in eastern Colorado. Future research that quantifies habitat loss and fragmentation in eastern Colorado might be helpful in determining if land use change is a major driver of burrowing owl spatial distribution and abundance.

We recommend smaller-scale studies to get better estimates of burrowing owl productivity and determine what factors drive this population parameter in Colorado's eastern plains. Our large-scale study was extremely valuable in describing burrowing owl occupancy, density, and abundance; however, the large scale limited the strength of our productivity methods. Given the nature of our large study area, we could only count the numbers of juveniles on our survey plots and could not conduct fine-scale nest searching efforts. Obtaining updated estimates of nest success from large scale nest searching efforts and identifying the factors that drive nest success amidst land use change may be a valuable addition to our working knowledge of burrowing owl populations in eastern Colorado. However, this study provides a framework for estimating juvenile abundance when resources and logistics can't support nest-searching on a large scale.

Future burrowing owl surveys should be conducted to track changes in burrowing owl populations in eastern Colorado through time since burrowing owls are considered a state-threatened species at the time of this thesis. We recommend conducting large scale surveys at more frequent intervals than the ~17 year time period between this assessment and the last population assessment in 2005. An achievable frequency might be surveying for burrowing owls every 5 years because this period exceeds the time lag between local extinction of prairie dogs on a colony, and the cessation of burrowing owls nesting on that colony, and can coincide with the Colorado Natural Heritage Program's black-tailed prairie dog mapping efforts in eastern Colorado. We recommend that future monitoring efforts by Colorado Parks and Wildlife use a combination of new survey plots and a subset of the plots from this study to expand spatial coverage of burrowing owl surveys and track burrowing owl populations through time. In addition, revisiting plots from this study may cut down on resources needed to reach out to private landowners for survey permission. This study thus provides a baseline for future efforts. Funding and resources will ultimately determine the scale, frequency, and duration of these future monitoring efforts.

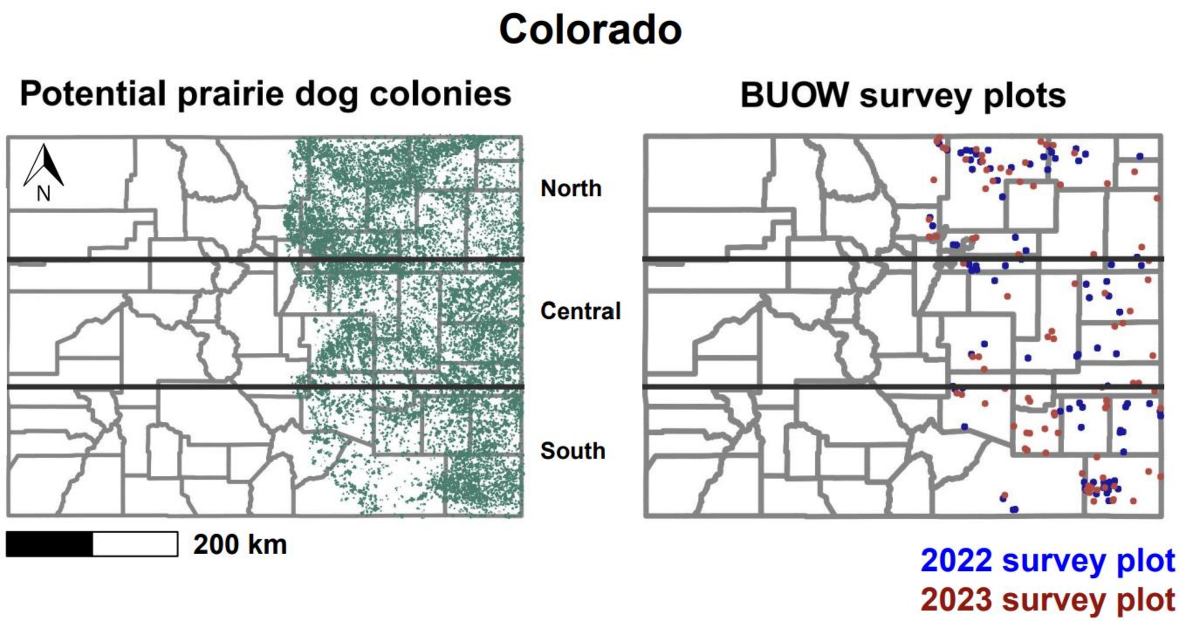

Figure 2.1: Maps of the study area with potential black-tailed prairie dog colonies (left) and burrowing owl survey plots (right). In the left map, the green area contains the potential black-tailed prairie dog colonies in eastern Colorado identified from 2019 NAIP imagery (Colorado Parks and Wildlife 2020). The map on the right shows survey plots from each year of the study (2022 and 2023), selected by spatially-balanced random sampling.

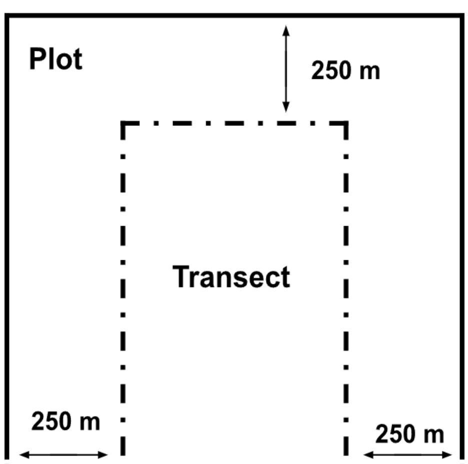

Figure 2.2: Diagram of the plot and transect used for 2022 and 2023 burrowing owl surveys. The transect is represented by the dashed line within the plot. Vegetation data were collected ~1 m off the transect.

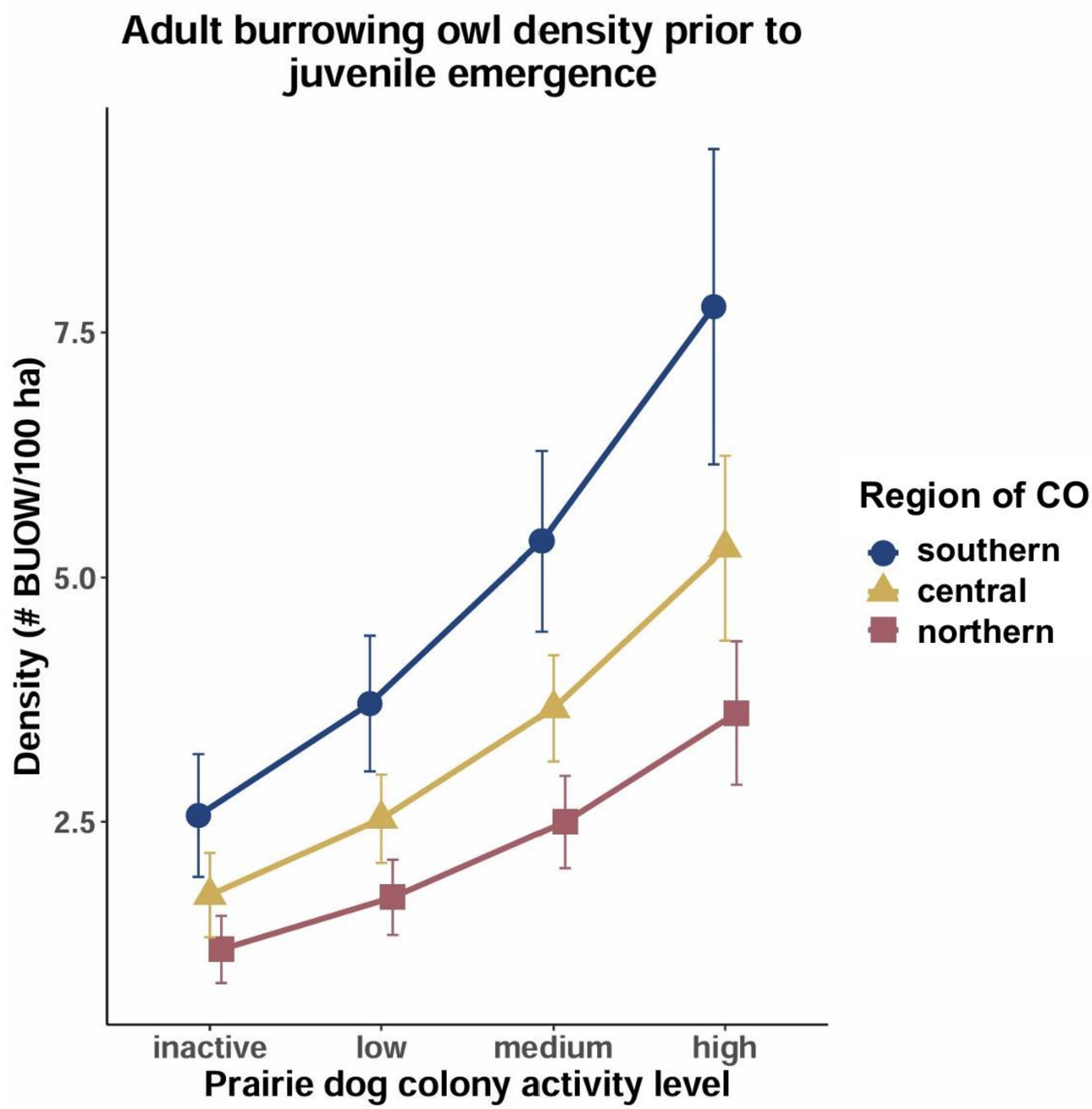

Figure 2.3: Adult burrowing owl density on prairie dog colonies prior to juvenile emergence for each prairie dog activity level in the southern, central, and northern regions of eastern Colorado. Density data were collected during the 2022 and 2023 burrowing owl breeding seasons.

