

Weather effects on avian breeding performance and implications of climate change

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Abstract. The influence of recent climate change on the world's biota has manifested broadly, resulting in latitudinal range shifts, advancing dates of arrival of migrants and onset of breeding, and altered community relationships. Climate change elevates conservation concerns worldwide because it will likely exacerbate a broad range of identified threats to animal populations. In the past few decades, grassland birds have declined faster than other North American avifauna, largely due to habitat threats such as the intensification of agriculture. We examine the effects of local climatic variations on the breeding performance of a bird endemic to the shortgrass prairie, the Lark Bunting (*Calamospiza melanocorys*) and discuss the implications of our findings relative to future climate predictions. Clutch size, nest survival, and productivity all positively covaried with seasonal precipitation, yet relatively intense daily precipitation events temporarily depressed daily survival of nests. Nest survival was positively related to average temperatures during the breeding season. Declining summer precipitation may reduce the likelihood that Lark Buntings can maintain stable breeding populations in eastern Colorado although average temperature increases of up to 3°C (within the range of this study) may ameliorate declines in survival expected with drier conditions. Historic climate variability in the Great Plains selects for a degree of vagility and opportunism rather than strong site fidelity and specific adaptation to local environments. These traits may lead to northerly shifts in distribution if climatic and habitat conditions become less favorable in the drying southern regions of the Great Plains. Distributional shifts in Lark Buntings could be constrained by future changes in land use, agricultural practices, or vegetative communities that result in further loss of shortgrass prairie habitats.

Key words: *Calamospiza melanocorys*; climate change; clutch size; Lark Bunting; nest survival; North American prairie birds; paleoclimate; precipitation; shortgrass prairie.

INTRODUCTION

Effects of recent climate change on world's biota are emerging with implications for many species (Root et al. 2003). Climate affects many aspects of a species' ecological niche, including the abiotic conditions determined by weather patterns, habitat structure as vegetation responds to climatic changes, and biotic components such as the timing, composition, and abundance of the food supply, and the foraging patterns of local predators. Several types of bird responses to ecological changes recently have been attributed to climate change, including latitudinal range shifts (Parmesan and Yohe 2003, Zuckerman et al. 2009), advancing springtime arrival dates of migrants (Walther et al. 2002, Miller-Rushing et al. 2008), changes in the timing of breeding (Crick and Sparks 1999, Walther et al. 2002), changes in clutch size, parental provisioning rates and metabolic effort (Sanz 2003, Sanz et al. 2003), and altered competitive relationships among residents and migrants (Ahola et al. 2007). Although various

influences of weather and climate cycles on adult survival and annual fecundity of passerines have been documented (George et al. 1992, Sillett et al. 2000), accounts explicitly linking recent climate change with avian reproductive output are rare (but see Dickey et al. 2008).

In the past four decades, grassland birds across North America have undergone dramatic population declines; as a group, they have declined more quickly and consistently than any other group of North American birds (North American Bird Conservation Initiative, U.S. Committee 2009). For example, between 1966 and 2009, Lark Buntings (*Calamospiza melanocorys*) have declined annually by 4.6% in Colorado and 5.7% in the Central Breeding Bird Survey region (extending from the Mississippi River west to the Rocky Mountains; Sauer et al. [2011]; a map of BBS regions is *available online*).² Climate change poses additional threats of unknown magnitude to these already declining populations. The climate of the Great Plains, renowned for its year-to-year variability, is projected to further increase in variability and frequency of extreme events such as

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² http://www.mbr-pwrc.usgs.gov/bbs/bbs_regions.png

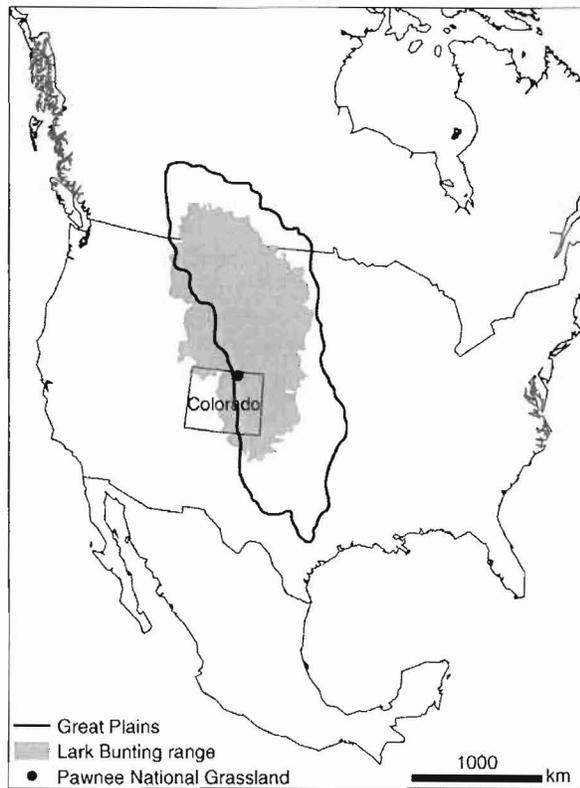


FIG. 1. Spatial extent of the Great Plains of North America, the range of Lark Buntings (*Calamospiza melanocorys*) from the Breeding Bird Survey (range of densities of ≥ 4 Lark Buntings per survey route; Sauer et al. 2011), and location of the Pawnee National Grassland, eastern Colorado, USA.

droughts and large rainstorms. Across Colorado, temperatures have increased about 1.1°C in the past 30 years, and climate models project a continued warming of 1.4°C by 2025 and 2.2°C by 2050, and seasonal shifts in precipitation to yield greater midwinter, but decreased late spring and summer precipitation (Ray et al. 2008). Under the scenario of increasing temperatures driving species northward, birds of the interior prairies of North America (the Great Plains) are predicted to experience greater range contractions than montane species of western North America (Peterson 2003). This prediction follows from the reasoning that birds restricted to flatlands face intense reductions in area of suitable habitat, especially if the area remains bounded to the north by forest (Peterson 2003).

Species endemic to the interior grasslands of North America have been exposed to extreme climate variability through evolutionary time and presumably have evolved mechanisms to cope with such variability. These evolved responses to weather-related phenomena (e.g., drought, storms) and climate variability may yield insights into how animals might respond to future changes in climate. Knowledge of demographic parameters of bird populations across years of varying climatic conditions allows for the development of models that

may prove to be highly informative in light of anticipated climate change in the Great Plains of North America.

This manuscript presents a detailed analysis of the effect of local climate variation on reproductive parameters of an endemic prairie passerine, the Lark Bunting (see Plate 1). This species is suited to the study of climate change impacts because of the availability of long-term data on reproduction, demography, and local climate (Simmons et al. 2004). It also can serve as a model to examine potential impacts of climate on other bird species that are similar in ecology and habitat preference, such as Baird's Sparrow (*Ammodramus bairdii*), Horned Lark (*Eremophila alpestris*), and other prairie-nesting birds. During seven breeding seasons, we quantified vegetative features, clutch size, nest survival, and productivity of grassland birds in 27 randomly selected study sites. Weather during our study was fairly representative of the past 70 years of recent climate. Here we model the influence of weather variables on reproductive parameters while controlling for the influences of nest age, vegetation characteristics of the site, and seasonal timing. We use our best-approximating model to generate predictions of reproductive parameters under various future climate scenarios. We discuss the implications of our findings for declining prairie bird populations relative to future climate predictions within the context of paleoclimatic conditions on the Great Plains of North America and the evolutionary history of prairie breeding birds.

