



Extremes of heat, drought and precipitation depress reproductive performance in shortgrass prairie passerines

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Climate change elevates conservation concerns worldwide because it is likely to exacerbate many identified threats to animal populations. In recent decades, grassland birds have declined faster than other North American bird species, a loss thought to be due to habitat loss and fragmentation and changing agricultural practices. Climate change poses additional threats of unknown magnitude to these already declining populations. We examined how seasonal and daily weather conditions over 10 years influenced nest survival of five species of insectivorous passerines native to the shortgrass prairie and evaluate our findings relative to future climate predictions for this region. Daily nest survival ($n = 870$) was best predicted by a combination of daily and seasonal weather variables, age of nest, time in season and bird habitat guild. Within a season, survival rates were lower on very hot days (temperatures ≥ 35 °C), on dry days (with a lag of 1 day) and on stormy days (especially for those species nesting in shorter vegetation). Across years, survival rates were also lower during warmer and drier breeding seasons. Clutch sizes were larger when early spring temperatures were cool and the week prior to egg-laying was wetter and warming. Climate change is likely to exacerbate grassland bird population declines because projected climate conditions include rising temperatures, more prolonged drought and more intense storms as the hydrological cycle is altered. Under varying realistic scenarios, nest success estimates were halved compared to their current average value when models both increased the temperature (3 °C) and decreased precipitation (two additional dry days during a nesting period), thus underscoring a sense of urgency in identifying and addressing the current causes of range-wide declines.

Keywords: climate change, clutch size, grassland birds, nest survival, reproductive success, temperature, weather.

Scientists increasingly agree that there is compelling, comprehensive and consistent evidence of anthropogenic climate change, the warming of the planet and alterations in Earth's hydrological cycles (Gleick *et al.* 2010). These changes lead to cascading events in diverse ecosystems worldwide, and affect individuals, populations and species. Changing climate alters many aspects of a species' ecological niche, including the phenology, composition and abundance of

the food supply, the foraging patterns of local predators and habitat structure as vegetation responds to changes in weather patterns (Crick 2004, Parmesan 2006). Depending on both the magnitude of climate change and the breadth of a given species' ecological niche, one might expect differential impacts. Some species may retain site fidelity but exhibit plasticity in resource use, whereas others may redistribute to new areas with suitable environmental conditions (Nicotra *et al.* 2015). Regardless of movement patterns, species may experience strong demographic consequences.

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The shortgrass prairie ecosystem of North America experiences extreme weather conditions because of its inland location east of a large mountain barrier, resulting in large inter- and intra-seasonal fluctuations in weather patterns (Pielke & Doesken 2008). Climate models for this region predict a future of hotter and drier summers (Lukas *et al.* 2014). Across Colorado, temperatures have increased about 1.1 °C in the past 30 years, and climate models project continued warming (from a 1950–99 baseline) of 2.2 °C by 2050 (Ray *et al.* 2008) and 2–7 °C by 2100, depending on emissions scenarios (Denning pers. comm., <http://biocycle.atmos.colostate.edu/shiny/gaussian/>). Seasonal shifts in precipitation are projected to yield greater midwinter but reduced late spring and summer precipitation (Lukas *et al.* 2014). The frequency of extreme events such as droughts and intense rainstorms is predicted to increase (Karl *et al.* 2008), and the highly variable climate characterizing the Great Plains is projected to become even more variable (Shortgrass Steppe Long Term Ecological Research 2010, Lukas *et al.* 2014).

Birds endemic to the North American shortgrass prairies have evolved under extreme climate variability and have evolved mechanisms to cope with such unpredictability. Understanding the reproductive consequences of weather-related phenomena (e.g. drought, storms) may yield insights into how animals might respond to future changes in climate. Policy-makers and managers tasked with conserving biodiversity can use empirical information on how avian communities respond to weather, including extreme events, across their breeding areas to inform conservation in the face

of impending climate change (Glick *et al.* 2011, Stein *et al.* 2014).

Potential negative effects of climate change on birds can be exacerbated by ongoing anthropogenic alterations of habitat structure and quality. Native grassland landscapes in North America, expansive and structurally diverse prior to European settlement, are now fragmented, structurally homogeneous and interspersed with agricultural fields (Lomolino *et al.* 2001, Brockway *et al.* 2002, Brennan & Kuvlesky 2005). The Homestead Act of 1862 attracted 1.5 million people, many to the Great Plains region, to acquire native prairie land and convert it to agricultural uses. By 2000, nearly 70% of untilled grassland systems across the Great Plains were lost, including about 50% of the shortgrass prairie (Samson *et al.* 2004). Grasslands have been altered to a greater extent than any other biome in North America, and populations of their associated avifauna have declined more rapidly than any other avian guild over the past century (Knopf 1994, Samson *et al.* 2004). Climate change poses additional threats of unknown magnitude to these already declining populations, including exposure to invasive species, disruption of community interactions, challenges to reproductive performance, and mismatch in timing of seasonal activities and resources (Walther *et al.* 2002, Crick 2004, Parmesan 2006).

We examined how seasonal and daily weather conditions influenced nest survival of five declining passerine species of northern Colorado shortgrass prairies over 10 non-consecutive years between 1997 and 2012 (Table 1). Our objectives were to assess whether temperature and precipitation at

Table 1. Study area details, sample sizes and distances from nests to the nearest weather station for grassland passerines in northern Colorado, USA, 1997–2012.

Study areas (location)	Years	Number (size) of plots	Number of nests	Distance to nearest weather station (in km; mean ± sd, (range))
Pawnee National Grassland, Weld County, CO, USA 40°34'–41°00'N, 103°30'–104°50'W	1997–1999, 2001	33 (64.7 ha)	165	17.96 ± 5.13 (7.82–26.14)
Washington County, CO, USA 39°34'–40°27'N, 102°48'–103°28'W	2000	20 (7–200 ha)	98	15.62 ± 8.08 (1.59–30.25)
Soapstone Prairie Natural Area, Larimer County, CO, USA 40°57'–41°00'N, 105°00'–105°09'W	2006–2007, 2010	8 (56.3 ha)	322	15.46 ± 1.73 (12.18–18.26)
Central Plains Experimental Range, Weld County, CO, USA 40°47'–40°52'N, 104°40'–104°47'W	2011–2012	12 (3 × 64.7 ha, 9 × 16.2 ha)	285	2.34 ± 1.31 (0.35–5.88)

seasonal or daily time scales influence the outcome of nesting attempts, to determine what weather conditions during the breeding season favour nest survival, and to project overall nest survival based on likely future climate scenarios for the region. We also examined how spring and breeding season weather conditions influence clutch size.

