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Research Papers

Drought and Cooler Temperatures Are Associated with Higher Nest Survival in Mountain Plovers

La sécheresse et les températures fraîches sont associées au taux de survie des nids supérieur chez le Pluvier montagnard

Victoria J. Dreitz^{1,2}, Reesa Yale Conrey³, and Susan K. Skagen⁴

ABSTRACT. Native grasslands have been altered to a greater extent than any other biome in North America. The habitats and resources needed to support breeding performance of grassland birds endemic to prairie ecosystems are currently threatened by land management practices and impending climate change. Climate models for the Great Plains prairie region predict a future of hotter and drier summers with strong multiyear droughts and more frequent and severe precipitation events. We examined how fluctuations in weather conditions in eastern Colorado influenced nest survival of an avian species that has experienced recent population declines, the Mountain Plover (*Charadrius montanus*). Nest survival averaged 27.2% over a 7-yr period (n = 936 nests) and declined as the breeding season progressed. Nest survival was favored by dry conditions and cooler temperatures. Projected changes in regional precipitation patterns will likely influence nest survival, with positive influences of predicted declines in summer rainfall yet negative effects of more intense rain events. The interplay of climate change and land use practices within prairie ecosystems may result in Mountain Plovers shifting their distribution, changing local abundance, and adjusting fecundity to adapt to their changing environment.

RÉSUMÉ. Les prairies naturelles ont été plus grandement modifiées que tout autre biome en Amérique du Nord. L'habitat et les ressources nécessaires pour favoriser la performance reproductrice des oiseaux de prairie endémiques de ces écosystèmes sont actuellement menacés par les pratiques de gestion des terres et les changements climatiques imminents. Les modèles climatiques pour les prairies des Grandes Plaines prévoient des étés plus chauds et plus secs, des sécheresses sévères durant plusieurs années et des événements de précipitation plus fréquents et intenses que ce qu'on observe présentement. Nous avons examiné les effets des fluctuations des conditions météorologiques dans l'est du Colorado sur la survie des nids chez une espèce aviaire ayant subi un récent déclin des populations, le Pluvier montagnard (*Charadrius montanus*). Le taux de survie des nids s'élevait à 27,2 % en moyenne sur une période de 7 ans (n = 936 nids) et diminuait à mesure que progressait la saison de reproduction. La survie des nids était supérieure quand les conditions étaient sèches et les températures fraîches. Les changements prévus dans les tendances régionales des précipitations influenceront vraisemblablement la survie des nids : tandis que la diminution des précipitations estivales prévue entraînera un effet positif sur la survie, les événements de précipitation plus intenses prévus auront, quant à eux, un effet négatif. L'interaction des changements climatiques et des pratiques d'utilisation des sols dans les écosystèmes de prairie amènera peut-être le Pluvier montagnard à modifier sa répartition, son abondance locale et sa fécondité pour s'adapter à l'environnement changeant.

Key Words: *Charadrius montanus*, climate change, Mountain Plover, nest survival, weather

INTRODUCTION

Native grasslands have been altered to a greater extent than any other biome in North America (Samson et al. 2004), resulting in the conversion of the once diverse grassland landscape into a collection of homogenous grassland fragments interspersed with agricultural fields (Lomolino et al. 2001, Brockway et al. 2002, Brennan and Kuvlesky 2005). These alterations are likely to have contributed to the

continental-scale declines in grassland avifauna, which have been steeper and more consistent than declines in any other avian guild over the past century (Knopf 1994).

Although direct anthropogenic changes can contribute to loss and degradation of avian habitat in the North American prairies, shifts in weather patterns also may result in changes in the condition, quality, and viability of prairie ecosystems, and thus the distribution, phenology, and reproductive output

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of many grassland birds. Presumably by affecting food resources, habitat structure, or predator abundance and behavior, higher levels of precipitation favor reproductive success of several grassland and shrubland passerines, such as Brewer's Sparrow (*Spizella breweri*), Rufous-crowned Sparrow (*Aimophila ruficeps*), and Lark Bunting (*Calamospiza melanocorys*; Rotenberry and Wiens 1989, 1991; Morrison and Bolger 2002, Skagen and Yackel Adams 2012). Precipitation, however, may not lead to higher reproductive output in the Mountain Plover (*Charadrius montanus*), a unique grassland species at the extreme of grassland bird habitat niches that prefers highly disturbed or exposed ground (Knopf 1996) within the prairie ecosystems of North America.

Mountain Plovers are short-distance migratory birds that breed in grasslands and recently tilled agricultural fields in interior North America from Montana to northern New Mexico and the panhandles of Oklahoma and Texas, and winter in dry plains from California to Texas with the largest concentration in the Imperial Valley, California (Knopf and Wunder 2006). During the breeding season, female plovers split their clutches between two nest sites, incubating at the second site while the males incubate at the first nest site (Knopf and Wunder 2006). Steep declines in population size have been reported for Mountain Plovers across their range since 1966, presumably stemming from loss of grassland habitats to agriculture and declining prairie dog populations. In 1999, the U.S. Fish and Wildlife Service was petitioned for 'threatened' status of the Mountain Plover, but a decision in 2003 found that listing was not warranted (USFWS 2003). Listing of the Mountain Plover as threatened was reconsidered in 2010 and the proposed listing was withdrawn (USFWS 2011). Regardless of legal conservation status, a better understanding of the factors that affect life history traits is imperative for the development of conservation strategies for this species that breeds and winters within the borders of the Great Plains region of North America.