METHODS

Study area and study organism

The study was conducted in and near the Pawnee National Grassland (PNG), northeastern Colorado USA ($40^{\circ}43' \text{ N}$, $104^{\circ}29' \text{ W}$) within an ecoregion dominated by shortgrass steppe (Fig. 1). The shortgrass steppe has a semiarid climate with average annual precipitation of 340 mm. Precipitation in this region is episodic, dominated by high inter- and intra-annual variability, and is the primary driver of plant productivity in the region (Pielke and Doesken 2008). Small rainfall events ($<5 \text{ mm}$) comprise more than 70% of the total precipitation during the growing season and are responsible for the intra-annual variation, whereas large precipitation events ($>10 \text{ mm}$) account for most of the interannual variation (Sala et al. 1992). Precipitation records over 65 years (1939–2004) from the 6280-ha Central Plains Experimental Range bordering the PNG in northeastern Colorado reveal interannual variation ranging from 32% to 170% of the long-term annual average and an increase of 1.8 mm per year; temperature records show no discernable changes in monthly minimum or maximum temperatures (Shortgrass Steppe Long Term Ecological Research 2010).

Our study area is a moderately fragmented grassland landscape composed of shortgrass prairie (62%), irrigated and nonirrigated crops (29%), and Conservation

Reserve Program (CRP) fields (8%). Through the seven years of the study, we randomly selected 27 study sites (64.7 ha, quarter section), which included 19 shortgrass prairie sites from a sampling frame of U.S. Forest Service land and eight CRP sites from a sampling frame of private CRP lands. All sites are contained within a 30 × 61 km area. The number of sites studied varied among years due to short-term research questions and funding and totaled 16, 16, 22, 1, 11, 2, and 3 from 1997 to 2003, respectively. In 2002, we increased the size of the two sites to include parts of 1–3 adjacent quarter sections to augment numbers of nests monitored.

Shortgrass prairie study plots were dominated by native xeric grasses such as buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*), with occasional shrub components of four-winged saltbush (*Atriplex canescens*) and broom snakeweed (*Gutierrezia sarothrae*). Study sites in CRP lands were primarily exotic grasses such as smooth brome (*Bromus inermis*), intermediate wheatgrass (*Agropyron intermedium*), and crested wheatgrass (*A. cristatum*). Low- to moderate-intensity grazing by cattle (≤ 0.6 AUM/ha, where AUM is animal unit month and animal refers to a cow–calf pair; Augustine et al. 2012) occurred in the shortgrass prairie sites managed by the U.S. Forest Service except in 2002 when forage production was reduced by drought. CRP sites were not grazed by cattle during our study.

Our study species, the Lark Bunting, is an insectivorous and granivorous endemic passerine of the shortgrass and midgrass prairie regions of North America, inhabiting regions with annual precipitation <586 mm (Shane 2000). During May to July, males and females build open-cup nests on the ground, often sheltered by grass clumps or small shrubs. Both males and females participate in incubation and care of nestlings and fledglings (Shane 2000). Lark Buntings are primarily single-brooded (2–6 eggs per clutch; average 4), although they frequently renest after nest failure (Yackel Adams et al. 2007). Their nesting period requires 23–28 days (2–3 d for nest building, 1 d per egg laid, 11–12 d for incubation, and 8 d for nestling care). Potential nest predators include thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), coyote (*Canis latrans*), swift fox (*Vulpes velox*), long-tailed weasel (*Mustela frenata*), bullsnake (*Pituophis melanoleucus*), western hognose snake (*Heterodon nasicus*), and Burrowing Owl (*Athene cunicularia*).

Field procedures

From mid-May to early-August 1997–2003, we located and monitored bird nests. We searched all sites systematically for nests by dragging a rope between two observers 25 m apart and by observing adult behavior. To determine incubation stage, we floated two eggs (to minimize nest disturbance) from each nest and used Westerskov's (1950) technique recalibrated for our study species. We recorded number, age (based on maximum

value of the two eggs), and status of eggs and nestlings at 2–4 day intervals until nests were empty. During the last nest check, we noted signs of fledging (parents feeding young or calling in vicinity, fecal droppings outside of nest).

We sampled vegetation structure and composition of sites using two field techniques. The first technique was used during late May and early June 1997–2001, and the second technique was used in early August of 2001–2003. In 2001, both techniques were used; about 50% of nests were on sites associated with each technique. With the first technique, we sampled 12 points 300 m apart along point transects systematically placed at the center of each study site. At each point, we visually estimated the percent cover of grasses, sedges, forbs, shrubs, cacti, and bare ground within 5 m radius plots, and we measured grass and vegetation height at distances of 1, 3, and 5 m from the point in one direction (east). With the second technique, we sampled 45 points at 15-m intervals along a randomly placed 700-m transect. At each point, we estimated percent cover of grasses, sedges, forbs, shrubs, cacti, and bare ground within a 20 × 50 cm frame (Daubenmire 1959) and measured heights of all vegetation types at 5, 25, and 45 cm along the center line of the frame and maximum vegetation height within the frame. For all data, we calculated average and median heights and average percent cover of all vegetation types, and we constructed new variables based on products of height and cover variables to indicate vegetation density (Table 1). The same field crew sampled vegetation in all years except 1998 (the observers in 1998 were trained in 1997). The difference in sample timing between the two techniques is partially mitigated by the measurement of standing dead vegetation. We assume that, despite use of two sampling methods and scales of measurement, we captured the relative differences in vegetation structure between sites.

Data analyses

We acquired historical weather data for 1997–2003 from the Western Regional Climate Center (*available online*)³ and the Shortgrass Steppe Long Term Ecological Research group (see *Acknowledgments*). Preliminary models for productivity parameters included several forms of daily and seasonal precipitation and temperature from four weather stations within the boundaries of our Colorado study area (NOAA Coop Station 050945 [Briggsdale], 055922 [New Raymer Coop], 055934 [New Raymer 21N], and weather station of the Central Plains Experiment Station). We chose a range of daily and seasonal precipitation metrics that might reveal short- and long-term effects of precipitation both on vegetation structure and on reproductive parameters. Fall and winter precipitation determine soil moisture at the beginning of the next growing season, which in turn

³ <http://www.wrcc.dri.edu/>

TABLE 1. Predictor variables with the most support ($\Delta AIC_c = 0.00$), indicating their influence on clutch size, nest survival, and productivity of the Lark Bunting (*Calamospiza melanocorys*) in and near the Pawnee National Grassland, northeastern Colorado, USA.

