



Research Article

Mountain Plover Nest Survival in Relation to Prairie Dog and Fire Dynamics in Shortgrass Steppe

DAVID J. AUGUSTINE,¹ *Rangeland Resources Research Unit, USDA—Agricultural Research Service, 1701 Centre Avenue, Fort Collins, CO 80526, USA*

SUSAN K. SKAGEN, *Fort Collins Science Center, US Geological Survey, 2150 Centre Ave, Fort Collins, CO 80526, USA*

ABSTRACT Disturbed xeric grasslands with short, sparse vegetation provide breeding habitat for mountain plovers (*Charadrius montanus*) across the western Great Plains. Maintaining local disturbance regimes through prairie dog conservation and prescribed fire may contribute to the sustainability of recently declining mountain plover populations, but these management approaches can be controversial. We estimated habitat-specific mountain plover densities and nest survival rates on black-tailed prairie dog (*Cynomys ludovicianus*) colonies and burns in the shortgrass steppe of northeastern Colorado. Mountain plover densities were similar on prairie dog colonies (5.9 birds/km²; 95% CI = 4.7–7.4) and sites burned during the preceding dormant season (6.7 birds/km²; 95% CI = 4.6–9.6), whereas the 29-day nest survival rate was greater on prairie dog colonies (0.81 in 2011 and 0.39 in 2012) compared to the burned sites (0.64 in 2011 and 0.17 in 2012). Reduced nest survival in 2012 compared to 2011 was associated with higher maximum daily temperatures in 2012, consistent with a previous weather-based model of mountain plover nest survival in the southern Great Plains. Measurements of mountain plover density relative to time since disturbance showed that removal of prairie dog disturbance by sylvatic plague reduced mountain plover density by 70% relative to active prairie dog colonies after 1 year. Plover densities declined at a similar rate (by 78%) at burned sites between the first and second post-burn growing season. Results indicate that black-tailed prairie dog colonies are a particularly important nesting habitat for mountain plovers in the southern Great Plains. In addition, findings suggest that prescribed burning can be a valuable means to create nesting habitat in landscapes where other types of disturbances (such as prairie dog colonies) are limited in distribution and size. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS black-tailed prairie dogs, *Cynomys ludovicianus*, disturbance regimes, grassland birds, prescribed fire, rangeland management, spatial heterogeneity, vegetation structure.

Avian species that breed in the North American Great Plains evolved with dynamic disturbances associated with herbivores, fire, and drought that together shaped the avifaunal habitats, food, and predator communities (Samson et al. 2004, Fuhlendorf et al. 2006, Derner et al. 2009). Anthropogenic influences have altered these historical disturbance regimes and habitats and may be contributing to the gradual decline of many grassland bird populations (Brennan and Kuvleskey 2005, Askins et al. 2007). The development of effective management strategies to enhance habitat for grassland birds requires an understanding of how different disturbances influence the distribution, abundance, and vital rates of bird species, particularly those of conservation concern.

The mountain plover (*Charadrius montanus*) is a migratory bird that breeds in rangelands of the western Great Plains

and in montane rangelands immediately west of the Great Plains. Populations of the species have been declining since the 1960s, particularly in portions of the western Great Plains (Knopf and Wunder 2006, Augustine 2011). Although processes underlying this decline are not known, mountain plovers have been shown to select heavily disturbed rangelands with high exposure of bare soil distributed over a broad area as breeding habitat (Knopf and Wunder 2006, Augustine and Derner 2012, Gougen 2012). Factors suspected to reduce the quality of breeding habitat in rangelands of the Great Plains include the suppression of disturbances from fire and black-tailed prairie dogs (*Cynomys ludovicianus*). Although previous studies have suggested that management through prescribed fire and prairie dog conservation may contribute to mountain plover conservation in the western Great Plains (Dinsmore et al. 2005, 2010; Augustine and Derner 2012; Gougen 2012), these practices can be controversial (Vermeire et al. 2004, Miller et al. 2007). In particular, prescribed fire has costs and risks associated with implementation, and prairie dog conservation can have consequences for livestock production (Derner et al. 2006,

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¹E-mail: david.augustine@ars.usda.gov

Augustine and Springer 2013). As a result, measures of how specific habitats, such as prescribed burns and prairie dog colonies, influence mountain plover vital rates are needed.

