



RESEARCH ARTICLE

Mountain Plover habitat selection and nest survival in relation to weather variability and spatial attributes of black-tailed prairie dog disturbance

Courtney J. Duchardt,^{1,*} Jeffrey L. Beck,^{1,*} and David J. Augustine^{2,*}

¹ Department of Ecosystem Science and Management and Program in Ecology, University of Wyoming, Laramie, Wyoming, USA

² USDA-ARS Rangeland Resources and Systems Research Unit, Fort Collins, Colorado, USA

*Corresponding author: cduchard@uwyo.edu

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ABSTRACT

Habitat loss and altered disturbance regimes have led to declines in many species of grassland and sagebrush birds, including the imperiled Mountain Plover (*Charadrius montanus*). In certain parts of their range Mountain Plovers rely almost exclusively on black-tailed prairie dog (*Cynomys ludovicianus*) colonies as nesting habitat. Previous studies have examined Mountain Plover nest and brood survival on prairie dog colonies, but little is known about how colony size and shape influence these vital rates or patterns of habitat selection. We examined how (1) adult habitat utilization, (2) nest-site selection, and (3) nest success responded to a suite of local- and site-level variables on large prairie dog colony complexes in northeastern Wyoming. Abundance of adult Mountain Plovers was highest on points within older, “medium”-sized (100–500 ha) colonies with high cover of annual forbs and bare ground (5.8 birds km⁻²), but lower on extremely large (>2,000 ha) colonies (2.1 birds km⁻²). Nest sites were characterized by high proportions of annual forbs and bare ground and low cactus cover and vegetation height. Nest survival was higher for older nests, and nests with lower cactus cover, and decreased with increasing temperatures. Uncertainty was high for models of daily nest survival, potentially because of 2 competing sources of nest failure: nest depredation and nest abandonment or inviability of eggs. Drivers of these 2 sources of nest failure differed, with inclement weather and higher temperatures associated with nest abandonment or egg inviability. We highlight how prairie dogs alter vegetation structure and bare ground heterogeneously across the landscape, and how this in turn influences bird abundance and nest distribution at different temporal and spatial scales. Furthermore, our work reveals how partitioning the causes of nest failure during nest survival analyses enhances understanding of survival rate covariates.

Keywords: black-tailed prairie dog, breeding ecology, *Charadrius*, conservation, disturbance, grassland, habitat selection, nest survival

Selección de hábitat y supervivencia del nido de *Charadrius montanus* en relación a la variabilidad del clima y los atributos espaciales de los disturbios de *Cynomys ludovicianus*

RESUMEN

La pérdida de hábitat y la alteración de los regímenes de disturbio han llevado a la disminución de muchas especies de aves de pastizal y de artemisa, incluyendo la especie en peligro *Charadrius montanus*. En algunas partes de su rango, *C. montanus* utiliza casi exclusivamente colonias de *Cynomys ludovicianus* (perro de las praderas de cola negra) como hábitat de anidación. Estudios previos han examinado la supervivencia del nido y de las crías de *C. montanus* en las colonias de *C. ludovicianus*, pero poco se sabe sobre cómo el tamaño y la forma de la colonia influyen estas tasas vitales o los patrones de selección de hábitat. Examinamos cómo (1) la utilización del hábitat del adulto, (2) la selección del sitio de anidación, y (3) el éxito de anidación respondieron a un conjunto de variables a nivel local y de sitio en grandes complejos de colonias de *C. ludovicianus* en el noreste de Wyoming. La abundancia de individuos adultos de *C. montanus* fue máxima en puntos dentro de colonias más viejas y de tamaño “medio” (100–500 ha) con alta cobertura de forbas anuales y suelo desnudo (5.8 aves km⁻²), pero menor (2.1 aves km⁻²) en colonias extremadamente grandes (>2,000 ha). Los sitios de anidación se caracterizaron por altas proporciones de forbas anuales y suelo desnudo, y baja cobertura de cactus y altura de la vegetación. La supervivencia del nido fue más alta para los nidos más viejos y los nidos con cobertura más baja de cactus, y disminuyó con aumentos de la temperatura. Los modelos de supervivencia diaria del nido tuvieron una alta incertidumbre, potencialmente debido a dos fuentes opuestas de fracaso del nido: la depredación del nido y el abandono del nido o la inviabilidad de los huevos. Los factores responsables de estas dos fuentes de fracaso del nido fueron diferentes, estando el mal tiempo y las temperaturas más altas asociadas con el abandono del nido o la inviabilidad de los huevos. Resaltamos cómo *C. ludovicianus* altera la estructura de la vegetación y el suelo desnudo de modo heterogéneo a través del paisaje, y cómo esto a su vez influye la abundancia de las aves y la distribución de los nidos a diferentes escalas temporales y espaciales. Más aún, nuestro trabajo revela cómo la división de las causas de

fracaso del nido durante los análisis de supervivencia del nido aumenta el entendimiento de las covariables que afectan las tasas de supervivencia.

Palabras clave: *Charadrius*, conservación, *Cynomys ludovicianus*, disturbio, ecología reproductiva, pastizal, selección de hábitat, supervivencia del nido

INTRODUCTION

Among the numerous conservation challenges facing North American wildlife are precipitous declines in grassland and sagebrush bird populations (Brennan and Kuvlesky 2005, Sauer et al. 2017, Rosenberg et al. 2019). These declines are driven in large part by habitat loss via conversion to row crop agriculture (Wright and Wimberly 2013), energy extraction (Allred et al. 2015), and exurban development (Sala et al. 2017), and have led to the loss of 70–99% of grassland habitat in many regions of the United States (Samson and Knopf 1994). On grasslands that remain, many species are negatively affected by the absence of disturbance, since many of these species evolved with natural disturbance regimes (Brawn et al. 2001, Fuhlendorf and Engle 2001). Fire, ungulate grazing, and burrowing mammals play integral roles as ecosystem engineers in grasslands (Davidson et al. 2012, Fuhlendorf et al. 2017), but throughout North America these disturbance regimes have been severely altered, potentially leading to reduced biodiversity (Fuhlendorf et al. 2006). Conversely, where historical disturbance regimes have been restored, avian biodiversity has increased (Coppedge et al. 2008, Augustine and Derner 2015, Duchardt et al. 2016).

The Mountain Plover (*Charadrius montanus*) is a declining disturbance-associated bird currently listed as near-threatened on the IUCN Redlist (Knopf 1996, Birdlife International 2018). The species is sexually monomorphic, socially monogamous, and employs a simultaneous multiple-clutch system (e.g., Beck et al. 2005), where females lay 2 separate 3-egg clutches, the first nest typically tended by the male and the second by the female (Knopf and Wunder 2006). The species breeds mainly within the Intermountain West and western Great Plains, overwintering in the southern United States and Mexico with localized breeding areas within the winter range. Mountain Plovers are patchily distributed throughout their relatively small breeding range (Figure 1), and typically breed on relatively flat landscapes (Graul 1975) with extensive bare ground exposure (often >30%; Knopf and Miller 1994), as well as short (Graul 1975, Olson and Edge 1985, Augustine and Derner 2012) and sparse (Knopf and Wunder 2006) vegetation. Individual studies have also noted potential associations with shrubs (Schneider et al. 2006) or forb cover (Olson and Edge 1985).