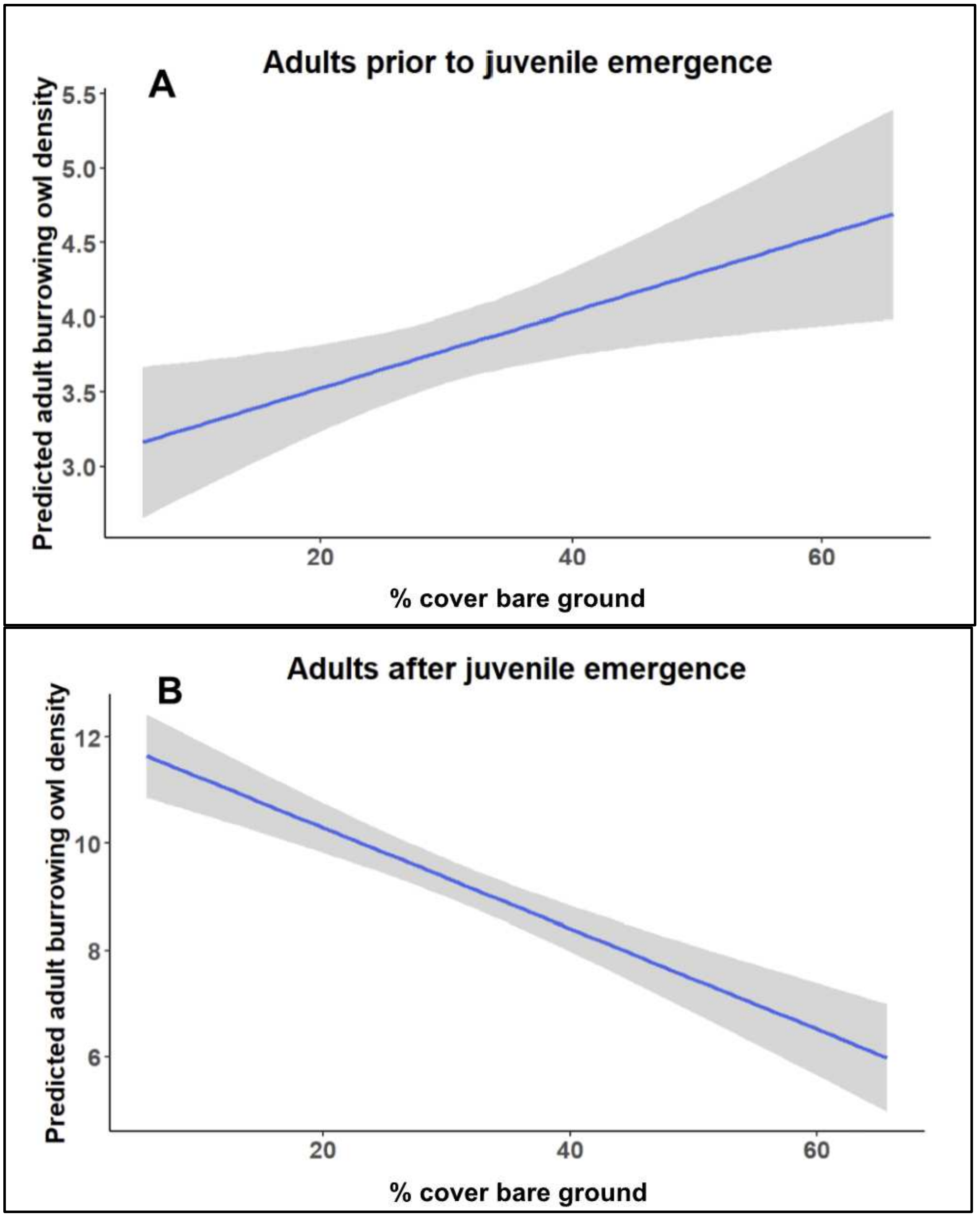

Figure 2.4: Effect of bare ground cover on adult burrowing owl densities on prairie dog colonies in eastern Colorado prior to (A) and after (B) juvenile emergence.

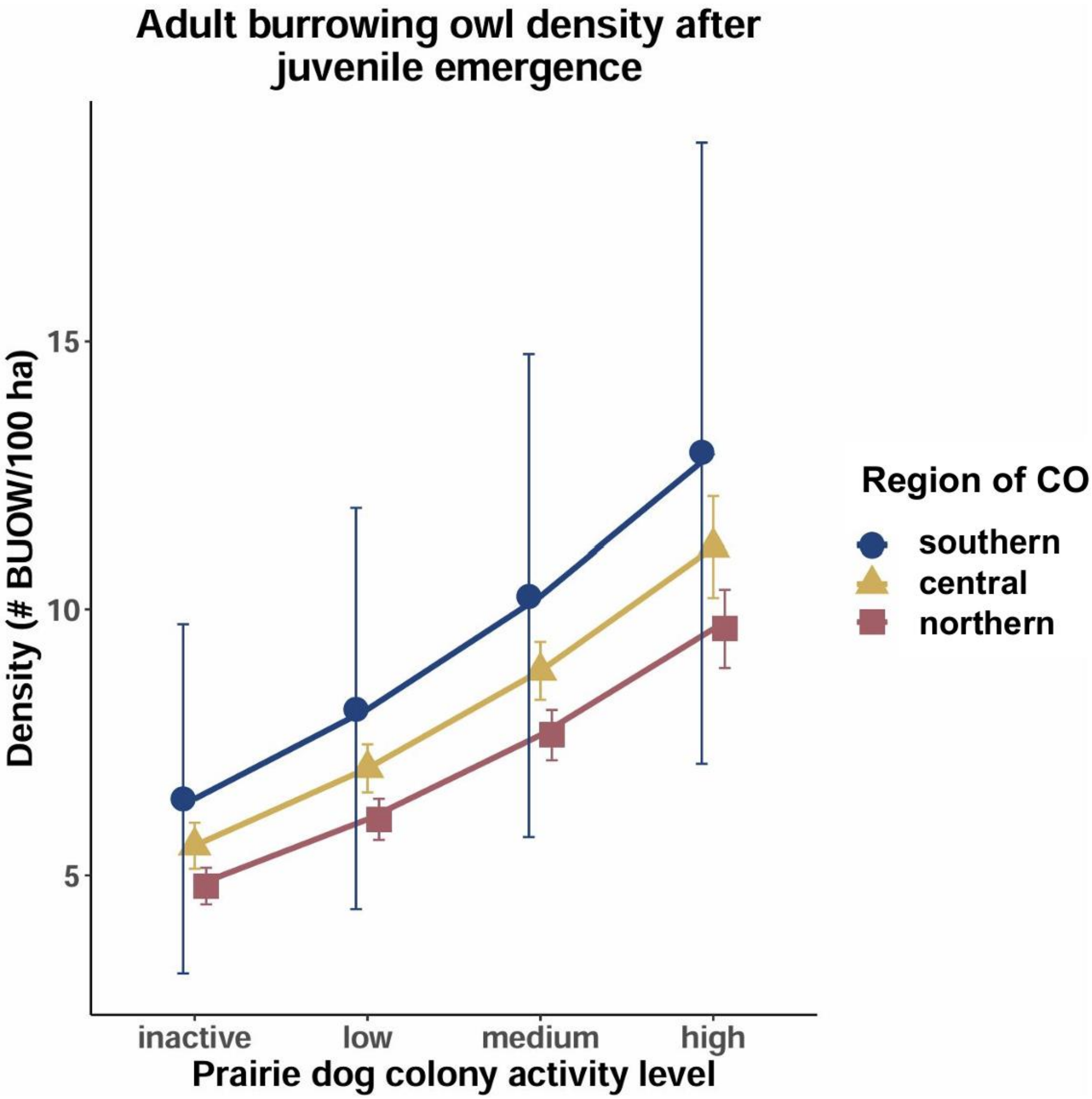

Figure 2.5: Adult burrowing owl density on prairie dog colonies after juvenile emergence for each prairie dog activity level in the southern, central, and northern regions of eastern Colorado. Density data were collected during the 2022 and 2023 burrowing owl breeding seasons.