Reproductive output is one crucial component in determining population performance of a migratory species. An element of reproductive performance, nest survival, is defined as the probability that a nest will be successful with ≥ 1 egg hatching (precocial species) or ≥ 1 nestling fledging (altricial species; Dinsmore et al. 2002). Nest survival of Mountain Plover, a precocial species, has been estimated across the species' breeding range, including areas in Colorado (e.g., Graul 1975, Knopf and Rupert 1996, Knopf and Wunder 2006, Mettenbrink et al. 2006, Dreitz and Knopf 2007) and Montana (e.g., Knowles et al. 1982, Knowles and Knowles 1984, Dinsmore et al. 2002), and ranges from 26% (Knopf and Rupert 1996) to 65% (Graul 1975). Studies examining factors influencing nest survival have found higher survival of nests attended by males rather than females (Dinsmore et al. 2002), that nest survival does not differ with land use, i.e., rangeland

vs. agricultural lands (Dreitz and Knopf 2007), and is independent of the distance from anthropogenic edges (Mettenbrink et al. 2006). Dinsmore et al. (2002) examined the influence of daily weather measures on nest survival of Mountain Plovers in Montana, the northern fringe of the species' range. Their findings suggest that daily precipitation events decreased daily nest survival, i.e., the probability a nest will survive one day, but maximum daily temperature had no effect.

Colorado is considered the stronghold for Mountain Plovers, because over half of the continent's population is believed to breed in the state, particularly on the eastern plains (Kuenning and Kingery 1998). The eastern plains of Colorado is an expansive area of $> 90,000$ km² of shortgrass prairie bordered by the foothills of the Rocky Mountains to the west and the state's borders to the east, north, and south. Drought is the primary ecological driver that maintains the shortgrass prairie ecosystem (Askins et al. 2007) in eastern Colorado. Annual variation in precipitation is the key mechanism influencing the function and structure of the area (Collins et al. 2008). Within-year in spatial variation in precipitation is relatively low at distances < 40 km and nearly equal in magnitude to annual temporal variation at distances of 120-160 km (Augustine 2010). The shortgrass prairie ecosystem experiences extreme weather conditions because of its location inland and east of a large mountain barrier resulting in large inter- and intra-seasonal fluctuations in weather patterns (Pielke and Doesken 2008). Climate models for this area predict a future of hotter and drier summers with strong multiyear droughts and more frequent and severe precipitation events (Matthews 2008).

We examined how seasonal and daily weather conditions influenced nest survival of Mountain Plovers across the eastern plains of Colorado during a 7-yr period. Our objectives were to distinguish whether temperatures and precipitation levels at seasonal or daily time scales influence the outcome of nesting attempts within the core range of Mountain Plovers, and secondly, to determine what weather conditions during the breeding season favored nest survival of Mountain Plovers. Knowledge of how mountain plovers respond to shifts in weather events across their breeding area will be invaluable to inform conservation practices and management agendas in the face of impending climate change.

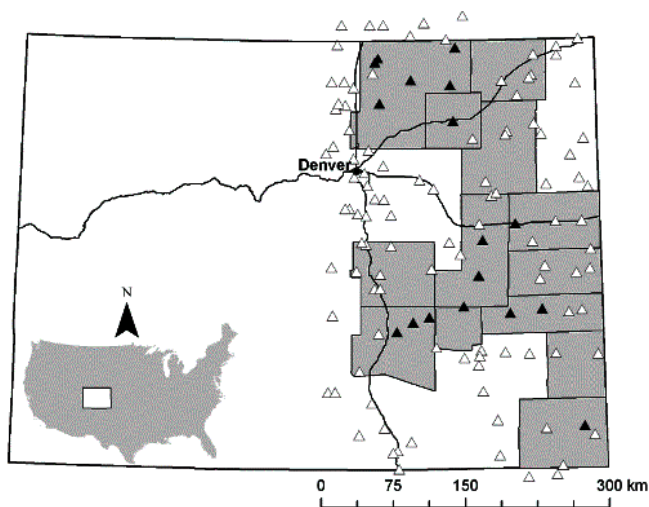
METHODS

Study area

The study area covered 13 counties in the eastern plains of Colorado, USA (Fig. 1) consisting of private and public lands. The eastern Colorado landscape is relatively flat, dominated by rangeland pastures vegetated by low-growing buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*), and grazed to varying degrees by domestic livestock, native

ungulates, and black-tailed prairie dogs (*Cynomys ludovicianus*). Pastures were interspersed with patches of agricultural fields and to a lesser extent, native shrublands and riparian areas. Agricultural fields were comprised predominately of dryland crops with some irrigated crops near arid river systems.

Fig. 1. Map of study area in eastern Colorado and the weather stations that provided data. Mountain Plover (*Charadrius montanus*) nests were located in the shaded counties, mainly on private land. Fewer than 20% of nests were on public land located in the Pawnee National Grassland, which borders Wyoming. Nests were located near the northern and southern borders of Colorado, but none were near the eastern border with Kansas. The nearest weather stations to each nest are shown with closed black triangles. Additional stations, located east of -105.35 degrees longitude, with available data but that were not nearest to nests are shown with open triangles. Black lines represent the major highways in eastern Colorado.