METHODS

Study area

The study area in north-central and northeastern Colorado, USA, is located in the shortgrass steppe, the driest and warmest part of the USA's central grasslands (Lauenroth & Burke 1995, Pielke & Doesken 2008). Land cover included crop fields, shortgrass prairie and Conservation Reserve Program (CRP) lands. Sampling occurred across 10 non-consecutive breeding seasons between 1997 and 2012 at four sites: Pawnee National Grassland in Weld County, private lands in Washington County, Soapstone Prairie Natural Area in Larimer County and the Central Plains Experimental Range in Weld County (Table 1). Study sites included 58 shortgrass prairie, eight mixed-grass prairie and seven CRP study plots. Land ownership was a mixture of public (USDA Forest Service manages Pawnee National Grassland, City of Fort Collins Natural Areas Program manages Soapstone Prairie and the USDA Agricultural Research Service manages the Central Plains Experimental Range) and private (Washington County). Dryland wheat fields were the main cover type surrounding study plots in Washington County, shortgrass prairie was the dominant matrix in Pawnee National Grassland and Central Plains Experimental Range, and a mixture of short and mixed grasses surrounded the Soapstone Prairie study plots. Most prairie study plots were grazed by cattle at low to moderate stocking densities (≤ 0.6 animal unit months (AUM)/ha). Shortgrass prairie was dominated by xeric C_4 grasses, especially Blue Grama *Bouteloua gracilis* and Buffalograss *Bouteloua dactyloides*, with an occasional shrub component. Mixed-grass prairie and CRP fields contained grasses that are taller than native shortgrasses, mainly C_3 grasses such as Western Wheatgrass *Pascopyrum smithii* and Needle-and-thread *Hesperostipa comata* (mixed-grass prairie) and exotic Smooth Brome *Bromus inermis*, Intermediate Wheatgrass *Thinopyrum*

intermedium and Crested Wheatgrass *Agropyron cristatum* (CRP fields).

Our focal bird species were Horned Lark *Eremophila alpestris*, McCown's Longspur *Rhynchophanes mccownii*, Chestnut-collared Longspur *Calcarius ornatus*, Lark Bunting *Calamospiza melanocorys* and Western Meadowlark *Sturnella neglecta*. Of these five species, three are considered endemic to the Great Plains and two (Horned Lark and Western Meadowlark) are more widespread in distribution (Knopf 1996). Populations of all five species declined significantly within the Central Breeding Bird Survey Region between 1966 and 2013 (Sauer *et al.* 2014). Nests of all species were dispersed across the study sites except that no McCown's Longspur nests were found in Washington County and no Chestnut-collared Longspur nests were found at Soapstone Prairie or the Central Plains Experimental Range. Survival of Lark Bunting broods from the Pawnee National Grassland was reported elsewhere (Skagen & Yackel Adams 2012) and those nests are not included here.

The focal species are insectivorous and granivorous native passerines that occupy shortgrass and midgrass habitats of North America and whose distributions range from highly restricted (McCown's Longspur; With 2010, and Chestnut-collared Longspur; Bleho *et al.* 2015) and fairly restricted (Lark Bunting; Shane 2000) to widespread (Horned Lark; Beason 1995, and Western Meadowlark; Davis & Lanyon 2008). Within our study region, Horned Larks and McCown's Longspurs inhabit relatively barren areas with grasses of short height and bare ground, whereas Chestnut-collared Longspurs, Lark Buntings and Western Meadowlarks are associated with taller grasses interspersed with forbs and low shrubs. Potential nest predators included Thirteen-lined Ground Squirrel *Spermophilus tridecemlineatus*, Coyote *Canis latrans*, Swift Fox *Vulpes velox*, Long-tailed Weasel *Mustela frenata*, American Badger *Taxidea taxus*, Striped Skunk *Mephitis mephitis*, Bullsnake *Pituophis melanoleucus*, Western Hognose Snake *Heterodon nasicus*, Prairie Rattlesnake *Crotalus viridis* and Burrowing Owl *Athene cunicularia*.

Nest monitoring and fate

We located nests by observing adult behaviour and by dragging a rope between two observers 25–28 m apart to flush birds (Winter *et al.* 2003). To

aid in estimating age of nests, we determined incubation stage by floating two eggs from each nest using methods described in Skagen and Yackel Adams (2012). Nests were monitored and eggs and chicks counted every 2–4 days until nests were empty. Evidence of success (parents feeding young or calling in vicinity, faecal droppings outside of nest) or failure (eggshell fragments, nest damage) was noted.

Data required to estimate daily survival rate (DSR) of nests included the date the nest was found, date it was last known to be active, date when it fledged or was known to have failed, and its fate. Nests were considered successful if at least one fully-feathered juvenile left the nest ('fledged'), as determined by cues recorded in the field (as above). As recommended by Manolis *et al.* (2000), for nests of uncertain fate (7%), the final observation interval was truncated to the date when the nest was last known to be active, and fate was coded as successful; we recognize, however, that predation was a possible outcome for these nests (Ball & Bayne 2012). All animal handling methods and protocols were approved by the Institutional Animal Care and Use Committee of the USGS Fort Collins Science Center and the Rocky Mountain Bird Observatory.

Vegetation structure data

We sampled vegetation structure across the four study areas using protocols that yielded comparable estimates for average grass height and per cent cover of vegetation. Within study plots, we estimated per cent cover of vegetation types and measured grass height (cm) in six or 12 5-m-radius plots or within 36 or 45 20-cm × 50-cm Daubenmire frames (Daubenmire 1959). See Skagen *et al.* (2005), Skagen and Yackel Adams (2012), and Augustine and Derner (2015) for further details of vegetation sampling methodology.

Weather data

We obtained daily precipitation and temperature values from the weather station nearest each nest. The 12 weather stations were administered by the National Oceanic and Atmospheric Administration, Shortgrass Steppe Long Term Ecological Research project and USDA Agricultural Research Service. If the nearest station had missing data on a given day, we used data from the next nearest

station. This occurred for only 2% of the days represented in our dataset, and in all but four of those cases, the second nearest station was only 5.2 km away and nearly as close to the nest as the nearest station; therefore, missing weather data had very little impact on analyses. Because the timing of data collection differed among stations (00:00–00:30, 06:00–08:00 or 18:00 h MDT), some measurements were offset by 1 day so that nest fate was associated with the most recent minimum temperature (early morning ~05:00 MDT), maximum temperature (previous afternoon) and precipitation event (assumed previous afternoon). Daily values were averaged (for temperature) or summed (for precipitation) over 15 May–15 July (encompassing 90% of the nesting season) to produce seasonal values. Using ArcGIS, we measured distances from individual nests to the nearest weather station for nests with UTM coordinates (2001–2012). For nests with no associated UTM coordinates (1997–2000), we measured the distance from the centroid of the plot to the weather station. On average, nests were 11.60 km (\pm 7.62 sd, range 0.35–30.25) from the nearest weather station (Table 1). Within distances of 40 km, we expect minimal spatial variation in precipitation patterns (Augustine 2010).