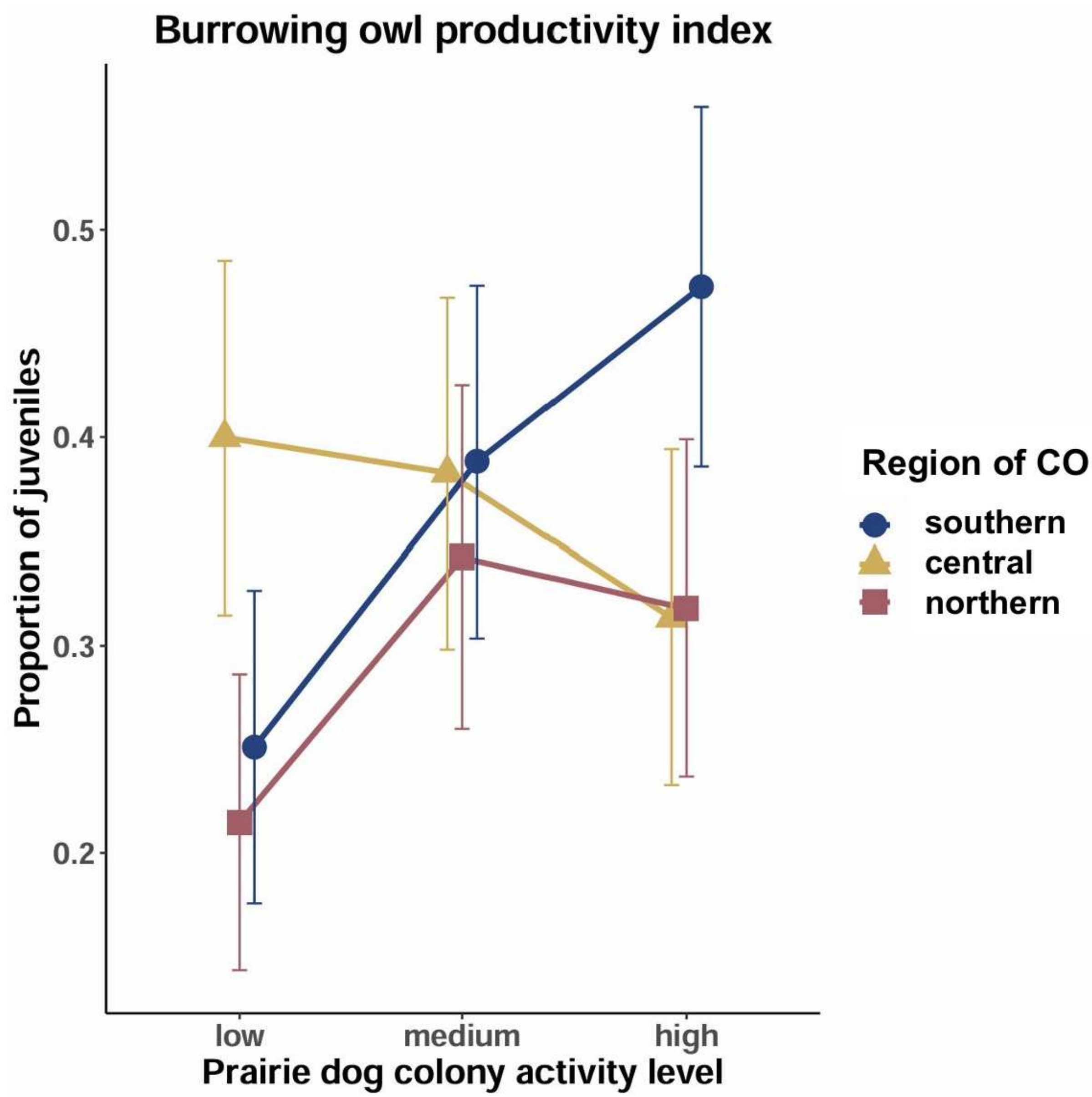

Figure 2.6: Burrowing owl productivity index on prairie dog colonies for each region of eastern Colorado and prairie dog activity level. The productivity index was defined as the proportion of owls that are juveniles. Productivity data were collected during the 2022 and 2023 burrowing owl breeding seasons.

Table 2.1: Covariates explored in unmarked distance sampling analysis for burrowing owls on prairie dog colonies in eastern Colorado. Density data were collected during the 2022 and 2023 burrowing owl breeding seasons.

Covariate	Parameter(s)	Covariate	Parameter(s)
Prairie dog colony activity status	λ	% cover shrub	λ
Prairie dog colony activity level	λ	% cover bare ground	λ
Grazing	λ	Coverage of prairie dog colony in survey plot (ha)	λ
Prairie dog colony size	λ	Wind (mph)	p, ϕ
Ordinal latitude	λ	Temperature (°F)	p
Continuous latitude	λ	% cloud cover	p
Survey time	λ	Observer team	p
Vegetation height (cm)	λ, p	Precipitation season sum (mm)	p
% cover grass	λ	Average precipitation one week before survey (mm)	p
% cover forb	λ	Survey year	p

Parameters and descriptions:

λ: Density
ϕ: Availability of burrowing owl for detection
p: Probability of detecting burrowing owls on a survey plot

Table 2.2: Top three models of adult burrowing owl density on prairie dog colonies in eastern Colorado prior to juvenile emergence. We ran 28 density models.

Model	ΔAICc	Model weight
λ(ordinal latitude+activity level+bare ground cover) ϕ(temp+wind) *p*(wind+cloud)	0	0.61
λ(ordinal latitude+activity level) ϕ(temp+wind) *p*(wind+cloud)	0.89	0.39
λ(ordinal latitude) ϕ(temp+wind) *p*(wind+cloud)	47.50	0

Parameters and descriptions:

λ: Density
ϕ: Availability of burrowing owl for detection
p: Probability of detecting burrowing owls on a survey plot

Table 2.3: Adult burrowing owl densities on prairie dog colonies in eastern Colorado prior to juvenile emergence (early in the breeding season, visits 1 and 2) for each combination of region of Colorado and prairie dog activity level.

Region of Colorado	Prairie dog colony activity level	Density (# owls/km^2)	95% Confidence Interval
South	Inactive	2.56	[1.93, 3.19]
	Low	3.71	[3.01, 4.40]
	Medium	5.36	[4.44, 6.28]
	High	7.76	[6.14, 9.37]
Central	Inactive	1.74	[1.31, 2.18]
	Low	2.53	[2.07, 2.98]
	Medium	3.66	[3.12, 4.20]
	High	5.29	[4.35, 6.23]
North	Inactive	1.19	[0.85, 1.54]
	Low	1.72	[1.34, 2.11]
	Medium	2.49	[2.02, 2.97]
	High	3.61	[2.87, 4.35]

Table 2.4: Top three models of adult burrowing owl density on prairie dog colonies in eastern Colorado after juvenile emergence. We ran 41 density models.

Model	ΔAICc	Model weight
λ(ordinal latitude+activity level+bare ground cover) ϕ(.) *p*(precip)	0	0.71
λ(ordinal latitude+activity level+bare ground cover) ϕ(temp) *p*(precip)	1.83	0.29
λ(bare ground) ϕ(.) *p*(precip)	14.29	0

Parameters and descriptions:

λ: Density
ϕ: Availability of burrowing owls for detection
p: Probability of detecting burrowing owls on a survey plot

Table 2.5: Adult burrowing owl densities on prairie dog colonies after juvenile emergence (later in the breeding season, visits 3 and 4) for each combination of region of eastern Colorado and prairie dog activity level.

Region of Colorado	Prairie dog colony activity level	Density (# owls/km^2)	95% Confidence Interval
South	Inactive	6.43	[3.15, 9.71]
	Low	8.12	[4.36, 11.87]
	Medium	10.24	[5.72, 14.76]
	High	12.91	[7.09, 18.73]
Central	Inactive	5.55	[5.12, 5.99]
	Low	7.01	[6.55, 7.46]
	Medium	8.84	[8.29, 9.28]
	High	11.15	[10.21, 12.09]
North	Inactive	4.79	[4.45, 5.14]
	Low	6.05	[5.66, 6.43]
	Medium	7.63	[7.63, 8.10]
	High	9.63	[9.63, 10.36]

Table 2.6: Top three models of juvenile burrowing owl density on prairie dog colonies in eastern Colorado. We ran 27 density models.

Model	ΔAICc	Model weight
λ(vegetation height) ϕ(.) *p*(.)	0	1
λ(shrub cover) ϕ(.) *p*(.)	33.88	0
λ(ordinal latitude + activity level) ϕ(.) *p*(.)	34.26	0

Parameters and descriptions:

λ: Density

ϕ: Availability of juvenile burrowing owls for detection

p: Probability of detecting juvenile burrowing owls on a survey plot

Table 2.7: Estimates of burrowing owl abundance on prairie dog colonies in eastern Colorado for each of the map correction factors. Abundances are listed for owls in different age classes (adult and juvenile) and timing of the breeding season (prior to and after juvenile emergence). BUOW=burrowing owl.

BUOW Classification	No colonies removed	False positive colonies removed	NAIP eliminated colonies removed	NAIP eliminated + false positives removed
Adults prior to juvenile emergence	6,230 owls [5,009-7,453]	4,913 owls [3,948-5,875]	4,490 owls [3,609-5,371]	3,171 owls [2,549-3,794]
Adults after juvenile emergence	14,730 owls [8,502-20,959]	11,613 owls [5,333-17,893]	10,616 owls [4,875-16,357]	7,499 owls [3,443-11,554]
Juveniles	33,714 owls [24,889-42,538]	26,580 owls [19,623-33,537]	24,297 owls [12,228-20,875]	17,163 owls [12,680-21,647]

Descriptions of map correction factors:
No colonies removed: We did not remove any area of prairie dog colony prior to expanding burrowing owl density estimates to eastern Colorado.
False positive colonies removed: Prior to expanding our density estimates, we removed 21.16% of prairie dog colony area from the mapping layer to adjust for the rate of ground-truthed false positive colonies from our surveys. False positives arose when the 2019 NAIP imagery of potential prairie dog colonies in eastern Colorado indicated the presence of a colony, but then they were determined by observers to have no prairie dog colony present during the initial survey.
NAIP eliminated colonies removed: Prior to expanding our density estimates, we removed 27.93% of potential prairie dog colony area from the mapping layer to account for plots identified in 2021 and 2022 NAIP imagery that were unlikely to contain prairie dog colony.
NAIP + false positives removed: Prior to expanding our density estimates, we removed 49.09% of potential prairie dog colony area from the mapping layer to account for both ground-truthed false positives and NAIP eliminated plots.

Table 2.8: Top three beta regression models of burrowing owl productivity on prairie dog colonies in eastern Colorado. Productivity was defined as the proportion of owls that were juveniles on each survey plot. We ran 12 zero-inflated beta regression models.