These conditions can occur on high-elevation sites (e.g., South Park, Colorado; Wunder et al. 2003) or in desert shrublands (Wyoming; Plumb et al. 2005); however, in

grasslands throughout the western Great Plains of North America, Mountain Plovers often breed in highly disturbed areas including cropfields (Shackford et al. 1994, Woolley 2016), recently burned sites (Augustine and Derner 2012), and heavily grazed areas (Plumb et al. 2005, Uresk 2017). Throughout much of their range, Mountain Plovers are especially dependent on black-tailed prairie dogs (*Cynomys ludovicianus*) to engineer suitable habitat through soil disturbance and vegetation clipping (Dinsmore et al. 2005, Augustine and Derner 2012, Duchardt et al. 2018). Although all species of prairie dog consume vegetation and cause some level of soil disturbance by burrowing, black-tailed prairie dogs actively clip vegetation to maintain visibility for predators and live at extremely high densities. These activities lead to substantial soil and vegetation disturbance (Hoogland 1995); this combination of traits make black-tailed prairie dog colonies ideal habitat for Mountain Plovers.

The association of Mountain Plovers with prairie dog colonies across much of their range (Figure 1) may be another factor contributing to declines in Mountain Plover populations. Widely recognized as both an ecosystem engineer and keystone species (Kotliar et al. 1999, Van Nimwegen et al. 2008), black-tailed prairie dogs can also compete with cattle for forage (Derner et al. 2006, Augustine and Springer 2013) and as such are often subject to lethal control via poisoning and shooting on lands managed for livestock (Miller et al. 2007). In addition to lethal control, outbreaks of sylvatic plague (*Yersinia pestis*) regularly lead to drastic local population reductions (>95% mortality in black-tailed prairie dogs; Cully and Williams 2001). These factors have severely reduced black-tailed prairie dog populations (occupying <3% of their historical range; Mulhern and Knowles 1997), pushing colony associates like the black-footed ferret (*Mustela nigripes*) to the brink of extinction (Dobson and Lyles 2000). Given the observed impacts on other colony associates, Mountain Plover populations that rely on prairie dogs for breeding habitat may be especially vulnerable.

Many aspects of Mountain Plover breeding biology on prairie dog colonies have been studied (Dinsmore et al. 2005, Dreitz and Knopf 2007, Augustine et al. 2008, Goguen 2012, Augustine and Skagen 2014), but these studies have occurred in landscapes with a limited range of colony sizes (5–480 ha), and with smaller total area of colony complexes (a “complex” is a cluster of colonies within the same landscape; Hoogland 2006). Within certain landscapes, Mountain Plovers occupy colonies >4,000 ha in

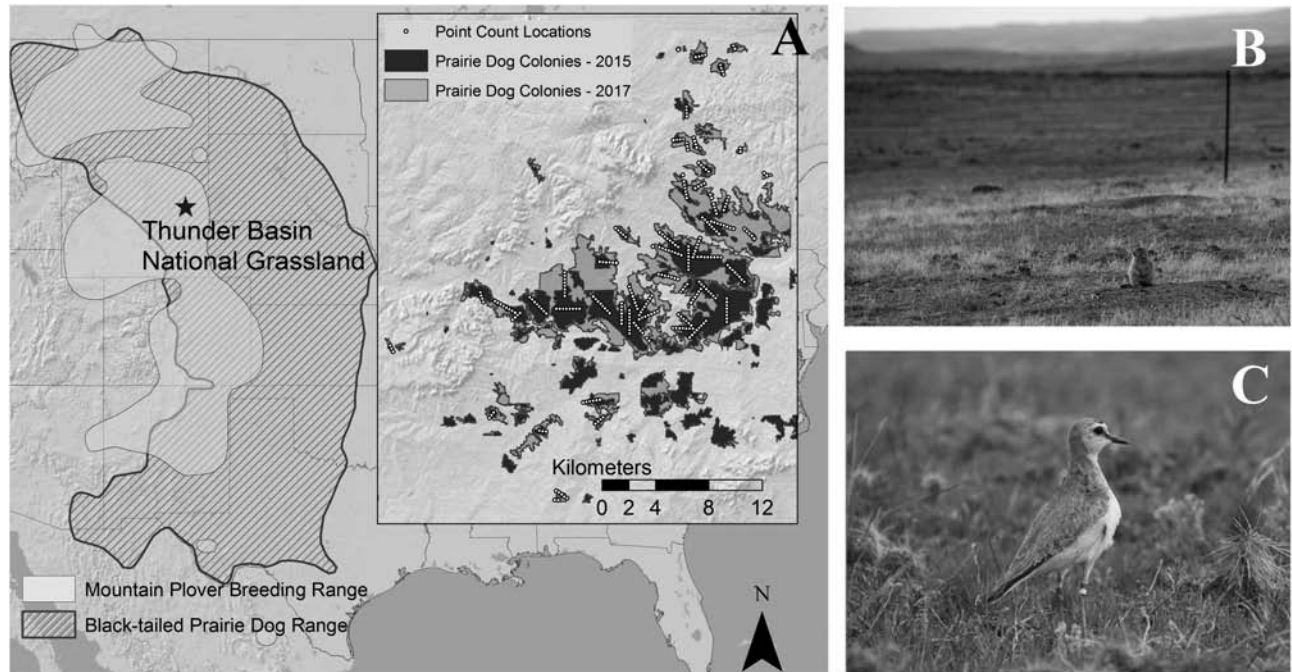


FIGURE 1. Location of the Thunder Basin National Grassland in eastern Wyoming in relation to breeding range of Mountain Plover and annual range of black-tailed prairie dog, with inset representing study area (A). Black-tailed prairie dog colony (B) and Mountain Plover (C) in Thunder Basin National Grassland.

size in colony complexes exceeding 15,000 ha (Duchardt et al. 2019), but little is known about Mountain Plover breeding ecology on large colonies. To address this gap in knowledge, we studied Mountain Plover habitat selection and nest survival in the Thunder Basin National Grassland of northeastern Wyoming, USA (Figure 1), where we focused on 4 questions: (1) How does variation in prairie dog colony size and within-colony variation in vegetation structure influence adult abundance (density) during the nesting season? (2) How does fine-scale variation in habitat structure influence Mountain Plover nest placement? (3) What are the effects of habitat structure, weather, and predation on Mountain Plover nest survival? (4) Can we separate drivers of different sources of nest loss for Mountain Plovers?

