BioOne COMPLETE

Reproductive response of Arizona Grasshopper Sparrows to weather patterns and habitat structure

Authors: Ruth, Janet M., and Skagen, Susan K.

Source: The Condor, 120(3) : 596-616

Published By: American Ornithological Society

URL: https://doi.org/10.1650/CONDOR-17-128.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 120, 2018, pp. 596–616
DOI: 10.1650/CONDOR-17-128.1

RESEARCH ARTICLE

Reproductive response of Arizona Grasshopper Sparrows to weather patterns and habitat structure

Janet M. Ruth[1]* and Susan K. Skagen[2]*

[1] U.S. Geological Survey, Fort Collins Science Center, Arid Lands Field Station, Albuquerque, New Mexico, USA
[2] U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado, USA
* Corresponding authors: Janet Ruth, janet_ruth@usgs.gov; Susan Skagen, skagens@usgs.gov

Submitted July 7, 2017; Accepted May 7, 2018; Published July 18, 2018

ABSTRACT

Avian species endemic to desert grasslands of North America contend with significant ecological challenges, including monsoonal rains, droughts, and variable temperatures. These birds have evolved physiological and behavioral means of coping with such extremes, but ongoing changes to temperature and precipitation patterns are affecting their breeding phenology, reproductive success, and population growth rates. We examined how seasonal and daily weather conditions and habitat structure were associated with the nest survival of Arizona Grasshopper Sparrows (*Ammodramus savannarum ammolegus*) in the semidesert and plains grasslands of southeastern Arizona, USA. The mean ± SE daily survival rate (DSR) of nests was 0.960 ± 0.006, corresponding to overall nest success of 46%. The previous season's precipitation, large rain events, and nest concealment were the most important factors explaining DSR. Grasshopper Sparrow nest survival decreased with a wetter previous growing season and with large rain events on previous days. Nests that were more concealed had lower survival rates. There was some evidence that nest survival was lower later in the nesting season. In addition, when nest concealment was included in models, there were positive but weak associations between other vegetation variables and DSR—nests with higher visual obstruction at the nest and nest plot scales, and nests that were farther from shrubs >2 m tall, showed higher survival rates. Predation was the major cause of nest failure, suggesting complex interactions among predation, precipitation, and nest concealment. Further, our findings suggest tradeoffs in the potential effects of future climate change on *A. s. ammolegus*. The increased frequency of extreme storm events predicted for the region may result in reduced nest survival of *A. s. ammolegus*, but, conversely, lower seasonal precipitation prior to nesting may positively influence nest survival.

Keywords: *Ammodramus savannarum ammolegus*, daily survival rate, desert grasslands, Arizona Grasshopper Sparrow, reproductive success, precipitation, temperature, vegetation structure

Respuesta reproductiva de *Ammodramus savannarum ammolegus* a los patrones meteorológicos y a la estructura del hábitat

RESUMEN

Las especies de aves endémicas de los pastizales del desierto de América del Norte lidian con desafíos ecológicos significativos, incluyendo lluvias monzónicas, sequía y temperaturas variables. Estas aves han evolucionado medios fisiológicos y comportamentales para hacer frente a estos extremos, pero los cambios en curso en los patrones de temperatura y precipitación afectan su fenología reproductiva, el éxito reproductivo y las tasas de crecimiento poblacional. Examinamos cómo las condiciones meteorológicas estacionales y diarias y la estructura del hábitat estuvieron asociados con la supervivencia del nido de *Ammodramus savannarum ammolegus* en los pastizales semidesérticos y las planicies del sudeste de Arizona. La tasa de supervivencia diaria promedio ± EE de los nidos (TSD) fue 0.960 ± 0.006, correspondiendo a un éxito global de anidación de 46%. La precipitación estacional previa, los eventos de mucha lluvia y el ocultamiento de los nidos fueron los factores más importantes para explicar la TSD. La supervivencia del nido de *Ammodramus savannarum ammolegus* disminuyó con una mayor humedad en la estación de crecimiento anterior y con los eventos de mucha lluvia de los días previos. Los nidos que estuvieron más ocultos tuvieron tasas de crecimiento más bajas. Hubo cierta evidencia de que la supervivencia de los nidos fue más baja hacia fines de la estación reproductiva. Adicionalmente, una vez que se incluyó en los modelos al ocultamiento del nido, hubo asociaciones débiles pero positivas entre otras variables de la vegetación y la TSD—los nidos con obstrucción visual más alta en el nido y las escalas de parcela del nido, y los nidos que estuvieron más lejos de arbustos > 2 m de alto, mostraron tasas de supervivencia más altas. La depredación fue la mayor causa de fracaso del nido, sugiriendo interacciones complejas entre depredación, precipitación y ocultamiento del nido. Más aún, nuestros resultados sugieren la existencia de soluciones de compromiso en los efectos potenciales del cambio climático futuro en *A. s.*

© 2018 American Ornithological Society. ISSN 0010-5422, electronic ISSN 1938-5129
Direct all requests to reproduce journal content to the AOS Publications Office at pubs@americanornithology.org

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

ammolegus. El aumento en la frecuencia de eventos extremos de tormenta predichos para la región puede originar una reducción de la supervivencia del nido de *A. s. ammolegus*, y por el contrario, una menor precipitación estacional antes de la anidación puede influenciar positivamente la supervivencia del nido.

Palabras clave: Ammodramus savannarum ammolegus, Arizona, estructura de la vegetación, éxito reproductivo, pastizales del desierto, precipitación, tasa de supervivencia diaria, temperatura

INTRODUCTION

Species that inhabit arid ecosystems in the southwestern United States and northern Mexico contend with significant ecological challenges, most of them related to climate. Birds and other arid-land species have long been exposed to extreme and variable monsoonal rains, drought conditions, and temperatures, and have presumably evolved physiological and behavioral means of coping with such extremes and variability (Wolf et al. 1996, Williams and Tieleman 2001, Gardner et al. 2009, Martin et al. 2015). However, in spite of evolved adaptations, recent studies have indicated that temperature increases and changes in precipitation patterns are affecting the breeding phenology, reproductive success and population growth rates of species as varied as Loggerhead Shrikes (*Lanius ludovicianus*; Borgman and Wolf 2016), Black-throated Sparrows (*Amphispiza bilineata*; Hargrove and Rotenberry 2011), deer mice (*Peromyscus maniculatus*; Reed et al. 2007), and vespertilionid bats (Adams 2010).

Increases in temperature, changes in the amount or timing of precipitation, or changes in the frequency of extreme weather events may affect birds that breed in arid systems directly through effects on survival and reproductive success (Skagen and Yackel Adams 2012, Cunningham et al. 2013, Öberg et al. 2015, Conrey et al. 2016) or indirectly through effects on primary productivity, grassland structure, food resources, and foraging behavior (Morrison and Bolger 2002, Joern and Laws 2013, Mowll et al. 2015, Öberg et al. 2015). In addition, sparrows, an important component of arid-land avian communities, contend with a diverse assemblage of nest predators that exert strong selective pressure on sparrow use of breeding habitat and are likewise affected by climate (Ernest et al. 2000, Witecha 2011, Joern and Laws 2013, Ibáñez-Álamo et al. 2015).

Across its overall distribution, the Grasshopper Sparrow (*Ammodramus savannarum*) shows a long-term declining population trend (Sauer et al. 2014) and has been designated a Common Bird in Steep Decline (NABCI–US 2014, Rosenberg et al. 2016). It has been designated by the U.S. Fish and Wildlife Service (USFWS) as a focal species (Ruth 2015). Southeastern Arizona, USA, is the core of the distribution of the Arizona Grasshopper Sparrow (*A. s. ammolegus*). This subspecies is endemic to the desert grasslands of the southwestern U.S. and northern Mexico, with a breeding distribution that includes southeastern Arizona and southwestern New Mexico, USA, south to northern Sonora, Mexico (Vickery 1996). The subspecies is considered a Bird of Conservation Concern in USFWS Region 2 (USFWS 2008) and is listed as Endangered in the state of New Mexico (NMDGF 2016) due to population declines and threats of loss, degradation, and fragmentation of its native grassland habitat (Ruth 2008, 2017, USFWS 2008, NMDGF 2016).

In these grasslands, Arizona Grasshopper Sparrows and Cassin's Sparrows (*Peucaea cassinii*), another desert grassland specialist, have adapted to the arid climate by delaying nest initiation until the arrival of summer monsoons in July and August (McClaran and Van Devender 1995, Ruth 2000, 2017, Corman and Wise-Gervais 2005). In Arizona, Grasshopper Sparrow nest entrances are oriented to the north, likely to provide protection from solar radiation and prevailing winds (Long et al. 2009, Ruth 2017). Arizona Grasshopper Sparrows are smaller than more northern subspecies (Ruth 2017), possibly facilitating heat loss following Bergmann's rule (Ashton 2002). In spite of these adaptations, recent literature suggests that changes in temperature and precipitation patterns may still affect the reproductive success of grassland species such as the Grasshopper Sparrow. The Grasshopper Sparrow was 1 of 5 grassland species in the northern mixed-grass prairie (Badlands and Prairies Bird Conservation Region 17) whose abundance was significantly associated with precipitation and temperature (Gorzo et al. 2016). Gorzo et al. (2016) noted that increased frequencies of droughts could negatively affect this species, and suggested that more in-depth assessments of the effects of weather on grassland birds were needed.

Climate affects avian abundance primarily through changes in demographic parameters such as survival, productivity, and phenology (Robinson et al. 2007, Seavy et al. 2008). Therefore, understanding how weather affects reproductive success is an important means of improving our understanding of how climate change may affect bird populations. We examined how seasonal and daily weather conditions and nest microhabitat (vegetation structure) were associated with daily nest survival of Arizona Grasshopper Sparrows in the desert grasslands of southeastern Arizona during a 3-yr period. Our objectives were to determine the relative importance of the influence of daily and seasonal weather conditions and grassland structure on reproductive success, and to determine which weather and habitat conditions affected reproductive

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

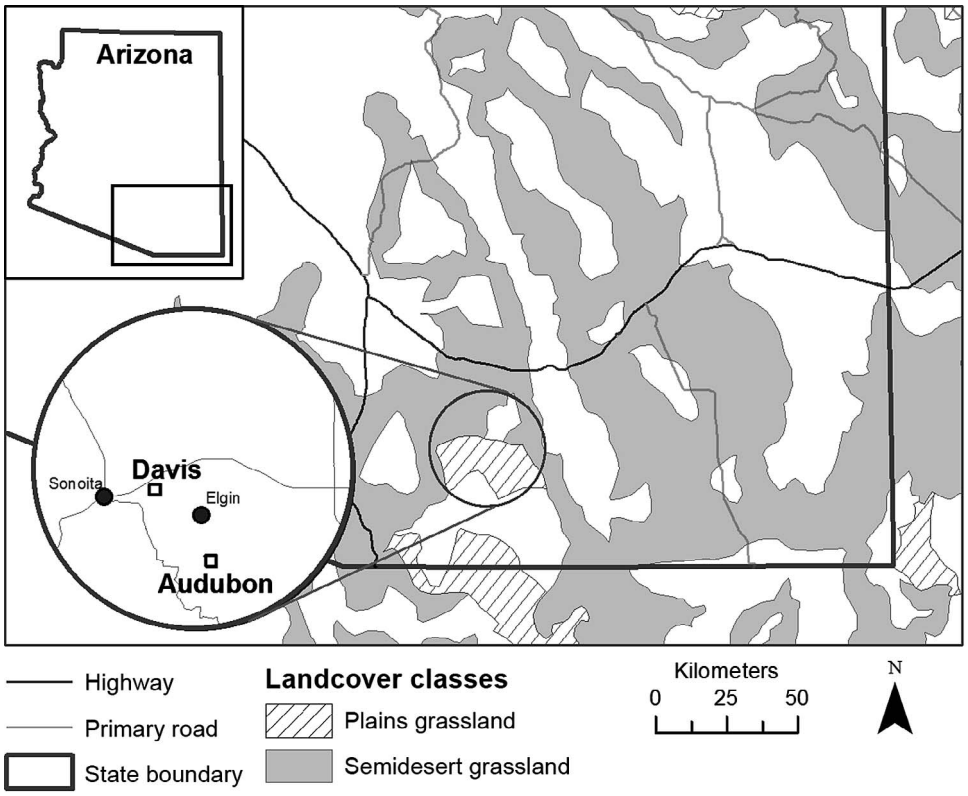


FIGURE 1. Location of study sites (Davis and Audubon) in the Sonoita Valley of southeastern Arizona, USA, where we examined how seasonal and daily weather conditions and habitat structure were associated with the nest survival of Arizona Grasshopper Sparrows in 2011–2013. Mapping of grassland biotic communities is modified from Brown et al. (2007). The blank areas on the map (not shaded or hatched) represent all land cover classes other than the 2 grassland types.

success. Knowledge about Grasshopper Sparrow responses to shifts in weather and grassland structure will be valuable to natural resource managers as they plan for anticipated climate change (Wolf 2000).