Model	ΔAICc	Model weight
P(ordinal latitude * activity level)	0	0.98
P(ordinal latitude + activity level)	8.55	0.01
P(activity level)	9.65	0.01

Parameter and description:

P: burrowing owl productivity index

REFERENCES

Askins, R. A., F. Chávez-Ramírez, B.C. Dale, C.A. Haas, J.R. Herkert, F.L. Knopf, P.D. Vickery 2007. Conservation of Grassland Birds in North America: Understanding Ecological Processes in Different Regions: “Report of the AOU Committee on Conservation.” *Ornithological Monographs*, *64*, iii–46.

Berardelli, D., M.J. Desmond, and L. Murray. 2010. Reproductive success of Burrowing Owls in urban and grassland habitats in southern New Mexico. *The Wilson Journal of Ornithology*, *122*(1), 51–59.

Brooks M.E., K. Kristensen, K.J. van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H.J. Skaug, M. Maechler, B.M. Bolker 2017. “glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling.” *The R Journal*, **9**(2), 378–400.

Chandler, R.B., J.A. Royle, and D.I. King. 2011. Inference about density and temporary emigration in unmarked populations. *Ecology*. 92:1429–1435.

Chamberlain S. and D. Hocking. 2023. rnoaa: 'NOAA' Weather Data from R. R package version 1.4.0, <https://CRAN.R-project.org/package=rnoaa>.

Colorado Parks and Wildlife. 2015. State Wildlife Action Plan: a strategy for conservation of wildlife in Colorado. Denver, Colorado. https://cpw.state.co.us/aboutus/Pages/StateWildlifeActionPlan.aspx

Colorado Parks and Wildlife. 2020. Colorado Black-tailed Prairie Dog Range-wide Monitoring Report. Denver, Colorado.

Conrey, R. Y. 2010. Breeding success, prey use, and mark-resight estimation of burrowing owls nesting on black-tailed prairie dog towns: plague affects a non-susceptible raptor. Ph.D. dissertation, Colorado State University, Fort Collins, CO.

Conway, C. J., and J. C. Simon. 2003. Comparison of detection probability associated with burrowing owl survey methods. *Journal of Wildlife Management* 67: 501-511.

Conway, C.J. 2018. Spatial and Temporal Patterns In Population Trends and Burrow Usage of Burrowing Owls In North America. *Journal of Raptor Research*.52 (2): 129–142.

Crowe D. and K. Longshore 2010. Population status and reproduction ecology of the western burrowing owl (*Athene cunicularia hypugaea*) in Clark County, Nevada. Final Report USGS-582-P. United States Geological Survey; 31

Cully, J. F., S.K. Collinge, R.E. VanNimwegen, C. Ray, W.C. Johnson, B. Thiagarajan, D.B. Conlin, B.E. Holmes, 2010. Spatial variation in keystone effects: small mammal diversity associated with black-tailed prairie dog colonies. *Ecography 33*(4): 667–677.

Davidson, A. D., D.J. Augustine, H. Jacobsen, D. Pellatz, L.M. Porensky, G. McKee, C. Duchardt. 2022. Boom and bust cycles of black-tailed prairie dog populations in the Thunder Basin grassland ecosystem, *Journal of Mammalogy* 103(5): 1112–1126.

Dechant, J. A., M. L. Sondreal, D. H. Johnson, L. D. Igl, C. M. Goldade, P. A. Rabie, B. R. Euliss. 1999 (revised 2002). Effects of management practices on grassland birds: Burrowing Owl. Northern Prairie Wildlife Research Center, Jamestown, ND.

Decker, K. 2007. Central Shortgrass Prairie Ecological System: Ecological Integrity Assessment. Colorado Natural Heritage Program.

Desmond, M.J. and J.A. Savidge. 1996. Factors influencing Burrowing Owl (*Speotyto cunicularia*) nest densities and numbers in western Nebraska. *American Midland Naturalist* 136:143- 148.

Desmond, M. J., J.A. Savidge, and K.M. Eskridge. 2000. Correlations between Burrowing Owl and Black-Tailed Prairie Dog Declines: A 7-Year Analysis. *The Journal of Wildlife Management 64*(4): 1067–1075.

Dickinson, C. E., and J.L. Dodd. 1976. Phenological Pattern in the Shortgrass Prairie. *The American Midland Naturalist 96*(2): 367–378.

Douma J.C. and J.T. Weedon. 2019. Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. *Methods Ecol Evol*. 10: 1412–1430.

Fiske I. and R. Chandler. 2011. “unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance.” *Journal of Statistical Software*, **43**(10), 1–23.

Flanders-Wanner, B. L., White, G. C., & McDaniel, L. L. 2004. Validity of Prairie Grouse harvest-Age Ratios as Production Indices. *The Journal of Wildlife Management 68*(4): 1088–1094.

Griebel, R.L. and J.A. Savidge. 2007. Factors influencing burrowing owl reproductive performance in contiguous shortgrass prairie. *Journal of Raptor Research* 41:212-221.

Helmig, D. 2020. Air quality impacts from oil and natural gas development in Colorado. *Elementa: Science of the Anthropocene*, 8(4).

Herrick, J.E., J.W. Van Zee, S.E. McCord, E.M. Courtright, J.W. Karl, L.M. Burkett. 2021. Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems. USDA-ARS Jornada Experimental Range.

Howlin, S. and J. Mitchell. 2016. Monitoring black-tailed prairie dogs in Colorado with the 2015 NAIP imagery. Western Ecosystems Technology, Laramie, WY.

Huggins, R. M. (1989). On the statistical analysis of capture-recapture experiments. *Biometrika* 76:133-140.

Hurvich, C.M., and Tsai, C.L. 1989. Regression and time series model selection in small samples, *Biometrika*, *76*(2):297–307.

Jones, S.R. 1998. Burrowing Owl. pp. 220-221 *in* Kingery, H.E., ed. Colorado Breeding Bird Atlas. Colorado Bird Atlas Partnership, Denver, Colorado. 636pp.

Jones, N. F. and L. Pejchar 2013. Comparing the ecological impacts of wind and oil & gas development: a landscape scale assessment. *PloS one*, *8*(11), e81391.

Kellner K.F., A.D. Smith, J.A. Royle, M. Kery, J.L. Belant, R.B. Chandler. 2023. "The unmarked R package: Twelve years of advances in occurrence and abundance modeling in ecology." *Methods in Ecology and Evolution*, **14**(6), 1408–1415.

Klute, D. S., L. W. Ayers, M. T. Green, W. H. Howe, S. L. Jones, J. A. Shaffer, S. R. Sheffield, T. S. Zimmerman. 2003. Status Assessment and Conservation Plan for the Western Burrowing Owl in the United States. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication FWS/BTP-R6001-2003, Washington, D.C.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15:247–257.

Lancia R,A., J.D. Nichols, and K.H. Pollock. 1994. Estimating the number of animals in wildlife populations. In *Research and Management Techniques for Wildlife and Habitats*, 5th edn, Bookout TA (ed.). The Wildlife Society: Bethesda, MD; 215-253.

Lutz, R. S. and D. L. Plumpton. 1999. Philopatry and nest site reuse by Burrowing Owls: implications for productivity. *Journal of Raptor Research* 33:149-153.

Macías-Duarte, A. 2011. Change in migratory behavior as possible explanation for burrowing owl population declines in northern latitudes. Ph.D. Dissertation, University of Arizona, Tucson, AZ, USA

Macías-Duarte, A. and Conway, C.J. 2015. Distributional Changes in the Western Burrowing Owl (*Athene cunicularia hypugaea*) in North America from 1967 to 2008. *Journal of Raptor Research.* 49(1), 75-83.

Morin, D. J., C.B. Yackulic, J.E. Diffendorfer, D.B. Lesmeister, C.K. Nielsen, J. Reid, E.M. Schauber. 2020. Is your ad hoc model selection strategy influencing your multimodal inference? *Ecosphere* 11(1): 1-16.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. *Conservation Biology* 8: 677-681.

Neely, B., S. Kettler, J. Horsman, C. Pague, R. Rondeau, R. Smith, L. Grunau, P. Comer, G. Belew, F. Pusateri, B. Rosenlund, D. Runner, K. Sochi, J. Sovell, D. Anderson, T. Jackson and M. Klavetter. 2006. Central Shortgrass Prairie Ecoregional Assessment and Partnership Initiative. The Nature Conservancy of Colorado and the Shortgrass Prairie Partnership. 124 pp. and Appendices

Nichols, J. D., J.E. Hines, J.R. Sauer, F.W. Fallon, J.E. Fallon, P.J. Heglund. (2000). A Double-Observer Approach for Estimating Detection Probability and Abundance From Point Counts, *The Auk* 117(2): 393–408.

Parker, R., Duchardt, C., Dwyer, A., Painter, C., Pierce, A., Michels, T., Wunder, M. 2019. Troc Ecology Warrants Multispecies Management in a Grassland Setting: Proposed Species Interactions on Black-tailed Prairie Dog Colonies. Rangelands. 41:135-144.

Plumpton, D.L. and R.S. Lutz. 1993. Nesting habitat use by burrowing owls in Colorado. *Journal of Raptor Research* 27(4): 299-304.

Poulin, R. & Todd, L.D., Haug, E.A., Millsap, B.A., Martell, M. 2011. Burrowing Owl (Athene cunicularia). The Birds of North America Online.

Pollock, K. H., J.D. Nichols, T.R. Simons, G.L. Farnsworth, L. Bailey, J.R. Sauer. (2002). Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics,* 13, 105–19

R Core Team 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, J.D. 2016. Factors influencing burrowing owl abundance in prairie dog colonies on the southern high plains of Texas. *Journal of Raptor Research*. 50(2), 185-193.

Royle, J. A., D. K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. *Ecology* 85:1591–1597.