Data analyses

DSR of nests was modelled in Program MARK version 6.2 (White & Burnham 1999) using the logit link function. *A priori*, we identified several factors other than weather that were expected to influence DSR based on the literature for grassland and shrubsteppe birds (Rotenberry & Wiens 1989, George *et al.* 1992, Dinsmore *et al.* 2002). These factors were grouped in five categories: (i) age of the nest (linear and quadratic), (ii) time in season (linear and quadratic; day 1 = 9 May, the date on which the first nest was found), (iii) bird species and bird habitat guild, (iv) landscape context and patch fragmentation and (v) grassland structure. The two bird habitat guilds were defined as species nesting in shorter vegetation (Horned Lark and McCown's Longspur) and those nesting in taller vegetation (Chestnut-collared Longspur, Lark Bunting and Western Meadowlark). Preliminary analyses with separate model sets for each guild suggested that the two guilds were responding similarly to the other variables we tested; thus we combined all species into one model set while

continuing to test for guild and species differences. Landscape context was defined for the broader area containing our study sites as a three-level ordinal variable: highly fragmented (< 32% grassland remaining; Washington County study site), moderately fragmented (32–60% grassland remaining; most of Pawnee Grassland study site) and intact (60–100% grassland remaining; Soapstone Prairie and Central Plains Experimental Range study sites). Patch fragmentation was measured as the amount of land immediately surrounding the study plot (within 1.6 km) that remained as grassland, expressed as a two-level categorical variable: fragmented $\leq 30\%$ grassland and intact = 100% grassland.

To limit the number of models evaluated, we used a hierarchical model selection procedure, using Akaike's information criterion (AIC_c) to infer support for models (Akaike 1973, Burnham & Anderson 2002). For each of the five variable categories, we first used univariate models to determine the best expression of the category to carry forward to more inclusive models. If two variables were highly correlated ($r \geq 0.7$), only one was included within a given model. We then chose the most parsimonious model based on non-weather variables as our overall baseline model from which to evaluate the effects of weather on DSR of nests.

To evaluate the influence of weather on DSR, we added variables describing daily and seasonal temperature and precipitation to the base model, first in a univariate manner to choose the best one to two expressions of each of these four variable categories, and then in balanced combinations until we identified the most parsimonious model. After inclusion of the weather variables, we checked the variables in the original base model for parsimony. We thought that threshold effects might exist for some continuous weather variables; for example, very wet and very dry weather might be associated with lower daily nest survival. Quadratic effects were therefore modelled for daily precipitation, and binary variables, such as daily precipitation ≥ 10 mm or otherwise, were also tested. After determining the most parsimonious model, we substituted closely competing variables (those from univariate models with $\Delta AIC_c \leq 2$) of all categories back into the best model as a final check of their relative performance. Finally, we considered interactions of bird guild and weather; for example, we expected that intense heat and heavy rains might affect exposed ground nests

more so than nests positioned under taller vegetation. In total, we tested 14 candidate models to build the base model (Table S1) and an additional 49 candidate models to evaluate weather covariates (Tables 2 and 3) and interactions.

We calculated overall nest success as DSR^x , where x is the total length of the incubation and nestling stages. We used the following values (in days) for the duration of incubation and nestling periods, respectively, based on Baicich and Harrison (1997): Horned Lark (12,10), McCown's Longspur (12,10), Chestnut-collared Longspur (12,10), Lark Bunting (12,8) and Western Meadowlark (12,11). We calculated standard errors on nest success estimates using the delta method, and we calculated 95% confidence intervals on the logit scale before back-transforming to the real scale.

We evaluated the effects of daily and seasonal weather conditions on clutch size using generalized linear models (McDonald & White 2010) in SYSTAT 13 (SYSTAT 2009). In these models, we accounted for average clutch sizes of the five focal species and for time in season (Skagen & Yackel Adams 2012). As for the nest survival models, we first chose the best one or two expressions of each of the four weather variable categories by fitting univariate models. We then ran models in combinations until we identified the most parsimonious model. After inclusion of the weather variables, we checked the variables in the original base model for parsimony, and substituted closely competing variables (those from univariate models with $\Delta AIC_c \leq 2$) of all categories back into the best model to assess their relative performance. We \ln -transformed explanatory variables to improve normality when necessary. We evaluated several expressions of daily and seasonal temperature and precipitation in these models; daily temperature and precipitation values were associated with the days preceding the laying period (up to a week before), and seasonal weather included temperature and precipitation for spring (April to mid-May) as well as for the breeding season (mid-May to mid-July). We tested four candidate models to build the base model and an additional 64 candidate models to evaluate weather covariates (Tables S2 and 3).

We calculated nest success for future climatic conditions that are projected for this region using our top (minimum AIC_c) model. Increases of 2–3 °C (or more) are expected by 2050 with

Table 2. Preliminary analyses for the effects of weather on nest survival for grassland passerines in northern Colorado, USA, 1997–2012. These models indicated the initially most supported variables ($\Delta AIC_c = 0$; indicated in bold) for daily temperature and precipitation, and seasonal temperature and precipitation variables when added to the base model. The preliminary baseline model included nest age (Age + Age²), time in season (Time), bird guild (Guild), degree of fragmentation in the surrounding landscape (Land), and habitat structure (per cent cover of grass: GrassPct). Closely competing variables ($\Delta AIC_c \leq 2.0$) were substituted into final best-approximating models to determine if they provided a better fit.

		Nest survival ($n = 870$)	
		AIC_c	ΔAIC_c
Daily temperature			
Base model		2576.71	5.88
Minimum temperature	Min Temp	2578.14	7.30
Minimum temperature on previous day	LagMinTemp	2578.63	7.80
Maximum temperature	MaxTemp	2572.00	1.16
Maximum temperature on previous day	LagMaxTemp	2573.48	2.64
Mean temperature	MeanTemp	2574.00	3.16
Mean temperature on previous day	LagMeanTemp	2575.56	4.72
Maximum temperature ≥ 35 °C*	Over35C	2571.46	0.62
Maximum temp ≥ 35 °C on previous day*	LagOver35C	2570.84	0
Minimum temperature ≤ 0 °C*	Under0C	2578.31	7.47
Minimum temperature ≤ 0 °C* on previous day	LagUnder0C	2578.33	7.49
Daily precipitation			
Base model		2576.71	12.14
Daily precipitation	Precip	2577.69	13.12
Precipitation on previous day	LagPrecip	2578.19	13.62
(Daily precipitation) ²	Precip2	2578.14	13.56
(Precipitation on previous day) ²	LagPrecip2	2578.61	14.03
No rain (dry day)*	0 mm	2569.75	5.17
No rain on previous day*	Lag0 mm	2564.58	0
No rain for 10 days (drought)*	10DayDrought	2577.00	12.43
Rain event ≥ 10 mm*	Over10 mm	2573.52	8.95
Rain ≥ 10 mm on previous day*	LagOver10 mm	2577.31	12.74
Seasonal temperature			
Base model		2576.71	9.40
Average daily minimum temperature	AvgMin	2574.17	6.85
Average daily maximum temperature	AvgMax	2572.01	4.69
Average daily mean temperature	AvgMean	2572.46	5.14
Number of days w/max temp ≥ 35 °C	Days35C	2567.32	0
Number of days w/min temp ≤ 0 °C	Days0C	2571.54	4.22
Seasonal precipitation			
Base model		2576.71	9.49
Total summer precipitation	TotalPcp	2577.42	10.20
Number of days with no rain	Days0 mm	2567.22	0
Number of days with rain ≥ 10 mm	Days10 mm	2578.61	11.39