METHODS

Study Area

In North America, desert grasslands occur from the southwestern United States into northern Mexico at elevations of 1,100–1,800 m (McClaran and Van Devender 1995). In our study region of southeastern Arizona, these grasslands include what other sources name semidesert grassland interspersed in a mosaic with plains grassland (Brown and Makings 2014). The climate here is dry, hot, and sunny. Mean annual precipitation in desert grasslands ranges from 300 mm to 450 mm (Brown and Makings 2014); in southeastern Arizona, ~60% of annual precipitation occurs between July and September, with significant spatial and temporal variation (McClaran and Van Devender 1995). The mean annual temperature is 13–16°C. The region typically experiences 20 summer days hotter than 40°C; as a result, annual potential evaporation is often 2–3 times greater than annual rainfall (McClaran and Van Devender 1995). The main ecological drivers in this system are precipitation and drought; secondary drivers are fire and grazing (Askins et al. 2007).

We worked in 2 sites spaced ~13 km apart in the desert grasslands of Santa Cruz County, southeastern Arizona (Figure 1): Audubon Appleton-Whittell Research Ranch (hereafter, 'Audubon'; 3,200 ha, 31.60°N, 110.51°W, elevation 1,497 m); and the Davis pasture in the Bureau of Land Management (BLM) Las Cienegas National Conservation Area (NCA; hereafter, 'Davis'; 1,560 ha, 31.70°N, 110.60°W, elevation 1,430 m). We selected these 2 sites because of access and adequate Arizona Grasshopper Sparrow sample sizes. We considered the sites to be representative of Arizona Grasshopper Sparrow habitat based on surveys throughout the range of the subspecies in New Mexico and Arizona (Ruth 2008). We worked in randomly selected representative portions of the 2 study sites: ~50 ha at Audubon and ~67 ha at Davis.

Long-term mean annual precipitation for Audubon (NOAA 1981–2010 Normals; Arguez et al. 2012) was 454 mm. Consistent with the regional pattern (McClaran and Van Devender 1995), 55% of long-term annual

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

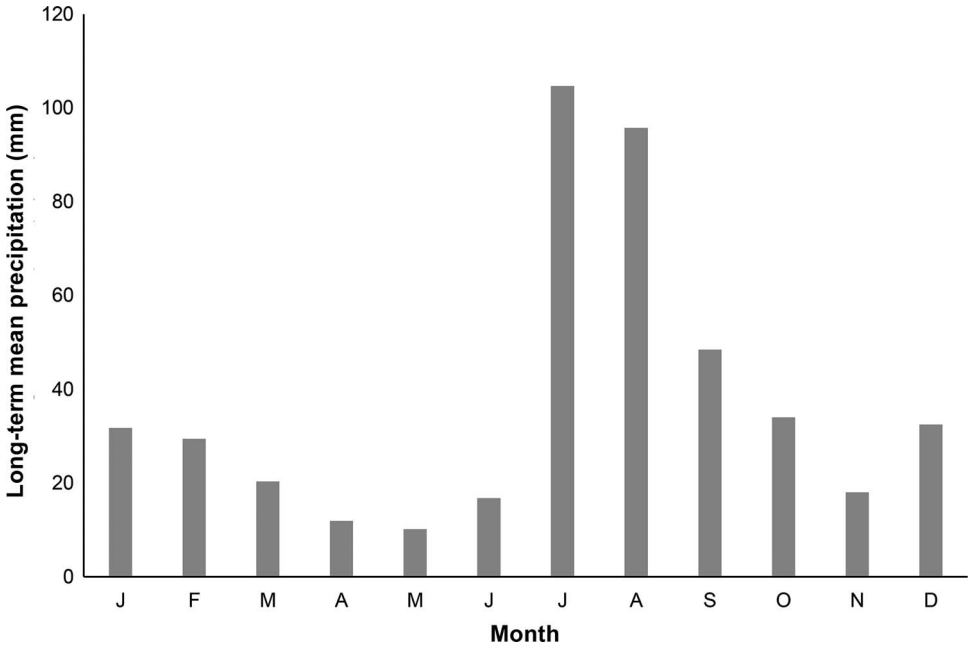


FIGURE 2. Long-term monthly precipitation averages for the Audubon Appleton-Whittell Research Ranch from NOAA 1981–2010 Normals (Arguez et al. 2012) taken from the Elgin 5S AZ station.

precipitation at Audubon occurred during the months of July through September (Figure 2). The long-term mean daily summer temperature (summer = June–August) at Audubon was 23.8°C, and the long-term mean daily summer maximum temperature was 31.6°C (NOAA 1981–2010 Normals; Arguez et al. 2012). Although specifically documented long-term averages were not available for the Las Cienegas NCA, it has been described as "only slightly lower, warmer, and drier" than the Audubon Research Ranch (page 12 in McClaran and Van Devender 1995), and average annual precipitation in nearby Sonoita was 433 mm (http://www.usa.com/sonoita-az-weather.htm).

Upland grasslands in these sites were dominated by a variety of native annual and perennial bunchgrasses, including gramas (*Bouteloua* spp.), cane bluestem (*Bothriochloa barbinodis*), threeawns (*Aristida* spp.), bristly wolfstail (*Lycurus setosus*), curly-mesquite (*Hilaria belangeri*), and plains lovegrass (*Eragrostis intermedia*), as well as exotic grasses, predominantly Lehmann lovegrass (*Eragrostis lehmanniana*) and some Boer lovegrass (*E. curvula* var. *conferta*). Varying densities of shrubs, succulents, and short trees, predominantly velvet mesquite (*Prosopis velutina*), were also present (McClaran and Van Devender 1995, Ruth 2017, Ruth and Skagen 2017). Although both sites included some areas with much higher densities of trees, our study focused on the relatively open grassland portions of both sites. Audubon is managed as a desert grassland research facility and has been ungrazed since 1968. Davis, as part of the Las Cienegas NCA, is managed for multiple uses, including grazing. During the period of this study, cattle grazing occurred in the Davis site for 1 mo in 2012.

Arizona Grasshopper Sparrow Breeding Biology

In our study sites, males selected territories with sparser vegetation structure than random and with more tall shrubs than random where shrub densities were low (Ruth and Skagen 2017). Females located nest sites within male territories in areas where the density of small shrubs was lower than in the territory overall when possible. Females constructed domed nests on the ground beneath bunchgrasses, preferentially selecting native bunchgrasses (Ruth and Skagen 2017), with nest openings oriented northward (Ruth 2017). Females incubated eggs and brooded young (Vickery 1996), with 11 days for incubation and 8 days for the nestling period, for a total nesting period of 19 days (Ruth 2017).

Field Methods

Nest searching. We conducted nest searches and nest monitoring from 2011 to 2013. We searched for nests 3–5 times per week from early July through to the end of August, using a combination of rope dragging, opportunistic foot flushing, behavioral observations, and occasional visual sightings of nests (Winter et al. 2003; see also Ruth and Skagen 2017). Once a nest was found, we marked it for relocation. In addition to recording the GPS location, we tied colored flagging to vegetation ~3 m from the nest in the direction that the nest entrance faced, and at ~3 m

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

in the opposite direction. We monitored nests every 2–4 days. We assigned nest age (onset of incubation = day 0) as soon as possible after discovery by candling eggs (Lokemoen and Koford 1996) or by estimating the age of nestlings (Jongsomjit et al. 2007). We back-calculated the date of incubation initiation (with the penultimate egg; Vickery 1996) from estimates of nestling or egg age or from hatching or fledging date.

We assigned nest fates as: (1) successfully fledged at least one Grasshopper Sparrow young; (2) depredated; (3) abandoned (eggs left permanently unattended); (4) trampled; or (5) unknown or uncertain. Evidence of reproductive success included observations of fledglings near the nest or within 3 days of expected fledging, adults carrying food for new fledglings or uttering alarm calls near the nest within 3 days of expected fledging, presence of fecal sacs or feather scales in the nest, and presence of fecal sacs near the nest (Jones et al. 2010). We assumed that predation had occurred when any of the following was documented: eggs were destroyed, eggs disappeared, or nestlings were too young to have fledged at the time that either they disappeared or their nest was destroyed.

We used the following data to estimate the daily survival rate of nests (DSR): date that the nest was found, date that it was last known to be active, date when it fledged or was known to have failed, and fate. For nests of uncertain fate, the final observation interval was censored such that the observation data were truncated to the date when the nest was last known to be active, and fate was coded as successful (Manolis et al. 2000). Dates were scaled so that day 1 was the first date when a nest was found (July 11) during the study.

Nest-site vegetation measurements. We sampled vegetation at the nest (Nest) and in a nest plot (NPlot) centered on the nest following fledging or nest failure. We typically measured nest vegetation within a week of fledging or failure, with the exception of 17 nests in the first year of nest monitoring when nest measurements were taken later (8–20 days after fledging or failure). For the nest plot, we placed 5-m transects in the 4 cardinal directions centered on the nest, and took measurements at the nest (plot center) and at 1-, 3-, and 5-m intervals, resulting in 13 sample points per nest plot.

Measurement protocols were the same as those used in these sites for wintering grassland bird research (Ruth et al. 2014) and for research on territory and nest-site selection (Ruth and Skagen 2017) conducted synchronously with this study. In summary, we measured vertical vegetation density at the nest (NestVVgDen) and in the 5-m radius nest plot (NPlotVVgDen), visual obstruction at the nest (NestVO) and in the nest plot (NPlotVO), bare ground in the nest plot (NPlotBare), distance from the nest to the nearest shrub 1–2 m tall (DistNShrb1–2m), and distance from the nest to the nearest shrub >2 m tall (DistNShrb>2m). Vertical vegetation density and visual obstruction measurements were taken using the same 6-mm diameter pole following Wiens (1969) and Robel et al. (1970). Shrub data were collected using Bonham's (1989) point-centered quarter (PCQ) measurements.