Ruiz Ayma, G., A. Olalla Kerstupp, A. Macías Duarte, A. Guzmán Velasco, J.I. González Rojas. 2016. Population density of the western burrowing owl (*Athene cunicularia hypugaea*) in Mexican prairie dog (*Cynomys mexicanus*) colonies in northeastern Mexico. *BMC Ecol* 16, 38.

Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary Production of the Central Grassland Region of the United States. *Ecology, 69*(1), 40-45.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: Past, present, and future. *Wildlife Society Bulletin* 32:6–15.

Santini, L., Tobias, J. A., Callaghan, C., Gallego-Zamorano, J., & Benítez-López, A. 2023. Global patterns and predictors of avian population density. *Global Ecology and Biogeography*, 32, 1189–1204.

Sidle, J.G., M. Ball, T. Byer, J.J. Chynoweth, G. Foli, R. Hodorff, G. Moravek, R. Peterson, D.N. Svingen. (2024). Occurrence of Burrowing Owls in Black-tailed Prairie Dog Colonies on Great Plains National Grasslands. *Journal of Raptor Research*, *35*(4): 316-321

Skagen, S. K, A.Y. Yackel Adams, and R.D. Adams. 2005. Nest survival relative to patch size in a highly fragmented shortgrass prairie landscape. *Wilson Bulletin 117*(1): 23-34.

Smith, G. A., and M.V. Lomolino. 2004. Black-Tailed Prairie Dogs and the Structure of Avian Communities on the Shortgrass Plains. *Oecologia 138*(4): 592–602.

Stevens, D. L., and Olsen, A. R. (2004). Spatially Balanced Sampling of Natural Resources. *Journal of the American Statistical Association*, *99*(465), 262–278.

Tipton, H.C, and P.F. Doherty, Jr. 2008. Occupancy of mountain plover and burrowing owl in Colorado. *Journal of Wildlife Management* 72:1001-1006

Tipton, H. C., P. F. Doherty Jr., and V. J. Dreitz. 2009. Abundance and density of mountain plover (*Charadrius montanus*) and burrowing owl (*Athene cunicularia*) in eastern Colorado. *The Auk* 126(3):493-499.

VerCauteren, T.L., S.W. Gillihan, and S.W. Hutchings. 2001. Distribution of burrowing owls on public and private lands in Colorado. *Journal of Raptor Research* 35(4): 357-361.

Wilsey, C.B., J. Grand, J. Wu, N. Michel, J. Grogan-Brown, B. Trusty, B. 2019. North American Grasslands. National Audubon Society, New York, New York, USA.

Woodard, J.D. 2002. The influence of diet, habitat, and recreational shooting of prairie dogs on burrowing owl demography. M.S. Thesis, Colorado State University, Fort Collins, Colorado.

Zarn, M. 1974a. Burrowing owl, Speotyto cunicularia hypugaea. U.S. Dep. Inter., Bur. Land Manage., Wash. DC. Tech. Note No. 250. 25pp.

APPENDIX

Appendix table 1.1: Full AICc model selection table from analysis of multistate burrowing owl occupancy on prairie dog colonies in eastern Colorado during 2022 - 2023.

Model	AICc	ΔAICc	AICc Weights	K
ψ(state*activity level, state*ordinal latitude) p(state*year) δ(year, temp)	2251.982	0	0.35486	13
ψ(state*activity level, state*continuous latitude) p(state*year) δ(year, temp)	2252.1307	0.148	0.32944	13
ψ(state*activity level, state*ordinal latitude) p(state*year) δ(year, temp, visit precip)	2254.1503	2.1683	0.12001	14
ψ(state*activity level, state*ordinal latitude) p(state*year) δ(year, temp, sum precip)	2254.1707	2.1887	0.11879	14
ψ(state*activity level, state*ordinal latitude) p(state*year) δ(year)	2256.0895	4.1075	0.04551	12
ψ(state*activity level, state* ordinal latitude) p(state*year) δ(temp)	2257.314	5.332	0.02467	12
ψ(state*activity level, state* ordinal latitude) p(state*year) δ(survey time)	2260.3576	8.3756	0.00539	12
ψ(state*activity level, state* ordinal latitude) p(state*year) δ(.)	2265.6959	13.7139	0.00037	11
ψ(state*activity level, state* ordinal latitude) p(state*year) δ(season sum precip)	2266.0324	14.0504	0.00032	12
ψ(state*activity level, state+activity status, state* ordinal latitude) p(state*year) δ(.)	2266.7581	14.7761	0.00022	12
ψ(state*activity level, state* ordinal latitude) p(state*year) δ(veg height)	2267.4053	15.4233	0.00016	12

ψ(state*activity level, state* ordinal latitude) p(state*year) δ(precip)	2267.7566	15.7746	0.00013	12
ψ(state*activity level, state+ ordinal latitude) p(state*year) δ(.)	2268.1961	16.2141	0.00011	10
ψ(state*continuous latitude) p(state*year) δ(.)	2273.8774	21.8954	0.00001	9
ψ(state*activity level) p(state*year) δ(.)	2273.9315	21.9495	0.00001	9
ψ(state*ordinal latitude) p(state*year) δ(.)	2275.0045	23.0225	0.00001	9
ψ(state+ordinal latitude) p(state*year) δ(.)	2277.4605	25.4785	0	8
ψ(state+activity status) p(state*year) δ(.)	2277.5205	25.5385	0	8
ψ(state+ categorical latitude) p(state*year) δ(.)	2277.8789	25.8969	0	8
ψ(state+ continuous latitude) p(state*year) δ(.)	2278.2895	26.3075	0	8
ψ(state+activity level) p(state*year) δ(.)	2278.8	26.818	0	8
ψ(state* categorical latitude) p(state*year) δ(.)	2279.9462	27.9642	0	9
ψ(state) p(state*year) δ(.)	2281.1589	29.1769	0	7
ψ(state*bareground) p(state*year) δ(.)	2281.5566	29.5746	0	9
ψ(state+shrub) p(state*year) δ(.)	2282.5227	30.5407	0	8
ψ(state*shrub) p(state*year) δ(.)	2282.6533	30.6713	0	9
ψ(state+bareground) p(state*year) δ(.)	2282.9017	30.9197	0	8
ψ(state+colony size) p(state*year) δ(.)	2282.9412	30.9592	0	8
ψ(state+grass) p(state*year) δ(.)	2283.075	31.093	0	8

ψ(state+proportion prairie dog colony) p(state*year) δ(.)	2283.003	31.0211	0	8
ψ(state+year) p(state*year) δ(.)	2283.1022	31.1202	0	8
ψ(state) p(state+temp) δ(.)	2283.2293	31.2473	0	6
ψ(state+forb) p(state*year) δ(.)	2283.2888	31.3068	0	8
ψ(state+veg height) p(state*year) δ(.)	2283.2891	31.3071	0	8
ψ(state) p(state*season sum precip) δ(.)	2283.6022	31.6202	0	7
ψ(state) p(state*temp) δ(.)	2283.6797	31.6977	0	7
ψ(state) p(state) δ(.)	2284.0695	32.0875	0	5
ψ(state) p(state+cloud) δ(.)	2284.5138	32.5318	0	6
ψ(state*veg height) p(state*year) δ(.)	2284.8169	32.8349	0	9
ψ(state*colony size) p(state*year) δ(.)	2284.8863	32.9043	0	9
ψ(state*year) p(state*year) δ(.)	2284.9279	32.9459	0	9
ψ(state*grass) p(state*year) δ(.)	2285.0461	33.0641	0	9
ψ(state*forb) p(state*year) δ(.)	2285.2783	33.2963	0	9
ψ(state) p(state+year) δ(.)	2285.5519	33.5699	0	6
ψ(state) p(state+season sum precip) δ(.)	2285.5665	33.5845	0	6
ψ(state) p(state+precip) δ(.)	2285.9499	33.9679	0	6
ψ(state) p(state+veg height) δ(.)	2286.09	34.108	0	6
ψ(state) p(state*cloud) δ(.)	2286.119	34.137	0	7
ψ(state) p(state+wind) δ(.)	2286.179	34.197	0	6
ψ(state) p(state+survey time) δ(.)	2286.2145	34.2325	0	6

ψ(state) p(state*veg height) δ(.)	2286.4784	34.4964	0	7
ψ(state) p(state*wind) δ(.)	2287.2602	35.2782	0	7
ψ(state) p(state*time) δ(.)	2288.0451	36.0631	0	7
ψ(state) p(state*precip) δ(.)	2288.1096	36.1276	0	7
ψ(.) p(.) δ(.)	2336.8327	84.8507	0	3

Parameters and descriptions:

ψ: burrowing owl occupancy where the two states are ψ_1: probability plot is occupied regardless of reproductive state and ψ2: probability of successful reproduction on an occupied plot
p: probability of detection where the two states are *p*1: probability of detecting at least one owl and *p*2: probability of detecting at least one owl on a plot where juveniles are present
δ: probability of detecting a juvenile owl (detecting successful reproduction)
ΔAICc: AICc difference between top model and model being compared
K:number of parameters in the model

Appendix table 1.2: Full AICc model selection table from analysis of dynamic burrowing owl occupancy on prairie dog colonies in eastern Colorado during 2022 - 2023.