Nesting monitoring

Each year from 2001 to 2006 and in 2009, data collection began in mid-April and continued until the last nest hatched. Study plots were systematically searched for Mountain Plover nests ≥ 4 times throughout the nesting period. We either slowly drove a motorized vehicle or walked, dependent on access requirements, across each pasture or agriculture field and periodically stopped to scan for plovers. Individual adult plovers were observed until they returned to the nest or their behavior indicated they did not have a nest, e.g., flew out of area, exhibited courting behavior, or had chicks present. We defined a nest as a structure with ≥ 1 egg. Multiple nest structures or scrapes may be constructed within a nest site, but

only one nest structure contains eggs (Knopf and Wunder 2006). We marked nests with a small flag and/or “natural” marker consisting of dried cattle droppings or agricultural vegetation.

Nests were checked every 3-12 d until the eggs hatched or failed. Mountain Plovers do not begin incubation until the clutch is complete, with the incubation period lasting ~ 29 d (Dinsmore et al. 2002). Nests were considered successful if ≥ 1 egg hatched, regardless of the size of the clutch. If hatching was not directly observed, evidence at nests such as small eggshell fragments (Mabee 1997) and/or finding young near the nest was used to assess hatching. As with many ground nesting precocial species, the first small eggshell fragments made by the hatching young remain in the nest while the adults remove the larger fragments (Knopf and Wunder 2006). These small “pip chips” are quite visible with their contrasting blue-green and white coloration. Nests were classified as failed when no small eggshell fragments were present in the nest, eggs were missing or broken, or the adult abandoned the nest. In 2004-2009, nests were checked more often as hatch date approached, resulting in increased accuracy of hatch date estimation.

Weather variables

We obtained daily precipitation and temperature values from the weather station closest to each nest. Stations (Fig. 1) were administered by the National Oceanic and Atmospheric Administration (NOAA; data requested from www.ncdc.noaa.gov/oa/climate/stationlocator.html), the Shortgrass Steppe Long Term Ecological Research project, and U.S. Department of Agriculture-Agricultural Research Service. If weather data in a given day were unavailable from the nearest weather station, we used data from the next nearest station. Because the timing of data collection differed among stations (00:00–00:30, 06:00–08:00, or 17:00–18:00 hours), some measurements were offset by one day so that nest fate was associated with the most recent minimum temperature (early morning $\sim 05:00$), maximum temperature (previous afternoon), and precipitation event (previous afternoon). The distance between weather stations and nests was < 42 km; at these distances, spatial variation in precipitation within a year is relatively low compared with annual variation (Augustine 2010). Daily values were averaged (for temperature) or summed (for precipitation) over May–June, encompassing 90% of the nesting season, to produce seasonal values.

Data analysis

Daily nest survival (DNS), the probability that a nest will survive a single day, was calculated using the nest survival model in Program MARK, version 5.1 (White and Burnham 1999). Daily nest survival could be influenced by a large number of patterns in daily and seasonal weather conditions. To limit the number of models evaluated, we developed a set of a priori biological hypotheses and used these to choose

Table 1. Explanatory variables used to model daily nest survival of Mountain Plovers (*Charadrius montanus*).

Daily Variable		Seasonal Variable	
Variable Name	Variable Name	Variable Name	Variable Name
Precipitation			
Precip	daily precipitation	TotalPcp	total precipitation
Over5mm [†]	day had ≥ 5 mm rain	Days5mm	# days with ≥ 5 mm rain
Over10mm [†]	day had ≥ 10 mm rain	Days10mm	# days with ≥ 10 mm rain
0mm [†]	day had no rain	Days0mm	# days with no rain
5DayDrought [†]	5+ consec. days w/ total rain ≤ 1 mm		
7DayDrought [†]	7+ consec. days w/ total rain ≤ 1 mm		
10DayDrought [†]	10+ consec. days w/ total rain ≤ 1 mm		
Temperature			
MinTemp	daily minimum temp	AvgMin	average daily minimum temp
MaxTemp	daily maximum temp	AvgMax	average daily maximum temp
MeanTemp	daily mean temp	AvgMean	average daily mean temp
TempRange	daily temp range (max – min)	AvgRange	average daily temp range
Over29C [†]	day had max temp ≥ 29°C	Days29C	# days with max temp ≥ 29°C
Over32C [†]	day had max temp ≥ 32°C	Days32C	# days with max temp ≥ 32°C
Over35C [†]	day had max temp ≥ 35°C	Days35C	# days with max temp ≥ 35°C
Under0C [†]	day had min temp ≤ 0°C	Days0C	# days with min temp ≤ 0°C
Under4C [†]	day had min temp ≤ 4°C	Days4C	# days with min temp ≤ 4°C
Time-in-Season			
Time	linear trend (day 1 – 110)		
Year			
		2001-2003 [†]	2001-2003 vs. 2004-2009

Seasonal weather variables were created by summing or averaging daily values for May–June of each year. For each daily weather variable, 1-day lag effects (previous day’s weather) were also modeled. Droughts were defined as periods when at least 5, 7, or 10 days had passed with ≤ 1 mm total rainfall. Hatch dates were known with greater accuracy beginning in 2004 because nests were visited more often as hatch date approached. Quadratic effects were modeled for continuous variables when AIC_c-based model selection indicated at least moderate support for the main effect (Appendix 1).