In shortgrass steppe of northeastern Colorado, mountain plovers occur at similar densities on black-tailed prairie dog colonies and sites that were burned during the preceding dormant season, whereas mountain plovers only rarely occur in rangeland lacking these disturbances (Augustine 2011). More recent work found that burns and prairie dog presence significantly increased bare soil exposure and reduced vegetation height compared to surrounding rangeland lacking these disturbances, and did so to a similar degree on burns and prairie dog colonies (Augustine and Derner 2012). Furthermore, mountain plovers selected nest sites with a fine-scale mosaic of prostrate (<4 cm tall) vegetation with >35% bare soil in a 100-m radius area surrounding the nest, which was similar to measurements surrounding random locations on sites burned during the preceding dormant season (referred to hereafter as recently burned sites) and active prairie dog colonies (Augustine and Derner 2012). However, the value of burns and prairie dog colonies may vary over time as vegetation conditions respond to time since disturbance. Prairie dog populations are periodically affected by epizootic outbreaks of sylvatic plague, caused by the introduced bacterium *Yersinia pestis*. Plague can result in >95% mortality of prairie dogs within a colony (Cully and Williams 2001), allowing vegetation conditions to revert towards non-colonized rangeland conditions over a period of several years (Hartley et al. 2009). Similar mortality can be achieved where prairie dogs are poisoned to reduce conflicts with livestock. Burns typically reduce vegetation cover and height during the first post-burn growing season, as plant productivity and height in burned areas recovers rapidly (Augustine and Milchunas 2009, Scheintaub et al. 2009). Knowledge of how long mountain plovers continue to use these sites after a burn or prairie dog removal occurs is needed to guide management efforts and assessments of habitat availability.

In addition, little is known about mountain plover breeding success on prairie dog colonies versus burns. Mountain plover brood rearing success can be nearly twice as great for broods raised on prairie dog colonies compared to those on rangeland lacking prairie dogs (Dreitz 2009), but studies have not examined how nesting success on prairie dog colonies compares to other habitats. Two long-term studies have provided estimates of mountain plover nesting success averaged across broad areas of Montana (Dinsmore et al. 2002) and Colorado (Dreitz and Knopf 2007, Dreitz et al., 2012). Dinsmore et al. (2002) and Dreitz et al. (2012) showed that nesting success is significantly influenced by precipitation and temperature patterns and provided models that could be used to predict nesting success as a function of daily weather parameters. However, the work by Dinsmore et al. (2002) in Montana all occurred on prairie dog colonies (Dinsmore et al. 2002), so nesting success was not compared with other habitats. In Colorado, Dreitz and Knopf (2007) documented similar nesting success on agricultural crop fields compared to rangeland habitats but did not report

variation in nesting success within the rangeland habitat, which included nests both on and off prairie dog colonies. Mean nest survival rate over a 29-day incubation period on prairie dog colonies in Montana (0.41) was greater than in rangeland habitats in Colorado (0.27), but many other factors differed between the 2 regions. Very little is known about mountain plover reproduction at burned sites; Svingen and Giesen (1999) reported an apparent nest survival rate of 0.49 on 1 burned site in southeastern Colorado but did not compare this to survival rates in other habitats.

We previously reported habitat-specific mountain plover densities in northeastern Colorado based on surveys conducted during 2008 and 2009 (Augustine 2011), and examined variation in vegetation attributes at mountain plover nest sites within burns and prairie dog colonies (Augustine and Derner 2012). We present habitat-specific mountain plover densities based on longer-term surveys conducted during 2008–2012, and compare nest survival rates during 2011 and 2012 at recent burns versus black-tailed prairie dog colonies.

STUDY AREA

The study encompassed approximately 60,900 ha of public lands in Weld County, Colorado, consisting of the Central Plains Experimental Range, all cattle allotments on the western unit of the Pawnee National Grassland, and 6 cattle allotments on the eastern unit of Pawnee Topography was flat to gently undulating, with slopes typically 0–3%. The climate was semiarid with cold, dry winters. More than 70% of precipitation fell as rain between April and September (Lauenroth and Milchunas 1992) with precipitation during April–May having the strongest influence on plant productivity and height (Milchunas et al. 1994). Long-term mean annual precipitation (1981–2012) measured at 3 gauges within the study area was 351 mm. Annual precipitation during 2008–2012 was 317, 379, 354, 349, and 217 mm, respectively. Two warm-season, perennial grasses, blue grama (*Bouteloua gracilis*) and buffalograss (*B. dactyloides*) dominated the vegetation; prickly pear cactus (*Opuntia polyacantha*) was also abundant, and scarlet globemallow (*Sphaeralcea coccinia*) was the dominant forb (Lauenroth and Burke 2008).