We also measured nest concealment in 2012 and 2013 by visually estimating the percentage of the nest concealed from view from directly above the nest and from 1 m away from the nest at ground level in the 4 cardinal directions. We used the arithmetic mean of these 5 measurements as the mean nest concealment (Conceal) value for each nest (Jones and Dieni 2007).

Choice of Model Variables

A variety of factors can affect the daily nest survival of grassland and shrubsteppe birds directly and indirectly and may vary in importance among species and habitats (Rotenberry and Wiens 1989, George et al. 1992, Dinsmore et al. 2002). Thus, we selected a priori a set of possible nest phenology, daily and seasonal climate, and habitat variables (Table 1) that we expected might influence the daily survival of Arizona Grasshopper Sparrow nests based on the literature and our knowledge (Ruth 2017, Ruth and Skagen 2017). The nest phenology variables that we selected were the age of the nest (linear, quadratic, and cubic polynomial), and the time in the season (linear and quadratic; Dreitz et al. 2012, Skagen and Yackel Adams 2012, Lusk and Koper 2013, Conrey et al. 2016).

To address the possibility that daily weather conditions might have direct effects on nest survival, we selected measures of daily precipitation and temperature. We selected daily maximum temperature because, in such an arid ecosystem, we assumed that high temperatures would have the strongest effect on nest survival (Dreitz et al. 2012, Skagen and Yackel Adams 2012, Öberg et al. 2015, Conrey et al. 2016). We considered it likely that there would be a slight time lag in the effect of daily precipitation or temperature on nest survival (Dreitz et al. 2012, Skagen and Yackel Adams 2012, Conrey et al. 2016). Therefore, we calculated precipitation and temperature on the days just prior to the nest check: precipitation 1 day prior (DaPrec1DP); precipitation 2 days prior (DaPrec2DP); maximum temperature 1 day prior (DaTMax1DP); and maximum temperature 2 days prior (DaTMax2DP).

In addition to these continuous daily weather variables, we also considered threshold effects of extreme rain or heat events on nest survival (Dreitz et al. 2012, Skagen and Yackel Adams 2012, Cunningham et al. 2013, Öberg et al. 2015, Conrey et al. 2016). In fact, there is reason to believe that there are effects on reproduction at temperatures far below the temperatures usually associated with mortality events (McKechnie et al. 2012). Based on the literature, we identified an extreme rain event threshold of $\geq$10 mm (Skagen and Yackel Adams 2012, Öberg et al. 2015, Conrey

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 1. Explanatory variables used to model the daily survival rate of Grasshopper Sparrow nests in southeastern Arizona, USA, 2011–2013.

Variable abbreviation	Variable explanation
Nest age (day)	
Age	Nest age (with day 0 at onset of incubation)
Age^2	Quadratic term of nest age
Age^3	Cubic polynomial term of nest age
Time in season (day)	
Time	Ordinal date when nest was initiated [a]
$Time^2$	Quadratic term of ordinal date
Seasonal precipitation (mm)	
PGSPrec	Cumulative previous growing season precipitation (previous June–September)
P12MPrec	Cumulative previous 12 mo precipitation (previous June–May)
PWPrec	Cumulative previous winter precipitation (previous October–February)
PSpPrec	Cumulative previous spring precipitation (previous March–June)
P30DPrec	Cumulative precipitation in the 30 days before initiation of incubation
Daily precipitation (mm)	
DaPrec1DP	Precipitation 1 day prior
DaPrec2DP	Precipitation 2 days prior
Over10mm1DP	Precipitation $\geq$10 mm 1 day prior (significant rain event, binary, 1 = yes)
Over10mm2DP	Precipitation $\geq$10 mm 2 days prior (significant rain event, binary, 1 = yes)
Daily temperature (°C)	
DaTMax1DP	Maximum temperature 1 day prior
DaTMax2DP	Maximum temperature 2 days prior
Over33°1DP	Maximum temperature $\geq$33°C 1 day prior (binary, 1 = yes)
Over33°2DP	Maximum temperature $\geq$33°C 2 days prior (binary, 1 = yes)
Over34°1DP	Maximum temperature $\geq$34°C 1 day prior (binary, 1 = yes)
Over34°2DP	Maximum temperature $\geq$34°C 2 days prior (binary, 1 = yes)
Grassland structure	
NPlotBare	Cover of bare ground within 5-m radius nest plot (%)
NPlotVVgDen	Vertical vegetation density within 5-m radius nest plot (mean vegetation contacts in 4 dm)
NPlotVO	Visual obstruction within 5-m radius nest plot (dm)
DistNShrb1–2m	Distance from nest to nearest shrub 1–2 m tall (m)
DistNShrb>2m	Distance from nest to nearest shrub >2 m tall (m)
NestVVgDen	Vertical vegetation density at nest (mean vegetation contacts in 4 dm)
NestVO	Visual obstruction at nest (dm)
NestPlNat	Nest plant native (binary, 1 = yes)
Nest concealment	
Conceal	Mean nest concealment (%)

[a] Ordinal date calculated with day 0 as the first date of nest initiation (July 11) in any year.

et al. 2016) and extreme daily maximum temperature event thresholds of $\geq$33°C (Cunningham et al. 2013) and $\geq$34°C. We had insufficient data to test the daily maximum temperature threshold of >35°C (Dreitz et al. 2012, Conrey et al. 2016). Again, to consider lags in the effects of these extreme daily weather events on nest survival, we identified the occurrence of precipitation events $\geq$10 mm 1 day prior (Over10mm1DP) and 2 days prior (Over10mm2DP), and the occurrence of daily maximum temperature events $\geq$33°C and $\geq$34°C 1 day prior (Over33°1DP and Over34°1DP) and 2 days prior (Over33°2DP and Over34°2DP). These 6 extreme weather variables were binary.

We considered that previous season precipitation might have indirect effects on nest survival (Morrison and Bolger 2002, Skagen and Yackel Adams 2012, McCreedy and van Riper 2015, Borgman and Wolf 2016). We selected previous season precipitation variables to represent time periods that affect factors such as primary and secondary productivity, vegetation structure, food resources, and predator communities that indirectly affect nest survival (Table 1). Precipitation varies seasonally, with different effects on habitat. Most grass and forb growth occurs during the growing season associated with summer monsoons, but trees and shrubs benefit most from winter precipitation (McClaran and Van Devender 1995). Seasonal precipitation summaries were calculated relative to the breeding season in which nests were monitored (e.g., for nests monitored in summer 2012, previous growing season precipitation was calculated for summer 2011). Values were calculated by summing monthly precipitation values for the appropriate time period: previous 12 mo precipitation (P12MPrec), previous growing season precipitation (PGSPrec), previous spring precipitation

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

(PSpPrec), and previous winter precipitation (PWPrec). To address the possibility that nest survival was associated with precipitation in the period immediately prior to individual nest initiation, we also calculated precipitation in the 30 days before initiation of incubation (P30DPrec).

We also considered that vegetation structure and composition could explain variation in nest survival (Davis 2005, Jones and Dieni 2007, Skagen and Yackel Adams 2012), given our findings regarding male territory and female nest-site selection (Ruth and Skagen 2017). We selected the following vegetation measurements for analysis: vertical vegetation density, visual obstruction, bare ground, nest plant, distance to the nearest shrub, and nest concealment (described by Ruth and Skagen 2017).

Climatic Data

Precipitation data were downloaded from the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information Global Historical Climatology Network–Daily (GHCN–D; http://www.ncdc.noaa.gov). Precipitation data for the Audubon site were taken from the Elgin 5S AZ (Arizona) station (GHCND: USW00053132), which was ~1.5 km from the study site, and precipitation data for the Davis site were taken from the Sonoita 1.3 SE AZ station (GHCND: US1AZSC0001), which was ~4 km from the study site. Monthly and annual precipitation data were from monthly summaries (NOAA GHCN–D). Daily precipitation data were gathered from the NOAA GHCN–D (Menne et al. 2012a, 2012b). There was a difference in the time of precipitation data collection between the 2 sites. For the Elgin 5S AZ station, part of the U.S. Climate Reference Network, daily summaries were for the 24-hr period ending at local midnight (Menne et al. 2012a, 2012b), whereas for the Sonoita 1.3 SE AZ station, part of the Community Collaborative Rain, Hail, and Snow Network (CoCoRaHS), daily summaries were for the 24-hr period ending at local noon (http://www.cocorahs.org/ViewData/StateDailyPrecipReports.aspx?state=AZ). Most summer monsoon precipitation in Arizona is of a convective nature and occurs in the afternoons and evenings (Hendricks 1985, Vera et al. 2006). To provide consistent data across the 2 sources, we assumed that rain occurred in the afternoon (after 12:00 hours), and manipulated the 2 datasets to present precipitation from the 1 day prior and 2 days prior to the nest check.

We used daily maximum temperatures from the Elgin 5S AZ station for the Audubon site (NOAA GHCN–D; Menne et al. 2012a, 20121b). Because the Sonoita 1.3 SE AZ station did not collect temperature data, we used an Interagency Remote Automatic Weather Station (RAWS) dataset (QEMA3 Empire station) available through MesoWest (http://mesowest.utah.edu) that provided daily temperature data for Davis. The Empire station was the nearest source (distance ~11 km from the Davis site) with available temperature data from approximately the same elevation (Davis: 1,430 m elevation; Empire station: 1,417 m elevation).

Data Analyses

We quantified reproductive output by estimating the daily survival rate (DSR) of nests, defined as the probability that a nest will survive one day, and overall nest success, defined as DSR^x, where x is the total number of days in the nesting period. For calculations of DSR and analyses of effects of weather and vegetation structure, we excluded 7 nests for which there were no vegetation data.

We used program MARK 6.2 (White and Burnham 1999) to model our data and estimate DSR. Program Mark uses generalized linear modeling based on a binomial likelihood. We used Akaike's information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i) to identify models with the most support (Akaike 1973, Burnham and Anderson 2002). We interpreted the strength of the response to a given variable by determining whether the confidence intervals around the coefficient estimate incorporated zero.

We used a hierarchical model selection procedure to limit the number of models when evaluating the associations between nest survival and nest phenology, weather, and habitat structure (see Winter et al. 2006, Arnold 2010, Skagen and Yackel Adams 2012).

In step one, we constructed a "base" model using 5 sets of phenological and weather variables (nest age, time in season, seasonal precipitation, daily precipitation, and daily temperature), initially excluding vegetation variables. We generated univariate models to determine which form of variable in a given set (including the constant model) performed the best (lowest AIC_c). If the constant model was the best model for a given set, but a second-best model was very closely ranked ($\Delta AIC_c < 0.10$), the variable in the second-best model was carried forward to the next step.

In step 2, we ran multivariate models that included the most competitive form of each of the 5 sets of variables in all combinations and determined the best model based on the lowest AIC_c value.

In step 3, the final step in building the base model, we substituted or added competitive variables, defined as being within 1 AIC_c of the best-performing variable in the same set, into the best model from step 2 to see if the model improved. We considered the resulting best-performing model in step 3 to be our base model.

In the final step, step 4, we evaluated the effects of grassland structure and composition on DSR by adding each of 8 vegetation variables individually to the base model. We calculated Pearson product moment correlation coefficients using SYSTAT 13 (Systat Software, San

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 2. Seasonal precipitation by year and site for our southeastern Arizona, USA, study sites (see Figure 1 for locations). Data are from the NOAA Global Historical Climatology Network (GHCN), from the Elgin 5S AZ station for the Audubon site, and from the Sonoita 1.3 SE AZ station for the Davis site.