Each nest was individually associated with the nearest weather station. Droughts were defined as periods when at least 10 consecutive days had passed with ≤ 1 mm total rainfall. In the daily precipitation category, we ran models that included both dry conditions and storms on consecutive days (Lag0 mm + Over10 mm or 0 mm + LagOver10 mm). Seasonal weather variables were created by summing or averaging daily values for 15 May–15 July of each year. *Binary variable.

increasing frequency and severity of heat waves (Lukas *et al.* 2014); we assumed that daily maximum and minimum temperatures would increase proportionally. Increased drought (Lukas *et al.* 2014) during the breeding season is also expected, but we are not aware of any results quantifying this. So, in our projections, we used the maximum

number of dry days observed during this study and a value intermediate between the average and maximum value. Other variables (storms) from our top model were set at their mean value, because specific predictions for precipitation extremes from climate models are lacking. Projected nest success estimates under future climate scenarios were

based on a 22-day period, the average sum of the incubation and nestling periods for these five species (range 20–23 days). In these climate projections, temperatures and precipitation levels all remain within the ranges of observed data from the 12 weather stations used in our study.

RESULTS

Maximum temperature during the breeding season in our study averaged 28.0 ± 6.2 °C (range 0–40.6 °C; Fig. 1), and 11.4% of days exceeded 35 °C, mainly in July. The first 35 °C day typically occurred in late June or early July, but the earliest seasonal occurrence was on 23 May in 2001. Minimum temperature during the breeding season averaged 10.3 ± 4.8 °C (range –5.6 to

21.1 °C; Fig. 1). Only 2.6% of days (0–7 days per breeding season) had minimum temperatures below 0 °C, and all but two were in May, with the latest freeze occurring on 8 June in 2007. Minimum temperature during April, just prior to the breeding season, averaged -1.3 ± 4.4 °C (range –17.8 to 10.3 °C). Daily precipitation during the breeding season averaged 2.06 ± 5.72 mm (range 0–91.44 mm; Fig. 1). No rainfall occurred on 73.4% of days, and dry periods lasted up to 22 days. Storms with ≥ 10 mm of rainfall occurred on 5.5% of days.

In the first phase of the nest survival analysis, the baseline model with the most explanatory power incorporated age of the nest (quadratic), time in season, bird habitat guild, landscape connectivity (whether intact, or moderately or highly fragmented) and grassland structure (per cent cover of grass) (Table S1). Incorporating this base model, we determined that the best daily and seasonal weather metrics to include were daily maximum temperature on the previous day ≥ 35 °C (LagOver35C); previous day with no rain (Lag0 mm); days with rain events ≥ 10 mm (Over10 mm; storm events); the number of days exceeding 35 °C (Days35C); and the number of days with no rain (Days0 mm; Table 2). After the addition of weather covariates, the re-evaluated base model included only age of the nest (quadratic), time in season and bird habitat guild.

DSR for 870 passerine nests was best predicted by a combination of daily and seasonal weather variables along with age of the nest, time in season and bird habitat guild (Table 3). Within a season, survival rates were lower after very hot days and dry days (with a lag of 1 day for each), and on stormy days (Table 4, Fig. 2). This was true in both the incubation and the nestling phases (Fig. 3). Across the 10 years of the study, survival rates were also lower during warmer and drier breeding seasons (Table 4, Fig. 2). Daily temperature effects were best modelled using very hot days when maximum temperatures exceeded 35 °C on the previous day (LagOver35C), with strong negative effects on DSR (Tables 3 and 4, Figs 2 and 3). Daily precipitation effects were best modelled using dry weather on the preceding day (Lag0 mm) and storms on the current day (Over10 mm), with strong negative effects on DSR (Tables 3 and 4, Figs 2 and 3). Seasonal temperature effects were best modelled using the number of days exceeding 35 °C. As this variable

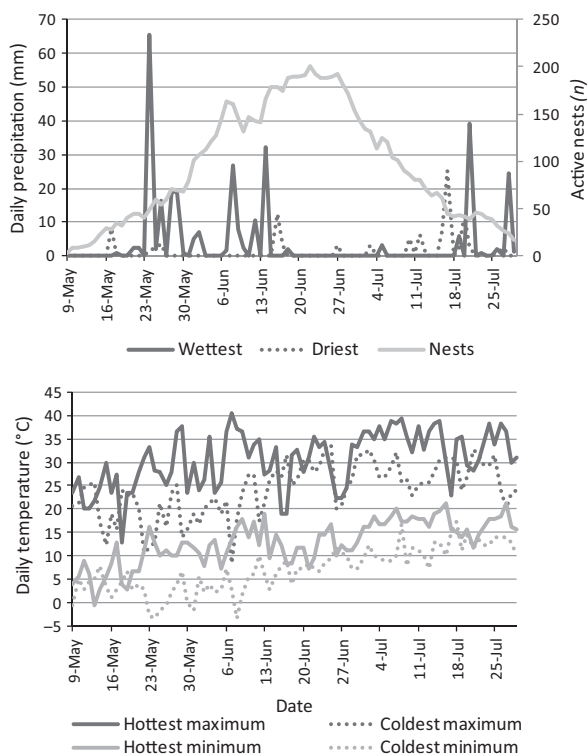


Figure 1. Range of daily precipitation, maximum and minimum temperature values for northern Colorado, USA, in 1997–2012 and the number of active grassland passerine nests per day included in this study. These values depict the wettest, driest, hottest and coldest seasons encountered during this study and illustrate the range of extremes that characterize the region. Wettest season: 1997 (New Raymer 21 N, Weld County). Driest season: 2000 (Akron 4 E, Washington County). Hottest season: 2000 (Yuma 10 NW, Washington County). Coldest season: 2007 (Virginia Dale 7 ENE, Larimer County).

Table 3. Nest survival and clutch size models for grassland passerines in northern Colorado, USA, 1997–2012. We ran 63 models with minimum $AIC_c = 2541.38$ for the nest survival model set and 68 models with minimum $AIC_c = 1449.27$ for the clutch size model set. All models included an intercept. Nest survival models with AIC_c weights > 0.05 also included covariates of the final base model (nest age², time in season and guild). Clutch size models with AIC_c weights > 0.05 also included average clutch size per species. w_i are Akaike weights and K is the number of parameters in each model.