Although fire and grazing by black-tailed prairie dogs were widespread disturbances in shortgrass steppe prior to European settlement (Wright and Bailey 1982, Knowles et al. 2002), both were suppressed in the southern Great Plains during the 20th century. Quantitative estimates of historical fire return intervals in the shortgrass steppe are not available because of the lack of trees to record fire scars. Over the past 15 years, the area affected by fires and prairie dogs has increased within the study area (Augustine 2011). Prescribed and wildfires in the study area primarily occur when the vegetation is dormant (typically during Oct–Apr). Such fires have not been found to alter herbaceous plant species composition or productivity but can reduce the abundance of prickly pear cactus (Augustine and Milchunas 2009, Scheintaub et al. 2009). Prairie dogs alter the vegetation by reducing cover of the dominant C₄ grasses,

increasing bare soil exposure, and increasing the relative abundance of forbs, although perennial graminoids continue to be the most abundant plant functional group on prairie dog colonies (Stapp 2007, Hartley et al. 2009).

METHODS

Mountain Plover Density

During 2008–2012, we conducted point counts annually to estimate mountain plover densities on burns and black-tailed prairie dog colonies. Augustine (2011) reported survey methods and results from 2008 to 2009 when the objective was to compare mountain plover densities on prairie dog colonies and burns to rangeland lacking these disturbances. During 2010–2012, surveys focused exclusively on sites affected by prairie dogs or burning, with objectives to 1) compare mountain plover densities on recent burns versus active black-tailed prairie dogs over the 5-year period, and 2) evaluate the degree to which plover density declines on these sites as a function of years since disturbance (e.g., years since burning or years after prairie dogs are extirpated from a site by epizootic plague).

We surveyed all known burns in the study area each year. These included prescribed burns conducted in late winter (Mar 2008, 2009, and 2012) and fall (Oct or Nov 2007, 2008, 2009, and 2010), and wildfires that occurred during the fall or winter of 2009–2010, 2010–2011, and 2011–2012. Previous studies showed that vegetation structure (bare soil exposure and vegetation cover and height) was similar on fall and late-winter burns (Augustine and Derner 2012). Burns varied in size from 16 ha to 332 ha. At each burn, we conducted counts at a grid of points spaced at 250 m; the number of points per burn varied with burn shape and size, from 2 up to a maximum of 10 per burn. We surveyed 10, 7, 6, 8, and 4 recent burns (76, 46, 39, 40, and 22 points) during 2008, 2009, 2010, 2011, and 2012, respectively. During 2010–2012, we also resurveyed a randomly selected subset of sites that had been burned 2 and 3 years prior to the survey (12, 24, and 26 points, respectively) to evaluate whether mountain plovers continue to use these sites beyond the first post-burn growing season.

For black-tailed prairie dog colonies, our sampling design addressed spatiotemporal variability in the size and location of active colonies caused by epizootic plague outbreaks (Stapp et al. 2004, Hartley et al. 2009). In April of each year, we used a map of prairie dog colony boundaries created by Pawnee National Grassland staff during the previous year to determine point count locations on colonies. We overlaid a grid of points with 250-m spacing over each active colony and selected those points where >50% of the area within a 125-m radius of the point was within the boundary of an active colony, which resulted in 1 up to a maximum of 10 points per colony. Beginning in 2009, we continued to sample points from the prior year's survey that originally occurred on an active black-tailed prairie dog colony, but where prairie dogs had been extirpated by plague. Plague affected some portion of the study area every year, so the number of plague-affected colony sites that we surveyed

increased each year. Over the 5-year study period, we surveyed 53 different colonies, with 55, 108, 135, 155, and 169 points surveyed on active colony sites and 29, 51, 77, 103, and 119 points surveyed on plague-affected colony sites during 2008, 2009, 2010, 2011, and 2012, respectively.

Point counts followed the method described by Augustine (2011). Briefly, the field team used radial distance point count surveys (Buckland et al. 2001) to sample mountain plovers during 21 April–10 May each year. Most mountain plovers arrive during March or early April and establish territories during April (Graul 1975). We conducted surveys between sunrise and 1030 hours MDT during standardized weather conditions (no precipitation, 0–24 km/hr wind speed). We used a Global Positioning System (GPS) with pre-programmed point locations to navigate to all points. The observer drove to each point using an all-terrain or 4-wheel drive vehicle and then exited the vehicle for the count. Vehicles are recommended for use in mountain plover surveys because plover flushing distances may be within 3 m for vehicles, but 50–100 m for humans approaching on foot (U.S. Fish and Wildlife Service 2002). If a bird was flushed as the observer approached the point, we estimated the distance from the survey point to the initial location where the bird was first detected. At each survey point, the observer searched for 5 minutes using 8 × 42 binoculars and used a laser rangefinder to measure the exact distance from the point to any plover(s) detected.