		2011		2012		2013	
Precipitation variable [a]	Abbreviation [a]	Audubon	Davis	Audubon	Davis	Audubon	Davis
Growing season precipitation (mm)	GSPrec	213	250	297	279	259	265
Previous growing season precipitation (mm)	PGSPrec	305	239	213	250	297	279
Previous 12 mo precipitation (mm)	P12MPrec	338	317	319	389	390	386
Previous winter precipitation (mm)	PWPrec	29	70	82	103	86	104
Previous spring precipitation (mm)	PSpPrec	14	8	28	46	23	11

[a] Seasonal precipitation variables are defined in Table 1.

Jose, CA, USA) to assure that no 2 variables within models were highly correlated ($r \geq 0.7$; Dormann et al. 2013).

Nest concealment, an alternative measure of vegetation structure, incorporates both natural structure (the grass clump under which a female constructs her nest) and female sparrow-created structure (the dome and tunnel that a female constructs over her nest). To determine whether nest concealment was associated with nest survival, we used a subset of data from the 2 yr in which we measured nest concealment. In developing a new base model for this data subset, we modified the process used for the full dataset in order to reduce the number of models and utilize prior information gained from analysis of the full dataset. We referenced the best 4 models from the full dataset to identify the most important phenological and weather variable sets to carry forward in this analysis. First, we ran univariate models for the 2 best-performing variables (from step one, including the constant model) from each of these important variable sets. Next, we ran all combinations of the resulting top variable from each important set. We then added concealment to the resulting top model to determine whether this addition improved model performance. The resulting top model was designated as the new base model. As in step 4, we evaluated the effects of grassland structure and composition on DSR by adding each of 8 vegetation variables individually to the base model.

For graphical purposes, we projected daily survival rates for the most important variables across a range of values. To do so, we ran the best models with specified values for the variable of interest and held other influential variables at their mean values; the exception to this latter rule was that we specified no extreme rain event.

We ln-transformed variables to improve normality when necessary. Estimates ± SE are presented unless otherwise specified.

RESULTS

Annual precipitation during all 3 yr of this study (2011–2013; Table 2) was lower than the long-term average of 430–455 mm (Audubon Research Ranch website: http://researchranch.audubon.org/, NOAA 1981–2010 Normals: Arguez et al. 2012), with seasonal patterns that varied among sites and years. Annual precipitation for the year prior to our study (2010) was higher (Audubon: 508 mm; Davis: 514 mm) than the long-term average. Mean ± SD daily precipitation during our study period (July 11–August 30) across sites and years was 3.4 ± 7.6 mm (range: 0.0–60.2 mm). Daily maximum temperature was 30°C ± 3°C (range: 24–38°C). On average, there were 5 ± 2 days per field season (range: 3–9 days) with rain events that exceeded 10 mm (Figure 3), 9 ± 4 days per field season (range: 6–14 days) with maximum temperatures that exceeded 33°C, and 5 ± 3 days per field season (range: 3–9 days) with maximum temperatures that exceeded 34°C (Figure 4).

Nests

We located and monitored 128 nests (Audubon: $n = 54$ nests; Davis: $n = 74$ nests) over the 3 yr of our study (2011: $n = 37$; 2012: $n = 30$; 2013: $n = 61$). The percentages of nests found using various techniques were: rope dragging = 38%, opportunistic foot flushing = 31%, behavioral observations = 28%, and visual sightings = 3%. Across the 3 yr, the earliest incubation initiation dates ranged from July 8 to July 17 (Ruth 2017). Overall, 36% ($n = 46$ nests) of nests were unsuccessful, with 87% ($n = 40$ nests) of unsuccessful nests depredated, 7% ($n = 3$ nests) abandoned or infertile, 4% ($n = 2$ nests) trampled by cattle, and 2% ($n = 1$ nest) unsuccessful due to unknown causes. We did not observe Brown-headed Cowbird (*Molothrus ater*) eggs in any nests.

Nest-Site Vegetation Characterization

The means ± SD of the vegetation variables used in the DSR analyses (Table 1) were: percent bare ground on nest plot (NPlotBare) = 3% ± 5% (range: 0–23%); vertical vegetation density on nest plot (NPlotVVgDen) = 6.2 ± 1.1 vegetation contacts in 4 dm (range: 3.6–9.5 contacts); visual obstruction on nest plot (NPlotVO) = 0.8 ± 0.3 dm

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

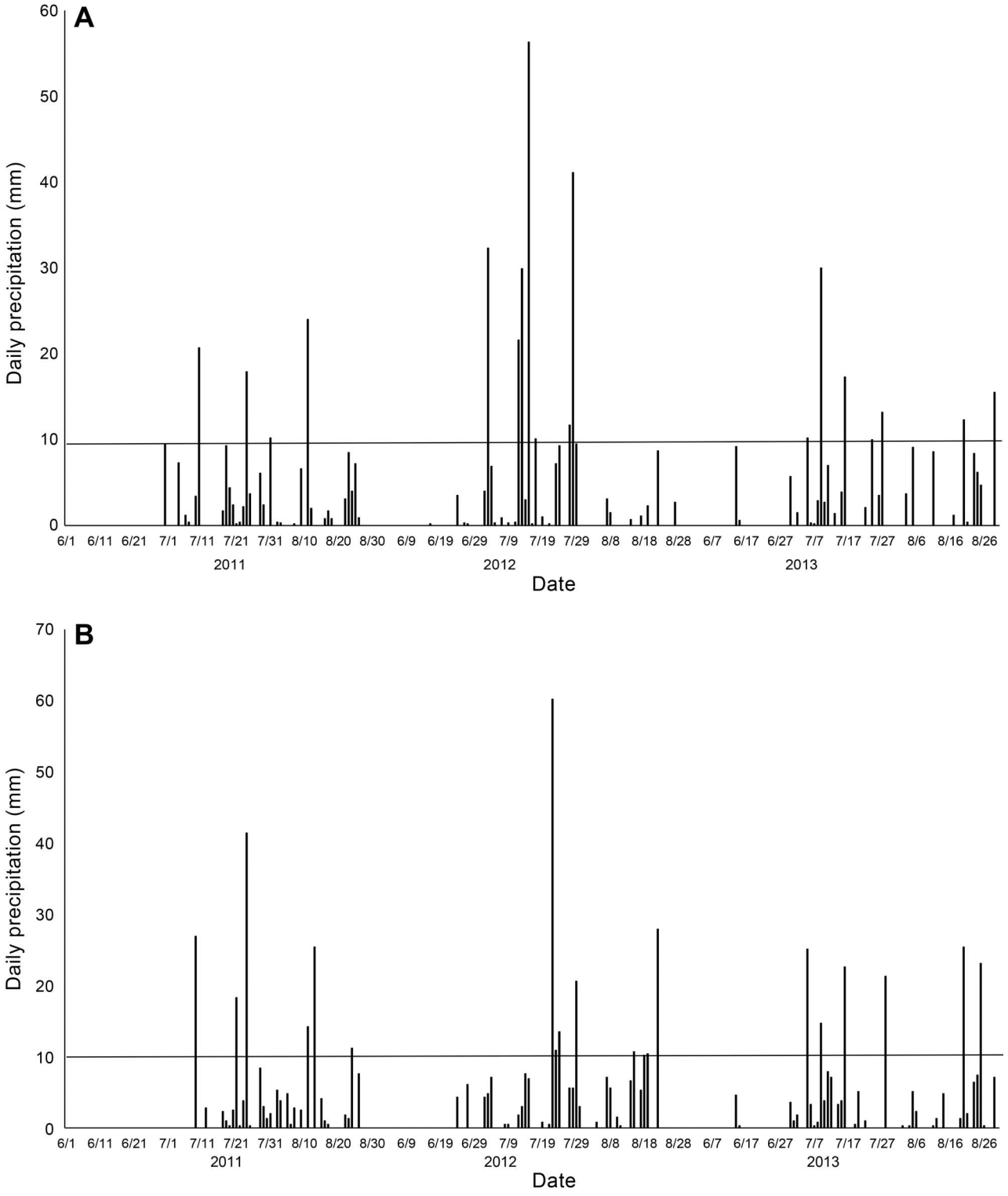


FIGURE 3. Daily precipitation for June 1 through August 30 in 2011–2013 for our 2 study sites: (**A**) Audubon, and (**B**) Davis. The heavy horizontal line indicates the threshold for an extreme daily rain event ($\geq$10 mm).

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

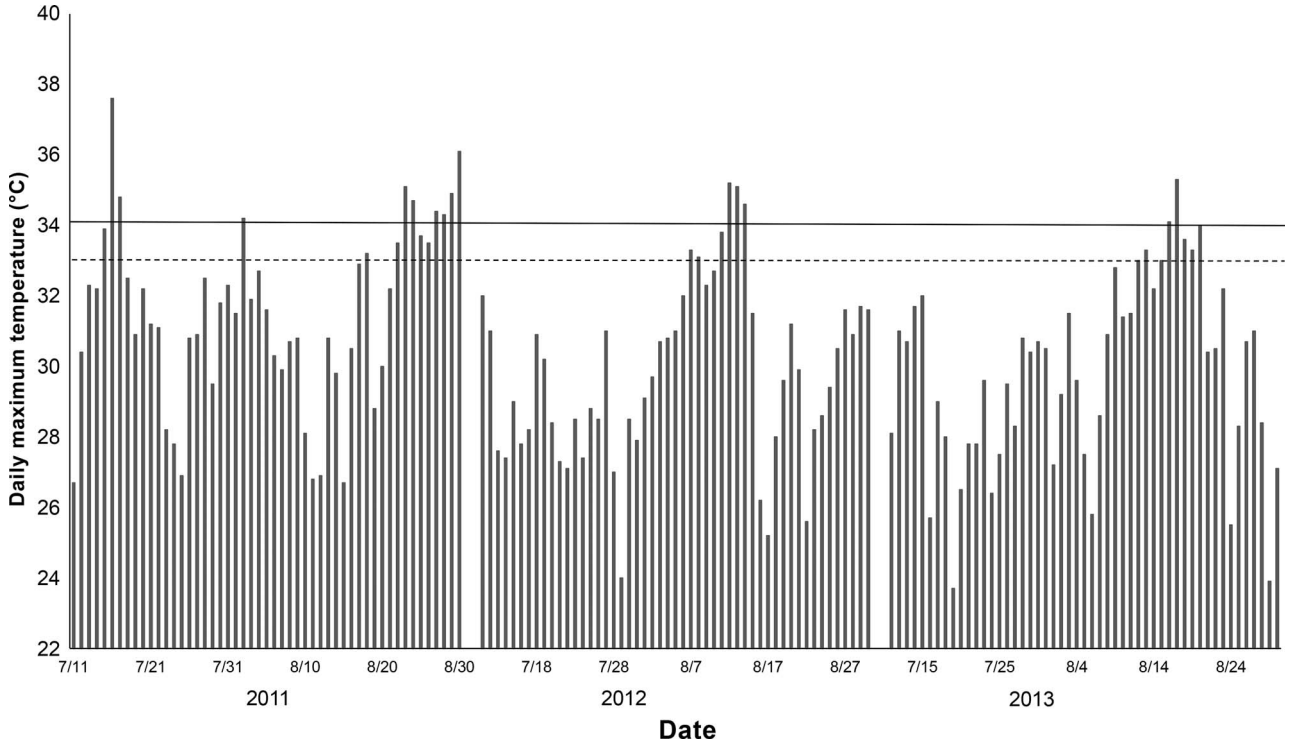


FIGURE 4. Daily maximum temperatures during the nesting period (July 11 through August 30) in 2011–2013 at the Audubon study site. Dotted and heavy horizontal lines indicate thresholds for extreme daily maximum temperature events identified from the literature (≥33°C and ≥34°C).