Variable	Clutch size (<i>n</i> = 731 nests)		Nest survival (<i>n</i> = 811 nests)		Productivity (<i>n</i> = 301 nests)	
	AIC _c	ΔAIC_c	AIC _c	ΔAIC_c	AIC _c	ΔAIC_c
Nest age						
Constant model	2012.34		2676.76	21.84	941.86	
Age			2677.17	22.25		
Age + Age ²			2678.45	23.53		
Age + Age ² + Age ³			2654.92	0.00		
Time in season (covariates in model)						
	none		nest age + clutch size		clutch size	
Covariates only	2012.34	116.14	2634.14	0.00	904.61	0.00
Date	1908.25	12.04	2636.04	1.90	905.52	0.91
Date + Date ²	1896.21	0.00	2637.97	3.83	907.52	2.91
Date + Date ² + Date ³	1896.78	0.57	2639.81	5.67	908.80	4.19
Habitat structure (covariates in model)						
	date ²		nest age + clutch size		clutch size	
Covariates only	1896.21	21.84	2634.14	4.06	904.61	4.26
Average grass height (AvGrHt)	1892.93	18.57	2631.66	1.59	900.35	0.00
Median grass height (MedGrHt)	1888.12	13.76	2630.07	0.00	904.46	4.12
Quadratic of median grass height	1889.87	15.51	2631.24	1.16	905.94	5.60
Average height of forbs and shrubs	1895.23	20.86	2636.01	5.93	906.33	5.98
Average height of all vegetation	1885.95	11.58	2632.25	2.18	903.93	3.58
Percent cover of grasses and sedges	1884.61	10.29	2633.76	3.68	906.12	5.77
Percent cover of forbs and shrubs	1893.73	19.36	2636.02	5.94	903.41	3.06
Percent cover of all vegetation (VegCover)	1874.37	0.00	2634.46	4.39	903.35	3.00
Product of median grass height and cover	1883.62	9.25	2633.55	3.47	904.91	4.56
Product of forb/shrub height and cover	1896.30	21.93	2639.38	9.31	902.02	1.67
Product of vegetation height and cover	1884.67	10.31	2636.13	6.05	906.06	5.71
Daily precipitation (covariates in model)						
	date ² + VegCover		nest age + clutch size + MedGrHt			
Daily precipitation	1874.44	2.42	2631.87	4.33		
Precipitation the previous day	1872.02	0.00	2632.04	4.51		
Rain event ≥ 5 mm	1874.06	2.04	2632.08	4.54		
Rain event ≥ 10 mm	1875.54	3.52	2627.54	0.00		
Rain event ≥ 20 mm	1876.04	4.02	2631.49	3.95		
Previous day with ≥ 5 mm	1876.01	3.98	2632.02	4.48		
Previous day with ≥ 10 mm	1873.40	1.38	2631.95	4.41		
Previous day with ≥ 20 mm	1875.00	2.97	2630.20	2.66		
Seasonal precipitation (covariates in model)						
	date ² + VegCover		nest age + clutch size + MedGrHt		clutch size + AvGrHt	
Precipitation Sep–Aug	1852.95	0.00	2632.04	3.26	895.39	0.00
Precipitation Apr–Jun	1858.66	5.67	2630.59	1.81	901.25	5.86
No. days with ≥ 5 mm precipitation	1865.86	12.81	2628.78	0.00	896.33	0.94
No. days with ≥ 10 mm precipitation	1860.91	7.88	2630.79	2.01	902.42	7.03
No. days with ≥ 20 mm precipitation	1868.67	15.67	2631.75	2.97	902.14	6.76
Temperature (°C) (covariates in model)						
	date ² + VegCov		nest age + clutch size + MedGrHt		clutch size + AvGrHt	
Daily minimum	1876.05	22.58	2630.60	2.48		
Daily mean	1872.98	18.47	2629.65	1.55		
Daily maximum	1867.69	14.15	2629.52	1.41		
Average daily minimum	1870.25	16.99	2628.88	0.77	899.82	4.03
Average daily mean	1859.98	5.75	2628.10	0.00	896.64	0.85
Average daily maximum	1853.33	0.00	2628.43	0.32	895.79	0.00

Notes: Each nest is individually associated with the nearest weather station. Variables ultimately used in models are indicated in boldface. In some cases, closely competing variables ($\Delta AIC_c < 2.0$) provided a better fit when substituted into best-approximating models. Blank cells indicate variables that were not included in models.

positively influences vegetation growth as well as spring and summer precipitation (Pielke and Doesken 2008). Seasonal precipitation was expressed as the amount of precipitation from September of the previous year through August of the study year (annual) or the amount of precipitation April through June of the study year. For daily precipitation variables, we evaluated

measured precipitation, binary variables that denoted rain events of different magnitudes (>5 mm, >10 mm, and >20 mm), and amount of rainfall on the previous day as a surrogate for varying predator behavior after rainstorms (Dinsmore et al. 2002). Temperature was expressed as daily and average daily maximum, minimum, and mean temperatures during the study season.

Because the timing of data collection differed among stations (01:00, 07:00–08:00, or 18:00 hours), some measurements were offset by one day so that nest fate was associated with most recent minimum temperature (early morning), maximum temperature (previous afternoon), and precipitation events (previous afternoon). For clutch size analyses, we used the recorded daily weather values from the day prior to the laying of the first egg. We assigned weather data to each individual nest based on the nearest weather station. The average distance of sites from the nearest weather station was 7.9 km (SE = 0.08, range = 4–17 km, with the exception of one outlying site that was 40.8 km from its nearest weather station).

In addition to temperature and precipitation, we used several other predictive variables (nest age, clutch size, time in season, habitat structure) in our models, the number of which depended on the particular response variable. We chose these explanatory variables because the scientific literature suggests they influence breeding success and because of our interest in the repercussions of predicted increases in temperature and reduced precipitation in the shortgrass prairie region on avian reproductive performance. Nest age, vegetation structure, and time in season (with day 1 designated as May 18, the onset of incubation of the first nest of all seasons) are all known to influence nest survival in other grassland birds, although responses can be highly variable and include linear and nonlinear effects; specifically, higher order polynomials of time in season (quadratic) and nest age (cubic) have been reported (Dinsmore et al. 2002, Davis 2005, Grant et al. 2005, Winter et al. 2005). Further, we suspect that clutch size may influence nest survival positively if it indicates parents that are more experienced (older) or in better body condition or negatively if it results in increased activity around the nest or longer parental inattentive periods during foraging bouts (Bolton et al. 1993, Westneat et al. 2009). The inclusion of nest age, clutch size, habitat structure, and time in season in our regression models may allow for improved estimates of the effects of temperature and precipitation on nest survival if they explain portions of the variance surrounding the estimates of nest survival.

We determined the relationships among clutch size, nest survival, and productivity and their respective explanatory variables using general linear models (for clutch size and productivity, SYSTAT 2009) and the robust nest survival model in MARK Version 4.3 (White and Burnham 1999), which uses generalized linear modeling based on a binomial likelihood. We assumed the duration of incubation and nestling periods to be 12 and 8 days, respectively. For nests of uncertain fate, the final observation interval was censored and nests were coded as successful, as recommended by Manolis et al. (2000). Nests of unknown age were assigned the age of the average initial age of nests found for each year. Records for four nests that were

abandoned during laying or early incubation were censored. For nests with incomplete information to determine clutch size ($n = 81$ of 811 nests in nest survival analyses and $n = 26$ of 301 nests in productivity analyses), we used average clutch size calculated from our data set (Cooch and White 2011).

We selected the best expression for each variable of interest (nest age, time in season, habitat structure, daily and seasonal precipitation, and temperature, including quadratics and polynomials of time in season and nest age, respectively), then using the selected expressions, we formed balanced model sets with respect to the weather variables. In preliminary analyses, variables yielding the lowest AIC_c values were chosen to represent time in season, habitat structure, daily and seasonal precipitation, and temperature. Table 1 presents all metrics considered in preliminary analyses. Closely competing expressions of variables (from models <2 AIC_c from that of the selected metric) were reevaluated post hoc by substituting into the final best-fitting model containing the variable with closely competing forms.

After the preliminary analyses, we formulated sets of eight candidate models for clutch size and nest survival and four candidate models of productivity to explore the influence of climatic variables on reproductive parameters using covariates in all models to control for as much variability as possible. Covariates considered in clutch size models were time in season and habitat structure; in nest survival models were nest age, clutch size, time in season, and habitat structure; and in productivity models were clutch size, time in season, and habitat structure. The candidate model sets were balanced with respect to weather-related variables (daily precipitation, seasonal precipitation, and temperature), in that they appear equally in the model set. For example, sets of models for clutch size and nest survival analyses included a model with all three weather variables, three models with two weather variables (in all combinations), models with each variable alone, and a model with only covariates (to serve as a null model). Productivity models evaluated seasonal precipitation and temperature only.