	ΔAIC_c	w_i	K
Nest survival models			
LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm	0	0.185	10
LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm + Guild * Over10 mm	0.709	0.130	11
LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm + Guild * Lag0 mm	1.018	0.111	11
LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm + Guild * Days0C	1.350	0.094	11
LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm + Guild * LagOver35C	1.776	0.076	11
LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm + GrassHt	1.786	0.076	11
LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm + Guild * Days0 mm	1.791	0.075	11
LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm + Guild * Over10 mm + Guild * Lag0 mm	2.115	0.064	12
Clutch size models			
TMax7d + Prec7d + AprAvgMin + TotalPrec	0	0.291	6
TMax7d + Prec7d + AprAvgMin	0.314	0.249	5
TMax4d + Prec7d + AprAvgMin	2.466	0.085	5
-----+ Prec7d + AprAvgMin	2.478	0.084	4
-----+ Prec7d + AprAvgMin + TotalPrec	2.786	0.072	5
-----+ Prec7d + AprAvgMin + ----- + Time	2.941	0.067	5

The top ranked nest survival model included age of nest (quadratic), time in season, bird habitat guild (species nesting in short (Horned Lark, McCown's Longspur) vs. tall (Chestnut-collared Longspur, Lark Bunting, Western Meadowlark) vegetation), daily temperature (maximum ≥ 35 °C on previous day), daily precipitation (no rain the previous day and ≥ 10 mm rain on the current day), seasonal temperature (number of days with minimum ≤ 0 °C) and seasonal precipitation (number of days with no rain). Lower ranked nest survival models included interactions between bird guild and weather, as well as grass height in the plot. The top ranked clutch size model included average clutch size (species-specific), daily temperature (average maximum temperature during 7 days prior to egg-laying), daily precipitation (total for 7 days prior to egg-laying), seasonal temperature (average minimum temperature in April) and seasonal precipitation (total precipitation 1 April–15 July). Lower ranked clutch size models also contained time in season when incubation began and/or substituted average maximum temperature during 4 days (rather than 7 days) prior to egg-laying. Dashes indicate that a variable category was not included in the model.

was highly correlated ($r > 0.7$) with Days0 mm, however, we substituted the second ranking seasonal temperature variable, the number of days experiencing freezing temperatures (Days0C), in subsequent models. Days0C exhibited weak positive effects on DSR (Tables 3 and 4, Fig. 2). Other seasonal temperature variables such as average daily minimum, mean and maximum temperature all suggested higher nest survival in cooler years. Seasonal precipitation effects were best modelled using the number of dry days (Days0 mm), with weak negative effects on DSR (Tables 3 and 4, Fig. 2).

The guild of birds nesting in the shortest vegetation (Horned Lark and McCown's Longspur) had lower nest DSR and clutch sizes than birds associated with taller grasses (Tables 4 and 5). In the nest survival analyses, interactions between habitat guild and climate variables were not supported by AIC_c -based model selection; models that added interactions of guild and weather to the top

model yielded larger AIC_c values (Table 3). Guilds differed only in the magnitude (not direction) of their climate responses, with DSR of Horned Lark and McCown's Longspur nests responding more strongly to dry days and storms than DSR of Chestnut-collared Longspur, Lark Bunting and Western Meadowlark nests (Table 4, Fig. 2), although this may be an artefact of different sample sizes (Table 5). Further species differences lacked support. Average DSR ($n = 870$ nests) from a constant survival model was estimated to be 0.938 ± 0.003 , and nest success over the 20- to 23-day development period averaged $22.8 \pm 1.5\%$ to $27.7 \pm 1.6\%$. Nest age had an effect size on DSR of 4–5%, which was maximized at the onset of incubation and minimized 1 day post-hatch (Fig. 3).

Weather during spring and the breeding season also influenced clutch sizes, specifically with larger clutches associated with cooler springs and with wet and warming conditions the week prior to

Table 4. Variable coefficient estimates from the top ranked models for daily nest survival and clutch size containing the variable of interest for grassland passerines in northern Colorado, USA, 1997–2012. The best variables in each category are shown, including weather variables and non-weather variables from the base model.

	β Estimate \pm se	95%CI	Effect
Variables: nest survival models ($n = 870$ nests)			
Age	-0.122 ± 0.033	$-0.188, -0.057$	Strong
Age ²	0.005 ± 0.001	$0.002, 0.008$	Strong
Time in season (Time)	0.005 ± 0.003	$-0.001, 0.011$	Weak positive
Guild: species nesting in short vs. tall vegetation (Guild)	-0.217 ± 0.109	$-0.431, -0.003$	Strong negative
Landscape (Land)*	0.028 ± 0.090	$-0.150, 0.205$	No relationship
Habitat: grass height (GrassHt)*	0.006 ± 0.013	$-0.019, 0.031$	No relationship
Daily Temperature: hot day (LagOver35C)	-0.511 ± 0.222	$-0.946, -0.076$	Strong negative
Daily Precipitation: dry day (Lag0 mm)	-0.676 ± 0.190	$-1.048, -0.304$	Strong negative
Daily Precipitation: stormy day (Over10 mm)	-0.924 ± 0.219	$-1.354, -0.494$	Strong negative
Seasonal Temperature: cold season (Days0C)	0.038 ± 0.023	$-0.007, 0.082$	Weak positive
Seasonal Precipitation: dry season (Days0 mm)	-0.022 ± 0.011	$-0.043, -0.000$	Strong negative
Intercept	4.743 ± 0.565		
Variables: clutch size models ($n = 652$ nests)			
Average clutch size (AvgClutch)	0.928 ± 0.054	$0.822, 1.034$	Strong positive
Time in season (Time)*	-0.002 ± 0.002	$-0.006, 0.002$	No relationship
Daily Temperature: avg maximum for 7 days prior to egg-laying (TMax7d)	0.017 ± 0.008	$0.001, 0.033$	Strong positive
Daily Precipitation: total for 7 days prior to egg-laying (Prec7d)	0.008 ± 0.002	$0.004, 0.012$	Strong positive
Seasonal Temperature: April minimum temperature (AprAvgMin)	-0.061 ± 0.024	$-0.108, -0.014$	Strong negative
Seasonal Precipitation: total for spring & breeding season (TotalPrec)	0.001 ± 0.001	$-0.001, 0.003$	Weak positive
Intercept	-0.499 ± 0.269		

The top ranked nest survival model included age of nest (quadratic), time in season, bird habitat guild (species nesting in short (Horned Lark, McCown's Longspur) vs. tall (Chestnut-collared Longspur, Lark Bunting, Western Meadowlark) vegetation), daily temperature (maximum $\geq 35^\circ\text{C}$ on previous day), daily precipitation (no rain the previous day and ≥ 10 mm rain on the current day), seasonal temperature (number of days with minimum $\leq 0^\circ\text{C}$) and seasonal precipitation (number of days with no rain). Lower ranked nest survival models also contained a measure of fragmentation in the surrounding landscape and grass height within the plot. The top ranked clutch size model included average clutch size (species-specific), daily temperature (average maximum temperature during 7 days prior to egg-laying), daily precipitation (total for 7 days prior to egg-laying), seasonal temperature (average minimum temperature in April) and seasonal precipitation (total precipitation 1 April–15 July). Lower ranked clutch size models also contained time in season when incubation began. Effects were considered strong if the 95% confidence intervals (CIs) did not span zero, weak if the 85% CIs did not span zero (and a variable appeared in the top model) and as having no relationship with the dependent variable if the 85% CIs spanned zero (unsupported embellishments of the top model: Arnold 2010). *Variables not included in the top ranked model.

egg-laying (Tables 3 and 4). The top two models of our final model set received most of the weight, with AIC_c weights totaling 0.540; all other model weights were < 0.085 . The top model, with an AIC_c weight of 0.291, included average clutch size (for each species) and four weather variables: average minimum temperature in April (AprAvgMin), total precipitation during spring and the breeding season (TotalPrec), average maximum temperature in the 7 days prior to egg-laying (TMax7d) and total precipitation in the 7 days prior to egg-laying (Prec7d). The second-best model, with an AIC_c weight of 0.249, did not include TotalPrec (Table 3). After the preliminary analyses (Table S2), we ran 24 additive models to find the most parsimonious clutch size model.