METHODS

Study Area

We conducted our field sampling from 2015 to 2017 on and around prairie dog colonies on public lands within the Thunder Basin National Grassland, located in Campbell, Converse, and Weston counties, Wyoming (Figure 1). The study area was composed of rangeland with low to moderate stocking rates (0.1–0.4 animal unit months [AUM] ha⁻¹; Connell et al. 2019) of both domestic sheep and cattle. Elevation within our study area ranged between 1,200 and 1,500 m. Mean

annual precipitation averaged 25–35 cm per year, with most precipitation occurring in spring and summer. Shrublands in this system were dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), greasewood (*Sarcobatus vermiculatus*), broom snakeweed (*Gutierrezia sarothrae*), and other sagebrush species including silver sagebrush (*A. cana*). Common perennial grass species included blue grama (*Bouteloua gracilis*), threadleaf sedge (*Carex filifolia*), needle-and-thread (*Hesperostipa comata*), and cheatgrass (*Bromus tectorum*), an invasive annual. Prairie dog colonies were characterized by a high proportion of bare ground and dominated by western wheatgrass (*Pascopyrum smithii*), plains pricklypear (*Opuntia polyacantha*), and various forb species. Dominant land uses in our study area included livestock grazing, energy extraction, and recreation.

Perimeters of black-tailed prairie dog colonies in the study area were mapped by the U.S. Forest Service and researchers from 2014 to 2016 (Cully et al. 2010, Parker et al. 2019). Prairie dog colonies ranged in size from 6 to 1,700 ha in 2015. Colony expansion in 2016 and 2017 led to colony sizes exceeding 4,000 ha; the largest colonies in Thunder Basin were nearly an order of magnitude larger than where Mountain Plovers have been studied in Montana (Olson and Edge 1985, Dinsmore et al. 2005), Colorado (Augustine and Skagen 2014), and New Mexico (Goguen 2012).

Adult Mountain Plover Density

Data collection. We surveyed point transects located entirely within colonies ($n = 10$; 8 points per transect) and across colony edges into adjacent undisturbed habitat ($n = 41$; 5–8 points per transect) during 2015–2017 as a part of a larger study assessing grassland and sagebrush bird responses to prairie dogs (Figure 1). All transects contained 4–8 points spaced 250 m apart, and no point in any transect was closer than 250 m to another point. Although the complete dataset included some points outside of colonies, previous analyses indicated that plovers are almost entirely restricted to colony habitat in this system (Duchardt et al. 2018); therefore, we only used points located within colonies for the following analyses. However, this study design allowed us to capture more points each year due to colony growth over the study period, because many points that were located outside colonies in 2015 were within colonies by 2017. As such, this dataset includes 196, 236, and 280 points surveyed each year, respectively.

We conducted 2 rounds of avian surveys on these transects between mid-May and late June each year from 2015 to 2017, surveying between sunrise and 1000 hours on days with low wind and no rain (Pavlacky et al. 2017). We conducted discrete 6-min point counts at each point within transects, recording all birds detected within the survey period at an unlimited distance. By traveling to many points via off-road vehicle we ensured more effective detection of Mountain Plovers, which display more cryptic behavior in response to observers on foot (Dinsmore 2003).

We collected habitat data each year along 30-m transects radiating from each point. We measured visual obstruction, a metric incorporating both vegetation height and density, using a Robel pole (Robel et al. 1970) placed at 5-m increments along transects. We also measured vegetation cover and bare soil exposure using the line-point intercept method at 1-m increments (Herrick et al. 2009). We recorded basal and canopy contacts for perennial C_3 and C_4 grasses, annual grasses, and forbs. Ground cover categories included bare ground and litter, in addition to basal cover of plant functional groups. Shrub and cactus canopy cover were only measured in 2015 using the line-intercept method (measuring gaps in shrub and cactus canopy along the transect; Canfield 1941, Herrick et al. 2009) because we reasoned that these cover measurements would remain relatively static over the course of our study. Because both topography and soil type may also influence habitat use, we used a digital elevation model to generate a topographic roughness index within a 100-m buffer around each point (Gesch 2007, Porensky et al. 2018) and the SSURGO database (NRCS 2017) to characterize average soil texture (percent clay, silt, and sand) from 0 to 30 cm depth at each point.

Modeling framework. We began our overall modeling process by identifying variables likely to be important to Mountain Plover habitat selection (Table 1). These included structural variables often tested in the literature (e.g., bare ground and visual obstruction; Knopf and Miller 1994), topography and soil type, which have been shown previously to be important for shortgrass bird habitat use in this system (Duchardt et al. 2018), as well as a number of variables related to prairie dog disturbance. These included aspects of disturbance itself (colony size, duration of disturbance at a given point [i.e. colony age], and distance to colony edge), as well as proportions of cover in different vegetation classes (C_3 perennial grasses, C_4 perennial grasses, annual forbs). We included the latter because while it is widely recognized that black-tailed prairie dogs alter vegetation composition (Winter et al. 2002, Johnson-Nistler and Sowell 2004), it is unclear whether these effects impact habitat quality for Mountain Plover.

To adjust for detectability, we modeled Mountain Plover abundance (truncated to within 200 m of a point) using program DISTANCE 6.0, comparing models including hazard rate and half-normal key functions along with covariates including sky cover, wind, temperature, visual obstruction, and use of ATV; the best model explaining detectability included an effect of wind and use of off-road vehicle (see Supplementary Table A2 and Duchardt et al. 2019 for more detail concerning distance sampling methods).

Counts of Mountain Plovers were zero-inflated, so we employed a zero-inflation Poisson model in the package *glmmTMB* in R (Brooks et al. 2017) to model variation in abundance. Each model included variables specified under the traditional conditional model (“conditional model”) as well as variables expected to predict structural zeroes in the dataset (“zero-inflated model”). Because program DISTANCE output is in the form of density estimates, we modeled instead the response of raw plover abundance with an offset variable in all models to include the effect of species detectability (Aldridge et al. 2011, Timmer 2017). We also included a random effect of transect to account for spatial autocorrelation within transects (Duchardt et al. 2019) and calculated Moran’s I to ensure independence (Moran 1950).

We examined univariate models of each target variable specified in either the conditional (c) or zero-inflated (zi) portion of the model, and compared these models to a base model (in this case, a model including the random effect of spatial autocorrelation and detectability offset term), selecting those models with an Akaike’s information criterion for small samples (AIC_c ; Burnham and Anderson 2002) smaller than the base model to be incorporated into a global model. Where multiple highly correlated variables were all better than the null, we selected the variable from the model with the lowest AIC_c .

TABLE 1. Variables used in models predicting Mountain Plover habitat use, nesting habitat use, and nest survival for data collected in the Thunder Basin National Grassland, USA, 2015–2017.