[†] = binary variable.

explanatory variables (Table 1) and guide construction of the model set (Appendix 1). The types of weather variables that we considered to have the greatest potential influence on DNS, based on the scientific literature for plovers and other grassland and shrubsteppe bird species, were daily precipitation, daily temperature, seasonal precipitation, and seasonal temperature (Rotenberry and Wiens 1989, George et al. 1992, Dinsmore et al. 2002). Within each of these four categories, we included variables such as total daily precipitation, daily maximum temperature, total precipitation during the breeding season, and average daily maximum temperature during the breeding season, respectively. Two additional climate-related variables, time-in-season and year, were also included in the model set (Table 1) because previous studies suggested their importance to DNS (Dinsmore et al. 2002, Davis 2005, Grant et al. 2005, Dreitz and Knopf 2007).

We first ran univariate models to evaluate the importance of time-in-season (linear or quadratic) and year and to identify the weather variables in each category that best explained DNS. Akaike’s information criterion for small samples (AIC_c) was used to infer support for the models (Akaike 1973, Burnham and Anderson 2002). We selected the weather variables that appeared in univariate models with $\Delta AIC_c \leq 2$ within each weather category. If no variables met this criterion

because none of them improved the model beyond a constant survival model, we selected the top two (minimum AIC_c) variables within that weather category. We then developed additive models with the selected weather effects, time-in-season, and year (Table 1), including a maximum of one weather variable per category. We thought that threshold effects might occur for some continuous variables; for example, very low and very high temperatures might be associated with lower daily nest survival, with higher nest survival at moderate temperatures. Therefore, quadratic effects were modeled for continuous variables when AIC_c-based model selection indicated at least moderate support for the main effect (Appendix 1). If two variables were highly correlated ($r \geq 0.7$), only one was included within a given model.

We calculated nest success as DNS^x, where x is the number of days of incubation (29 in Mountain Plovers) following Dinsmore et al. (2002) and Dreitz and Knopf (2007). Dates were scaled so that day 1 was the first date when a nest was found (Apr 18) during the study. In total, we considered 94 candidate models and used the logit link function to evaluate covariate effects on DNS (Appendix 1). Because nest survival data are a known fate data type, a saturated model with one parameter per day for each nest would fit the data perfectly;

Table 2. Nest survival models for Mountain Plover (*Charadrius montanus*). We ran 94 models with minimum AICc = 2204.43 for the model set. Models with weight ≥ 0.05 are shown. All models contain an intercept.

Model	ΔAIC_c	w_i	K	Deviance
Time + 10DayDrought + MaxTemp	0	0.13	4	2196.43
Time + 10DayDrought + MaxTemp + TotalPcp	0.13	0.12	5	2194.56
Time + 10DayDrought + MaxTemp + Days10mm	0.96	0.08	5	2195.39
Time + Time ² + 10DayDrought + LagOver35C	1.15	0.07	5	2195.58
Time + Time ² + 10DayDrought + MaxTemp	1.22	0.07	5	2195.65
Time + 10DayDrought + LagOver35C	1.36	0.06	4	2197.78
Time + Time ² + 10DayDrought + MaxTemp + TotalPcp	1.47	0.06	6	2193.89
Time + Time ² + 10DayDrought + LagOver35C + TotalPcp	1.47	0.06	6	2193.90
Time + 10DayDrought + LagOver35C + TotalPcp	1.61	0.06	5	2196.03
Time + 10DayDrought + MaxTemp + MaxTemp ²	1.83	0.05	5	2196.25

The top ranked model included time-in-season (linear trend beginning 18 April), daily precipitation (binary variable indicating drought occurrence, defined as ≥ 10 consecutive days with ≤ 1 mm total rainfall), and daily maximum temperature ($^{\circ}\text{C}$). Lower ranked models included seasonal precipitation (total precipitation and number of days with ≥ 10 mm rain), an alternative maximum temperature variable (previous day's maximum $\geq 35^{\circ}\text{C}$), and quadratic effects of time-in-season and maximum temperature.

therefore, there is no goodness-of-fit test implemented in Program MARK for nest survival models (Dinsmore et al. 2002, Rotella 2011).

RESULTS

Over the seven years of the study, we monitored the fate of 936 nests, ranging from 92 nests in 2001 to 215 nests in 2006. Only 35 nests were monitored in 2009 because of the specific study objective for this year. Average DNS was 0.956 (SE = 0.002), and nest success over the 29-day incubation period was 0.272 (SE = 0.016). The earliest and latest days of nest activity from 2001-2009 were 18 April-6 August, with $> 90\%$ of the nesting season occurring May-June.

Mountain Plover DNS was best predicted by time-in-season and daily weather conditions (Table 2) with higher survival rates early in the nesting season, during dry periods, and on cooler days (Fig. 2, Table 3). Daily precipitation effects were best modeled using droughts when ≥ 10 days had passed with ≤ 1 mm total rainfall (10DayDrought), with strong positive effects of drought on DNS (Tables 2, 3, Appendix 2). Daily temperature effects were best modeled using daily maximum temperature (MaxTemp) or days when the previous afternoon's temperature exceeded 35°C (LagOver35C), with strong negative effects of heat on DNS. Daily minimum temperature (MinTemp) was correlated with time-in-season ($r = 0.79$); because time-in-season had a stronger effect on DNS than minimum temperature, we removed minimum temperature from the final analyses. Models containing minimum temperature instead of time had $\Delta AIC_c \geq 7$ and weight < 0.004 (Appendix 1).