We used program DISTANCE (Thomas et al. 2006) to model the probability of detecting a plover as a function of the distance from a given survey point (referred to as the detection function) and to derive habitat-specific density estimates and associated confidence intervals based on the number of plover detections, number of survey sites, and number of survey points per site in each habitat in combination with the derived detection function. We considered 6 robust models for the detection function as suggested by Buckland et al. (2001): 1) uniform key with cosine expansion, 2) uniform key with simple polynomial expansion, 3) half-normal key with cosine expansion, 4) half-normal key with hermite polynomial expansion, 5) hazard-rate key with cosine expansion, and 6) hazard-rate key with simply polynomial expansion. We also fitted models that included year and observer as covariates for the detection function (Marques and Buckland 2004). Because of the low number of detections on 2- and 3-year old burns, we estimated the detection function for burns based on detections in all burn age classes. Similarly, because of the low number of detections on plague-affected prairie dog colony sites, we estimated the detection function for colony sites based on detections from both active and plague-affected colony sites (see also Childers and Dinsmore 2008, Augustine 2011). We also examined models with year and observer as covariates, and selected the model that minimized Akaike's Information Criterion (AIC). For both burns and prairie dog colonies, the best model had $\Delta AIC > 2$, so we did not consider model averaging. Prior to fitting models, the dataset was truncated at a detection distance of 175 m which corresponded to the distance at which the detection

probability was approximately 0.1, as recommended by Buckland et al. (2001).

After estimating the detection function, we calculated mountain plover densities in each habitat category according to years since disturbance, timing of the burns (fall vs. late winter), and disturbance size class. We compared 95% confidence intervals to evaluate differences among density estimates. We classified each burn as occurring either in the fall (Oct–Dec) or late winter (Feb–Mar). We also classified each burn (varying from 11 ha to 500 ha) and prairie dog colony (varying from 4 ha to 211 ha) into 1 of 3 size classes consisting of small (≤ 16 ha), medium (17–82 ha), and large (> 82 ha) to examine whether mountain plover density varied with burn or colony size. We selected these size classes because our sample of prairie dog colonies was distributed relatively evenly across these size classes.

Mountain Plover Nest Survival

During May of 2011 and 2012, we returned to all recent burns and active prairie dog colonies where we detected mountain plovers during the point counts and conducted nest surveys. To find nests, we followed the method of Dinsmore et al. (2002); we traversed the site on an all-terrain vehicle until we located a mountain plover. We then observed the plover until we located the nest site or the bird displayed behaviors indicating that it did not have a nest. We recorded the nest location with a GPS unit with sub-meter accuracy (Trimble GeoXT; Trimble Navigation Limited, Sunnyvale, CA) and placed dried cattle dung at locations 5 m north and south of the nest to aid in relocation. We then revisited nests every 3–7 days until the eggs hatched, were predated, or the nest was determined to have been abandoned. We defined successful nests as those where > 1 egg hatched as either determined by direct observation of chicks in the nest or the presence of small eggshell fragments in the material lining the nest. As with many precocial, ground-nesting bird species, the first small eggshell fragments made by hatching mountain plover chicks remain in the nest while the adults remove the larger fragments (Knopf and Wunder 2006, Dreitz et al. 2012). If we did not observe eggshell fragments in the field, we collected the nest lining material and carefully re-checked it in the laboratory. We defined failed nests as those with no eggshell fragments and those that the adult abandoned. During this study, we did not measure specific attributes of the vegetation at nest sites, but previous work showed that within this study area, vegetation surrounding mountain plover nest sites was similar to that surrounding randomly located sites on burns and active prairie dog colonies in terms of amount and spatial heterogeneity of bare soil exposure and vegetation height (Augustine and Derner 2012).

We estimated daily nest survival (DNS), defined as the probability that a nest will survive for a 1-day period, and 95% confidence intervals using the nest survival model in Program MARK, version 6.2 (White and Burnham 1999). We evaluated DNS models using three covariates: habitat (burn or prairie dog colony), year (2011 or 2012), and time in season (Julian date) in all combinations. We assumed an

incubation period of 29 days and calculated nest survival as DNS^{29} . We evaluated the relative importance of variables in the model by contrasting associated t -values (beta estimate divided by standard error; Bring 1994), specifically by expressing a ratio of the t -value of the variable of interest divided by the maximum t -value of all considered variables.