Model	AICc	ΔAICc	AICc Weights	K
ψ(overall activity status) γ(2022_2023 activity status, ordinal latitude) ε(active to inactive transition) p(season+observer)	1025.2825	0	0.58966	8
ψ(overall activity status) γ(2022_2023 activity status*ordinal latitude) ε(active to inactive transition) p(season+observer)	1028.3585	3.076	0.12667	10
ψ(overall activity status) γ(2022_2023 activity status) ε(active to inactive transition) p(season+observer)	1028.723	3.4405	0.10556	8
ψ(overall activity status) γ(ordinal latitude) ε(active to inactive transition) p(season+observer)	1029.9724	4.6899	0.05652	8
ψ(overall activity status) γ(.) ε(active to inactive transition) p(season+observer)	1031.6781	6.3956	0.02409	7
ψ(overall activity status) γ(inactive to active transition) ε(active to inactive transition) p(season+observer)	1032.2213	6.9388	0.01836	8
ψ(overall activity status) γ(.) ε(2022_2023 activity status) p(season+observer)	1032.2602	6.9777	0.01801	6
ψ(overall activity status) γ(proportion colony w/in2250m) ε(active to inactive transition) p(season+observer)	1032.6124	7.3299	0.0151	8
ψ(overall activity status) γ(proportion colony w/in1500m) ε(active to inactive transition) p(season+observer)	1033.411	8.1285	0.01013	8
ψ(overall activity status) γ(proportion colony w/in500m) ε(active to inactive transition) p(season+observer)	1033.4476	8.1651	0.00994	8

ψ(overall activity status) γ(2019 colony size) ε(active to inactive transition) p(season+observer)	1033.7173	8.4348	0.00869	8
ψ(overall activity status) γ(occupancy 2005) ε(active to inactive transition) p(season+observer)	1033.7547	8.4722	0.00853	8
ψ(overall activity status) γ(continuous latitude) ε(active to inactive transition) p(season+observer)	1033.7989	8.5164	0.00834	8
ψ(overall activity status) γ(.) ε(ordinal latitude) p(season+observer)	1040.6061	15.3236	0.00028	7
ψ(overall activity status) γ(.) ε(.) p(season+observer)	1045.5816	20.2991	0.00002	6
ψ(overall activity status) γ(.) ε(proportion colony w/in1500m) p(season+observer)	1046.7374	21.4549	0.00001	7
ψ(overall activity status) γ(.) ε(proportion colony w/in2250m) p(season+observer)	1046.7543	21.4718	0.00001	7
ψ(overall activity status) γ(.) ε(2005 burrowing owl density) p(season+observer)	1046.8644	21.5819	0.00001	7
ψ(overall activity status) γ(.) ε(colony size) p(season+observer)	1046.9167	21.6342	0.00001	7
ψ(overall activity status) γ(.) ε(proportion colony w/in500m) p(season+observer)	1047.0115	21.729	0.00001	7
ψ(overall activity status) γ(.) ε(continuous latitude) p(season+observer)	1047.4159	22.1334	0.00001	7
ψ(overall activity status) γ(.) ε(2005 occupancy) p(season+observer)	1047.6743	22.3918	0.00001	7
ψ(overall activity status) γ(.) ε(2005 activity status) p(season+observer)	1047.6864	22.4039	0.00001	7
ψ(proportion colony w/in2250m) γ(.) ε(.) p(season+observer)	1048.5307	23.2482	0.00001	6

ψ(proportion colony w/in1500m) γ(.) ε(.) p(season+observer)	1049.7696	24.4871	0	6
ψ(2019 colony size) γ(.) ε(.) p(season+observer)	1050.9442	25.6617	0	6
ψ(proportion colony w/in500m) γ(.) ε(.) p(season+observer)	1051.131	25.8485	0	6
ψ(ordinal latitude) γ(.) ε(.) p(season+observer)	1053.777	28.4945	0	6
ψ(.) γ(.) ε(.) p(season+observer)	1054.4869	29.2044	0	5
ψ(latitude) γ(.) ε(.) p(season+observer)	1055.6894	30.4069	0	6
ψ(.) γ(.) ε(.) p(season+temp)	1055.964	30.6815	0	6
ψ(.) γ(.) ε(.) p(season)	1056.0443	30.7618	0	5
ψ(.) γ(.) ε(.) p(season+cloud)	1057.1152	31.8327	0	6
ψ(.) γ(.) ε(.) p(season+wind)	1058.077	32.7945	0	6
ψ(.) γ(.) ε(.) p(.)	1107.5582	82.2757	0	4

Parameters and descriptions:

ψ: probability that a plot is occupied by burrowing owls
γ: probability of burrowing owl local colonization
ε: probability of burrowing owl local extinction
p: probability of detection
ΔAICc: AICc difference between top model and model being compared
K:number of parameters in the model

Appendix table 1.3: Correlations between survey plot covariates from the Pearson correlation test for burrowing owl multistate occupancy models. Correlation coefficients (*r*) >0.5 indicate moderate correlation between covariates. Covariates with moderate correlations were explored separately.

	Activity level	Grazing	Colony size	Ordinal latitude	Continuous latitude	Veg height	Grass	Forb	Shrub	Bare ground	Sum precip	Activity status	Year	Pdog coverage
Activity level	1	0.028	0.066	0.164	0.203	0.045	-0.204	0.22	0.078	0.034	-0.058	0.416	-0.008	0.028
Grazing	0.028	1	-0.29	0.089	0.083	0.176	0.182	0.122	0.067	-0.098	0.126	0.003	0.293	-0.151
Colony size	0.066	-0.29	1	-0.061	-0.099	-0.139	-0.145	-0.082	-0.042	0.25	-0.181	0.046	-0.194	0.438
Ordinal latitude	0.164	0.089	-0.061	1	0.951	0.39	0.166	0.048	0.228	-0.397	-0.139	-0.079	-0.012	-0.267
Continuous latitude	0.203	0.083	-0.099	0.951	1	0.369	0.144	0.074	0.256	-0.393	-0.138	-0.02	-0.023	-0.315
Veg height	0.045	0.176	-0.139	0.39	0.369	1	0.359	0.476	0.099	-0.485	0.433	0.067	0.62	-0.305
Grass	-0.204	0.182	-0.145	0.166	0.144	0.359	1	-0.321	0.074	-0.588	0.23	-0.019	0.252	-0.135
Forb	0.22	0.122	-0.082	0.048	0.074	0.476	-0.321	1	-0.086	-0.092	0.36	0.109	0.581	-0.01
Shrub	0.078	0.067	-0.042	0.228	0.256	0.099	0.074	-0.086	1	-0.091	-0.022	0.085	-0.061	-0.144
Bare ground	0.034	-0.098	0.25	-0.397	-0.393	-0.485	-0.588	-0.092	-0.091	1	-0.189	0.043	-0.23	0.264

Appendix table 1.4: Correlations between probability of detection covariates from the Pearson correlation test for burrowing owl multistate occupancy models. Correlation coefficients (*r*) >0.5 indicate moderate correlation between covariates. Covariates with moderate correlations were explored separately.

	Veg height	Wind	Temp	Cloud	Precip	Observer	Time
veg height	1	-0.39	-0.211	0.307	0.39	0.483	0.265
Wind	-0.39	1	0.322	-0.084	-0.305	-0.299	-0.153
Temp	-0.211	0.322	1	-0.177	-0.255	-0.13	-0.093
Cloud	0.307	-0.084	-0.177	1	0.178	0.261	0.27
Precip	0.39	-0.305	-0.255	0.178	1	0.346	0.259
Observer	0.483	-0.299	-0.13	0.261	0.346	1	0.377
Time	0.265	-0.153	-0.093	0.27	0.259	0.377	1

Appendix table 1.5a: First half of correlations between probability of detection covariates from the Pearson correlation test for burrowing owl dynamic occupancy models. Correlation coefficients (*r*) >0.5 indicate moderate correlation between covariates. Covariates with moderate correlations were explored separately. Pdog_pr500m, Pdog_pr1500m, Pdog_pr2250m describe the proportion of land that is a prairie dog colony within 500 m, 1,500 m, and 2,250 m, respectively, of Tipton et al.'s (2008) survey plot in 2005. The overall prairie dog status describes if the colony ever had active prairie dogs, such that if it was active in 2005, but not in 2022/2023, the colony is considered active. BUOW=burrowing owl.

	Overall activity status	2005 Activity status	22_23 Activity status	2005 occupancy	Continuous latitude	2019 colony size	2005 BUOW density
Overall activity status	1	0.482	0.489	0.027	-0.022	0.007	0.154
2005 Activity status	0.482	1	-0.328	0.246	-0.239	-0.015	0.198
22_23 Activity status	0.489	-0.328	1	0.016	0.09	0.012	-0.016
2005 occupancy	0.027	0.246	0.016	1	-0.077	-0.101	0.209
Continuous latitude	-0.022	-0.239	0.09	-0.077	1	-0.134	-0.038
2019 colony size	0.007	-0.015	0.012	-0.101	-0.134	1	-0.03
2005 BUOW density	0.154	0.198	-0.016	0.209	-0.038	-0.03	1
pdog_pr500m	-0.112	-0.119	-0.015	-0.123	-0.067	0.062	-0.383
pdog_pr1500m	-0.172	-0.196	-0.048	-0.164	-0.032	0.085	-0.36
pdog_pr2250m	-0.162	-0.199	-0.038	-0.183	-0.031	0.094	-0.367
Active to inactive transition	-0.062	-0.159	-0.408	-0.173	0.193	-0.049	0.025
Inactive to active transition	-0.091	-0.546	0.101	-0.432	0.249	0.064	-0.161
Ordinal latitude	-0.047	-0.16	0.024	-0.083	0.236	-0.06	-0.032
Temp	-0.026	0.058	-0.048	-0.03	-0.047	-0.022	0.029
Cloud	0.049	-0.056	0.061	0.025	-0.036	-0.073	0.022
Observer	0.276	-0.452	0.669	-0.035	0.301	-0.061	0.044
Wind	0.062	0.121	0.031	-0.015	-0.155	-0.091	0.111