Seasonal climate variables were not useful predictors of Mountain Plover DNS. The best seasonal precipitation variables were total precipitation (TotalPcp) and number of

days with ≥ 10 mm rain (Days10mm). Both variables had weak negative effects on DNS (lower DNS in wetter seasons: Table 3) but did not improve upon the top-ranked model (Table 2). The best seasonal temperature variable, number of days with maximum temperature $\geq 32^{\circ}\text{C}$ (DaysOver32C), appeared only in a model with $\Delta AIC_c > 45$ and weight near zero (Appendix 1).

Fig. 2. Daily nest survival of Mountain Plovers (*Charadrius montanus*) in eastern Colorado, 2001-2009, as a function of daily maximum temperature, drought, and time-in-season. Dry periods were defined as droughts in which ≥ 10 consecutive days had ≤ 1 mm total precipitation, while wet periods had > 1 mm total precipitation. Days 21 (early = 8 May) and 58 (late = 14 June) were the 12.5% and 87.5% points in the nesting season and thus bound the middle 75% of nest activity. Nest survival over the entire nesting period = (daily nest survival)²⁹.

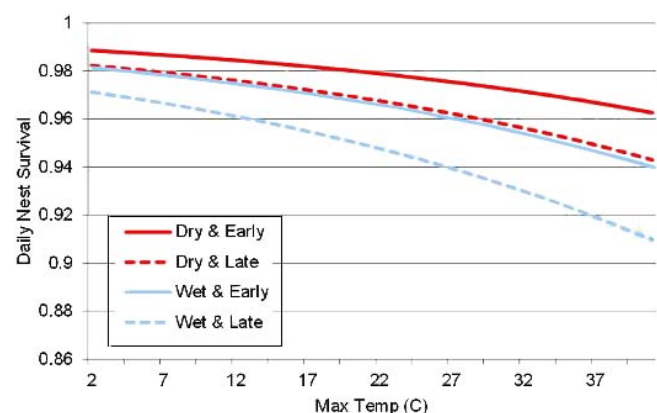


Table 3. Coefficient estimates for the top three models ($\Delta AIC_c < 1$) with weights totaling 0.322 used to calculate the logit of daily nest survival probability of Mountain Plover (*Charadrius montanus*).

Model	Variable	β Estimate \pm SE	95% CI
Time + 10DayDrought + MaxTemp	Time	-0.012 \pm 0.003	(-0.019, -0.005)
	10DayDrought	0.498 \pm 0.161	(0.182, 0.814)
	MaxTemp	-0.031 \pm 0.013	(-0.056, -0.006)
	Intercept	4.276 \pm 0.293	(3.703, 4.850)
Time + 10DayDrought + MaxTemp + TotalPcp	Time	-0.011 \pm 0.003	(-0.018, -0.005)
	10DayDrought	0.467 \pm 0.163	(0.148, 0.785)
	MaxTemp	-0.034 \pm 0.013	(-0.059, -0.009)
	TotalPcp	-0.002 \pm 0.001	(-0.005, 0.001)
	Intercept	4.499 \pm 0.338	(3.836, 5.162)
Time + 10DayDrought + MaxTemp + Days10mm	Time	-0.012 \pm 0.003	(-0.018, -0.005)
	10DayDrought	0.466 \pm 0.164	(0.144, 0.787)
	MaxTemp	-0.032 \pm 0.013	(-0.057, -0.007)
	Days10mm	-0.030 \pm 0.029	(-0.087, 0.027)
	Intercept	4.368 \pm 0.307	(3.765, 4.970)

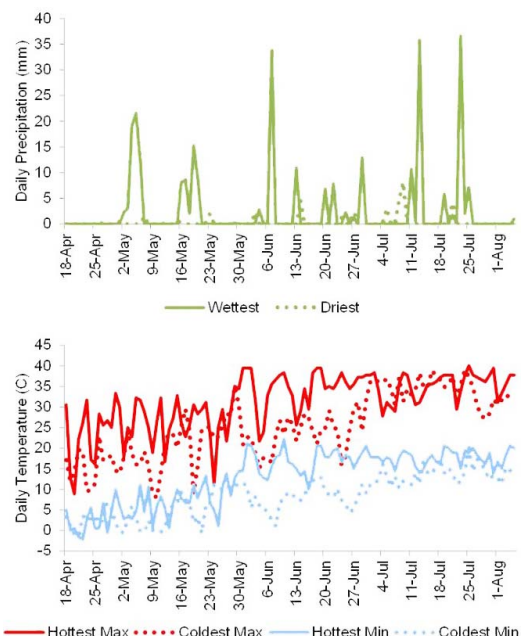
The top ranked models include a linear trend throughout the breeding season starting with 18 April (Time), ≥ 10 consecutive days with ≤ 1 mm total rainfall (10DayDrought), daily maximum temperature ($^{\circ}\text{C}$; MaxTemp), total precipitation during May and June (mm; TotalPcp), and ≥ 10 consecutive days with ≥ 10 mm precipitation (Days10mm). Coefficients for additional models are shown in Appendix 2.

For perspective on weather conditions during our study, 75.7% of days had no rainfall, droughts lasted up to 45 days, and droughts lasting at least 10 days occurred in each year of the study. Daily precipitation (Fig. 3) averaged 1.59 ± 5.13 mm and ranged from 0 - 71.12 mm over all sites and years. Maximum temperature (Fig. 3) averaged $27.7 \pm 7.4^{\circ}\text{C}$ and ranged from 2.2 - 41.1°C ; 18.4% of days exceeded 35°C , occurring in late May-August. The earliest occurrence of a 35°C day advanced monotonically during the study from 9 June in 2001 to 19 May in 2009.