We tested for strong correlation (Pearson's $|r| \geq 0.7$) among the independent variables contained in the same model so that we could avoid using highly correlated predictor variables. To evaluate the relative importance of the three weather variables in this balanced model set, we computed the relative variable importance by summing Akaike weights ($\sum w_i$) over models containing the variable of interest (Burnham and Anderson 2002:167). We based our interpretations of the relative influence of all variables on (1) the AIC_c values with the addition of a variable to a model, (2) the relative variable importance (for the three weather variables), and (3) whether or not the confidence intervals (CI) spanned zero. A relative variable importance weight <0.40 suggests that a variable has little influence (G. White, *personal communication*). Effects were considered

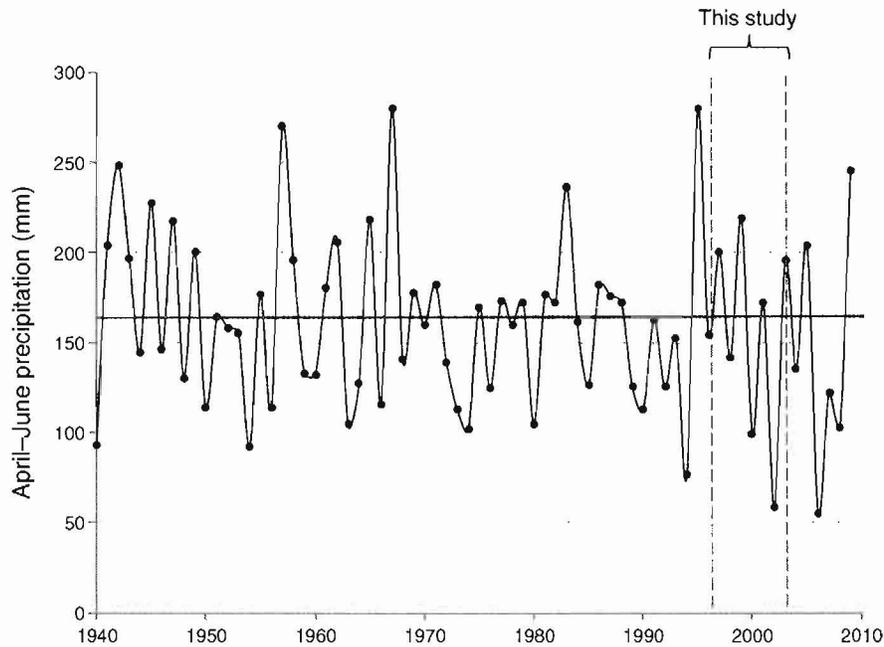


FIG. 2. April–June precipitation from 1940 to 2009 for the Pawnee National Grassland and vicinity, northeastern Colorado, USA. The seven years of this study are contained between the vertical dashed lines (1997–2003) and represent four wet years and three dry years. The 70-year April–June precipitation average of 160 mm is denoted by the solid horizontal gray line. Precipitation data are from PRISM (Parameter–elevation Regressions on Independent Slopes Model, Oregon State University; PRISM Climate Group 2010).

strong if the 95% CI did not span zero, weak if the 90% CI did not span zero, and as having no relationship with the predictor variable if the 90% CI spanned zero. Nest success was calculated as $(\text{daily survival})^{20}$ (where 20 is the total number of days for incubation plus nestling periods), and variance estimates were calculated using the delta method (Seber 2002). Reported values are means or regression coefficients \pm SE, unless otherwise noted.

Last, we applied the best-approximating models to predict clutch size, daily nest survival, and productivity with increases in temperature and declines in precipitation. We applied the models to 12 future climate scenarios in which future average temperatures (mean and maximum) and precipitation (daily and seasonal) remain within the ranges of observed data from the four weather stations used in our study. The 12 scenarios included two temperature levels and six precipitation levels. We set future temperatures at the maximum observed in our study and at a value intermediate between current averages and the maximum. To specify precipitation levels, we calculated the span between the current average and minimum for the seasonal and daily precipitation variables in the models, and decreased values by 0%, 20%, 40%, 60%, 80%, and 100% of this amount. We treated vegetation variables in the same manner as precipitation, and we assumed the mean value for time in season. Predicted clutch sizes for the 12 scenarios were specified in the nest survival and productivity models. We estimated fecundity (number

of female young/female) for each scenario assuming a 50:50 nestling sex ratio and 1.66 nesting attempts per female (including re-nesting attempts; sensu Yackel Adams et al. 2007).

RESULTS

During the seven years of our study, the climate of our study area and its immediate vicinity was fairly representative of the past 70 years except that we witnessed no years of extremely high precipitation (Fig. 2). April through June precipitation was greater than the long-term (1940–2009) average for four of seven years and below the long-term average for three years. During the seven years of our study, average April through June precipitation across the Pawnee National Grassland and vicinity (155 ± 22 mm, range 62–216 mm) did not differ from the longer-term average (160 ± 6 mm, range 58–219 mm; PRISM Climate Group 2010). Temperature and precipitation levels averaged across the four weather stations during our study period were as follows: average mean temperature = $19.6^\circ \pm 0.04^\circ\text{C}$, range 17.7 – 22.5°C ; average maximum temperature = $28.2^\circ \pm 0.06^\circ\text{C}$, range 25.5 – 32.6°C ; precipitation during the months of April through June = 159 ± 23 mm, range 59–245 mm; annual precipitation = 395 ± 45 mm, range 216–557 mm. Rain occurred in 33% of the daily weather records (range 13–40% across years) and totaled >10 mm in 7% (range 1–13%) of records during our study.

During the seven breeding seasons of the study, we located and monitored 811 Lark Bunting nests (63, 58,

TABLE 2. Competing top-ranked ($w_i > 0.05$) models of effects of selected precipitation and temperature variables on reproductive parameters of Lark Buntings on and near the Pawnee National Grassland, 1997–2003.

Response variable	Models	AIC _c	ΔAIC _c	K	w _i
Clutch size (n = 731 nests)	TimeSeas ² + VegCover + DailyPrec + SeasPrec + Temp	1846.635	0	7	0.555
	TimeSeas ² + VegCover + SeasPrec + Temp	1847.671	1.036	6	0.331
Nest survival (n = 811 nests)	Age ³ + Clutch + MedGrHt + DailyPrec + SeasPrec + Temp	2621.001	0	9	0.712
	Age ³ + Clutch + MedGrHt + SeasPrec + Temp	2624.050	3.049	8	0.155
	Age ³ + Clutch + McdGrHt + DailyPrec + Temp	2625.721	4.720	8	0.067
Productivity (n = 301 nests)	Clutch + AvGrHt + SeasPrec	895.386	0	4	0.398
	Clutch + AvGrHt + SeasPrec + Temp	895.613	0.227	5	0.355
	Clutch + AvGrHt + Temp	896.636	1.250	4	0.213

Notes: All clutch size models contained the quadratic of time in season and the percent cover of all vegetation (indicated as TimeSeas² + VegCover); all nest survival models contained nest age³, clutch size, and median grass height (indicated as Age³ + Clutch + MedGrHt). Quadratic and cubic polynomial forms included the lower-level terms. All productivity models contained clutch size and average grass height (indicated as Clutch + AvGrHt). AIC_c weights (w_i) indicate the relative likelihood of each model, given the model set. DailyPrec is daily rainfall the day prior to egg formation (clutch size models) and daily rainfall of ≥ 10 mm (nest survival models); SeasPrec is total rainfall (in cm) from September through August of each study year (for clutch size and productivity models), and total rainfall from April through June of each study year (for nest survival models); Temp is average daily maximum temperature (°C) in each study year (clutch size and nest survival models) and average daily mean temperature (productivity models).