A long-term study of mountain plover nest survival in Colorado showed that weather patterns such as large precipitation events, extended periods of time without rain, and maximum daily temperatures can influence nest survival rates (Dreitz et al. 2012). We compared our nesting success rates to rates predicted by the Dreitz et al. (2012) model after accounting for the weather conditions that occurred during our study. To do this, we obtained daily precipitation and temperature data for 2011 and 2012 from a weather station located within the study area. For each day, we used measurements of maximum air temperature and whether < 1 mm of precipitation had occurred in the previous 10 days to predict DNS on logit and non-logit scales, and then extrapolated to a 29-day nest survival rate.

RESULTS

Mountain Plover Density

For prairie dog colony sites, a detection function based on the half-normal key with cosine expansion that included observer identity as a covariate was selected over a models with no covariate ($\Delta AIC = 13.1$) and year as a covariate ($\Delta AIC = 17.0$), and gave an effective sampling radius of 102.6 m. For burns, a detection based on the half-normal key with cosine expansion and observer identity as a covariate was selected over models with no covariate ($\Delta AIC = 4.55$) and year as a covariate ($\Delta AIC = 6.42$), and gave an effective sampling radius of 120.0 m.

During 2008–2011, mountain plover density was similar at recently burned sites and active black-tailed prairie dog colonies, whereas in 2012, density was greater at recent burns than at colonies (Fig. 1). Averaged over all 5 years, mountain plover density was similar at active prairie dog colonies (5.9 birds/km²; 95% CI = 4.7–7.4) and at recently burned sites (6.7 birds/km²; 95% CI = 4.6–9.6; Fig. 2). When prairie dogs were extirpated from a locality by epizootic plague, mountain plover density at the same site declined dramatically to 1.8 birds/km² (95% CI = 1.3–2.7) during the first post-plague growing season and 0.7 birds/km² (95% CI = 0.4–1.2) at sites where prairie dogs had been extirpated for 2 or more years. We did not detect mountain plovers at any of the 8 sites that were in their second post-burn growing season during 2009–2011, but detected plovers at 1 of 5 such sites in 2012. Averaged across all 4 years in which we surveyed burns of multiple ages, plover density on burn sites during the second post-burn growing season was 1.5 birds/km² (95% CI = 1.1–2.2). We did not observe plovers using burn sites during the third post-burn growing season (Fig. 2). During the first post-burn growing season, mountain plover density did not differ between sites burned in the fall (95% CI = 5.4–11.8 birds/km²) versus sites burned in late winter (95% CI = 4.2–8.8 birds/km²), and mountain plover density

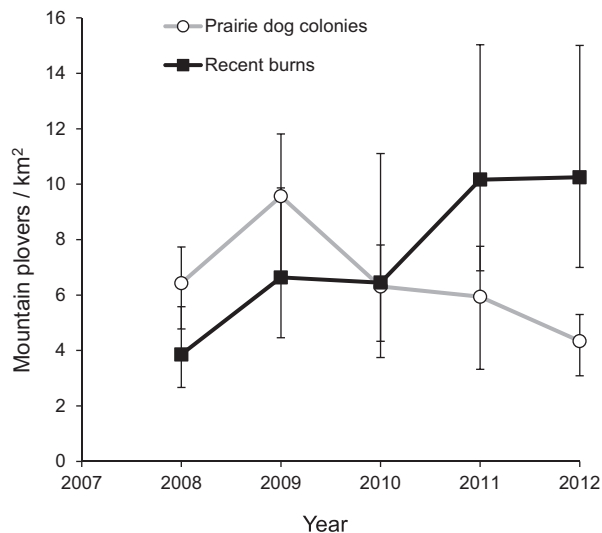


Figure 1. Annual density of mountain plovers on active black-tailed prairie dog colonies and recent burns (first post-burn growing season) estimated using distance sampling in shortgrass steppe of northeastern Colorado during 2008–2012. Error bars show 95% confidence intervals.

did not vary across burns of different sizes (small burns: 95% CI = 5.7–14.1 birds/km²; medium burns 95% CI = 5.5–14.7 birds/km²; large burns 95% CI = 4.4–9.2 birds/km²). In contrast to the lack of influence of burn size, mean mountain plover density was significantly greater on large prairie dog colonies (10.6 birds/km²; 95% CI = 7.9–14.4 birds/km²) compared to small colonies (3.8 birds/km²; 95% CI = 2.7–5.3 birds/km²) and medium colonies (3.2 birds/km²; 95% CI = 2.4–4.3 birds/km²).