DISCUSSION

Daily precipitation depressed nest survival of Mountain Plovers both in the core of the species' range in eastern Colorado (this study) and at the northern edge of their range in Montana (Dinsmore et al. 2002). The role of drought as an ecological driver of plover population recruitment is further supported by the correlation of annual survival of adult Mountain Plovers with dry climatic conditions (Dinsmore 2008) and drought-induced recruitment of young (Wunder 2007). The Colorado and Montana nest survival studies differed in the actual metric that best described the relationship; the best-fitting daily precipitation metric in our study was an extended lack of precipitation (droughts when ≥ 10 days had passed with ≤ 1 mm total rainfall), whereas Dinsmore et al. (2002) reported lower survival with rain events ≥ 2.54 cm.

Fig. 3. Range of daily precipitation, maximum and minimum temperature values for eastern Colorado in 2001–2009. Wettest season: 2001. Driest season: 2002. Hottest season: 2002. Coldest season: 2003.



The effect of temperature on nest survival differed among studies, with cooler temperatures favoring nest survival of plovers in Colorado (this study) but no effect of temperature in Montana (Dinsmore et al. 2002). The inconsistency in the role of temperature between Colorado and Montana might be explained by the average breeding season temperatures in the two locales, with long-term average and maximum temperatures in our study area averaging higher than those near the study site of Dinsmore et al. (2002) in north central Montana by 1.9°C and 2.4°C, respectively (www.wrcc.dri.edu/COMPARATIVE.html). The higher temperatures in Colorado might expose plovers or their eggs to heat stress.

Precipitation and temperature likely influence the behavior of plovers, their prey, and their nest predators. Predation is the primary cause of nest failure across the range of the Mountain Plover and thus drives nest survival rates (Dinsmore et al. 2002, Dreitz and Knopf 2007). Higher nest mortality under wet conditions may result from higher activity levels and enhanced olfactory sensitivity of nest predators in wet than dry conditions (Dinsmore et al. 2002).

Climate change may exacerbate population declines in Mountain Plovers and result in shifts in distribution and changes in local abundance and fecundity. Temperatures across Colorado have increased by 1.1°C in the past 30 years, and continued warming of 2.2°C is expected by 2050 (Ray et al. 2008), potentially compromising nest survival. However, climate models for Colorado project seasonal shifts in precipitation with greater midwinter but decreased late spring and summer precipitation (Ray et al. 2008), potentially favoring nest survival. The frequency of extreme events such as droughts and intense rainstorms is predicted to increase, and the highly variable climate characterizing the Great Plains is projected to become even more variable (Ojima and Lockett 2002, Shortgrass Steppe Long Term Ecological Research 2010). Within the range of weather parameters recorded in this study, lower precipitation likely would favor Mountain Plover abundance and nest survival, but higher temperatures may apply negative selective pressures. Predicted increases in intense rain events, associated with lower nest survival of Mountain Plovers in Montana (Dinsmore et al. 2002), also may disfavor plover fecundity.

Changes in climate can modify aboveground vegetation structure and habitat suitability for prairie birds. Although one might presume that shortgrass prairie conditions may trend toward more extensive bare ground as temperatures and evapotranspiration rates rise and summer precipitation declines, recent evidence is to the contrary. Rather, as storm intensity increases, soil moisture and aboveground net primary productivity are predicted to increase, and proportional evaporative water loss to decrease, even if storms are separated by longer droughts (Knapp et al. 2008, Heisler-White et al. 2009).

Climate-related responses in breeding performance of Mountain Plovers likely result from direct effects on eggs, chicks, and adults, as well as indirect effects on vegetation structure, insect availability, and predator abundance and behavior. Nest survival is ultimately driven by factors affecting nest predators, such as coyote (*Canis latrans*), swift fox (*Vulpes velox*), and bull snake (*Pituophis catenifer*), and their alternate prey (Schmidt 1999). As climate variability increases across the Great Plains, investigations on how ambient temperature and rainfall affect predator activity levels and hunting efficiencies could provide insights into climate change impacts on bird communities.

Mountain Plovers have adapted to habitat fragmentation across prairie ecosystems by readily using agricultural fields for breeding activity (Knopf and Wunder 2006, Dreitz and Knopf 2007). Agriculture, defined as the production of livestock and crops for human food consumption, is the primary land use of prairie ecosystems in North America. Agricultural processes and mechanisms will also be impacted by climate change. Predicting the impacts of changes in prairie ecosystems produced by climate change and the associated changes in agricultural practices should also be considered when forecasting the response of Mountain Plover, or any species reliant on prairie ecosystems, to climate change.

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<http://www.ace-eco.org/vol7/iss1/art6/responses/>

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APPENDIX 1. Nest survival models for Mountain Plover (*Charadrius montanus*). We ran 94 models with minimum AICc = 2204.431 for the model set. All models contain an intercept.