	Adult habitat use	Nesting habitat	Nest survival
Response variable	Abundance, adjusted for detectability	Nest site use vs. non-use	Daily survival rate
Data source	Point counts	Nest searching	Nest monitoring
Modeling framework	Zero-inflated Poisson model	Logistic model	Logistic exposure model
Covariates			
Prairie dog colony - direct	Colony size ²	— ^a	Colony size ²
Vegetation structure	Colony age (years) ²	Colony age ²	Colony age ²
	Distance to colony edge ²	Distance to colony edge ²	Distance to colony edge ²
	Visual obstruction ^b	Visual obstruction (nest, 5 m, 10 m) ^b	Visual obstruction (nest, 5 m, 10 m) ^b
Vegetation composition	Maximum vegetation height ^b	Maximum vegetation height (nest, 5 m, 10 m) ^b	Maximum vegetation height (nest, 5 m, 10 m) ^b
	Bare ground	Bare ground (nest, nest site)	Bare ground (nest, nest site)
	Shrub cover (0/1)	Shrub cover (0/1)	Shrub cover (0/1)
	Sub-shrub cover (0/1)	Sub-shrub cover (0/1)	Sub-shrub cover (0/1)
	Cactus cover	Cactus cover	Cactus cover
	Annual forb	Annual forb (nest, nest site) ^c	Annual forb (nest, nest site)
	C3 perennial grass cover	C3 perennial grass cover (nest, nest site)	C3 perennial grass cover (nest, nest site)
	C4 perennial grass cover	C4 perennial grass cover (nest, nest site)	C4 perennial grass cover (nest, nest site)
Topo-edaphic	C3 annual grass cover	C3 annual grass cover (nest, nest site)	C3 annual grass cover (nest, nest site)
	% Clay ^b	% Clay ^b	% Clay ^b
	% Silt ^b	% Silt ^b	% Silt ^b
Periodic/Temporal	% Sand ^b	% Sand ^b	% Sand ^b
	Topographic roughness	Topographic roughness	Topographic roughness
	Year	Year	Year
			Day of season
			Day of season ²
			Nest age
			Precipitation ^d
			Thunder ^d
			Hail ^d
			Maximum Temperature ^d

^aBecause available paired points for nest-site selection analyses were located within the same colony, colony size was identical between used and available points at this scale.

^bIndicates variables that were highly (>0.6) correlated with at least one other variable; in multivariate model building, only the variable with the lowest AIC_c was used in building more complex models.

^cData were available at the nest cup and nest site for most composition variables, and at the nest cup, 5 m distant, and 10 m distant for measurements of VO and vegetation heights. Because of high correlation between measurements at different scales, for each variable the scale with lowest AIC_c was used in building more complex models.

^dWeather variables were calculated as the value at the midpoint of the exposure period.

for inclusion in the global model. This global model was then reduced by manually removing variables that appeared to be statistically less important (85% confidence intervals overlapping zero, beginning with the greatest overlap) until the AIC_c was minimized, resulting in a “best reduced” model. We then compared all univariate models and the global and reduced models with a “literature model” including visual obstruction and bare soil, 2 variables consistently identified as important traits of plover habitat in the literature (Knopf and Miller 1994, Knopf and Wunder 2006).

Nest-Site Selection

Data collection. Following point counts we returned to colonies where Mountain Plovers had been detected, either that year or historically, and conducted nest searches at these sites following the method of Dinsmore et al. (2002), utilizing all-terrain vehicles to survey the entire colony. Upon detecting a Mountain Plover, we observed the bird until we either located its nest or determined that it likely was not tending a nest based on behavioral cues. Once a nest was located, we recorded its geographic coordinates using a global positioning system device (Trimble GeoXT,

Sunnyvale, California, USA), and placed cow pats 5 m to the north and south of the nest to facilitate revisits to the nest site to determine nest fate, while avoiding detection of the nest by predators. We also floated one egg from each nest to determine nest age (Dinsmore et al. 2002; University of Wyoming IACUC Protocol Approval [#20150518]B00168-01], Wyoming Game and Fish Department Chapter 33 Permit 1017, USFWS Permit MB95551B-0). We visited each nest every 5–7 days during the incubation period (~30 days) to determine nest fate.

To assess patterns of nest-site selection we compared habitat data collected at survey points with data collected at the nest site and area around the nest. At the nest, we used a 40 cm × 40 cm point-intercept grid, centered on the nest (Augustine and Derner 2012). We measured ground cover (including basal vegetation) and canopy (measured as pin hits) at 25 systematically positioned points within this grid for the following cover classes: C_4 perennial grasses, C_3 perennial grasses, annual grasses, forbs, shrubs (to spp.), litter, and bare ground. We also overlaid two 30-m transects oriented N–S and E–W centered on the nest (i.e. representing a 15-m radius around the nest). Along each transect, we collected visual obstruction data using Robel pole readings in 4 directions at the nest, and at 5 m and 10 m from the nest. Along the E–W transect, we collected line-intercept data on shrubs and cactus. We also collected point-intercept data for the same vegetation categories as above at 1-m intervals along the E–W transect for a total of 30 points. These measurements were conducted from May to July each year, typically within 5 days of nest failure or fledging.

Modeling framework. We used logistic regression to model nest-site selection in Mountain Plovers (Keating and Cherry 2004). We implemented a use vs. non-use framework, randomly selecting “unused” sites from among previously sampled point count locations within colonies, using only points where no plovers were detected during surveys in that year and no nests were observed. Because we were interested in selection of nest sites at the within-colony scale, we limited our selection to an equal number of unused points per colony per year (e.g., where 4 nests were found on a colony in a given year, 4 random points were selected from that colony for that year).

As in analyses of adult density described above, we examined univariate models of each variable considered to be important for Mountain Plover nest-site selection (Table 1). Where data were available at the scale of both the nest site (15-m radius around the nest) and nest cup, we examined univariate models at both scales and selected the model at the scale with the lowest AIC_c (because the 2 scales were generally too correlated to include in the same model). We then selected all variables from univariate models that were $>2 AIC_c$ less than the null model, and

combined these in a global model. When variables were highly correlated ($|r| > 0.7$), we selected the variable with the lowest univariate AIC_c . Finally, this global model was then reduced by manually removing statistically unimportant variables (i.e. 85% CI overlapping zero) until AIC_c was minimized, resulting in a “best reduced” model. We then compared all univariate models and the best global and reduced models with a “literature model” including visual obstruction and bare soil, 2 variables typically identified as important in the literature (Knopf and Miller 1994).

Nest Survival

Modeling framework. To investigate the effects of vegetation, topographic factors, and weather on nest survival, we estimated daily survival rates (DSR) using the logistic exposure method (Shaffer 2004) in program R (Herzog and Bolker 2014). Because temporal variables (Table 1) have been identified as extremely important in predicting nest survival in this species (e.g., Dinsmore et al. 2002, Dreitz et al. 2012), we used a hierarchical approach to build models of nest survival. We began by examining all univariate temporal models (see Table 1). However, because nest survival is commonly influenced by interactions between temporal variables, in this step we also examined 2-way interactions between year, nest age, and day of season, as well as between year, nest age, and quadratic day of season to capture potential nonlinear effects. We then built a global model with all temporal variables better than the null. This temporal global model was reduced by manually removing statistically unimportant (i.e. 85% confidence interval overlapping zero) variables until the AIC_c was minimized, resulting in a “best reduced” temporal model. In step 2 of this approach, we used this best temporal model as a base to examine all variables related to vegetation structure and composition, building a complete global model with both temporal and structural variables, and again removing statistically unimportant variables until the AIC_c was minimized. We also included a literature-based model of nest survival including nest age and day of season.

We obtained weather data including temperature, precipitation, and inclement weather from a local weather station administered by the National Oceanic and Atmospheric Administration (NOAA; data requested from <https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00482725/detail>). Inclement weather measures included days with hail and days of thunder (Carver et al. 2017). We generated weather variables for the midpoint of the exposure interval of each nest (Table 1).