In future climate scenarios with 2–3 $^\circ\text{C}$ increases in daily maximum temperatures and 1–2 additional dry days experienced by each nest, projected 22-day nest success declined by 5% in the most conservative scenario (2 $^\circ\text{C}$ increase and one additional dry day: Fig. 4). Nest success declined by 8–10% in the least conservative scenario that we modelled (3 $^\circ\text{C}$ increase and two additional dry days). Increasing dryness had a slightly stronger negative effect than increasing temperature in terms of the resulting effect size for projected nest success. The combined effect of increasing temperature and declining precipitation was large; in the scenario with 3 $^\circ\text{C}$ increase and two additional dry days during a nesting period, nest success estimates were halved compared to their current value. Although we did not depict more severe scenarios

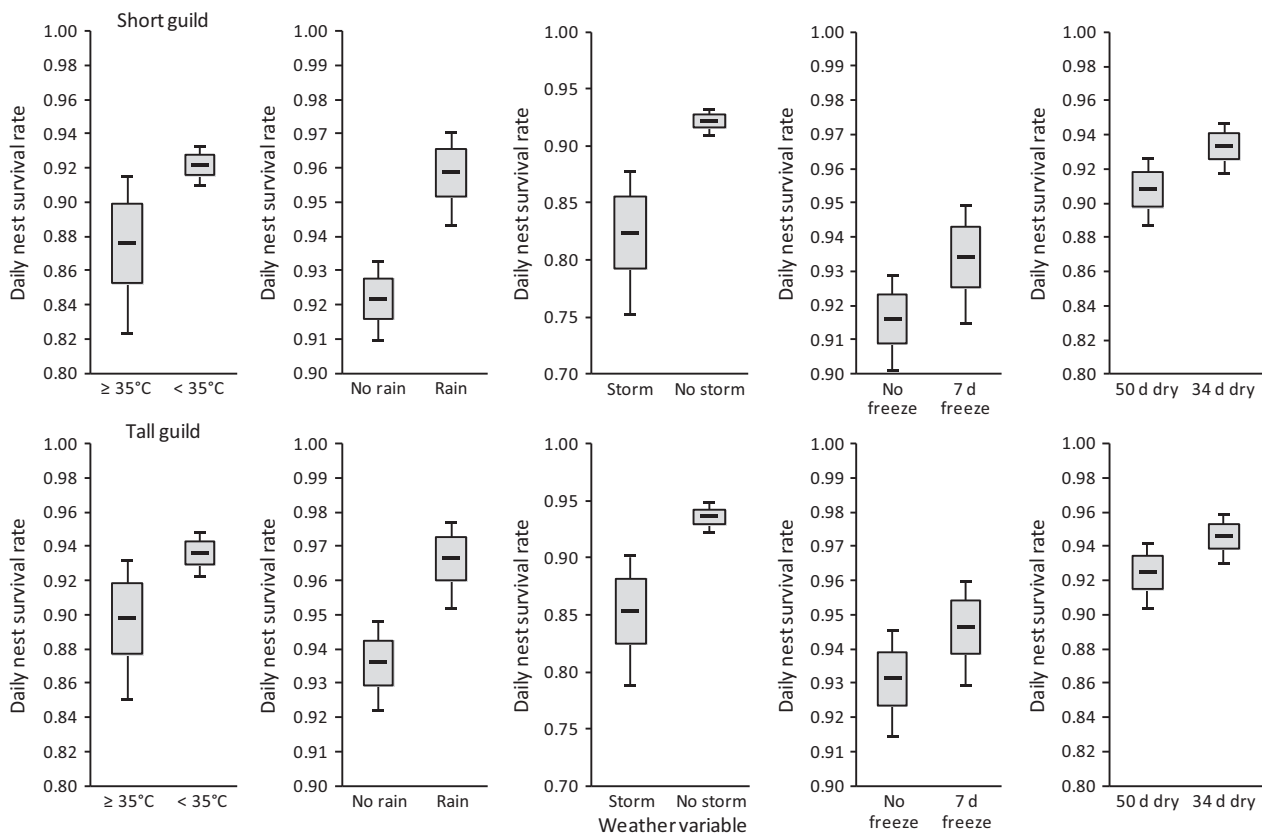


Figure 2. Effects of daily and seasonal weather on daily nest survival of grassland passerines associated with short (Horned Lark and McCown's Longspur) vs. tall (Chestnut-collared Longspur, Lark Bunting and Western Meadowlark) vegetation under varying weather scenarios in northern Colorado, USA, 1997–2012. Estimates were generated from the top ranked model (Table 2) by varying focal weather values while holding other variables at their median value. Over the 10-year dataset, the peak of the breeding season was 18 June (day 41), and mean nest age indicates an average nest initiation date of 7–8 June (day 29.5); thus, nest survival estimates depicted here correspond to a pre-hatch nest (11.5 days old). Box-and-whisker plots show median (midline) daily nest survival estimates \pm se (boxes) and 95% confidence intervals (bars).

in Fig. 4, further changes such as another degree of warming, an additional storm event or increasing numbers of dry days each caused projected nest success to decline by an additional 1% or more when other variables were held constant.

DISCUSSION

For the focal species in this study, one element of reproductive performance (whether a nest survived to fledge at least one young) was reduced under conditions of drought, high summer temperatures and storms. These findings suggest that grassland songbirds will be negatively affected by changing climate because these are the conditions likely to be encountered more commonly; climate models predict increasing temperatures, more

prolonged drought and more intense storms as the hydrological cycle is altered (Christensen *et al.* 2007, Karl *et al.* 2008, 2009, Lukas *et al.* 2014). Furthermore, clutch sizes responded positively to cool conditions in spring and warming conditions with adequate precipitation in the days prior to egg-laying. Although seasonal precipitation predictions for clutch size were equivocal for spring, increasing spring temperatures in the future may serve to depress clutch sizes.