(range: 0.2–1.6 dm); distance to nearest shrub 1–2 m tall (DistNShrb1–2m) = 80 ± 82 m (range: 3 to >200 m); distance to nearest shrub >2 m tall (DistNShrb>2m) = 123 ± 90 m (range: 10 to >200 m); vertical vegetation density at the nest (NestVVgDen) = 8.3 ± 3.1 vegetation contacts in 4 dm (range: 3.0–17.0 contacts); and visual obstruction at the nest (NestVO) = 0.9 ± 0.6 dm (range: 0.0–2.3 dm). The percentage of native nest plants (NestPlNat) was 78%. Mean ± SD nest concealment for 2012–2013 was 88% ± 8% (range: 63–100%; $n = 79$ nests).

Daily Survival Rate

Nest survival analyses were based on a sample of 121 nests from 2 sites (Audubon and Davis) and 3 yr (2011–2013), representing 1,141 exposure days. The fate of 8% ($n = 10$) of these nests was uncertain. Mean ± SE DSR was 0.960 ± 0.006 (95% CI: 0.947–0.969), corresponding to an overall nest success estimate of 46% for a 19-day nesting cycle. There was no statistically significant difference in DSR between sites based on overlapping confidence intervals: Audubon DSR = 0.954 ± 0.010 (95% CI: 0.929–0.970); Davis DSR = 0.963 ± 0.007 (95% CI: 0.947–0.975).

When considered individually in univariate models, no variable representing nest age, time in season, or daily temperature was associated with nest survival (i.e. performed better than the constant model; Appendix Table 4). In the seasonal precipitation set of univariate models, previous growing season precipitation (PGSPrec) performed the best (lowest AIC_c value), and in the daily precipitation set of univariate models, the variable for rain events exceeding 10 mm 2 days prior (Over10mm2DP) was within 0.05 AIC_c of the constant model (Appendix Table 4). The multivariate step 2 of the modeling process resulted in a top model that included PGSPrec and Over10mm2DP. No additions or substitutions of phenological or seasonal weather variables improved this model (Appendix Table 5). Therefore, the final base model included only seasonal (PGSPrec) and daily (Over10mm2DP) precipitation variables. This base model ultimately became the top final model, as no additional vegetation variable improved model fit (Appendix Table 5). Nest survival decreased with a wetter previous growing season and extreme rain events (Table 3, Figures 5A and 5B). The 95% CI for previous growing season rainfall did not include zero, and the 90% CI for extreme rain events did not include zero (Table 3).

The addition of neither time in season nor nest age improved the top model, yet some degree of association was collectively suggested by AIC_c values within 1.0 of the best model (Appendix Table 5) and CIs that were asymmetrically distributed around zero (Table 3). Nest survival was somewhat lower later in the nesting season

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 3. Variable coefficient estimates from the highest-ranked model in which the variable occurred (Appendix Table 5) for Arizona Grasshopper Sparrow nest daily survival rate (DSR) in southeastern Arizona, USA, 2011–2013. Variables are shown for models with Akaike weights (w_i) $\geq$ 0.05.

Variable [a]	β estimate ± SE	95% CI	90% CI
Full dataset (n = 121 nests)			
PGSPrec	−0.012 ± 0.006	−0.024, −0.000	−0.022, −0.002
Over10mm2DP	−0.813 ± 0.452	−1.708, 0.082	−1.562, −0.064
Time	−0.020 ± 0.015	−0.050, 0.010	−0.045, 0.005
Age	−0.036 ± 0.031	−0.097, 0.025	−0.087, 0.015
NPlotBare	3.043 ± 3.361	−3.612, 9.700	−2.530, 8.616
Intercept	6.587 ± 1.638		
Partial dataset that included concealment variable (n = 79 nests)			
Conceal	−0.084 ± 0.032	−0.148, −0.020	−0.138, −0.030
P12MPrec	−0.049 ± 0.052	−0.151, 0.053	−0.135, 0.036
Over10mm2DP	−1.002 ± 0.542	−2.075, 0.071	−1.903, −0.100
Time	−0.028 ± 0.019	−0.065, 0.009	−0.059, 0.003
NPlotVO	0.990 ± 0.685	−0.366, 2.347	−0.150, 2.130
NestVO	0.527 ± 0.421	−0.307, 1.360	−0.174, 1.227
DistNShrb>2m	0.003 ± 0.002	−0.002, 0.008	−0.001, 0.007
DistNShrb1–2m	−0.003 ± 0.003	−0.003, 0.008	−0.002, 0.007
NestVVgDen	−0.057 ± 0.071	−0.197, 0.083	−0.175, 0.061
NestPlNat	0.351 ± 0.666	−0.967, 1.669	0.756, 1.459
NPlotBare	1.546 ± 4.256	−6.881, 9.973	−5.536, 8.628
NPlotVVgDen	0.002 ± 0.206	−0.406, 0.411	−0.341, 0.346
Intercept	29.864 ± 20.172		

[a] See Table 1 for variable definitions.

and in older nests (e.g., when the nest contained nestlings; Table 3). NPlotBare was the only vegetation variable included in models with $w_i \geq 0.05$ (Appendix Table 5), although the variable appeared largely uninformative (Table 3).

Nest concealment had a strong negative effect on nest survival (Figure 5C). When considering the subset of nests for which measurements of nest concealment were available (n = 79 nests), the base model included daily precipitation (rain events exceeding 10 mm 2 days prior [Over10mm2DP]), seasonal precipitation (previous 12 mo precipitation [P12MPrec]), and time in season. The addition of the nest concealment variable to this base model resulted in a greatly improved model, with ΔAIC_c reduced by >3.3 (Appendix Table 5), suggesting a strong influence of concealment on DSR. One additional vegetation variable (visual obstruction in the nest plot [NPlotVO]) ultimately appeared in the top model. Nests that were more concealed had lower survival rates, with the 95% CI not including zero (Table 3). Large rain events 2 days prior suppressed nest survival (90% CI did not include zero; Table 3, Figure 5B), and nests later in the season had lower nest survival (85% CI did not include zero; –0.055 to –0.001). Although included in the best models (Appendix Table 5), previous 12 mo precipitation (P12MPrec) appeared largely uninformative (Table 3). Visual obstruction at both nest and nest plot scales (NestVO, NPlotVO) and distance from shrubs >2m (DistShrb>2m) were positively but weakly associated with DSR, with CIs asymmetrical around zero (Table 3). Although included in models with $w_i > 0.05$ (Appendix Table 5), additional vegetation variables appeared uninformative (Table 3).

DISCUSSION

Our overall DSR and nest success estimates for Arizona Grasshopper Sparrows were comparable with those for other Grasshopper Sparrow populations (Appendix Table 6). We found previous seasonal and daily precipitation and nest concealment to be most important for explaining nest survival. The strong performance of nest concealment indicates that it captured vegetative characteristics at the nest, possibly associated with domed nest structure, that are important to nest survival; measurement of nest concealment may be better at characterizing vegetation structure at the nest than other vegetation variables (such as those used by us in the full dataset). That Arizona Grasshopper Sparrow reproduction was apparently most affected by abiotic variables (weather), and only secondarily affected by the biotic variables (grassland structure) that we measured, may limit management options for natural resource managers.

Daily and Seasonal Weather Effects

The negative association of DSR with major rain events is consistent with results from other recent studies (Skagen

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

and Yackel Adams 2012, Webb et al. 2012, Fisher et al. 2015, Öberg et al. 2015). The most likely indirect reason for such an association might be predation, which can be affected by rain events. Both parental and predator activity may increase after rain events, increasing the chances of nest detection by predators (Moynahan et al. 2007, Webb et al. 2012). Wet conditions after rain may result in higher activity levels of snakes (Gibbons and Semlitsch 1987, Daltry et al. 1998, Christy et al. 2010), and higher humidity can increase scent production and facilitate olfactory detection (Gutzwiller 1990, Conover 2007, Webb et al. 2012). Additional factors associated with major rain events could include nestling mortality due to exposure or reduction in foraging opportunities for adults feeding nestlings (Öberg et al. 2015).

Understanding the negative association of DSR with previous growing season precipitation is more challenging. One might expect higher bird nest success in response to increased precipitation prior to the nesting season due to improved primary productivity (Sala et al. 1988, Mowll et al. 2015) and secondary productivity (e.g., abundance of invertebrate and seed resources; Jonas and Joern 2007, Joern and Laws 2013). Seasonal precipitation has been positively associated with nest survival or reproductive output of other grassland bird species (Morrison and Bolger 2002, Skagen and Yackel Adams 2012). However, our results are inconsistent with that expectation. Reduced DSR of Arizona Grasshopper Sparrows after wetter seasons may have been a response to a complex interaction between grassland structure and predation variables (Ibáñez-Álamo et al. 2015). First, increases in predator populations can result in reduced nest success (Weidinger 2002, Davis 2003). Greater primary productivity can result in increased vegetation structure and seed and invertebrate resources for both sparrows and small mammals that are also nest predators. This can lead to irruptions in small mammal populations, often with a lag of 3 mo to 1 yr depending on the timing or season of rainfall (Ernest et al. 2000, Bradley et al. 2006, Witecha 2011). Second, prior precipitation and increased vegetation structure may affect the foraging behavior of opportunistic or random-search nest predators (Vickery et al. 1992, Olson and Warner 2001). They may forage more frequently or intensely in thicker vegetation for their primary food items (seeds, invertebrates, or small mammals; Thompson 1982), thus increasing their chances of finding nests. Third, nest predators may spend more time in thick, tall vegetation to avoid becoming prey themselves (Dion et al. 2000, Weidinger 2002, Orrock et al. 2004, Davis 2005), or may place their burrows near substantial protective cover (With 1994). All 3 of these interactive factors may help to explain the negative associations between DSR and previous seasonal precipitation that we found in this study.

Although other studies have found that temperature affects nest productivity (Dreitz et al. 2012, Skagen and Yackel Adams 2012, Cunningham et al. 2013, Conrey et al. 2016), our results did not show this. Few days with extreme temperatures during the study period may have limited our ability to document any such effects.

Nest Concealment

The degree of nest concealment exhibited by Arizona Grasshopper Sparrows appears similar to that documented for other Grasshopper Sparrow subspecies (Sutter and Ritchison 2005, Jones and Dieni 2007). The highly concealed nests constructed by females, importance of predation as a cause of nest failure, and negative relationship between concealment and DSR in this study contradict the general hypothesis that reproductive success increases with greater nest concealment due to reductions in visual and auditory cues for predators (Martin 1993). Literature on the effects of nest concealment on grassland bird nest success, however, is equivocal, documenting positive effects (Davis 2005, Galligan et al. 2006, Stauffer et al. 2011), no clear effects (Colwell 1992, Davis 2005, Sutter and Ritchison 2005, Lusk and Koper 2013), and negative effects (Jones and Dieni 2007, Ribic et al. 2012, Lusk and Koper 2013).

The negative association between nest concealment and nest success in this study may have arisen from a complex response to a combination of factors related to vegetation structure and predators (Lima 2009). Equivocal evidence in the literature may reflect geographic diversity in predator communities, resulting in diverse predator avoidance and safe nest-site selection strategies and tradeoffs between concealment and detection of threats (Götmark et al. 1995, Jones and Dieni 2007).