We observed that, in addition to predation events, both nest abandonment and egg inviability (i.e. adult continued to tend eggs that never hatched) sometimes were causes of nest failure. We hypothesized that among all failed nests, different factors affected the probability of predation as

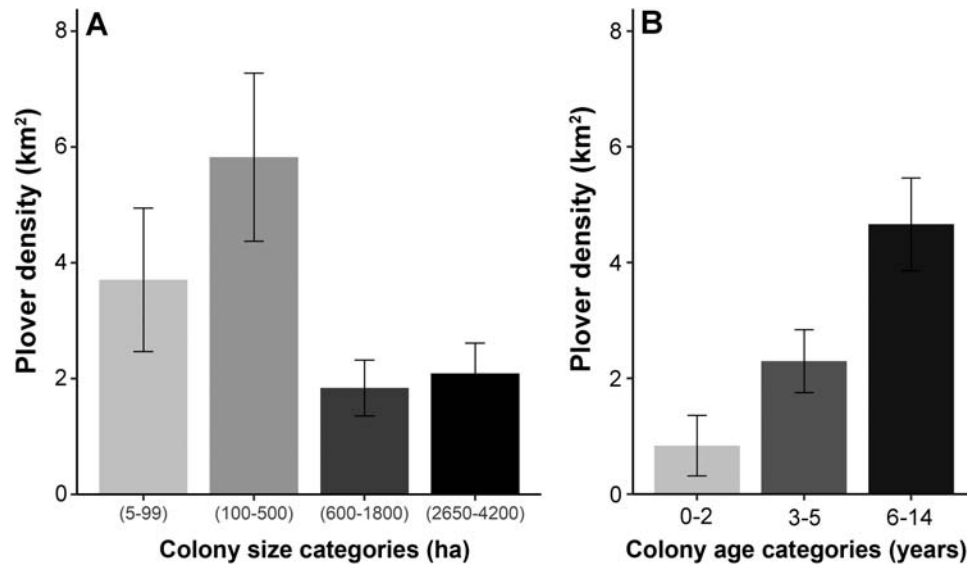


FIGURE 2. Mountain Plover density as a function of prairie dog colony size (A) and age (B) in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. The first 2 size categories (5–99 ha and 100–500 ha) represent small and large colonies, respectively, in previous studies (e.g., Dinsmore et al. 2005, Augustine et al. 2008, Goguen 2012). Colony sizes above 500 ha are unique relative to previous studies of breeding Mountain Plovers. Colony ages represent old (6–14 years), intermediate (3–5 years), and young (0–2 years) colonies. Error bars represent 85% confidence intervals. Note: these are observed distance-adjusted densities and not model-generated predictions.

compared to abandonment and inviability. We further explored these effects by predicting the source of nest failure, either in the form of depredation or abandonment/egg inviability. We used logistic regression with a reduced dataset only including failed nests to examine drivers of abandonment (1) vs. predation (0). We compared models including any competitive vegetation variables from above (>2 AIC_c better than the null) as well as all weather variables and year. Weather variables associated with causes of nest failure were either summed (“precipitation,” “hail,” “thunder”) or modeled as the maximum of these variables (“min temp” and “max temp”) over the duration of the nesting cycle.

RESULTS

Adult Mountain Plover Density

Adult Mountain Plover density on prairie dog colonies in the Thunder Basin National Grassland averaged 2.9 birds km⁻² (SE = 0.28). Density varied substantially across years, with the highest densities observed in 2015 (3.8 birds km⁻², SE = 0.67), but also varied with colony age and size (Figures 2A,B), with highest densities on colonies between 100 and 500 ha (5.82 birds km⁻², SE = 1.0). Overall, 6 variables in addition to colony area, distance to colony edge, and colony age were included in multivariate model exploration, including aspects of vegetation structure, composition, and topoedaphic features (Table 2, Supplementary Table A3; see Supplementary Table A1 for average covariate values for plover presence vs. absence).

The best multivariate model predicting Mountain Plover density had an $R^2 = 0.12$ and a model weight of 0.99 (Table 2). Most variables played a stronger role in predicting plover presence vs. absence on colonies, including maximum vegetation height ($\beta_{\text{maxheight}} = -0.1$, SE = 0.04), cover of annual forbs ($\beta_{\text{af}} = 3.19$, SE = 1.1), cover of C₃ annual grasses ($\beta_{\text{c3p}} = -5.81$, SE = 3.31), quadratic effects of colony age ($\beta_{\text{age}} = 0.55$, SE = 0.3; $\beta_{\text{age}}^2 = -0.04$, SE = 0.02), and distance to colony edge ($\beta_{\text{dist}} = 0.52$, SE = 0.3; $\beta_{\text{dist}}^2 = -0.06$, SE = 0.03). Bare ground ($\beta_{\text{bare}} = 0.81$, SE = 0.3), soil clay content ($\beta_{\text{clay}} = 2.35$, SE = 0.6), colony age ($\beta_{\text{age}} = 0.08$, SE = 0.03), and colony area (km) ($\beta_{\text{area}} = -0.026$, SE = 0.007) were included in the conditional portion of the model.

Nest-Site Selection

During 2015–2017, we located and monitored 144 Mountain Plover nests on colonies ranging from 15 to 4,000 ha in size. Because nest fate was uncertain in some cases, and in others vegetation data were not collected, we conducted nest-site selection analyses on 138 nests paired with 138 unused points. After comparing all univariate models (Supplementary Table A4), 9 variables were included in exploration of multivariate models. The best multivariate model ($R^2 = 0.58$; Table 3) included a negative response to vegetation height at the nest bowl ($\beta_{\text{h}} = -0.42$, SE = 0.07; Figure 3B) and to presence of shrubs ($\beta_{\text{shrub}} = -1.79$, SE = -0.49), cactus ($\beta_{\text{cactus}} = -23.0$, SE = 5.81; Figure 3D), topographic roughness ($\beta_{\text{rough}} = -0.84$, SE = 0.48) at the nest site, as well as a marginal response to colony

TABLE 2. Results of model-building and model comparison predicting adult Mountain Plover habitat utilization in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. The conditional and zero-inflated portions of the model are specified by (c) and (zi), respectively. The “Model” column indicates whether the model represents univariate model exploration from step one of our modeling approach, the global model built from competitive variables, the reduced global model, or an a priori model based on literature. Shown are the global and reduced model, as well as top univariate and quadratic models. For full model list see [Supplementary Table A3](#).

Model	Model	AIC _c	ΔAIC _c	k	w _i
(c) Clay + Colony area + Bare ground + Colony age (zi) Max. vegetation height + Colony age ² + Distance to colony edge ² + Annual forb + C3 Annual Grasses	Best reduced	869.30	0	15	0.99
(c) Clay + Colony area + Bare ground + Colony age ² + Distance to colony edge ² + Max. vegetation height (zi) Max. vegetation height + Colony age ² + Distance to colony edge ² + Annual forb + C3 Annual Grasses + Topographic Roughness + Bare ground	Best global	878.05	8.75	21	0.01
(zi) Colony Age ²	Quadratic	917.83	48.53	6	0
(zi) Colony Age	Univariate	920.17	50.87	5	0
(zi) Distance to edge ²	Quadratic	927.90	58.60	6	0
(c) Colony Age ²	Quadratic	929.53	60.23	6	0
(zi) Maximum vegetation height	Univariate	931.90	62.59	5	0
(zi) Visual obstruction + Bare ground	Best a priori model	933.59	64.28	6	0
(zi) Annual forb	Univariate	943.18	73.88	5	0
(zi) Bare ground	Univariate	943.38	74.07	5	0
Null	—	959.48	90.18	4	0

TABLE 3. Summary results of model-building and model comparison predicting Mountain Plover nest-site selection in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017, including the global model, reduced model, an a priori literature model, top univariate model, and null model. Full model set including all univariate models can be found in [Supplementary Table A4](#).