Mountain Plover Nest Survival

We monitored the fate of 84 mountain plover nests (41 in 2011, 43 in 2012), of which 38 were located on recent burns

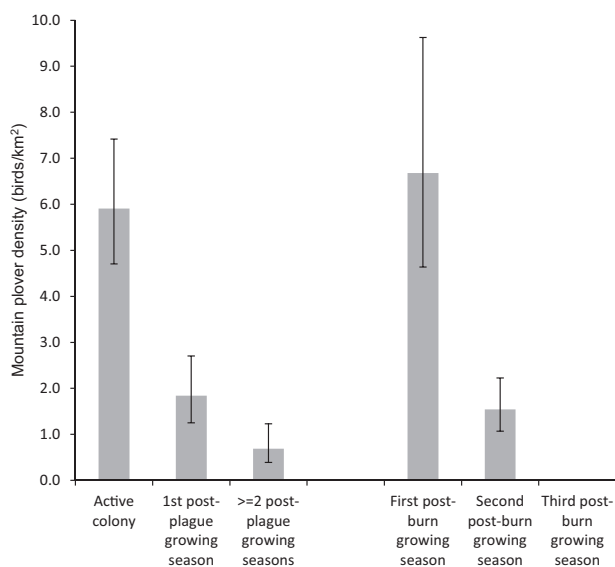


Figure 2. Mean densities of mountain plovers on black-tailed prairie dog colony sites and burned sites estimated using distance sampling in shortgrass steppe of northeastern Colorado during 2008–2012. Error bars show 95% confidence intervals.

and 46 were located on active prairie dog colonies. Across all samples, the daily probability of nest survival was 0.975 (± 0.004 SE, 0.965–0.982 95% CI). Daily nest survival was best predicted by a model that included habitat, year, and Julian date (Table 1); the 95% confidence limits for beta estimates of all 3 variables did not include 0 (Table 2). Based on the ratio of *t*-statistics, year ($t = 3.92$) had 1.6 times greater influence on DNS than Julian date ($t = 2.41$) and nearly twice the influence of habitat ($t = 1.98$; Table 2). When we converted daily survival rates to a non-logit scale and extrapolated to a 29-day nest survival rate, nest survival rates declined from 0.72 in 2011 to 0.28 in 2012, and on a habitat-specific basis, were 0.81 on prairie dog colonies compared to 0.64 on burns in 2011 and were 0.39 on prairie dog colonies compared to 0.17 on burns in 2012 (Table 3).

We also used the Dreitz et al. (2012) model to predict variation among years in nest survival rates based on daily weather conditions during the nesting season. For the 66-day period when we monitored nests in 2011, 5 days had < 1 mm of precipitation occurring during the prior 10 days, and mean daily maximum temperature was 18.7°C. For the 65-day period when we monitored nests in 2012, 30 days had < 1 mm of precipitation occurring during the prior 10 days, and mean daily maximum temperature was 24.6°C. The model predicted a 29-day nest survival rate of 0.47 in 2011 and 0.34 in 2012 (Table 3).

DISCUSSION

Disturbed xeric rangelands with short, sparse vegetation provide important breeding habitat for mountain plovers across the western Great Plains. Habitat conditions in these rangelands are spatially and temporally dynamic in response to local disturbance regimes. Mountain plovers select black-tailed prairie dog colonies for breeding habitat throughout the western Great Plains (Childers and Dinsmore 2008, Tipton et al. 2009, Gougen 2012, Augustine and Baker 2013). In the shortgrass steppe of Colorado, mountain plovers also select recent burns for breeding habitat (Svingen and Giesen 1999, Knopf and Wunder 2006) and occur at similar densities on burns and prairie dog colonies (Augustine 2011). Both types of habitat are transient as vegetation on burns reverts back to the height of unburned vegetation within 1–2 growing seasons, and vegetation on colonies reverts back to non-colony conditions within several years after a plague outbreak. Studies in northern portions of the mountain plover's range have documented reduced plover occupancy on prairie dog colony sites following plague (Augustine et al. 2008, Dinsmore and Smith 2010), but the magnitude of decline has not been quantified in the southern Great Plains.