Overall, our findings suggest that Arizona Grasshopper Sparrows do not select vegetation features that optimize reproductive output, in relation to the vegetation variables that we measured. We found that females preferentially selected native plants under which to place nests and, at least in sites with low shrub density, selected nest plots that had lower shrub density than the territories in which they were located (Ruth and Skagen 2017). However, nest plant and distance to the nearest shrub variables appeared largely uninformative for explaining DSR.

Predation

Predation was the major cause of nest failure of Arizona Grasshopper Sparrows, as it was for other Grasshopper Sparrow subspecies (Davis 1994, Giocomo et al. 2008, Jones et al. 2010). Understanding geographic variation in predator communities is crucial to understanding predator effects on nest success. Although identifying the primary nest predators in our sites was beyond the scope of this study, existing information about small mammal and snake

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

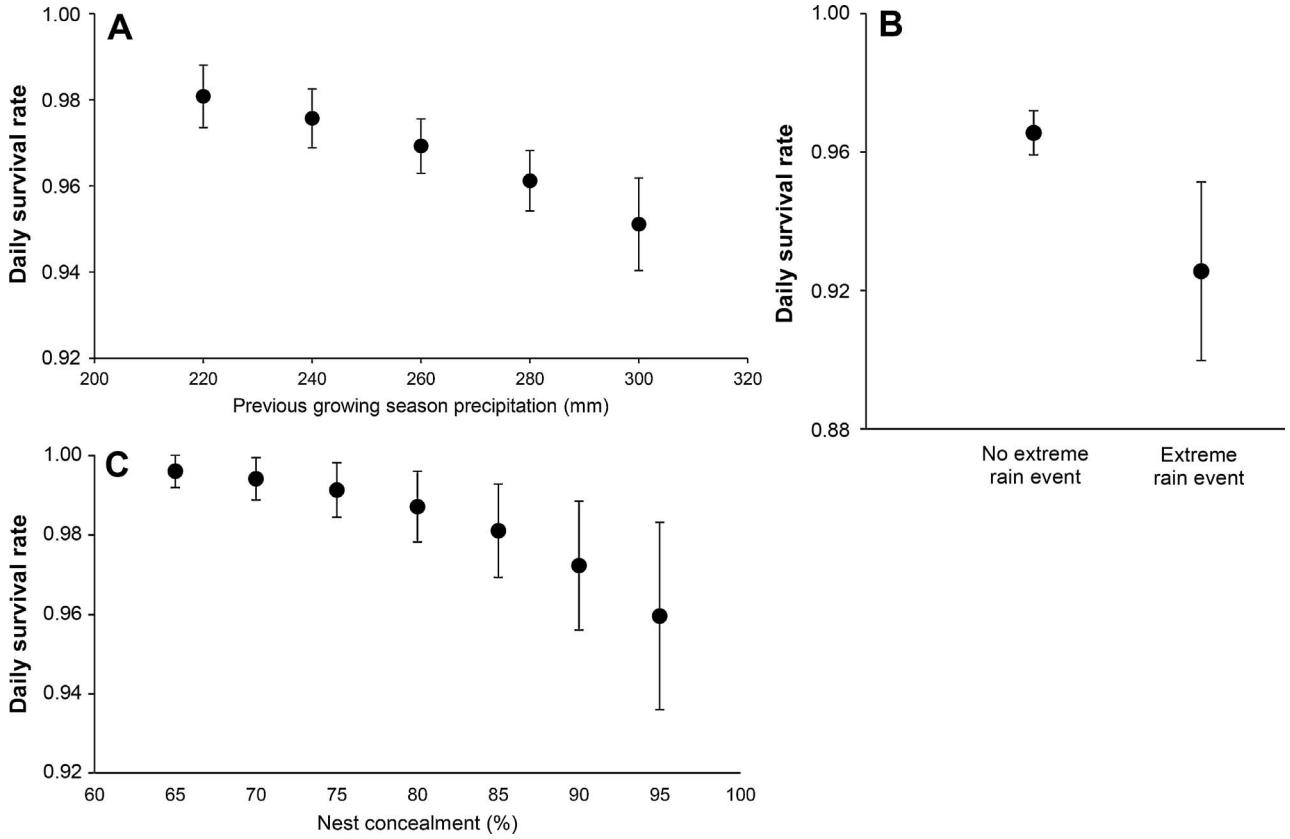


FIGURE 5. Daily survival rates (mean ± SE) of Grasshopper Sparrow nests predicted in relation to important variables based on best models (Appendix Table 4); predictions were made at specific values for the variable using its best model, while controlling for other variables in that model. (**A**) Previous growing season precipitation (mm), while specifying no extreme rain event; (**B**) presence–absence of an extreme rain event (≥10 mm) 2 days prior, while holding previous growing season precipitation at its mean value (270 mm); and (**C**) mean nest concealment (%), while specifying no extreme rain event, previous 12 mo precipitation at its mean value (380.4 mm), and visual obstruction at the nest plot at its mean value (0.829 dm).

communities in grasslands allows us to surmise which species might be nest predators in our study system. Rodents in 3 genera—*Peromyscus*, *Neotoma*, and *Sigmodon*—are known nest predators in grassland systems (DeGraaf and Maier 1996, Hernandez et al. 1997, Renfrew and Ribic 2003, Staller et al. 2005), and each of these genera is represented in Sonoita Valley grasslands (Jones et al. 2003, Bock et al. 2006, http://researchranch.audubon.org). Skunks (*Mephitis* spp.), raccoons (*Procyon lotor*), and coyotes (*Canis latrans*), all common grassland nest predators (Renfrew and Ribic 2003), occur in the Audubon site (http://researchranch.audubon.org). Snakes in 5 genera—*Thamnophis*, *Lampropeltis*, *Pituophis*, *Coluber*, and *Crotalus*—are also known nest predators (Beavers 1976, Thompson et al. 1999, Olson and Warner 2001, Rodríguez-Robles 2002, Renfrew and Ribic 2003, Lyons et al. 2015) and occur in southeastern Arizona grasslands (Mendelson and Jennings 1992, http://researchranch.audubon.org).

Implications for Future Climate Change

Small-bodied birds, such as sparrows, in arid ecosystems often survive near the limits of their physiological tolerances for heat and dehydration (Wolf and Walsberg 1996, Whitfield et al. 2015) and may be vulnerable to such stressors associated with climate change (McKechnie and Wolf 2010, McKechnie et al. 2012). The climate in the southwestern U.S. is projected to become hotter (Coe et al. 2012, Finch 2012) and, although more varied, many models also predict reduced annual rainfall, increased aridity, or changes in seasonality (Coe et al. 2012, Finch 2012, Bagne and Finch 2013). Increased frequency, intensity, duration, and spatial extent of droughts, heat waves, and extreme precipitation events are also predicted (Finch 2012, Garfin et al. 2013). In arid systems, this combination of climatic changes may lead to increases in avian mortality (McKechnie and Wolf 2010), as well as negative impacts on adult and nest survival, even at temperatures below those associated with mortality

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

(McKechnie et al. 2012, Cunningham et al. 2013, Gardner et al. 2016).

In this context, our results suggest climatic tradeoffs for Arizona Grasshopper Sparrows. Higher temperatures and increasingly frequent extreme storm events may result in reduced nest success. In contrast, nest success may benefit from a reduction in seasonal precipitation, much as Mountain Plover (*Charadrius montanus*) nest success is positively associated with drought (Dreitz et al. 2012). However, one would expect a threshold in precipitation decrease below which Grasshopper Sparrows would no longer benefit if food resources, adult survival, and grassland structure were to be negatively affected. In addition, although we did not find evidence of temperature effects at the temperatures observed during the years of our study, it is likely that higher maximum temperatures may also negatively affect nest survival at some level (Cunningham et al. 2013, Conrey et al. 2016).

Predictions of climate-induced changes in vegetation distribution could have additional implications for Arizona Grasshopper Sparrows. Although not all current desert grassland supports Arizona Grasshopper Sparrows, recent predictions of the future distribution of vegetation types, based on climate modeling, project that desert grassland vegetation could expand in area northward into the Great Basin, Colorado Plateau, and southern Great Plains (Rehfeldt et al. 2006, Finch 2012). If these predictions come about in a way that provides desert grassland habitat suitable for Arizona Grasshopper Sparrows, this could represent a fourfold increase in the area occupied by this habitat type compared with the present (Finch 2012).

ACKNOWLEDGMENTS

We thank field technicians Raymond Van Buskirk and Jason Kitting, who found most nests. We are also grateful to Leila Gass, Heather Swanson, and Kathleen Oliver for their help with dragging ropes and banding birds. The BLM and the Audubon Appleton-Whittell Research Ranch provided access to their lands. We also thank Colin Talbert, USGS Fort Collins Science Center, for the design of Figure 1.

Funding statement: This research was funded by the Bureau of Land Management's National Landscape Conservation System (NLCS) Science program and the U.S. Geological Survey (USGS). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States Government. This paper has been peer-reviewed and approved for publication consistent with USGS Fundamental Science Practices (https://pubs.usgs.gov/circ/1367).

Ethics statement: This research was conducted under USGS Master Station Bird Banding Permit 08566 and annual Arizona Game and Fish Department scientific collecting permits obtained for each year of the project. All bird and egg handling methods were approved by the Institutional Animal Care and Use Committee of the USGS Fort Collins Science Center.

Author contributions: J.M.R. conceived the idea and study design, developed methods, and conducted research; S.K.S. managed and analyzed the data with assistance from J.M.R.; and J.M.R. wrote the paper, with input from S.K.S.

Data deposits: Data associated with this work are available at: https://doi.org/10.5066/P9USE8CH

LITERATURE CITED

Adams, R. A. (2010). Bat reproduction declines when conditions mimic climate change projections for western North America. Ecology 91:2437–2445.

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In International Symposium on Information Theory, second edition (B. N. Petran and F. Csaki, Editors). Akadémiai Kiadó, Budapest, Hungary. pp. 267–281.

Ammer, F. K. (2003). Population level dynamics of Grasshopper Sparrow populations breeding on reclaimed surface mountaintop mines in West Virginia. Ph.D. dissertation, West Virginia University, Morgantown, WV, USA.

AOU (American Ornithologists' Union) (1957). Check-List of North American Birds. American Ornithologists' Union, Baltimore, MD, USA.

Arguez, A., I. Durre, S. Applequist, R. S. Vose, M. F. Squires, X. Yin, R. R. Heim, Jr., and T. W. Owen (2012). NOAA's 1981–2010 U.S. Climate Normals: An overview. Bulletin of the American Meteorological Society 93:1687–1697.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175–1178.

Ashton, K. G. (2002). Patterns of within-species body size variation of birds: Strong evidence for Bergmann's rule. Global Ecology and Biogeography 11:502–523.

Askins, R. A., F. Chávez-Ramírez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery (2007). Conservation of grassland birds in North America: Understanding ecological processes in different regions. Ornithological Monographs 64:1–52.

Bagne, K. E., and D. M. Finch (2013). Vulnerability of species to climate change in the Southwest: Threatened, endangered, and at-risk species at Fort Huachuca, Arizona. USDA Forest Service General Technical Report RMRS-GTR-302.

Balent, K. L., and C. J. Norment (2003). Demographic characteristics of a Grasshopper Sparrow population in a highly fragmented landscape of western New York State. Journal of Field Ornithology 74:341–348.