Prevailing weather conditions can influence rates of nest survival in prairie songbirds through interacting effects on food availability, predator behaviour and parental behaviour. Increased seasonal precipitation may enhance primary and secondary productivity (biomass of invertebrate prey), which may in turn influence patterns of nest

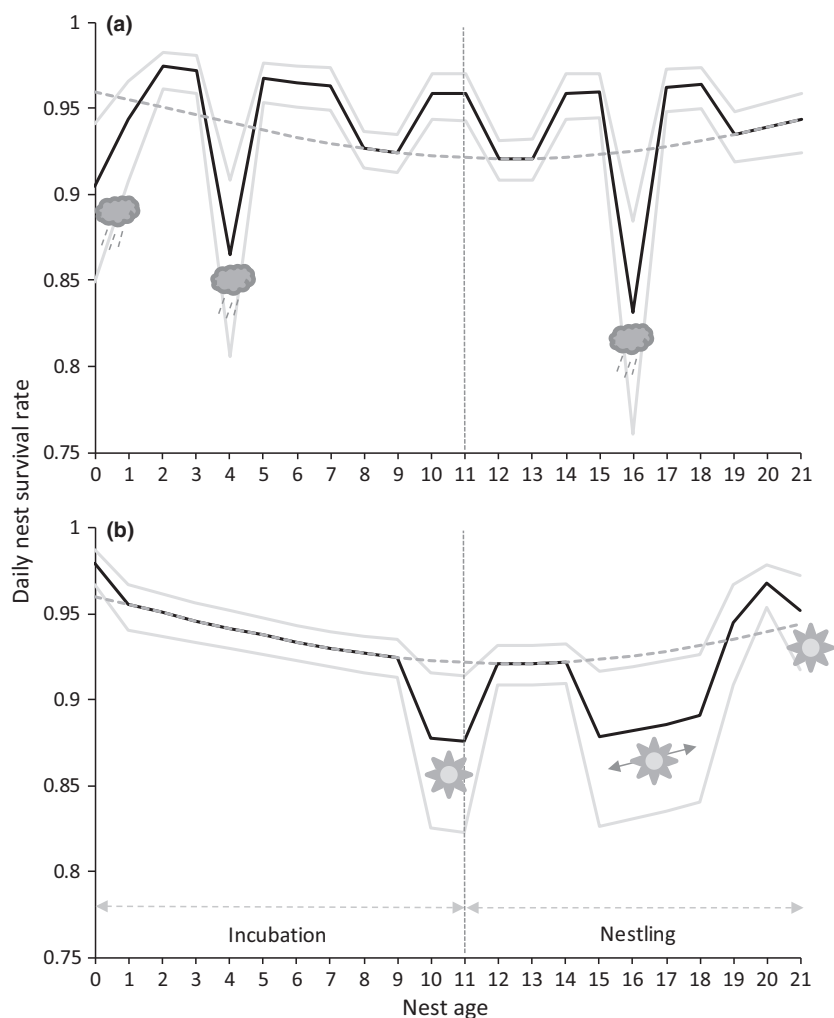


Figure 3. Daily nest survival rates for grassland passerines in the shorter grass guild in Colorado, USA, 1997–2012, in relation to age (days) of the nest and storm (a) and heat (b) events. Daily storm events (≥ 10 mm; (a)) and temperatures over 35 °C (modelled as a 1-day lagged effect; (b)) depressed daily nest survival rates (note downward spikes) during both incubation (days 0–11) and nestling (days 12–21) periods. Estimates, 95% confidence intervals (solid grey lines) and average rates (dashed line) were generated using the regression equation from the top model. Average conditions were dry days with maximum temperature below 35 °C in seasons with a total of 42 dry days and two freezes. Small daily rain events (averaging 2 mm, modelled as a 1-day lagged effect) resulted in increased nest survival (note upward bumps, particularly in (a)). Seasonal weather variables and nest age were held at their mean value, with an average nest initiation date of 8 June. Decreased survival rates associated with extreme weather events were similar across years and sites but are only illustrated for two cases, both in Weld County, Colorado: (a) Pawnee National Grassland, 1997, and (b) Central Plains Experimental Range, 2012.

attentiveness. During dry seasons, food scarcity may demand that parents have longer foraging bouts and thus spend less time actively defending the nest from predators (Schmidt 1999). Conversely, less frequent parental visits to the nest during dry periods may reduce the likelihood of predators discovering nests due to the movements of parents. Predation may also increase during drought if food scarcity increases the intensity of

spontaneous begging by underfed nestlings early in the nestling period (Haskell 1994).

As temperatures rose above 35 °C in our study, passerine nest survival declined, suggesting that eggs or nestlings may be vulnerable to heat stress unless shaded by parents. Wolf and Walsberg (1996) found that metabolic rates and evaporative water loss in Verdins *Auriparus flaviceps* increased at temperatures ≥ 36 °C. In general, the evidence

Table 5. Daily and overall nest survival, clutch size, and productivity (fledglings per successful nest) for grassland passerines in northern Colorado, USA, 1997–2012. Nest survival estimates were generated for average conditions: dry days with maximum temperature below 35 °C in seasons with a total of 42 dry days and two freezes. Clutch size and productivity are the empirical species-specific averages across all years of the study. *n* is the sample size of nests used in each analysis.

Species	Nest survival			Clutch		Productivity	
	<i>n</i>	Daily estimate ± se	Overall estimate ± se	<i>n</i>	Mean ± sd	<i>n</i>	Mean ± sd
Horned Lark	281	0.930 ± 0.006	0.204 ± 0.030	192	3.0 ± 0.05	85	2.5 ± 0.08
McCown's Longspur	339	0.930 ± 0.006	0.202 ± 0.027	262	3.2 ± 0.04	86	2.6 ± 0.10
Chestnut-collared Longspur	43	0.940 ± 0.012	0.254 ± 0.069	37	4.1 ± 0.14	10	3.4 ± 0.34
Lark Bunting	144	0.943 ± 0.007	0.306 ± 0.048	111	4.1 ± 0.08	54	3.4 ± 0.15
Western Meadowlark	63	0.951 ± 0.009	0.318 ± 0.068	50	4.6 ± 0.14	23	3.3 ± 0.19

Nest success estimates were based on a development period (incubation + nestling stage) of 20 days for Lark Bunting (LARB), 22 days for Horned Lark (HOLA), McCown's Longspur (MCLO) and Chestnut-collared Longspur (CCLO), and 23 days for Western Meadowlark (Baicich & Harrison 1997). Nest survival estimates were generated from the following model: HOLA + MCLO + CCLO + LARB + LagOver35C + Lag0 mm + Over10 mm + Days0C + Days0 mm + *Intercept*.