Model	Model	AIC _c	ΔAIC _c	k	w _i
Max. vegetation height (nest) + C4 perennial grass (nest) + cactus + Shrub + Bare (nest site) + Annual forb (nest) + Clay + Topographic roughness + Colony age	Reduced model	181.27	0.00	10	0.89
Max. vegetation height (nest) + C4 perennial grass (nest) + cactus + Shrub + Bare (nest site) + Annual forb (nest) + C3 perennial grass (nest) + Clay + Topographic roughness + Colony age ²	Global model	185.52	4.24	12	0.11
Max. vegetation height (nest)	Univariate	267.93	86.66	2	0.00
Visual obstruction (5 m) + Bare ground (site)	Literature Model	299.10	117.83	3	0.00
Null	Null	384.63	203.36	1	0.00

age ($\beta_{\text{colage}} = -0.15$, SE = 0.09). The model also included a positive response to annual forbs at the nest ($\beta_{\text{af}} = 4.45$, SE = 1.4), and bare ground ($\beta_{\text{bare}} = 2.45$, SE = 0.94) at the nest site, as well as marginal effects of soil clay content ($\beta_{\text{clay}} = 0.1$, SE = 0.03) and cover of C₄ perennial grasses at the nest ($\beta_{\text{C4}} = -3.75$, SE = 2.42; [Figure 3](#)).

Nest Success

Nesting began between April 24 and April 28 each year, but average nest initiation date was May 19 (range: April 24 to June 20) because many individuals renested in late May or June following nest failure. Fifty-three of 136 nests with complete survival data were successful (apparent survival = 39%), while 54 nests were depredated and 29 failed due to other causes (e.g., nest abandonment, egg inviability, egg damage). Daily nest survival across years was estimated at 0.96, with an estimated 30-day survival rate

of 34%. Univariate models with year, thunder, maximum temperature, and the interaction between nest age and day of season were all better supported than the null model ([Supplementary Table A5](#)). The reduced temporal model included the effects of thunder, maximum temperature, and the interaction between nest age and day of season ([Table 4](#)).

Second-stage models examining each habitat variable along with the best temporal variables indicated that cactus cover, shrub cover, C₄ perennial grasses at the nest, and C₃ perennial grasses at the site, and a quadratic effect of colony age, all influenced nest survival. The final reduced model included the effect of maximum temperature ($\beta = -0.036$, SE = 0.01), cactus cover ($\beta = -13.53$ SE = 4.8), thunder ($\beta = -0.54$, SE = 0.3), shrub cover ($\beta = -1.0$, SE = -0.4), nest age ($\beta = 0.10$, SE = 0.03), day of season ($\beta = 0.044$, SE = 0.02), and the interaction between nest age and day of season ($\beta = -0.002$, SE = 0.0008; [Figure 4](#)).

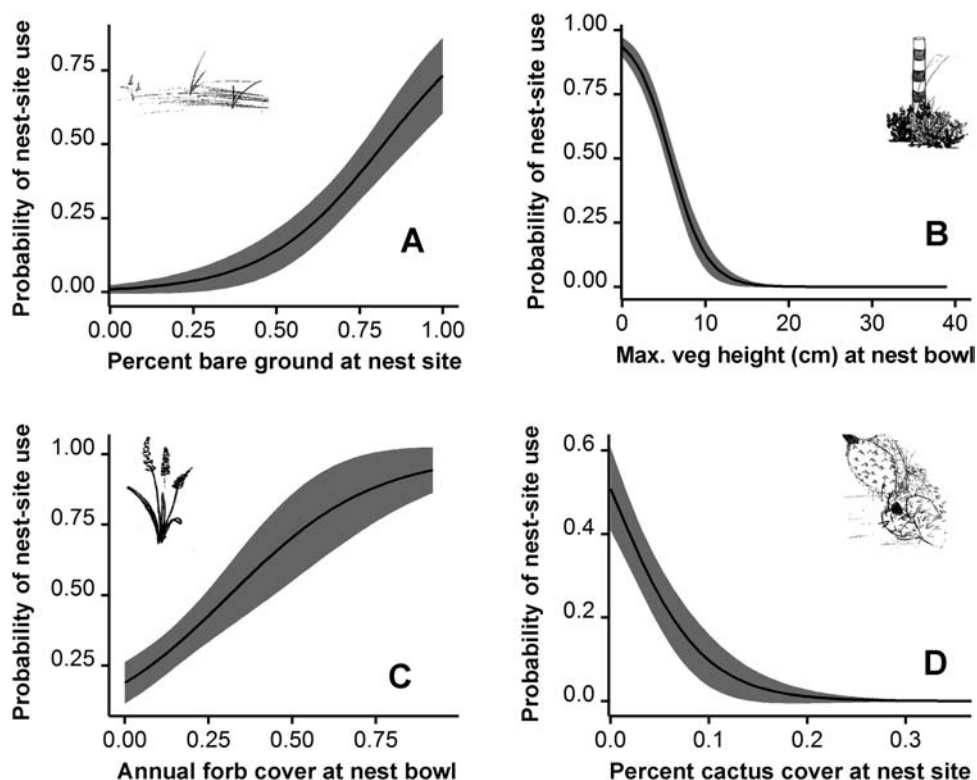


FIGURE 3. Probability of nest site use by Mountain Plovers as a function of percent bare ground (A), maximum vegetation height (B), annual forb cover (C), and cactus cover (D) in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. Gray envelopes represent 85% confidence intervals.

TABLE 4. Top models predicting daily nest survival for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. Full model set including all univariate models can be found in [Supplementary Table A5](#).

Model	Model type	AIC _c	ΔAIC _c	k	w _i
Cactus + Shrub + Nest Age*Day of season + Colony age ² + Max Temp + Thunder	Temporal + structure (reduced)	460.20	0	10	0.65
Cactus + Shrub + Colony Age ² + C3 perennial grass (Site) + C4 perennial grass (nest) + Nest Age*Day of season + Max Temp + Thunder	Temporal + Structure (global)	462.38	2.18	12	0.22
Cactus + Age*Day of season + Max. Temp + Thunder	Temporal + Cactus	464.02	3.83	7	0.10
Shrub + Age*Day of season + Max. Temp + Thunder	Temporal + Shrub	467.97	7.77	7	0.01
Age*Day of season + Max. Temp + Thunder	Best temporal model	471.99	11.29	6	0
Null	—	479.78	19.58	1	0
Max. Temp + Age + Day of season + Precipitation	Literature Model	480.64	20.45	5	0

This model also included a marginal effect of colony age ($\beta = -0.23$, SE = 0.2) and the quadratic effect of colony age ($\beta = 0.03$, SE = 0.02).