Model	ΔAIC_c	w_i	K	Deviance
Time + 10DayDrought + MaxTemp	0	0.126	4	2196.426
Time + 10DayDrought + MaxTemp + TotalPcp	0.133	0.118	5	2194.557
Time + 10DayDrought + MaxTemp + Days10mm	0.961	0.078	5	2195.386
Time + Time ² + 10DayDrought + LagOver35C	1.152	0.071	5	2195.577
Time + Time ² + 10DayDrought + MaxTemp	1.223	0.068	5	2195.648
Time + 10DayDrought + LagOver35C	1.357	0.064	4	2197.783
Time + Time ² + 10DayDrought + MaxTemp + TotalPcp	1.468	0.061	6	2193.890
Time + Time ² + 10DayDrought + LagOver35C + TotalPcp	1.474	0.060	6	2193.895
Time + 10DayDrought + LagOver35C + TotalPcp	1.608	0.056	5	2196.032
Time + 10DayDrought + MaxTemp + MaxTemp ²	1.826	0.051	5	2196.250
Time + Time ² + 10DayDrought + MaxTemp + Days10mm	2.231	0.041	6	2194.653
Time + Time ² + 10DayDrought + LagOver35C + Days10mm	2.389	0.038	6	2194.811
Time + 10DayDrought + LagOver35C + Days10mm	2.539	0.035	5	2196.963
Time + Time ² + 10DayDrought + MaxTemp + MaxTemp ²	3.206	0.025	6	2195.628
Time + 10DayDrought	4.369	0.014	3	2202.798
Time + Time ² + 10DayDrought	4.903	0.011	4	2201.330
Time + Lag10DDrought	5.371	0.009	3	2203.799
Time + 10DayDrought + TotalPcp	5.570	0.008	4	2201.996
Time + 10DayDrought + Days10mm	5.683	0.007	4	2202.110
Time + Time ² + Lag10DDrought	5.737	0.007	4	2202.163
Time + Time ² + 10DayDrought + TotalPcp	6.190	0.006	5	2200.614
Time + Time ² + 10DayDrought + Days10mm	6.262	0.006	5	2200.687
Time + Time ² + LagOver35C	6.890	0.004	4	2203.317
MinTemp + 10DayDrought	6.987	0.004	3	2205.415
Time + 10DayDrought + TotalPcp + TotalPcp ²	7.036	0.004	5	2201.460
Time + 10DayDrought + Days10mm + Days10mm ²	7.685	0.003	5	2202.110
Time + Time ² + 10DayDrought + TotalPcp + TotalPcp ²	7.690	0.003	6	2200.112
MinTemp + Lag10DDrought	8.035	0.002	3	2206.463
Time + Time ² + 10DayDrought + Days10mm + Days10mm ²	8.256	0.002	6	2200.678
Time + LagOver35C	8.347	0.002	3	2206.775
MinTemp + MinTemp ² + 10DayDrought	8.462	0.002	4	2204.889
Time + Time ² + MaxTemp	8.586	0.002	4	2205.013
Time + MaxTemp	8.643	0.002	3	2207.071
Time + Time ²	8.792	0.002	3	2207.220
Time + Time ² + Days10mm	9.013	0.001	4	2205.439
Time + Time ² + TotalPcp	9.121	0.001	4	2205.548
Time + Days10mm	9.264	0.001	3	2207.692
Time + TotalPcp	9.284	0.001	3	2207.712
Time	9.287	0.001	2	2209.716
MinTemp + MinTemp ² + Lag10DDrought	9.558	0.001	4	2205.985
Time + Days32C	11.003	0.001	3	2209.431
Time + 2001to2003	11.241	0.000	3	2209.669
Time + AvgMax	11.250	0.000	3	2209.678
MinTemp + Days10mm	14.739	0.000	3	2213.167
MinTemp + 2001to2003	15.023	0.000	3	2213.451
MinTemp	15.026	0.000	2	2215.456

MinTemp + TotalPcp	15.424	0.000	3	2213.852
MinTemp + AvgMax	15.500	0.000	3	2213.929
MinTemp + Days32C	15.585	0.000	3	2214.013
MinTemp + MinTemp ²	16.645	0.000	3	2215.073
LagMinTemp	17.833	0.000	2	2218.262
MeanTemp	17.935	0.000	2	2218.364
LagMeanTemp	22.311	0.000	2	2222.741
MaxTemp	25.673	0.000	2	2226.103
LagOver35C	26.103	0.000	2	2226.533
Under4C	27.355	0.000	2	2227.784
LagOver32C	27.858	0.000	2	2228.287
Over32C	29.051	0.000	2	2229.480
LagMaxTemp	30.110	0.000	2	2230.539
LagUnder4C	32.887	0.000	2	2233.317
Over29C	33.235	0.000	2	2233.665
LagOver29C	35.108	0.000	2	2235.538
10DayDrought	35.237	0.000	2	2235.667
Lag10DDrought	36.640	0.000	2	2237.069
Lag7DDrought	39.201	0.000	2	2239.630
7DayDrought	39.383	0.000	2	2239.812
Over35C	39.426	0.000	2	2239.856
Under0C	41.389	0.000	2	2241.819
LagUnder0C	41.727	0.000	2	2242.157
Lag5DDrought	41.730	0.000	2	2242.159
Days10mm	41.866	0.000	2	2242.295
TotalPcp	42.465	0.000	2	2242.894
5DayDrought	43.212	0.000	2	2243.641
Constant	44.173	0.000	1	2246.603
Lag5mm	44.436	0.000	2	2244.866
LagPrecip	44.697	0.000	2	2245.126
Over5mm	44.807	0.000	2	2245.236
Precip	45.076	0.000	2	2245.506
Days32C	45.183	0.000	2	2245.613
2001to2003	45.240	0.000	2	2245.670
Lag10mm	45.562	0.000	2	2245.992
AvgMax	45.576	0.000	2	2246.006
Days35C	45.588	0.000	2	2246.017
AvgMean	45.606	0.000	2	2246.035
Days29C	45.685	0.000	2	2246.115
AvgRange	45.739	0.000	2	2246.169
Days4C	45.901	0.000	2	2246.330
AvgMin	45.901	0.000	2	2246.331
Days0C	45.915	0.000	2	2246.344
0mm	46.069	0.000	2	2246.498
LagTempRange	46.075	0.000	2	2246.504
TempRange	46.108	0.000	2	2246.537
Over10mm	46.164	0.000	2	2246.593
Lag0mm	46.173	0.000	2	2246.603

Variables are defined in Table 1.