We documented patterns of plover density as habitats transitioned from suitable to unsuitable after a disturbance event. Mountain plover densities declined by 70% relative to active prairie dog colonies during the first growing season after plague. Plover densities declined at a similar rate (by 78%) at burned sites between first post-burn growing season, when bare ground was most extensive, and the second post-burn growing season, when vegetation had typically

Table 1. Model selection results using corrected Akaike's Information Criterion (AIC_c) for nest survival models for mountain plover (*Charadrius montanus*) in northeastern Colorado in 2011 and 2012. The habitat variable refers to the effect of nests being on recent burns versus active black-tailed prairie dog colonies.

Model	AIC _c	ΔAIC _c	AIC _c weights	Parameters	Deviance
Habitat + year + Julian day	167.41	0.00	0.64	4	159.38
Year + Julian day	169.29	1.88	0.25	3	163.27
Habitat + year	170.94	3.52	0.11	3	164.92
Null	179.37	11.95	0.00	1	177.36
Habitat + Julian day	249.04	81.63	0.00	3	243.02

recovered. Plovers still were present at a very low density (0.7 birds/km²) on some plague-affected colonies 2–3 years after loss of prairie dogs, whereas we did not find plovers using burns beyond the second post-burn growing season. We also note that we detected plovers on at least 1 plague-affected colony site each year of the study, whereas we detected plovers on 2-year old burn sites only in 2012, a year of relatively low rainfall. This suggests that plover use of burned sites beyond the first post-burn growing season may occur when vegetation recovery on burns is limited by low rainfall. In contrast, vegetation conditions on prairie dog colonies are more spatially variable compared to burns (Augustine and Derner 2012) and may continue to include some patches with relatively high bare soil exposure for 2 or more years after prairie dog removal, regardless of weather conditions.

For prescribed fire implementation, key considerations are the timing and size of fires. The low fuel loads characteristic of semiarid rangelands such as the shortgrass steppe restrict the use of growing season fires (McDaniel et al. 1997), but appropriate conditions for prescribed burning frequently occur during late winter (late Feb or Mar; e.g., Augustine and Milchunas 2009, Scheintaub et al. 2009) or in the fall (Oct–Nov; Augustine and Derner 2014). We found that mountain plover density did not vary with burn size (range of 11–500-ha burns studied), and did not differ between sites burned in fall compared to late winter, suggesting that managers have a wide range of flexibility in selecting the timing and size of burns to enhance habitat for mountain plovers.

In contrast to results for burn sizes, we found that large prairie dog colonies (82–126 ha) supported approximately 3 times greater mountain plover densities than small and medium (4–55 ha) colonies. Gougen (2012) also found that mountain plovers selected the largest colonies in a prairie dog colony complex in New Mexico. Thus, even after a plague-affected site is recolonized by prairie dogs and the colony expands over a series of years, mountain plovers may not return to pre-plague densities until the colony reaches a

Table 2. Parameter estimates for the top model used to calculate the logit of daily nest survival probability of mountain plover (*Charadrius montanus*), where year = 0 in 2011 and 1 in 2012, and habitat = 0 for prairie dog colonies and 1 for recent burns.

Variable	Estimate	SE	95% CL
Year	−1.867	0.476	(−2.801, −0.933)
Habitat	−0.785	0.396	(−1.562, −0.009)
Julian day	−0.041	0.017	(−0.074, −0.009)
Intercept	6.269	0.781	(4.739, 7.799)

relatively large size. Such large colonies (i.e., >82 ha) are often rare in plague-affected regions and persist at that size for only a few years before plague affects the colony again (Hartley et al. 2009, Cully et al. 2010).

To examine our findings for nest survival rates in the context of previous studies, we used the model of Dreitz et al. (2012), which predicts mountain plover nest survival in eastern Colorado as a function of weather parameters and date. Given the daily precipitation and temperature conditions during our study, the Dreitz model predicted a 29-day survival rate of 0.47 in 2011 and 0.34 in 2012. Lower predicted nest survival in 2012 was associated with greater daily maximum temperatures in 2012 compared to 2011, even though the drier conditions during 2012 would have predicted the opposite result had temperatures been similar. Our finding that nest survival rates were indeed lower in 2012 compared to 2011 provides further support for the conclusion of Dreitz et al. (2012) that maximum daily temperature is a key factor influencing mountain plover reproduction in the southern Great Plains. High temperatures could affect nesting plovers by requiring them to spend more time shading the nest, which under high temperatures can pose heat problems for the adults that requires raising the dorsal feathers, panting, exposing the legs, and facing away from the sun (Graul 1975); such activity could potentially increase nest detection by predators.