141, 29, 284, 83, and 153 from 1997 through 2003, respectively). These numbers varied due to differences the number of study sites searched each year, as well as the Buntings' tendency to drastically fluctuate in local numbers from year to year (Shane 2000). Adequate information existed to determine number of eggs laid (clutch size) for 732 of these nests. We suspected causes of nest failure to be inclement weather (a minimum of 3.4% of 504 failed nests), nest desertion (2.8%), cattle activity (0.6%), and predation (93.2%), although nest loss from starvation of chicks and inclement weather can be difficult to distinguish from predation. Brood parasitism did not occur. Fate and nest age were unknown for 3.0% and 3.2% of nests, respectively.

Preliminary analyses to select variable expressions

In our evaluation of the influence of weather patterns on clutch size, the quadratic of date, percent cover of all vegetation, precipitation on the day prior to egg formation, annual precipitation (from September of the previous year through August of the study year), and average daily maximum temperature were selected during preliminary analyses (Table 1). Substitution of closely competing expressions (from models < 2 AIC_c from that of the selected metric) into the best-approximating model did not improve model fit.

In preliminary analyses of nest survival, the cubic polynomial of nest age received substantially more support than other lower-order models (Table 1). The null model best described time in season. Habitat structure was best described by median grass height. In all cases, weather variables had more influence on nest survival when each individual nest was associated with data from the nearest weather station rather than when weather metrics were weighted by number of nests nearest the station, although the differences in AIC_c for various forms of temperature were slight. Daily precipitation was best described by whether a given day received > 10 mm of rainfall. Seasonal precipitation was

best represented by the number of days with ≥ 5 mm precipitation, and temperature was best represented by average daily mean temperature during the study season (Table 1). Closely competing variables for habitat structure, time in season, and daily precipitation did not improve fit of the best-approximating model (Δ AIC_c ranged from 1.72 to 7.31 and evidence ratios from 2.4 to 38.6, suggesting that the original models were more than 2.4–38.6 times as likely as the competing models). The original best models for seasonal precipitation and temperature were outcompeted by the total amount of precipitation during April through June (Δ AIC_c = 6.413, evidence ratio 24.7) and average daily maximum temperature (Δ AIC_c = 1.717, evidence ratio 2.4). Therefore, we used them in the nest survival candidate model set (Table 2).

In preliminary analyses for productivity (number of young fledged per successful nest), the best models included average grass height, precipitation from September of the previous year through August of the study year, and average daily maximum temperature. The addition of time in season did not improve the model consisting of covariates only (Table 1). Substitution of closely competing expressions into the best-approximating model improved model fit only for average mean temperature (Δ AIC_c = 0.373). We did not evaluate daily precipitation or daily temperature variables for productivity.

Models of clutch size

The balanced model set that we considered for clutch size contained time in season and habitat structure in all eight models. The best-approximating model included all weather variables (daily and seasonal precipitation, temperature) and yielded a model weight of $w_i = 0.555$ (Table 2). The combined weight of the top two models was $w_i = 0.885$. The relative variable importance of the weather variables indicate that seasonal precipitation (0.949), temperature (0.936), and daily precipitation

TABLE 3. Influence of nest age, clutch size, time of season, habitat structure, and weather on reproductive parameters of Lark Buntings on the Pawnee National Grassland and vicinity, 1997–2003.

Parameter	β (SE)	95% CL	Effect
Clutch size ($n = 731$ nests)			
Time of season	-0.008 (0.008)	-0.023, 0.007	
Time of season ²	-0.0002 (0.0001)	-0.0004, 0.0000	strong negative
VegCover	0.002 (0.004)	-0.006, 0.010	no relationship
Daily precipitation	0.010 (0.005)	0.000, 0.020	strong positive
Seasonal precipitation	0.012 (0.004)	0.004, 0.020	strong positive
Temperature	-0.063 (0.023)	-0.108, -0.018	strong negative
Nest survival ($n = 811$ nests)			
Age	0.223 (0.050)	0.125, 0.321	
Age ²	-0.021 (0.005)	-0.032, -0.011	strong
Age ³	0.0006 (0.0002)	0.0002, 0.0009	
Clutch size	0.278 (0.056)	0.168, 0.387	strong positive
MedGrHt	0.014 (0.012)	-0.010, 0.039	no relationship
Daily precipitation	-0.600 (0.235)	-1.060, -0.141	strong negative
Seasonal precipitation	0.030 (0.012)	0.007, 0.053	strong positive
Temperature	0.097 (0.033)	0.033, 0.162	strong positive
Productivity ($n = 301$ nests)			
Clutch size	0.455 (0.078)	0.301, 0.609	strong positive
AvGrHt	-0.043 (0.014)	-0.071, -0.015	strong negative
Seasonal precipitation	0.014 (0.005)	0.004, 0.024	strong positive
Temperature	-0.078 (0.059)	-0.194, 0.038	no relationship

Notes: Effect sizes (regression coefficient β with SE, and confidence limits, CL) are from the best-approximating models (from Table 2) containing the parameter. Time of season is date (day 1 = 18 May); Age is nest age and includes the three terms of the cubic polynomial model; VegCover is percent cover of all vegetation; MedGrHt is median grass height; AvGrHt is average grass height; Daily precipitation is rainfall on the day prior to egg formation (clutch size models) and daily rainfall of ≥ 10 mm (nest survival models); Seasonal precipitation is total rainfall (in cm) September–August of each study year (clutch size and productivity models) and total rainfall April–June of each study year (nest survival models); Temperature is average daily maximum temperature ($^{\circ}\text{C}$) in each study year (clutch size and nest survival models) and average daily mean temperature (productivity models). Effects were considered strong if the 95% CI did not span zero and as having no relationship with the predictor variable if the 90% CI spanned zero.

(0.630) influenced clutch size during the years of our study. Clutch size decreased nonlinearly as time in season progressed and was positively related to daily rainfall at the onset of egg formation (Table 3). Furthermore, clutch size was strongly (95% CI did not span zero) and positively related to annual precipitation and strongly negatively related to average maximum temperatures. There was no discernible relationship (90% CI spanned zero) between clutch size and the percent cover of all vegetation (Table 3).

Nest survival models

The balanced model set for nest survival contained nest age, clutch size, and habitat structure in all eight models. The best-approximating model of the balanced model set ($w_i = 0.712$; Table 2) included all of the weather predictor variables (daily and seasonal precipitation, temperature). The relative variable importance weights of the weather variables indicate that temperature (0.937), seasonal precipitation (0.895), and daily precipitation (0.828) all had strong influences on nest survival during the years of our study. No independent variables were strongly correlated (e.g., $|r| \geq 0.7$); thus they were retained in the models. Median grass height

was only moderately positively correlated with seasonal precipitation (April through June of the study year; $r = 0.446$), indicating that $<20\%$ of the variance in grass height was related to precipitation.

Nest age and clutch size had strong effects on survival of Lark Bunting nests, as evidenced by 95% CI that did not span zero for any of these terms (Table 3). Nest survival increased with nest age during early incubation and late in the nestling stage, but declined during late incubation and the early nestling stage. Broods from larger clutches had a higher likelihood of fledging at least one young. Part of the clutch size effect may have been confounded with time in season, but the two variables were only slightly negatively correlated ($r^2 = 0.135$). Habitat structure did not show a clear effect on nest survival, with 90% CI broadly spanning zero (Table 3).