Appendix table 1.5b: Second half of correlations between probability of detection covariates from the Pearson correlation test for burrowing owl dynamic occupancy models. Correlation coefficients (*r*) >0.5 indicate moderate correlation between covariates. Covariates with moderate correlations were explored separately. BUOW=burrowing owl. Pdog_pr500m, Pdog_pr1500m, Pdog_pr2250m describe the proportion of land that is a prairie dog colony within 500 m, 1,500 m, and 2,250 m, respectively, of Tipton et al.'s (2008) survey plot in 2005. The overall prairie dog status describes if the colony ever had active prairie dogs, such that if it was active in 2005, but not in 2022/2023, the colony is considered active.

	pdog_pr500m	pdog_pr1500m	pdog_pr2250m	Active to inactive transition	Inactive to active transition	Ordinal latitude	Temp	Cloud	Observer	Wind
Overall activity status	-0.112	-0.172	-0.162	-0.062	-0.091	-0.047	-0.026	0.049	0.276	0.062
2005 Activity status	-0.119	-0.196	-0.199	-0.159	-0.546	-0.16	0.058	-0.056	-0.452	0.121
22_23 Activity status	-0.015	-0.048	-0.038	-0.408	0.101	0.024	-0.048	0.061	0.669	0.031
2005 occupancy	-0.123	-0.164	-0.183	-0.173	-0.432	-0.083	-0.03	0.025	-0.035	-0.015
Continuous latitude	-0.067	-0.032	-0.031	0.193	0.249	0.236	-0.047	-0.036	0.301	-0.155
2019 colony size	0.062	0.085	0.094	-0.049	0.064	-0.06	-0.022	-0.073	-0.061	-0.091
2005 BUOW density	-0.383	-0.36	-0.367	0.025	-0.161	-0.032	0.029	0.022	0.044	0.111
pdog_pr500m	1	0.84	0.745	0.025	0.024	-0.033	-0.056	-0.04	-0.009	-0.058
pdog_pr1500m	0.84	1	0.961	0.077	0.166	-0.004	-0.087	-0.007	-0.056	-0.13
pdog_pr2250m	0.745	0.961	1	0.062	0.216	0.008	-0.087	0.02	-0.071	-0.125
Active to inactive transition	0.025	0.077	0.062	1	0.336	0.167	-0.085	0.041	0.073	-0.189
Inactive to active transition	0.024	0.166	0.216	0.336	1	0.258	-0.035	0.089	0.107	-0.077
Ordinal latitude	-0.033	-0.004	0.008	0.167	0.258	1	-0.216	0.179	0.102	-0.184
Temp	-0.056	-0.087	-0.087	-0.085	-0.035	-0.216	1	-0.163	-0.067	0.299
Cloud	-0.04	-0.007	0.02	0.041	0.089	0.179	-0.163	1	0.047	-0.004
Observer	-0.009	-0.056	-0.071	0.073	0.107	0.102	-0.067	0.047	1	-0.042
Wind	-0.058	-0.13	-0.125	-0.189	-0.077	-0.184	0.299	-0.004	-0.042	1

Appendix Table 2.1: Full AICc model selection table from analysis of adult burrowing owl density on prairie dog colonies in eastern Colorado prior juvenile emergence during 2022-2023.

Model	AICc	ΔAICc	AICc Weights	K
λ(ordinal latitude+activity level+bareground)ϕ(temp+wind)p(wind+cloud)	2948.83	0	0.61	11
λ(ordinal latitude+activity level)ϕ(.)p(wind+cloud)	2949.69	0.86	0.39	10
λ(ordinal latitude*activity level+bareground)ϕ(temp+wind)p(wind+cloud)	2970.59	21.76	1.14E-05	12
λ(ordinal latitude+activity level+bareground)ϕ(.)p(wind+cloud)	2988.64	39.81	1.38E-09	10
λ(ordinal latitude)ϕ(.)p(wind+cloud)	3000.51	51.68	3.63E-12	7
λ(activity level)ϕ(.)p(wind+cloud)	3005.35	56.52	3.24E-13	7
λ(shrub)ϕ(.)p(wind+cloud)	3011.16	62.33	1.77E-14	7
λ(activity status)ϕ(.)p(wind+cloud)	3024.83	76	1.90E-17	7
λ(grazing)ϕ(.)p(wind+cloud)	3026.3	77.47	9.14E-18	7
λ(forb)ϕ(.)p(wind+cloud)	3026.49	77.66	8.29E-18	7
λ(prairie dog colony cover)ϕ(.)p(wind+cloud)	3033.25	84.42	2.83E-19	7
λ(.)ϕ(.)p(.)	3036.36	87.53	5.95E-20	6
λ(bareground)ϕ(.)p(wind+cloud)	3037.47	88.64	3.43E-20	7
λ(.)ϕ(.)p(wind+cloud)	3038.69	89.86	1.86E-20	6
λ(.)ϕ(.)p(cloud)	3040.42	91.59	7.84E-21	5
λ(.)ϕ(.)p(wind)	3040.95	92.12	6.01E-21	5
λ(.)ϕ(temp)p(.)	3041.54	92.7	4.49E-21	5
λ(.)ϕ(wind)p(.)	3042.53	93.7	2.73E-21	5

λ(.)ϕ(.)p(year)	3043.09	94.26	2.06E-21	5
λ(.)ϕ(.)p(.)	3044.79	95.96	8.82E-22	4
λ(latitude)ϕ(.)p(wind+cloud)	3044.81	95.98	8.72E-22	7
λ(.)ϕ(.)p(time)	3045	96.17	7.92E-22	5
λ(.)ϕ(.)p(obsv)	3046.36	97.52	4.03E-22	5
λ(.)ϕ(.)p(temp)	3046.44	97.61	3.85E-22	5
λ(.)ϕ(.)p(precip)	3047.17	98.34	2.68E-22	5
λ(grass)ϕ(.)p(wind+cloud)	3069.37	120.54	4.06E-27	7
λ(veg.height)ϕ(.)p(wind+cloud)	3069.98	121.15	2.99E-27	7
λ(colony size)ϕ(.)p(wind+cloud)	3355.49	406.66	3.01E-89	7
λ(.)ϕ(.)p(sum precip)	3399.79	450.95	7.23E-99	5

Parameters and descriptions:

λ: Density
ϕ: Availability of burrowing owl for detection
p: Probability of detecting burrowing owls on a survey plot
ΔAICc: AICc difference between top model and model being compared
K:number of parameters in the model

Appendix Table 2.2: Full AICc model selection table from analysis of adult burrowing owl density on prairie dog colonies in eastern Colorado after juvenile emergence during 2022 - 2023.

Model	AICc	ΔAICc	AICc Weights	K
λ(ordinal latitude+activity level+bareground)ϕ(.)p(precip)	2161.97	0	0.66	8
λ(ordinal latitude+activity level+bareground)ϕ(temp)p(precip)	2163.80	1.83	0.26	9
λ(ordinal latitude*activity level+bareground)ϕ(temp)p(precip)	2166.23	4.26	0.08	10
λ(bareground)ϕ(.)p(precip)	2176.26	14.29	0	6
λ(ordinal latitude+activity level)ϕ(.)p(precip)	2176.73	14.75	0	7
λ(ordinal latitude+activity level)ϕ(temp)p(precip)	2178.07	16.10	0	8
λ(bareground)ϕ(temp)p(precip)	2178.39	16.42	0	7
λ(grazing)ϕ(.)p(precip)	2178.83	16.86	0	6
λ(grazing)ϕ(temp)p(precip)	2180.75	18.77	0	7
λ(forb)ϕ(.)p(precip)	2181.46	19.49	0	6

λ(.)ϕ(.)p(precip)	2182.55	20.58	0	5
λ(.)ϕ(.)p(.)	2183.64	21.67	0	4
λ(.)ϕ(.)p(cloud)	2183.94	21.97	0	5
λ(.)ϕ(.)p(wind)	2184.18	22.21	0	5
λ(shrub)ϕ(.)p(precip)	2184.19	22.21	0	6
λ(latitude)ϕ(.)p(precip)	2184.4	22.43	0	6
λ(.)ϕ(.)p(obsv)	2184.67	22.70	0	5
λ(ordinal latitude)ϕ(.)p(precip)	2184.76	22.79	0	6
λ(activity status)ϕ(.)p(precip)	2184.80	22.82	0	6
λ(.)ϕ(temp)p(.)	2185.19	23.21	0	5
λ(.)ϕ(.)p(veg.height)	2185.62	23.65	0	5

λ(.)ϕ(.)p(temp)	2185.66	23.68	0	5
λ(.)ϕ(.)p(year)	2185.68	23.71	0	5
λ(shrub)ϕ(temp)p(precip)	2185.72	23.75	0	7
λ(.)ϕ(.)p(time)	2185.81	23.84	0	5
λ(.)ϕ(wind)p(.)	2185.85	23.87	0	5
λ(activity status)ϕ(temp)p(precip)	2186.41	24.44	0	7
λ(activity level)ϕ(temp)p(precip)	2230.03	68.06	0	7
λ(activity level)ϕ(.)p(precip)	2232.35	70.38	0	6
λ(forb)ϕ(temp)p(precip)	2236.40	74.43	0	7
λ(grass)ϕ(temp)p(precip)	2237.20	75.23	0	7
λ(grass)ϕ(.)p(precip)	2238.29	76.31	0	6

λ(latitude)ϕ(temp)p(precip)	2240.12	78.15	0	7
λ(ordinal latitude)ϕ(temp)p(precip)	2240.59	78.61	0	7
λ(colony size)ϕ(.)p(precip)	2242.73	80.76	0	6
λ(.)ϕ(.)p(sum precip)	2263.80	101.82	0	5
λ(veg.height)ϕ(.)p(precip)	2264.62	102.64	0	6
λ(prairie dog colony coverage)ϕ(.)p(precip)	2265.27	103.29	0	6
λ(veg.height)ϕ(temp)p(precip)	2266.36	104.38	0	7
λ(prairie dog colony coverage)ϕ(temp)p(precip)	2266.82	104.84	0	7
λ(colony size)ϕ(temp)p(precip)	2312.69	150.72	0	7

Parameters and descriptions:
λ: Density
ϕ: Availability of burrowing owl for detection
p: Probability of detecting burrowing owls on a survey plot
ΔAICc: AICc difference between top model and model being compared
K:number of parameters in the model

Appendix Table 2.3: Full AICc model selection table from analysis of juvenile burrowing owl density on prairie dog colonies in eastern Colorado during 2022 - 2023.