Despite similar densities of plovers on prairie dog colonies and recent burns, the inclusion of a covariate for habitat in our nest survival model showed that nest survival rates were greater on prairie dog colonies compared to recent burns. We did not examine brood survival in these habitats, but Dreitz (2009) found enhanced brood survival on prairie dog colonies

Table 3. Estimates of 29-day nest survival rates based on nests monitored on prairie dog colonies and recent burns in northeastern Colorado during 2011–2012, compared with nest survival rates predicted by Dreitz et al. (2012) for mountain plovers nesting in eastern Colorado based on weather conditions that occurred during 2011–2012.

Daily nest survival	29-Day nest survival			
	Mean	Observed		Predicted
		Lower 95% CI	Upper 95% CI	
2011 prairie dog colonies	0.81	0.43	0.95	0.47
2011 recent burns	0.64	0.37	0.82	0.47
2012 prairie dog colonies	0.39	0.20	0.58	0.34
2012 recent burns	0.17	0.03	0.40	0.34
Prairie dog colonies	0.52	0.34	0.68	0.40
Recent burns	0.44	0.26	0.61	0.40
Both years and habitats	0.49	0.36	0.61	0.40

compared to other rangeland and cropland habitats in eastern Colorado. Our results in concert with Dreitz (2009) suggest prairie dog colonies are a particularly important breeding habitat for mountain plovers in the southern Great Plains. This premise is also consistent with the long-term studies of Dinsmore et al. (2002, 2003, 2005, 2010), which document a relatively stable mountain plover population breeding almost exclusively on a complex of prairie dog colonies in the northern Great Plains. Past models of mountain plover population dynamics have provided valuable insights concerning demographic factors affecting populations in different portions of the species range (Dinsmore 2003, Dinsmore et al. 2010) but have not incorporated habitat-specific vital rates. Future model refinements that incorporate variability in both weather and habitat availability could provide a means to examine how habitat management strategies may influence population dynamics. One notable difference between burns and prairie dog colonies is the fact that burns occur in different locations each year, whereas colonies can persist in the same approximate location for a series of years between plague outbreaks. Mountain plovers often return to the same breeding locality in successive years (Skrade and Dinsmore 2010), and familiarity with local site conditions (e.g., avoidance of sites with low prior reproductive performance) could be related to increased nest survival at prairie dog colonies. In addition, recent studies found that burrowing owls nesting at prairie dog colonies benefit from prairie dog alarm calls that indicate the presence of a predator near the site (Bryan and Wunder 2014); if mountain plovers can also recognize such cues, they could potentially benefit from increased predator detection.

Although nest survival was greater on prairie dog colonies compared to recent burns, nest survival on burns was not unusually low. In fact, our estimate of mean nest survival on recent burns (0.44; 95% CI = 0.26–0.61) was very similar to the point estimate predicted by the Dreitz model based on weather parameters (0.40; Table 3). Thus, our findings for nest survival rates at burned sites are not indicative of a sink habitat, and burns may represent an important source of breeding habitat for mountain plovers in years with favorable weather conditions and in landscapes where other disturbances (such as prairie dog colonies) are limited in distribution and size. Our study provides the first estimate of mountain plover nest survival on burns using methods that correct for the bias associated with traditional Mayfield approaches (Dinsmore et al. 2002). To adequately measure the value of recent burns as mountain plover breeding habitat, future work is needed to address how burns influence nest survival under varying weather conditions and regions of the Great Plains, and to measure brood-rearing success in recent burns.

MANAGEMENT IMPLICATIONS

Our findings indicate that black-tailed prairie dog conservation and prescribed burning are important management strategies to create nesting habitat for mountain plovers. Based on our nest survival rates combined with studies of brood survival by Dreitz (2009), prairie dog colonies appear

to be a particularly valuable breeding habitat for mountain plover populations in the southern Great Plains. A key challenge for rangeland managers is how to sustain prairie dog colonies in a spatial and temporal distribution that provides consistent breeding habitat for associated species such as mountain plovers, while still minimizing costs to livestock production (Derner et al. 2006, Augustine and Springer 2013). Given these costs and the fact that prairie dog colonies change locations and size dynamically over time in response to plague outbreaks (Stapp et al. 2004, Cully et al. 2010, Savage et al. 2011), management approaches that combine both prairie dog conservation and the strategic use of prescribed burning could contribute to achieving nest survival rates that advance mountain plover conservation in the region. In addition, management to mitigate or prevent plague outbreaks on existing large colonies may be particularly valuable for mountain plover habitat conservation.

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