Daily precipitation had a strong negative effect on nest survival, as indicated by a negative regression coefficient and 95% CI that did not span zero. To illustrate the role of daily precipitation events on nest survival, we ran models that allowed the slope for nest age to vary for each year–weather station combination. Nest survival dramatically decreased on days with >10

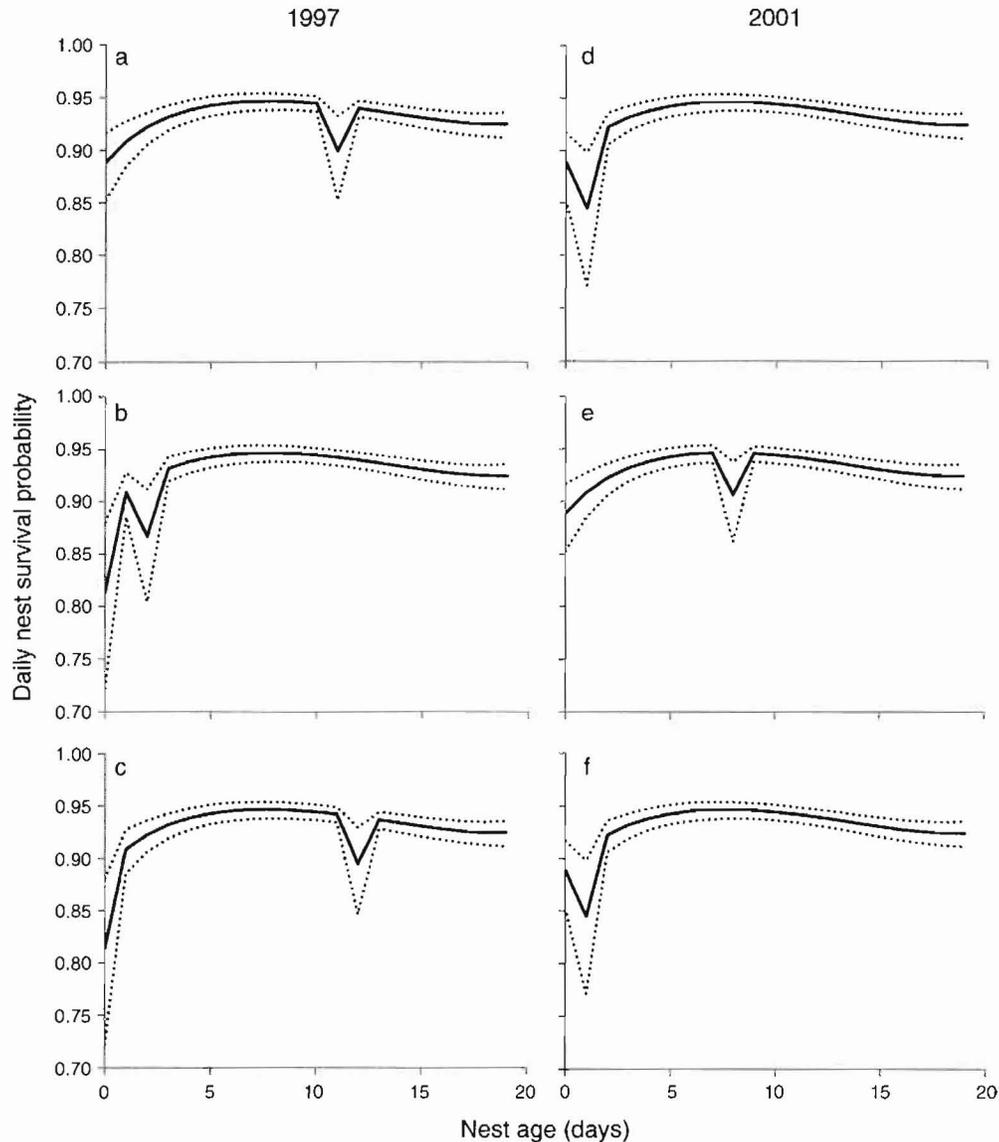


FIG. 3. Daily survival probabilities of Lark Bunting nests in and near the Pawnee National Grassland, Colorado 1997–2003 in relation to rain events during the nesting period. Daily rain events (>10 mm) depressed daily nest survival probabilities (note downward spikes). Estimates and 95% confidence intervals (dotted lines) were generated using the regression equation from the top nest survival model (Table 2) containing the effect and illustrated for only two years (1997 and 2001). Panels represent rain events recorded at the individual weather stations as follows: (a) day 11, Central Plains Experiment Station (CPEP); (b) days 0 and 2, New Raymer 21N; (c) days 0 and 12, New Raymer Coop; (d) day 1, Briggsdale, (e) day 8, CPEP; (f) day 1, New Raymer Coop. Weighted values for the following covariates were used to generate the figure: age set such that day 0 = 12 June, clutch size of 4.2, median grass height value 10.4 cm, seasonal precipitation 173 mm, and average maximum temperature 28.2°C.

mm rainfall (Fig. 3), resulting in an average decline in daily survival of $0.043 (\pm 0.001, n = 16)$ rainfall events for nests active during midseason) and a decrease in overall nest survival of 4.9% for each rainfall event.

In contrast, seasonal precipitation had a strong positive effect overall on nest survival, with greater nest survival in wetter than dry years (Tables 3 and 4). Temperature also had a strong positive effect, with increasing nest survival in years of higher average maximum temperatures; the 95% CI did not span zero.

Models of productivity

The balanced model set for productivity (number of young fledged per successful nest) contained clutch size and average grass height in all four models and evaluated two weather variables, seasonal precipitation and temperature. Temperature did not appear in the best-approximating model ($w_i = 0.398$), although it did in a closely competing model of similar weight ($w_i = 0.355$; Table 2). The relative variable importance weights of the weather variables suggest that both seasonal

TABLE 4. Influence of seasonal precipitation (April–June) on breeding performance of Lark Buntings during seven years of variable rainfall on the Pawnee National Grassland.

April–June precipitation (mm)	Year	Clutch size (total $n = 731$)			Nest survival (total $n = 811$)					Productivity (total $n = 302$)		
		Mean	SE	n	Daily survival		Nest success			Mean	SE	n
					Mean	SE	Mean	SE	n			
235	1999	4.6	0.07	115	0.943	0.006	0.309	0.039	141	3.7	0.16	60
227	1997	4.8	0.09	50	0.922	0.012	0.197	0.051	63	3.4	0.30	22
180	2001	4.3	0.08	260	0.938	0.005	0.278	0.030	284	3.2	0.11	108
167	1998	4.7	0.10	41	0.930	0.011	0.234	0.055	58	4.3	0.23	19
145	2003	4.3	0.08	153	0.928	0.007	0.224	0.034	153	3.0	0.15	47
128	2000	3.9	0.15	29	0.939	0.015	0.284	0.091	29	3.3	0.27	14
64	2002	3.6	0.12	84	0.916	0.011	0.173	0.042	83	3.2	0.17	32

Notes: Years are presented in order of decreasing precipitation; n is the number of nests. For this summary table only, precipitation was calculated as the average of the four weather stations weighted by the number of nearby nests. Nest success equals (daily survival)²⁰ (where 20 is the total number of days for incubation plus nestling periods), and variance estimates were calculated using the delta method (Seber 2002). Productivity is the number of young per successful nest. Data from the Western Regional Climate Data Center, Reno, Nevada, USA.

precipitation (0.754) and temperature (0.569) influenced productivity during the years of our study. Productivity increased with increasing clutch size, declined with increasing average grass height, and was greater in wetter years (Table 3). In contrast to the relative variable importance weight, the regression coefficient and confidence intervals did not suggest a relationship between productivity and temperature. The effect of temperature may have been masked by the effects of annual precipitation because the two variables were moderately negatively correlated ($r^2 = 0.274$).