Our simple approach to separating the drivers of nest predation from other sources of nest failure across the duration of the nesting cycle enhanced our ability to detect and understand factors related to nest survival rates (Table 5, [Supplementary Table A6](#)). After combining all variables better than the null into a multivariate global model, and then reducing from the global model, the resulting best model included the effects of maximum precipitation (2.67,

SE = 1.03), hail (2.21, SE = 1.0), maximum temperature (0.10, SE = 0.06), and an effect of C₄ perennial grasses at the nest site (−19.9, SE = 9.2). Thus, nests experiencing higher temperatures, hail, and more intense precipitation events were more likely to fail due to factors other than predation.

DISCUSSION

Our findings reinforce the importance of black-tailed prairie dogs as engineers of Mountain Plover habitat, but also identified novel responses of plovers to large prairie

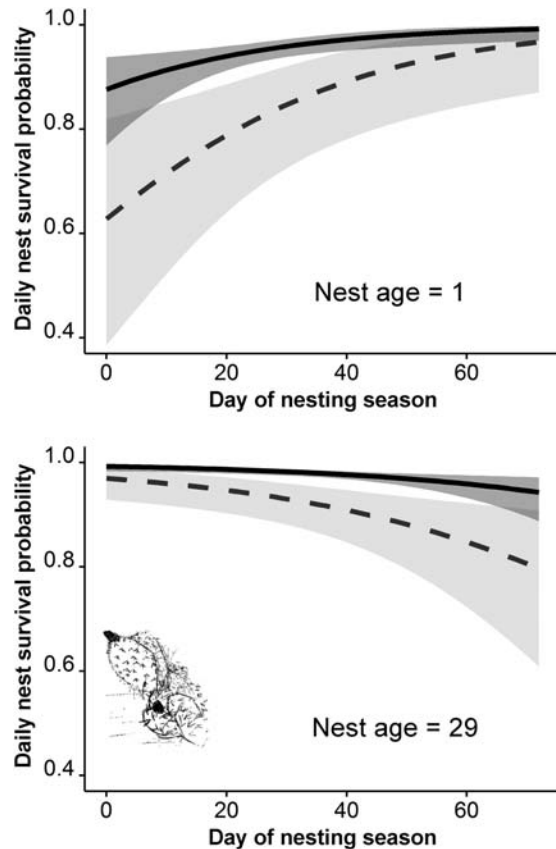


FIGURE 4. Daily nest survival for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017, increases across the nesting period for young nests (top), but decreases across the season for older nests (bottom). Solid and dashed lines represent 0% and 10% cactus cover, respectively. Gray envelopes represent 85% confidence intervals.

dog colonies. Prairie dog disturbance explained a large amount of variation in selection of breeding and nesting habitat, reinforcing the role of prairie dogs as identified in studies from other portions of the species' range (Dinsmore et al. 2005, Tipton et al. 2009, Augustine 2011, Goguen 2012). Aspects of prairie dog colonies directly influenced habitat suitability for adult plovers, with birds preferring older portions of moderately sized colonies, and habitat characteristics influenced by prairie dogs (e.g., vegetation height, bare ground exposure, and annual forb abundance; [Supplementary Table A1](#)) were quantitatively linked to habitat suitability both at the breeding-site and nest-site scales. Plover densities on moderately sized (100–500 ha) prairie dog colonies or at moderate distances from colony edges in the Thunder Basin were comparable with other identified hotspots in Wyoming (Plumb et al. 2005) and elsewhere in their range (Childers and Dinsmore 2008, Tipton et al. 2009, Augustine 2011, Pierce 2017). Nest survival rates for the Thunder Basin plover population also fell centrally within ranges reported in the literature (e.g.,

Dinsmore et al. 2002, Augustine and Skagen 2014, Pierce et al. 2019). As such, we posit that the Thunder Basin National Grassland, and specifically its prairie dog colonies, are an important resource in terms of range-wide Mountain Plover conservation.

Despite the importance of prairie dog colonies as breeding habitat, we found that not all colonies are equal in terms of habitat quality. Areas of longer-term prairie dog disturbance on colonies had higher Mountain Plover densities, likely because long-term disturbance is linked with increased bare ground exposure and lower vegetation height, as well as more annual forbs (Whicker and Detling 1988, Johnson-Nistler and Sowell 2004). More surprising was that extremely large colonies had lower average densities of adult Mountain Plovers and probability of site use declined near cores of large colonies. We had observed a similar trend in abundance responding to distance to colony edge previously (Duchardt et al. 2019), but this is the first direct evidence that colony size may negatively influence plover density. Observed densities were lowest on colonies >500 ha in size, while they were highest on colonies between 100 and 500 ha in size (Figure 2), although we note there was substantial variation in densities within this size class.

Similar findings are likely absent in the literature because most remaining black-tailed prairie dog colonies are comparatively small in size; maximum colony sizes in previous studies did not exceed ~480 ha (Dinsmore et al. 2005, Augustine et al. 2008, Goguen 2012, Augustine and Skagen 2014). In contrast, the largest colonies in Thunder Basin exceeded 4,000 ha in the final year of our study. While we did not directly examine mechanisms driving the response of plovers to colony size and distance to colony edge, one potential driver may be complementary resources (Ries et al. 2004). We have observed directly that vegetation height and shrub cover are higher outside of prairie dog colonies (Duchardt et al. 2019), which may be especially important for adults with broods; taller vegetation may provide protection from predators (Schneider et al. 2006), while vegetation and shrubs may provide better opportunities for thermoregulation, especially important for chicks in a region where daytime temperatures may exceed 38°C (Shackford 1996). These resources are lacking within colonies, and it may be easier for adults to travel with chicks if they nest nearer a colony edge than traveling >1 km from a colony core. However, our results indicated that while distance to colony edge was a strong driver of plover presence, total colony area influenced the abundance of birds; thus, there are likely factors associated directly with colony size in addition to complementary resources (e.g., predator abundances or food resources may vary with colony size).

Local-scale habitat attributes including reduced vegetation height and increased exposure of bare ground have been linked to enhanced Mountain Plover habitat quality in the literature (Knopf and Miller 1994, Dinsmore 2003,

TABLE 5. Top univariate models differentiating between nest failure by abandonment and nest failure by predation for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017, and the final combined global model, where positive parameter estimates indicate greater probability of abandonment.