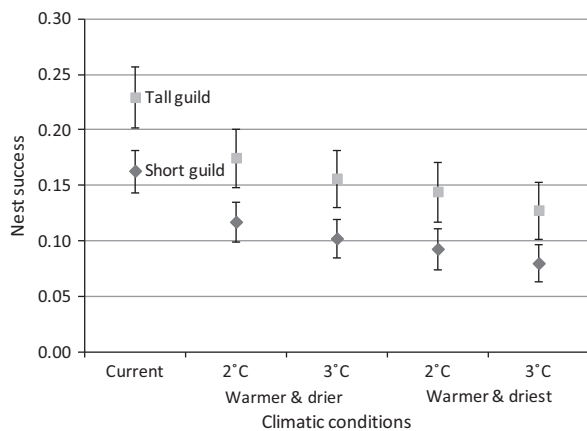


Figure 4. Estimates of nest success calculated using current average conditions in northern Colorado, USA, 1997–2012, and four projected future climate scenarios for bird habitat guilds associated with short (diamonds: Horned Lark and McCown's Longspur) vs. tall (squares: Chestnut-collared Longspur, Lark Bunting and Western Meadowlark) vegetation. Nest success was calculated for a 22-day nest period (the average for these five species) using daily nest survival estimates from the top ranked model (Table 2). Warmer conditions were modelled by increasing daily maximum and minimum temperatures by 2–3 °C. Drier conditions were modelled by increasing the number of dry days to the maximum value seen in our dataset and to a value intermediate between the average and the maximum values. Other variables (storms) from our top model were set at their mean value. Over the 10-year dataset, the peak of the breeding season was 18 June (day 41), and mean nest age indicates an average nest initiation date of 7–8 June (day 29.5); thus, nest survival estimates depicted here correspond to a pre-hatch nest (11.5 days old). Nest success estimates ± se (bars) are shown.

for effects of changing temperatures on nest survival of birds is equivocal. The inconsistency among studies is likely to be due to the variety of

factors, including the temperature variables considered (daily or seasonal), the range of temperatures during the study, nest substrates (cavity or open cup) and microclimates (open arid lands or forest; vegetation surrounding the nest) involved across the various studies (Rotenberry & Wiens 1991, Dinsmore *et al.* 2002, Drever & Clark 2007, Dickey *et al.* 2008, Dreitz *et al.* 2012, Skagen & Yackel Adams 2012).

Although predation has been considered the primary direct cause of nest failure in songbirds in general (Martin 1995), storm events can also directly lead to nest mortality through exposure to hail damage and flooding (Skagen & Yackel Adams 2012, Fisher *et al.* 2015). In this study, nest survival of the two species that place nests in scrapes or depressions in the ground, Horned Lark and McCown's Longspur, was more strongly and negatively affected by daily storms than was the case for the species that place their nests in and adjacent to taller grasses and shrubs (Chestnut-collared Longspur, Lark Bunting and Western Meadowlark). Flooded nests and periodic hail events causing direct mortality of adult grassland birds were observed by field crews. Storm events may also disrupt provisioning of young in the nest if parents halt foraging during the storm event (Fisher *et al.* 2015, Oberg *et al.* 2015). Immediately after, they may spend more time away from the nest and less time defending it from predators.

Weather conditions may indirectly influence nest survival through effects on vegetation structure and thus the probability of nest detection by predators. Although, theoretically, greater nest

concealment should favour higher nest survival (Martin 1993), evidence from grassland bird studies is equivocal (Dion *et al.* 2000, Davis 2005, Winter *et al.* 2005, Skagen & Yackel Adams 2012). In this study, we were unable to distinguish whether the lower DSR of bird species associated with shorter grasses and bare ground (Horned Lark and McCown's Longspur) was due to lower levels of concealment of these nests than those of species associated with taller grasses or due to other species-specific life-history traits.

More frequent drought conditions in concert with rising temperatures, increased storm intensity and enhanced carbon dioxide in the atmosphere will alter soil conditions and the plant community of the shortgrass prairie, and thus habitat suitability for prairie birds, in somewhat unpredictable ways. Although one might presume that shortgrass prairie conditions may tend toward more extensive bare ground as temperatures and evapotranspiration rates rise and summer precipitation declines, collectively, recent evidence suggests several alternative soil moisture and vegetative responses, from lower soil moisture (Dai 2013) to increasing soil moisture and above-ground net primary productivity (Knapp *et al.* 2008, Heisler-White *et al.* 2009). Furthermore, water dynamics associated with increasing carbon dioxide levels may lead to increased water use efficiency and deep soil moisture (Nelson *et al.* 2004). Prairies with high plant species diversity are expected to exhibit considerable resilience to climate change (Craine *et al.* 2013). Alternatively, Gonzalez *et al.* (2010) project that much of the central Great Plains, including eastern Colorado, may experience a biome shift from temperate grassland to temperate shrubland within the next 50 years in response to climate change (see Staudinger *et al.* 2012).

Increases in mean surface air temperatures of 3.5–4 °C in this century have been projected for the interior plains of North America, with greater increases in the north and in the summer (Christensen *et al.* 2007, Karl *et al.* 2009). Although precipitation is more difficult to forecast, wetter climates are predicted in the north and drier climates in the south by the end of the 21st century (Karl *et al.* 2009). Whether eastern Colorado experiences overall drier conditions or no effective change in the future is dependent upon emissions scenarios, although all scenarios predict precipitation to decrease in the summer relative to winter

months (Christensen *et al.* 2007), with declining spring snowpack (Lukas *et al.* 2014).

The habitat associations of breeding endemic short-mixed-grass species relative to vegetation structure are well defined, grading from the short-grass guild including McCown's Longspur to the guild of species nesting in or adjacent to taller forbs and small shrubs, such as Lark Bunting (Knopf 1996). Assuming that birds continue to select their currently favoured habitat types, the future distribution and abundance of breeding passerines will be strongly influenced by uncertain changes in the vegetative structure of the region. Presently the distribution of passerines of the interior prairies of North America, such as the Lark Bunting, is influenced by precipitation patterns, suggesting a degree of opportunism that enables birds to adjust to variation in habitat conditions associated with the highly dynamic weather in the midcontinent region (Price 1995, Niemuth *et al.* 2008). Because of this, one might expect to see shifts in distribution of bird populations with alterations in habitats and environmental conditions as the climate changes. Currently, however, the Breeding Bird Survey trend and species distribution information show no indication of a lasting directional shift in distribution of any of these five species; rather their populations are declining in northern as well as southern parts of the species' ranges (Sauer *et al.* 2014). Further research is needed to assess species-specific sensitivities to the interplay of changing climates, land uses and land management practices in the context of resilience and adaptive capacity (Williams *et al.* 2008, Nicotra *et al.* 2015). By integrating bird survey and demographic data with land use information and future climate scenarios, such an effort could indicate whether species' distributional shifts would be likely to occur in the future.

Climate change will exacerbate these population declines, underscoring a sense of urgency in identifying and addressing the current causes of decline. Given that predation is the greatest cause of mortality of eggs, nestlings and fledglings (Yackel Adams *et al.* 2006, Skagen & Yackel Adams 2012), knowledge of how predator communities respond to land use change, fragmentation and management practices in concert with climate change would be invaluable. Because there is little that land managers can do to address the sensitivity of species to climate change nor the exposure that species will experience, the primary

management options may come in the form of enhancing the adaptive capacity of the species of concern (Nicotra *et al.* 2015). For example, preventing population declines will help to maintain genetic diversity necessary for evolutionary adaptation (Frankham 1996, Reed & Frankham 2003). Further, managing grasslands for heterogeneity through the use of grazing, fire and control of invasive plants to provide a range of grassland structure, thus accommodating the full suite of grassland species, is an important component of conservation planning (Fuhlendorf & Engle 2001). Protection of grasslands across the interior prairies of North America would provide a buffer against climate change by allowing birds to redistribute into suitable areas as needed.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Non-weather variables tested in a base model for nest survival of grassland passerines.

Table S2. Variables tested in preliminary analyses of clutch size for grassland passerines.