Projections of reproductive parameters under future climate scenarios

Reproductive parameters were predicted at average mean temperature increases of 2° and 3°C during the breeding season (or similarly, average maximum temperature increases of 3.3° and 4.4°C). For all future scenarios, the number of young produced per 100 nests increased with increasing temperatures (due to increases in nest survival) but declined with reductions in precipitation. Higher temperatures with no accompanying change in precipitation led to 4–6% smaller clutches, 31–50% higher daily nest survival, and 5–8% lower productivity (Fig. 4). These changes yielded 22–32% additional young per 100 nests, corresponding to a rise in fecundity from 0.72 to 0.88–0.95. However, under scenarios of rising temperatures and declines in seasonal precipitation to the minimum observed in our study, clutch size, daily nest survival, and productivity all declined by 12–14%, 27–40%, and 7–10%, at 2–3°C increases, respectively. The number of young per 100 nests declined by 36–46% and fecundity declined to 0.39–0.46.

DISCUSSION

Species' responses to environmental change have consequences for population persistence through time. When challenged with climate change, species can evolve new physiological tolerances or behaviors, they can

maintain their current ecological niches and move spatially to track suitable conditions, or they can face extirpation. This study suggests that our focal species will be negatively affected by predicted climate change because several facets of reproductive performance were reduced under drought conditions. Decreased seasonal precipitation negatively influenced clutch size in Lark Buntings, as well as nest survival and productivity after the effects of clutch size were considered. Higher temperatures also depressed clutch size. With predicted temperature increases of 2–3°C, decreases in average precipitation beyond 30–40% could lead to declines in fecundity, further compromising the ability of local populations to persist in the absence of immigration (sensu Yackel Adams et al. 2007).

In semiarid environments, climatic influences on food abundance and predation may potentially yield the patterns of avian reproductive success that we observed. Increased precipitation may enhance primary and secondary productivity (e.g., biomass of invertebrate prey), which may then lead to greater clutch sizes and higher fledging success. Larger clutches of two passerine species, Brewer's Sparrow (*Spizella breweri*) in the northern Great Basin and Rufous-crowned Sparrow (*Aimophila ruficeps*) in coastal southern California (Rotenberry and Wiens 1989, 1991, Morrison and Bolger 2002) in wetter years support this idea. During drought periods, food scarcity may demand that parents have longer foraging bouts and thus spend less time defending the nest from predators (Schmidt 1999). Predation may also increase during drought if food scarcity results in greater intensity of spontaneous begging by underfed nestlings early in the nestling period (A. A. Yackel Adams, *personal observation*).

Although wet years of our study generally favored nest survival, large precipitation events (>10 mm) temporarily depressed daily survival of nests. In Colorado, 70–80% of the annual precipitation falls during the growing season, and severe thunderstorms and hail damage regularly occur (Doesken et al. 2003).

Daily precipitation events may have reduced foraging success of parents or compromised thermoregulation of eggs and nestlings via longer intervals between nest attentiveness or physical wetting or washing away of nests. Field crews observed flooded nests and periodic hail events that caused direct mortality of adult grassland birds attending nests. Presumably nest survival is favored by increasing nest concealment; however, we did not find a relationship between vegetation structure of the study plots and nest survival in this study. Because nest survival is largely determined by predator community structure and function, which in turn are influenced by a myriad of factors, including soil characteristics, vegetation structure, prey abundance, precipitation patterns, and land use (Stapp et al. 2008), it is not surprising that the relationship between nest survival and vegetation structure is highly variable among studies (Martin 1993, Davis 2005, Winter et al. 2005).

Average temperatures during the breeding season also were positively associated with survival of Lark Bunting eggs and nestlings to fledging age. Higher temperatures may enhance survival and growth rates of poikilothermic nestlings if they are better able to maintain body heat during parental inattentive periods (Franklin et al. 2000, Dawson et al. 2005). Warmer temperatures may also be associated with greater insect activity and bird foraging success (Avery and Krebs 1984) or with changes in incubation and brooding behavior, allowing longer foraging bouts away from the nest without incurring the adverse effects of cold on eggs and nestlings (Yom-Tov and Hilborn 1981, Conway and Martin 2000). The effect of temperature on nest survival of birds is not well established and is inconsistent among studies (Wiebe 2001, Dinsmore et al. 2002, Morrison and Bolger 2002, Drever and Clark 2007, Dickey et al. 2008).

Future scenarios of climate and implications for the Great Plains of North America

Increases in mean surface air temperatures of ~3.5–4°C in this century have been projected across the entire Great Plains by a composite of 21 climate models for the emissions scenario (A1b) that assumes carbon emissions at intermediate levels (Christensen et al. 2007). The range in this temperature response extends from an increase of only 1.4°C (low emissions scenario) to as high as 7.2°C (high emissions; Karl et al. 2009). Temperatures are predicted to increase more in the northern and western areas of the Great Plains and in the summer than in winter (Karl et al. 2009). Projected changes in spring precipitation forecast wetter climates in northern areas of the Great Plains to drier climates in southern areas by the end of the 21st century (Karl et al. 2009). Models incorporating various emissions scenarios differ in whether eastern Colorado experiences overall drier conditions (high emissions) or no effective change (low emissions), although under all scenarios, precipita-

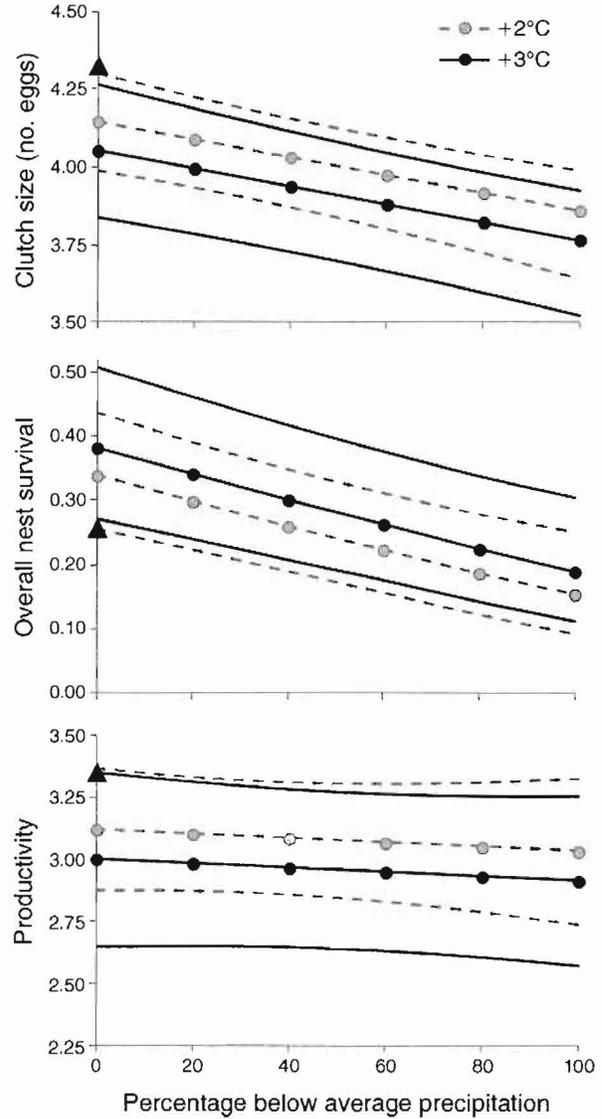


FIG. 4. Projected clutch size, overall nest survival, and productivity (number of young per successful nest) under climate scenarios of temperatures 2°C and 3°C higher than the current (1997–2003) average summer temperatures. To specify precipitation levels, we calculated the span between the current average and minimum for the seasonal precipitation ($SeasPrec_{avg} - SeasPrec_{min}$) and decreased values by 0%, 20%, 40%, 60%, 80%, and 100% to yield percentage below average precipitation. Projected values were based on the best-approximating models (Table 2), assuming time of season = day 25 (11 June) and no rain events >10 mm; nest age was set such that day 0 = 12 June. Habitat structure and daily precipitation were incremented downward in concert with seasonal precipitation values. Black triangles on the y-axes denote estimates of clutch size (95% CI: 4.25–4.41), overall nest survival (95% CI: 0.21–0.32), and productivity (95% CI: 3.23–3.48) at current average temperature and seasonal precipitation levels.