Model	AICc	ΔAICc	AICc Weights	K
λ(veg height)ϕ(.)p(.)	2262.3	0	1	5
λ(shrub)ϕ(.)p(.)	2296.18	33.88	0	5
λ(ordinal latitude+activity level)ϕ(.)p(.)	2296.55	34.26	0	6
λ(ordinal latitude+activity level+bare ground) ϕ(wind+temp)p(.)	2298.14	35.84	0	7
λ(activity level)ϕ(.)p(.)	2303.32	41.02	0	5
λ(statesection)ϕ(.)p(.)	2307.43	45.14	0	5
λ(latitude)ϕ(.)p(.)	2311.82	49.53	0	5
λ(.)ϕ(.)p(.)	2312.28	49.99	0	4
λ(.)ϕ(wind+temp)p(.)	2484.96	222.66	0	6
λ(.)ϕ(temp)p(.)	2509.16	246.86	0	5
λ(.)ϕ(wind)p(.)	2516.11	253.82	0	5
λ(grazing)ϕ(.)p(.)	2543.98	281.68	0	5
λ(prairie dog colony coverage)ϕ(.)p(.)	2558.58	296.28	0	5
λ(forb)ϕ(.)p(.)	2559.74	297.45	0	5
λ(activity status)ϕ(.)p(.)	2563.28	300.98	0	5
λ(grass)ϕ(.)p(.)	2567.55	305.26	0	5
λ(bare ground)ϕ(.)p(.)	2568.4	306.11	0	5
λ(.)ϕ(.)p(temp)	2568.75	306.45	0	5
λ(.)ϕ(.)p(wind)	2568.77	306.48	0	5

λ(.)ϕ(.)p(obsv)	2568.79	306.5	0	5
λ(.)ϕ(.)p(cloud)	2568.81	306.52	0	5
λ(.)ϕ(.)p(sum precip)	2568.82	306.52	0	5
λ(.)ϕ(.)p(precip)	2568.82	306.53	0	5
λ(.)ϕ(.)p(time)	2568.84	306.54	0	5
λ(.)ϕ(.)p(veg height)	2568.84	306.54	0	5
λ(.)ϕ(.)p(year)	2568.86	306.56	0	5
λ(colony size)ϕ(.)p(.)	2582.75	320.46	0	5

Parameters and descriptions:

λ: Density
ϕ: Availability of juvenile burrowing owl for detection
p: Probability of detecting juvenile burrowing owls on a survey plot
ΔAICc: AICc difference between top model and model being compared
K:number of parameters in the model

Appendix Table 2.4: Full AICc model selection table from analysis of burrowing owl productivity on prairie dog colonies in eastern Colorado during 2022 - 2023.

Model	AICc	ΔAICc	AICc Weights	K
P(ordinal latitude*activity level)	-1412.37	0	0.98	8
P(ordinal latitude+activity level)	-1403.82	8.55	0.01	6
P(activity level)	-1402.72	9.65	0.01	4
P(forb)	62.5	1474.87	0	4
P(veg.ht)	64.73	1477.1	0	4
P(ordinal latitude)	66.77	1479.13	0	5
P(shrub)	67.93	1480.3	0	4
P(grazing)	68.19	1480.56	0	4
P(colony size)	68.23	1480.6	0	4
P(prairie dog colony coverage)	68.66	1481.03	0	4
P(bareground)	68.74	1481.11	0	4
P(grass)	68.76	1481.13	0	4

Parameter and description:

P: proportion of burrowing owls that are juveniles

Appendix table 2.5: Correlations between survey plot covariates from the Pearson correlation test for burrowing owl density models. Correlation coefficients (*r*) >0.5 indicate moderate correlation between covariates. Covariates with moderate correlations were explored separately.

	Activity level	Grazing	Colony size	Ordinal latitude	Continuous latitude	Veg height	Grass	Forb	Shrub	Bare ground	Sum precip	Activity status	Year	Pdog coverage
Activity level	1	0.028	0.066	0.164	0.203	0.045	-0.204	0.22	0.078	0.034	-0.058	0.416	-0.008	0.028
Grazing	0.028	1	-0.29	0.089	0.083	0.176	0.182	0.122	0.067	-0.098	0.126	0.003	0.293	-0.151
Colony size	0.066	-0.29	1	-0.061	-0.099	-0.139	-0.145	-0.082	-0.042	0.25	-0.181	0.046	-0.194	0.438
Ordinal latitude	0.164	0.089	-0.061	1	0.951	0.39	0.166	0.048	0.228	-0.397	-0.139	-0.079	-0.012	-0.267
Continuous latitude	0.203	0.083	-0.099	0.951	1	0.369	0.144	0.074	0.256	-0.393	-0.138	-0.02	-0.023	-0.315
Veg height	0.045	0.176	-0.139	0.39	0.369	1	0.359	0.476	0.099	-0.485	0.433	0.067	0.62	-0.305
Grass	-0.204	0.182	-0.145	0.166	0.144	0.359	1	-0.321	0.074	-0.588	0.23	-0.019	0.252	-0.135
Forb	0.22	0.122	-0.082	0.048	0.074	0.476	-0.321	1	-0.086	-0.092	0.36	0.109	0.581	-0.01
Shrub	0.078	0.067	-0.042	0.228	0.256	0.099	0.074	-0.086	1	-0.091	-0.022	0.085	-0.061	-0.144
Bare ground	0.034	-0.098	0.25	-0.397	-0.393	-0.485	-0.588	-0.092	-0.091	1	-0.189	0.043	-0.23	0.264

Appendix table 2.6: Correlations between probability of detection covariates from the Pearson correlation test for burrowing owl density models. Correlation coefficients (*r*) >0.5 indicate moderate correlation between covariates. Covariates with moderate correlations were explored separately.

	Veg height	Wind	Temp	Cloud	Precip	Observer	Time
Veg height	1	-0.39	-0.211	0.307	0.39	0.483	0.265
Wind	-0.39	1	0.322	-0.084	-0.305	-0.299	-0.153
Temp	-0.211	0.322	1	-0.177	-0.255	-0.13	-0.093
Cloud	0.307	-0.084	-0.177	1	0.178	0.261	0.27
Precip	0.39	-0.305	-0.255	0.178	1	0.346	0.259
Observer	0.483	-0.299	-0.13	0.261	0.346	1	0.377
Time	0.265	-0.153	-0.093	0.27	0.259	0.377	1

Guidance for future Colorado Parks and Wildlife monitoring efforts

Given that the burrowing owl is considered a state-threatened species in Colorado at the time of this thesis, we recommend future burrowing owl monitoring efforts in Colorado to track population changes through time and understand what factors drive these changes. This section serves as our general guidance for these future efforts conducted by Colorado Parks and Wildlife and/or other management agencies. Future burrowing owl surveys should occur at more frequent time intervals than the ~17 year time period between this population assessment and the last assessment in 2005. A realistic time interval is 5 years because it exceeds the 2 - 3 year time lag between when a prairie dog colony goes locally extinct and cessation of burrowing owl breeding on that colony. In addition, this interval coincides with the frequency of the Colorado Natural Heritage Program's effort to map prairie dog colonies in eastern Colorado, from which we created our sampling frame. Burrowing owl surveys for this study were conducted 3- 4 years after the most recent black-tailed prairie dog colony mapping effort in 2019; therefore, the rate of colonies that were inactive for a period long enough for nesting conditions to deteriorate and cessation of burrowing owl breeding was likely higher than if this study had been conducted closer to the mapping year. Surveying more frequently would also identify finer scale population changes because major habitat issues are likely to affect burrowing owl density and productivity sooner than occupancy.

If future efforts are conducted at the scale of this study, we recommend revisiting a subset of the survey plots from this study to decrease the amount of time and resources needed to contact private landowners to secure permission to survey on private property. In addition, the comparison from this population assessment to the previous one in 2005 provided insight into how burrowing populations have changed. Therefore, future efforts should aim to revisit our survey plots to continue to track burrowing owl populations through time. The subset of Tipton et al's (2008, 2009) survey plots accounted for 18% of our total survey plots in this study. Future studies should aim for a higher proportion of revisited sites to increase the precision and power of a dynamic occupancy analysis.

In addition, we did not have the time and resources to assess the presence of false negative prairie dog colonies on the mapping layer; therefore this is a known source of bias in our study. Future studies could remedy this issue by using black-tailed prairie dog habitat suitability maps to identify potential prairie dog habitat and create the sampling frame from this instead of the map potential prairie dog colonies that we used. Overall, the scale, frequency, and duration of future monitoring efforts will be determined by funding and resources.