APPENDIX 2. Coefficient estimates used to calculate the logit of daily nest survival probability for models with $\Delta AICc \leq 2$ and weights ≥ 0.05 . Weights for these models total 0.753.

Model	Variable	β Estimate \pm SE	95% CI
Time + 10DayDrought + MaxTemp	Time	-0.012 \pm 0.003	(-0.019, -0.005)
	10DayDrought	0.498 \pm 0.161	(0.182, 0.814)
	MaxTemp	-0.031 \pm 0.013	(-0.056, -0.006)
	Intercept	4.276 \pm 0.293	(3.703, 4.850)
Time + 10DayDrought + MaxTemp + TotalPcp	Time	-0.011 \pm 0.003	(-0.018, -0.005)
	10DayDrought	0.467 \pm 0.163	(0.148, 0.785)
	MaxTemp	-0.034 \pm 0.013	(-0.059, -0.009)
	TotalPcp	-0.002 \pm 0.001	(-0.005, 0.001)
	Intercept	4.499 \pm 0.338	(3.836, 5.162)
Time + 10DayDrought + MaxTemp + Days10mm	Time	-0.012 \pm 0.003	(-0.018, -0.005)
	10DayDrought	0.466 \pm 0.164	(0.144, 0.787)
	MaxTemp	-0.032 \pm 0.013	(-0.057, -0.007)
	Days10mm	-0.030 \pm 0.029	(-0.087, 0.027)
	Intercept	4.368 \pm 0.307	(3.765, 4.970)
Time + Time ² + 10DayDrought + LagOver35C	Time	-0.032 \pm 0.014	(-0.059, -0.005)
	Time ²	0.0002 \pm 0.0001	(-0.0001, 0.0005)
	10DayDrought	0.420 \pm 0.159	(0.108, 0.731)
	LagOver35C	-0.635 \pm 0.239	(-1.102, -0.167)
	Intercept	3.943 \pm 0.306	(3.343, 4.543)
Time + Time ² + 10DayDrought + MaxTemp	Time	-0.024 \pm 0.014	(-0.052, 0.004)
	Time ²	0.0001 \pm 0.0001	(-0.0002, 0.0004)
	10DayDrought	0.475 \pm 0.163	(0.155, 0.795)
	MaxTemp	-0.030 \pm 0.013	(-0.055, -0.005)
	Intercept	4.487 \pm 0.382	(3.739, 5.235)
Time + 10DayDrought + LagOver35C	Time	-0.013 \pm 0.003	(-0.020, -0.007)
	10DayDrought	0.449 \pm 0.158	(0.139, 0.759)
	LagOver35C	-0.598 \pm 0.243	(-1.073, -0.122)
	Intercept	3.553 \pm 0.141	(3.277, 3.829)
Time + Time ² + 10DayDrought + MaxTemp + TotalPcp	Time	-0.022 \pm 0.014	(-0.050, 0.005)
	Time ²	0.0001 \pm 0.0001	(-0.0002, 0.0004)
	10DayDrought	0.448 \pm 0.164	(0.126, 0.769)
	MaxTemp	-0.033 \pm 0.013	(-0.058, -0.008)
	TotalPcp	-0.002 \pm 0.001	(-0.005, 0.001)
	Intercept	4.689 \pm 0.415	(3.877, 5.502)

Time + Time ² + 10DayDrought + LagOver35C + TotalPcp		
Time	-0.031 ± 0.014	(-0.058, -0.005)
Time ²	0.0002 ± 0.0001	(-0.0001, 0.0005)
10DayDrought	0.388 ± 0.160	(0.074, 0.702)
LagOver35C	-0.695 ± 0.240	(-1.165, -0.224)
TotalPcp	-0.002 ± 0.001	(-0.005, 0.001)
Intercept	4.075 ± 0.323	(3.443, 4.707)
Time + 10DayDrought + LagOver35C + TotalPcp		
Time	-0.013 ± 0.003	(-0.019, -0.006)
10DayDrought	0.415 ± 0.160	(0.101, 0.728)
LagOver35C	-0.660 ± 0.244	(-1.138, -0.182)
TotalPcp	-0.002 ± 0.001	(-0.005, 0.001)
Intercept	3.695 ± 0.177	(3.347, 4.043)
Time + 10DayDrought + MaxTemp + MaxTemp ²		
Time	-0.012 ± 0.003	(-0.019, -0.005)
10DayDrought	0.499 ± 0.162	(0.182, 0.816)
MaxTemp	-0.071 ± 0.099	(-0.265, 0.124)
MaxTemp ²	0.001 ± 0.002	(-0.003, 0.004)
Intercept	4.774 ± 1.277	(2.271, 7.277)

Variables are defined in Table 1.