tion is expected to decrease in the summer relative to winter months (Christensen et al. 2007, Ray et al. 2008). Increases in summer temperatures will increase evapotranspiration rates and potentially contribute to in-

creased frequency of meteorological droughts (Karl et al. 2008), especially in seasons and areas of stable or declining precipitation, such as summers in eastern Colorado.

The findings from this study suggest that, within a local area, the components of climate have different effects on reproductive success. In the immediate future, the negative effects of reduced spring and summer precipitation on daily nest survival may be offset partially by the positive influences of temperature increases up to 3°C (within the range of temperatures in our study) and of potential declines in frequency of large rain events (>10 mm). Declining seasonal precipitation and increasing temperatures (again, within the ranges measured during our study) could also contribute to smaller clutches, although there may be a slight increase in the proportion of eggs that survive to fledging.

Climate change and birds: an evolutionary perspective

Perspectives from paleoclimate and evolutionary history can help to refine questions and identify possible management directions/actions toward the conservation of native bird populations and their habitats in light of pending climate change. The highly variable climatic conditions experienced by prairie biota across several spatial and temporal scales are evidenced by the climate history of the Great Plains. Grassland birds, and presumably Lark Buntings, have persisted through millennia of both climate stasis and extreme variability throughout their evolutionary history. Passerines appeared in the northern hemisphere by 25 Mya [million years ago] (Steadman 2005). Fossil evidence of modern grassland songbirds dates to the early Pliocene, 4.3–4.8 Mya (Emslie 2007), with identified fossil remains specifically of Lark Buntings in southwestern Kansas in the late Pleistocene (26 700–29 000 yr BP; Downs 1954, Shane 2000). Extensive prairie and steppe habitat dominated the Great Plains during the early Pliocene when the climate was relatively stable; with the advent of the glacial–interglacial cycles of the Pleistocene beginning ca. 2.5 Mya, the prairie–steppe habitat periodically appeared and disappeared (Emslie 2007). During the past 10 000 years (the Holocene), relatively moist conditions on North American grassland landscapes were repeatedly interrupted with droughts intense enough to impact vegetation composition and mobilize sand dunes (Forman et al. 2001).

During the 20th century, the American West has experienced less frequent and less severe droughts than the conditions revealed in paleoclimate records of the last 1000 years (Ray et al. 2008). Over the past 400 years, droughts as intense or greater than the extreme droughts of the 1930s and 1950s occurred with some regularity, and prior to AD 1600, droughts were longer (often spanning decades) and more spatially extensive than droughts of the 20th century (Woodhouse and Overpeck 1998). Tree ring and lake salinity records extending back

2000 years also suggest overall drier conditions and more frequent and persistent droughts prior to AD 1200 than in modern times (Laird et al. 1996). Our study period included the drought of 2002 across the Great Plains of North America, one of the six driest periods of the past century (Ray et al. 2008).

At broad spatial and temporal scales, Lark Buntings and other prairie birds presumably have evolved strategies that allow them to cope with the extreme interdecadal and interannual climate variability of the Holocene. Selection for migratory behavior purportedly occurred in response to climate change during the Pleistocene ice ages (Emslie 2007). Historic climate variability in the Great Plains selects for a degree of vagility and opportunism rather than strong site fidelity to specific locations. Our study demonstrates a cost, in lower productivity, to breeding under dry conditions. To minimize this cost, Lark Buntings can seek alternative breeding sites where conditions are favorable. The distribution of Lark Buntings in any given year is strongly influenced by precipitation and the position and magnitude of the North Atlantic Oscillation, which largely drives Great Plains precipitation patterns (Price 1995, Niemuth et al. 2008).

Potential interplay of climate and land use change

Evidence that drought is negatively associated with Lark Bunting reproductive output, combined with knowledge that the 20th century was wetter and thus more favorable than much of the preceding millennia, leads us to hypothesize that the widespread population declines in Lark Buntings documented over the past four decades (Sauer et al. 2011) are not related primarily to weather and recent climate trends. Rather, population declines may be a response to anthropogenic factors such as a century or more of land use change and intensification of agriculture across the species' range (Brennan and Kuvlesky 2005). Although buntings will settle opportunistically in breeding areas with favorable rainfall conditions, they are geographically constrained by the occurrence of their primary vegetative associations, the shortgrass and mixed grass prairie communities (Shane 2000). Large portions (30–70%) of native vegetation within the central shortgrass prairie region, including northeastern Colorado, have been converted to dryland and irrigated croplands. In contrast to eastern Colorado populations, Lark Bunting populations have increased in eastern Montana (Sauer et al. 2011), a relatively intact grassland landscape where the climate is only slightly drier than eastern Colorado, based on data from the Western Regional Climate Center.

The behavioral traits of vagility and opportunism, which enable Lark Buntings to respond to long- and short-term habitat conditions influenced by weather variation, may lead to northerly and easterly shifts in distribution if precipitation and habitat conditions become more favorable there than in areas predicted



PLATE 1. (Top panel) Female sitting on nest and (lower panel) male with food. Both male and female Lark Buntings participate in the incubation and care of young. Photo credit: A. A. Yackel Adams.

to be drier: the southern and western regions of the Great Plains. However, distributional shifts in Lark Buntings may be constrained by changes in land use, agricultural practices, and vegetative communities that diminish the extent of short- and mixed-grass prairie habitats in areas with more favorable climatic conditions. For example, northward and eastward shifts in Buntings may be hindered if rising temperatures and increased evapotranspiration also push the optimum latitude and longitude for crops, and thus agricultural intensity, northward and eastward. Conversely, increased summer dryness in Colorado, coupled with the redirection of water used for agriculture to cities (Wiener et al. 2008), may cause a reduction in cropland in the region, yet this change would only lead to benefits

for prairie birds if habitat structure in abandoned croplands and prevailing climatic conditions were favorable.

It is useful to acknowledge that many modern birds have coped with changing climates during their evolutionary pasts (Lovette 2005), primarily by broadening niches or redistributing on the landscape. Birds currently exposed to extensive year-to-year climate variability, such as grassland birds in the Great Plains of North America, show responses to climate change in an ecological time frame. Our study species redistributes in response to precipitation (Price 1995, Niemuth et al. 2008), yet land use change and human perturbations of grassland systems may yield limited opportunities for such a redistribution. Our data and analyses demon-

strate the costs (lower reproductive output) of breeding in an area during a drought, and thus the costs of highly altered landscapes that constrain movements because there is no habitat suitable for immigration. Protection of grasslands through easement programs and management through the use of grazing and fire would provide a buffer against climate change by allowing the Lark Bunting to shift into suitable areas as needed.

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