Bart, J., and D. S. Robson (1982). Estimating survivorship when the subjects are visited periodically. Ecology 63:1078–1090.

Beavers, R. A. (1976). Food habits of the western diamondback rattlesnake, *Crotalus atrox*, in Texas. Southwestern Naturalist 20:503–515.

Berthelsen, P. S., and L. M. Smith (1995). Nongame bird nesting on CRP lands in the Texas southern high plains. Journal of Soil and Water Conservation 50:672–675.

Bock, C. E., Z. F. Jones, and J. H. Bock (2006). Rodent communities in an exurbanizing southwestern landscape. Conservation Biology 20:1242–1250.

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Bonham, C. D. (1989). Measurements for Terrestrial Vegetation. John Wiley & Sons, New York, NY, USA.

Borgman, C. C., and B. O. Wolf (2016). The indirect effects of climate variability on the reproductive dynamics and productivity of an avian predator in the arid Southwest. Oecologia 180:279–291.

Bradley, R. D., J. D. Hanson, B. R. Amman, B. D. Baxter, D. S. Carroll, N. D. Durish, M. L. Haynie, M. Kageyama, L. K. Longhofer, F. M. Mendez-Harclerode, S. A. Reeder, et al. (2006). Rapid recovery of rodent populations following severe drought. Southwestern Naturalist 51:87–93.

Brown, D. E., and E. Makings (2014). A Guide to North American Grasslands. Desert Plants Volume 29.

Brown, D. E., P. J. Umack, and T. C. Brennan (2007). Digitized map of biotic communities for plotting and comparing distributions of North American animals. Southwestern Naturalist 52: 610–616.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer-Verlag, New York, NY, USA.

Christy, M. T., A. A. Yackel Adams, G. H. Rodda, J. A. Savidge, and C. L. Tyrrell (2010). Modelling detection probabilities to evaluate management and control tools for an invasive species. Journal of Applied Ecology 47:106–113.

Coe, S. J., D. M. Finch, and M. M. Friggens (2012). An assessment of climate change and vulnerability of wildlife in the Sky Islands of the Southwest. USDA Forest Service General Technical Report RMRS-GTR-273.

Colwell, M. A. (1992). Wilson's Phalarope nest success is not influenced by vegetation concealment. The Condor 94:767–772.

Conover, M. R. (2007). Predator–Prey Dynamics: The Role of Olfaction. CRC Press, Boca Raton, FL, USA.

Conrey, R. Y., S. K. Skagen, A. A. Yackel Adams, and A. O. Panjabi (2016). Extremes of heat, drought and precipitation depress reproductive performance in shortgrass prairie passerines. Ibis 158:614–629.

Corman, T. E., and C. Wise-Gervais (Editors) (2005). Arizona Breeding Bird Atlas. University of New Mexico Press, Albuquerque, NM, USA.

Cunningham, S. J., R. O. Martin, C. L. Hojem, and P. A. R. Hockey (2013). Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: A study of Common Fiscals. PLOS One 8:e7461.

Daltry, J. C., T. Ross, R. S. Thorpe, and W. Wüster (1998). Evidence that humidity influences snake activity patterns: A field study of the Malayan pit viper *Calloselasma rhodostoma*. Ecography 21:25–34.

Davis, S. K. (1994). Cowbird parasitism, predation, and host selection in fragmented grasslands of southwestern Manitoba. M.S. thesis, University of Manitoba, Winnipeg, MB, Canada.

Davis, S. K. (2003). Nesting ecology of mixed-grass prairie songbirds in southern Saskatchewan. The Wilson Bulletin 115:119–130.

Davis, S. K. (2005). Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. The Condor 107:605–616.

DeGraaf, R. M., and T. J. Maier (1996). Effect of egg size on predation by white-footed mice. The Wilson Bulletin 108: 535–539.

Dinsmore, S. J., G. C. White, and F. L. Knopf (2002). Advanced techniques for modeling avian nest survival. Ecology 83: 3476–3488.

Dion, N., K. A. Hobson, and S. Larivière (2000). Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. The Condor 102:629–634.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, et al. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Dreitz, V. J., R. Y. Conrey, and S. K. Skagen (2012). Drought and cooler temperatures are associated with higher nest survival in Mountain Plovers. Avian Conservation and Ecology 7:art.6.

Ernest, S. K. M., J. H. Brown, and R. R. Parmenter (2000). Rodents, plants, and precipitation: Spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.

Finch, D. M. (Editor) (2012). Climate change in grasslands, shrublands, and deserts of the interior American West: A review and needs assessment. USDA Forest Service General Technical Report RMRS-GTR-285.

Fisher, R. J., T. I. Wellicome, E. M. Bayne, R. G. Poulin, L. D. Todd, and A. T. Ford (2015). Extreme precipitation reduces reproductive output of an endangered raptor. Journal of Applied Ecology 52:1500–1508.

Galligan, E. W., T. L. DeVault, and S. L. Lima (2006). Nesting success of grassland and savanna birds on reclaimed surface coal mines of the Midwestern United States. The Wilson Journal of Ornithology 118:537–546.

Gardner, J. L., T. Amano, W. J. Sutherland, M. Clayton, and A. Peters (2016). Individual and demographic consequences of reduced body condition following repeated exposure to high temperatures. Ecology 97:786–795.

Gardner, J. L., R. Heinsohn, and L. Joseph (2009). Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines. Proceedings of the Royal Society B 276:3845–3852.

Garfin, G., A. Jardine, R. Merideth, M. Black, and S. LeRoy (Editors) (2013). Assessment of Climate Change in the Southwest United States: A Report Prepared for the National Climate Assessment. Island Press, Washington, DC, USA.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen (1992). Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275–284.

Gibbons, J. W., and R. D. Semlitsch (1987). Activity patterns. In Snakes: Ecology and Evolutionary Biology (R. A. Seigel, J. T. Collins, and S. S. Novak, Editors). Macmillan, New York, NY, USA. pp. 396–421.

Giocomo, J. J., E. D. Moss, D. A. Buehler, and W. G. Minser (2008). Nesting biology of grassland birds at Fort Campbell, Kentucky and Tennessee. The Wilson Journal of Ornithology 120:111–119.

Gorzo, J. M., A. M. Pidgeon, W. E. Thogmartin, A. J. Allstadt, V. C. Radeloff, P. J. Heglund, and S. J. Vavrus (2016). Using the North American Breeding Bird Survey to assess broad-scale response of the continent's most imperiled avian community,

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

grassland birds, to weather variability. The Condor: Ornithological Applications 118:502–512.
Götmark, F., D. Blomqvist, O. C. Johansson, and J. Bergkvist (1995). Nest site selection: A trade-off between concealment and view of the surroundings? Journal of Avian Biology 26: 305–312.
Gutzwiller, K. J. (1990). Minimizing dog-induced biases in game bird research. Wildlife Society Bulletin 18:351–356.
Hargrove, L., and J. T. Rotenberry (2011). Breeding success at the range margin of a desert species: Implications for a climate-induced elevational shift. Oikos 120:1568–1576.
Hendricks, D. M. (1985). Arizona Soils. College of Agriculture, University of Arizona, Tucson, AZ, USA.
Hernandez, F., D. Rollins, and R. Cantu (1997). Evaluating evidence to identify ground-nest predators in West Texas. Wildlife Society Bulletin 25:826–831.
Hovick, T. J., J. R. Miller, S. J. Dinsmore, D. M. Engle, D. M. Debinski, and S. D. Fuhlendorf (2012). Effects of fire and grazing on Grasshopper Sparrow nest survival. The Journal of Wildlife Management 76:19–27.
Ibáñez-Álamo, J. D., R. D. Magrath, J. C. Oteyza, A. D. Chalfoun, T. M. Haff, K. A. Schmidt, R. L. Thomson, and T. E. Martin (2015). Nest predation research: Recent findings and future perspectives. Journal of Ornithology 156 (Suppl. 1):247–262.
Ingold, D. J. (2002). Use of a reclaimed stripmine by grassland nesting birds in east-central Ohio. Ohio Journal of Science 102:56–62.
Joern, A., and A. N. Laws (2013). Ecological mechanisms underlying arthropod species diversity in grasslands. Annual Review of Entomology 58:19–36.
Johnson, D. H. (1979). Estimating nest success: The Mayfield method and an alternative. The Auk 96:651–661.
Johnson, R. G., and S. A. Temple (1990). Nest predation and brood parasitism of tallgrass prairie birds. The Journal of Wildlife Management 54:106–111.
Jonas, J. L., and A. Joern (2007). Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison grazing and weather in North American tallgrass prairie: A long-term study. Oecologia 153:699–711.
Jones, S. L., and J. S. Dieni (2007). The relationship between predation and nest concealment in mixed-grass prairie passerines: An analysis using program MARK. In Beyond Mayfield: Measurements of Nest-Survival Data (S. L. Jones and G. R. Geupel, Associate Editors). Studies in Avian Biology 34: 117–123.
Jones, S. L., J. S. Dieni, and P. A. Gouse (2010). Reproductive biology of a grassland songbird community in northcentral Montana. The Wilson Journal of Ornithology 122:455–464.
Jones, Z. F., C. E. Bock, and J. H. Bock (2003). Rodent communities in a grazed and ungrazed Arizona grassland, and a model of habitat relationships among rodents in southwestern grass/shrublands. The American Midland Naturalist 149:384–394.
Jongsomjit, D., S. L. Jones, T. Gardali, G. R. Geupel, and P. J. Gouse (2007). A guide to nestling development and aging in altricial passerines. USDI Fish and Wildlife Service Biological Technical Publication FWS/BTP-R6008-2007.
Koford, R. R. (1999). Density and fledging success of grassland birds in Conservation Reserve Program fields in North Dakota and west-central Minnesota. In Ecology and Conservation of Grassland Birds of the Western Hemisphere (P. D. Vickery and J. R. Herkert, Editors). Studies in Avian Biology 19:187–195.
Lima, S. L. (2009). Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485–513.
Lokemoen, J. T., and R. R. Koford (1996). Using candlers to determine the incubation state of passerine eggs. Journal of Field Ornithology 67:660–668.
Long, A. M., W. E. Jensen, and K. A. With (2009). Orientation of Grasshopper Sparrow and Eastern Meadowlark nests in relation to wind direction. The Condor 111:395–399.
Lusk, J. S., and N. Koper (2013). Grazing and songbird nest survival in southwestern Saskatchewan. Rangeland Ecology and Management 66:401–409.
Lyons, T. P., J. R. Miller, D. M. Debinski, and D. M. Engle (2015). Predator identity influences the effect of habitat management on nest predation. Ecological Applications 25:1596–1605.
Manolis, J. C., D. E. Andersen, and F. J. Cuthbert (2000). Uncertain nest fates in songbird studies and variation in Mayfield estimation. The Auk 117:615–626.
Martin, R. O., S. J. Cunningham, and P. A. R. Hockey (2015). Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. Ostrich 86:127–135.
Martin, T. E. (1993). Nest predation and nest sites: New perspectives on old patterns. BioScience 43:523–532.
Mayfield, H. (1961). Nesting success calculated from exposure. The Wilson Bulletin 73:255–261.
Mayfield, H. F. (1975). Suggestions for calculating nest success. The Wilson Bulletin 87:456–466.
McClaran, M. P., and T. R. Van Devender (Editors) (1995). The Desert Grassland. University of Arizona Press, Tucson, AZ, USA.
McCoy, T. D., M. R. Ryan, E. W. Kurzejeski, and L. W. Burger (1999). Conservation Reserve Program: Source or sink habitat for grassland birds in Missouri? The Journal of Wildlife Management 63:530–538.
McCreedy, C., and C. van Riper, III (2015). Drought-caused delay in nesting of Sonoran Desert birds and its facilitation of parasite- and predator-mediated variation in reproductive success. The Auk: Ornithological Advances 132:235–247.
McKechnie, A. E., and B. O. Wolf (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biology Letters 6:253–256.
McKechnie, A. E., P. A. R. Hockey, and B. O. Wolf (2012). Feeling the heat: Australian landbirds and climate change. Emu 112: i–vii.
Mendelson, J. R., III, and W. B. Jennings (1992). Shifts in the relative abundance of snakes in a desert grassland. Journal of Herpetology 26:38–45.
Menne, M. J., I. Durre, B. Korzeniewski, S. McNeal, K. Thomas, X. Yin, S. Anthony, R. Ray, R. S. Vose, B. E. Gleason, and T. G. Houston (2012a). Global Historical Climatology Network–Daily (GHCN–Daily), Version 3. GHCND: USW00053132 – Elgin 5S, AZ US and GHCND: US1AZSC001 – Sonoita 1.3 SE, AZ US (2010–2013). NOAA National Climatic Data Center. doi:10.7289/V5D21VHZ
Menne, M. J., I. Durre, R. S. Vose, B. E. Gleason, and T. G. Houston (2012b). An overview of the Global Historical Climatology Network-Daily database. Journal of Atmospheric and Oceanic Technology 29:897–910.