Univariate model	AIC _c	ΔAIC _c	k	w _i	Parameter estimate (SE)	R ²
Max. Precipitation + Max. Temperature + Hail + C4 perennial grasses (nest site)	61.01	0	5	1	$\beta_{\text{precip}} = 2.67 (1.03)$ $\beta_{\text{maxtemp}} = 0.10 (0.06)$ $\beta_{\text{c4p2}} = -19.9 (9.3)$ $\beta_{\text{hail}} = 2.20 (1.04)$	0.42
Hail	77.95	16.93	2	0	2.13 (0.6)	0.15
Max. Precipitation	82.08	21.06	2	0	1.61 (0.56)	0.1
Max. Temperature	84.28	23.27	2	0	0.08 (0.03)	0.08
Visual obstruction at nest	85.25	24.23	2	0	0.52 (0.23)	0.07
C4 perennial grass (Nest site)	86.05	25.04	2	0	-9.89 (5.7)	0.06
Thunder	86.43	25.42	2	0	1.87 (1.07)	0.05
Null	89.04	28.03	1	0	—	

Augustine and Derner 2012) and were also important in our study. We note that we quantified 2 metrics of vegetation height/structure. The first was visual obstruction, or height at which the vegetation is sufficiently dense to obscure a 2.5-cm wide pole when viewed from a 1-m height (Robel et al. 1970). The second was maximum vegetation height, or the height of the tallest vegetation visible in front of a 2.5-cm wide pole, regardless of that vegetation's density. Because these 2 measurements covary strongly ($r = 0.82$), we did not consider models with both predictors. Our model comparison analysis found that maximum vegetation height was the better of the two in explaining variation in plover habitat use. Our selected model indicated that plovers avoided nesting in areas with a maximum vegetation height >11 cm, corresponding with an average visual obstruction of >5 cm. We suggest that the presence of sparse vegetation in the range of 3–5 cm, which is typically associated with a shorter layer (1–1.5 cm) of more dense vegetation, is ideal habitat because the short, dense layer can provide some concealment to a sitting plover's body, and the taller but sparse pieces of vegetation break up the outline of a plover while still affording them the ability to scan for and detect approaching ground predators (Knopf and Wunder 2006). Our models also identified high levels of bare soil exposure as an important component of plover habitat (Table 2), likely because plovers blend in especially well with bare soil when viewed by aerial predators.

Although cactus cover has been examined in the literature, responses of plovers to this variable have been mixed, with some reports of avoidance (Knopf and Miller 1994), but no apparent sensitivity in other systems (Augustine and Derner 2012). Our results show avoidance of cactus at the nest site, combined with lower nest survival in areas of unusually high cactus cover (Figure 4). Perhaps the reason this has not been detected in the past is the especially high cactus density in some portions of Thunder Basin, compared with more moderate cover in other locales, but

this is difficult to assess because maximum percent cover of cactus is not generally reported in the literature (e.g., Knopf and Miller 1994, Augustine and Derner 2012). We found that probability of plovers nesting in a locality declined most notably where cactus exceeded 10% cover. It is important to note that while we observed avoidance of extensive cactus cover at the nest site, low or moderate cactus cover may be beneficial to Mountain Plovers for crypsis at broader spatial scales, or during the brood-rearing period.

In addition to cactus cover, a number of other variables influenced nest survival, including nest age (Figure 4). Unlike altricial species, increased nest age in precocial species is often associated with increased probability of survival (Klett and Johnson 1982). We observed this trend, but it was paired with an interaction with day of season, such that older nests were less likely to survive late in the season. This may be related to stress on adults to complete the nesting season, or increased temperatures later in the nesting season. We found support for the latter proposed mechanism, as higher temperatures were also associated with lower nest survival. Temperature has been previously linked with Mountain Plover nest survival (Dreitz et al. 2012, Pierce et al. 2019), but the role of extreme minimum or maximum temperatures may vary because Mountain Plovers inhabit a fairly wide climatic envelope given their limited geographic range (Knopf and Wunder 2006). In the Thunder Basin and other lower-elevation sites, maximum temperature is likely to limit nest survival. In the Thunder Basin National Grassland, maximum temperatures exceeded 38°C for multiple days in all years, and high temperatures were often accompanied by altered adult behavior at the nest (e.g., drastically reduced flight initiation distance, panting while shading eggs), indicating increased stress associated with shading eggs at high temperatures.

Models of nest survival did not support the importance of precipitation as indicated in the literature (Dreitz et al. 2012), but precipitation was identified as important when

partitioning between depredated and abandoned/inviable nests. We identified several key differences in weather variables associated with nest depredation vs. nest abandonment or egg inviability, including higher precipitation associated with abandoned nests. We note that during field monitoring of nests, it can be difficult to determine whether a nest was inviable or just abandoned early during the incubation period, leading to a cessation of development in eggs. However, in at least one case we know that eggs were inviable and not noticeably damaged or abandoned; in 2017 we observed the same individual (identified by color bands outfitted by collaborators) attending a nest for at least 72 days, failing to abandon even after we determined eggs were inviable on day 35. We grouped these 2 sources of failure (nest abandonment and nest inviability) together because they can sometimes be difficult to discern from one another, and because they are likely influenced by similar drivers. Indeed, abandoned or inviable nests were characterized by exposure to higher temperatures and intense precipitation events. Dreitz et al. (2012) observed a similar trend in overall nest survival for Mountain Plovers in eastern Colorado, with higher rates of nest survival during drought and periods of cooler temperatures, although the authors did not indicate what proportion of nests failed due to predation as compared to other causes.

Management actions in many upland systems, especially for gamebirds, often focus on predator control (e.g., Schroeder and Baydack 2001, Fletcher et al. 2010), but this may not be appropriate if substantial numbers of nests are lost due to other causes. In the case of the Mountain Plover and other ground-nesting species exposed to climatic extremes, we encourage future research to explore the drivers of different sources of nest failure. Our own approach to this issue was relatively simple and was constrained by our dataset and research foci, but new methods are emerging for partitioning sources of variation in nest success (e.g., Darrah et al. 2018), providing opportunities to further explore this concept both for Mountain Plovers and other grassland and sagebrush bird species.

Conservation Implications

Mountain Plovers are strongly dependent on prairie dog colonies for nesting habitat in the Thunder Basin National Grassland, as evidenced by their near absence off colonies during the nesting season (Duchardt et al. 2019). However, our analyses of Mountain Plover adult distribution during the nesting season indicates that extremely large colonies are likely suboptimal in terms of habitat value for this species. While the mechanisms driving these responses warrant further exploration, this finding has important and immediate management implications. In addition to reduced habitat quality for Mountain Plovers, large prairie dog colony complexes can impact livestock production on

rangelands (Derner et al. 2006, Augustine and Springer 2013), creating tensions between land managers, livestock producers, and conservation organizations. Future management of black-tailed prairie dog colonies to support Mountain Plover conservation may be optimized by aiming to sustain complexes that include moderately sized colonies (100–500 ha). In addition to benefitting Mountain Plovers, this strategy would also sustain many other ecosystem services (e.g., sagebrush wildlife habitat, livestock forage) associated with off-colony plant communities.

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Ethics statement: We followed all ethics protocols as set forth by the University of Wyoming. All appropriate state and federal permissions were obtained, including University of Wyoming IACUC Protocol Approval [#20150518]B00168–01], Wyoming Game and Fish Department Chapter 33 Permit 1017, and USFWS Permit MB95551B–0.

Author contributions: CJD, JLB, and DJA conceived the idea, design, experiment (supervised research, formulated question or hypothesis). CJD and DJA performed the experiments (collected data, conducted the research). CJD, JLB, and DJA wrote the paper (or substantially edited the paper). CJD and DJA developed or designed methods. CJD analyzed the data. CJD, JLB, and DJA contributed substantial materials, resources, or funding.

Data depository: Analyses reported in this article can be reproduced using the data provided by Duchardt et al. (2020).

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