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Morrison, S. A., and D. T. Bolger (2002). Variation in a sparrow's reproductive success with rainfall: Food and predator-mediated processes. Oecologia 133:315–326.

Mowll, W., D. M. Blumenthal, K. Cherwin, A. Smith, A. J. Symstad, L. T. Vermeire, S. L. Collins, M. D. Smith, and A. K. Knapp (2015). Climatic controls of aboveground net primary production in semi-arid grasslands along a latitudinal gradient portend low sensitivity to warming. Oecologia 177:959–969.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas (2007). Factors affecting nest survival of Greater Sage-Grouse in northcentral Montana. The Journal of Wildlife Management 71:1773–1783.

NABCI–US (North American Bird Conservation Initiative, U.S. Committee) (2014). The State of the Birds 2014 Report. U.S. Department of the Interior, Washington, DC, USA.

NMDGF (New Mexico Department of Game and Fish) (2016). Threatened and Endangered Species of New Mexico: 2016 Biennial Review. New Mexico Department of Game and Fish, Wildlife Management and Fisheries Management Divisions, Santa Fe, NM, USA.

Öberg, M., D. Arlt, T. Pärt, A. T. Laugen, S. Eggers, and M. Low (2015). Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. Ecology and Evolution 5:345–356.

Olson, D. J., and R. E. Warner (2001). Grassland snakes. Diet. Herpetological Review 32:186–187.

Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff (2004). Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behavioral Ecology 15:433–437.

Patterson, M. P., and L. B. Best (1996). Bird abundance and nesting success in Iowa CRP fields: The importance of vegetation structure and composition. The American Midland Naturalist 135:153–167.

Perkins, D. W., P. D. Vickery, and W. G. Shriver (2003). Spatial dynamics of source–sink habitats: Effects on rare grassland birds. The Journal of Wildlife Management 67:588–599.

Reed, A. W., G. A. Kaufman, and B. K. Sandercock (2007). Demographic response of a grassland rodent to environmental variability. Journal of Mammalogy 88:982–988.

Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans (2006). Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Science 167:1123–1150.

Renfrew, R. B., and C. A. Ribic (2003). Grassland passerine nest predators near pasture edges identified on videotape. The Auk 120:371–383.

Ribic, C. A., M. J. Guzy, T. J. Anderson, D. W. Sample, and J. L. Nack (2012). Bird productivity and nest predation in agricultural grasslands. In Video Surveillance of Nesting Birds (C. A. Ribic, F. R. Thompson, III, and P. J. Pietz, Editors). Studies in Avian Biology 43:119–134.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert (1970). Relationships between visual obstruction measurements and weights of grassland vegetation. Journal of Range Management 23:295–298.

Robinson, R. A., S. R. Baille, and H. Q. P. Crick (2007). Weather-dependent survival: Implications of climate change for passerine populations. Ibis 149:357–364.

Rodríguez-Robles, J. A. (2002). Feeding ecology of North American gopher snakes (*Pituophis catenifer*, Colubridae). Biological Journal of the Linnean Society 77:165–183.

Rohrbaugh, R. W., Jr., D. L. Reinking, D. H. Wolfe, S. K. Sherrod, and M. A. Jenkins (1999). Effects of prescribed burning and grazing on nesting and reproductive success of three grassland passerine species in tallgrass prairie. In Ecology and Conservation of Grassland Birds of the Western Hemisphere (P. D. Vickery and J. R. Herkert, Editors). Studies in Avian Biology 19:165–170.

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, et al. (2016). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee.

Rotenberry, J. T., and J. A. Wiens (1989). Reproductive biology of shrubsteppe passerine birds: Geographical and temporal variation in clutch size, brood size, and fledging success. The Condor 91:1–14.

Ruth, J. M. (2000). Cassin's Sparrow (*Peucaea cassinii*) status assessment and conservation plan. Biological Technical Publication BTP-R6002-1999. U.S. Department of the Interior, Fish and Wildlife Service, Denver, CO, USA.

Ruth, J. M. (2008). Distribution and abundance of breeding Arizona Grasshopper Sparrow (*Ammodramus savannarum ammolegus*) in the southwestern United States: Past, present, and future. In Birds of the US-Mexico Borderlands: Distribution, Ecology, and Conservation (J. M. Ruth, T. Brush, and D. J. Krueper, Associate Editors). Studies in Avian Biology 37:113–124.

Ruth, J. M. (2015). Status assessment and conservation plan for the Grasshopper Sparrow (*Ammodramus savannarum*), Version 1.0. U.S. Fish and Wildlife Service, Lakewood, CO, USA.

Ruth, J. M. (2017). Life history attributes of Arizona Grasshopper Sparrow (*Ammodramus savannarum ammolegus*) compared with other North American species. The American Midland Naturalist 178:64–81.

Ruth, J. M., and S. K. Skagen (2017). Territory and nest site selection patterns by Grasshopper Sparrows in southeastern Arizona. The Condor: Ornithological Applications 119:469–483.

Ruth, J. M., T. R. Stanley, and C. E. Gordon (2014). Associations of wintering birds with habitat in semidesert and plains grasslands in Arizona. Southwestern Naturalist 59:199–211.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth (1988). Primary production of the central grassland region of the United States. Ecology 69:40–45.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link (2014). The North American Breeding Bird Survey, results and analysis 1966–2012. Version 02.19.2014. USGS Patuxent Wildlife Research Center, Laurel, MD, USA.

Seavy, N. E., K. E. Dybala, and M. A. Snyder (2008). Climate models and ornithology. The Auk 125:1–10.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. The Auk 121:526–540.

Skagen, S. K., and A. A. Yackel Adams (2012). Weather effects on avian breeding performance and implications of climate change. Ecological Applications 22:1131–1145.

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Staller, E. L., W. E. Palmer, J. P. Carroll, R. P. Thornton, and D. C. Sisson (2005). Identifying predators at Northern Bobwhite nests. The Journal of Wildlife Management 69:124–132.

Stauffer, G. E., D. R. Diefenbach, M. R. Marshall, and D. W. Brauning (2011). Nest success of grassland sparrows on reclaimed surface mines. The Journal of Wildlife Management 75:548–557.

Sutter, B., and G. Ritchison (2005). Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. Journal of Field Ornithology 76:345–351.

Thompson, F. R., III, W. Dijak, and D. E. Burhans (1999). Video identification of predators at songbird nests in old fields. The Auk 116:259–264.

Thompson, S. D. (1982). Microhabitat utilized and foraging behavior of bipedal and quadrupedal heteromyid rodents. Ecology 63:1303–1312.

USFWS (U.S. Fish and Wildlife Service) (2008). Birds of Conservation Concern 2008. U.S. Department of the Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, VA, USA.

Vera, C., W. Higgins, J. Amador, T. Ambrizzi, R. Garreaud, D. Gochis, D. Gutzler, D. Lettenmaier, J. Marnego, C. R. Mechoso, J. Nogues-Paegle, et al. (2006). Toward a unified view of the American monsoon systems. Journal of Climate 19:4977–5000.

Vickery, P. D. (1996). Grasshopper Sparrow (*Ammodramus savannarum*), version 2.0. In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.239

Vickery, P. D., M. L. Hunter, and J. V. Wells (1992). Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288.

Webb, S. L., C. V. Olsen, M. R. Dzialak, S. M. Harju, J. B. Winstead, and D. Lockman (2012). Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the Greater Sage-Grouse, in human-altered environments. Ecological Processes 1:1–15.

Weidinger, K. (2002). Interactive effects of concealment, parental behavior and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424–437.

White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Whitfield, M. C., B. Smit, A. E. McKechnie, and B. O. Wolf (2015). Avian thermoregulation in the heat: Scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. Journal of Experimental Biology 218: 1705–1714.

Wiens, J. A. (1969). An approach to the study of ecological relationships among grassland birds. Ornithological Monographs No. 8.

Williams, J. B., and B. I. Tieleman (2001). Physiological ecology and behavior of desert birds. Current Ornithology 16:299–353.

Winter, M., and J. Faaborg (1999). Patterns of area sensitivity in grassland-nesting birds. Conservation Biology 13:1424–1436.

Winter, M., S. E. Hawks, J. A. Shaffer, and D. H. Johnson (2003). Guidelines for finding nests of passerine birds in tallgrass prairie. Prairie Naturalist 35:197–211.

Winter, M., D. H. Johnson, J. A. Shaffer, T. M. Donovan, and W. D. Svedarsky (2006). Patch size and landscape effects of density and nesting success of grassland birds. The Journal of Wildlife Management 70:158–172.

Witecha, M. J. (2011). Effects of fire and precipitation on small mammal populations and communities. M.S. thesis, Texas A&M University, Kingsville, TX, USA.

With, K. A. (1994). The hazards of nesting near shrubs for a grassland bird, the McCown's Longspur. The Condor 96: 1009–1019.

Wolf, B. (2000). Global warming and avian occupancy of hot deserts; a physiological and behavioral perspective. Revista Chilena de Historia Natural 73:395–400.

Wolf, B. O., and G. E. Walsberg (1996). Respiratory and cutaneous evaporative water loss at high environmental temperatures in a small bird. Journal of Experimental Biology 199:451–457.

Wolf, B. O., K. M. Wooden, and G. E. Walsberg (1996). The use of thermal refugia by two small desert birds. The Condor 98: 424–428.

Wray, T., II, K. A. Strait, and R. C. Whitmore (1982). Reproductive success of grassland sparrows on a reclaimed surface mine in West Virginia. The Auk 99:157–164.

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

APPENDIX TABLE 4. Results of preliminary univariate analyses (step one in our modeling process) for Arizona Grasshopper Sparrow nest survival ($n = 121$ nests) in southeastern Arizona, USA, 2011–2013. The initially most-supported variables ($\Delta AIC_c = 0$; indicated by **boldface type**) within each set of phenological and seasonal weather variables (nest age, time in season, seasonal precipitation, and daily precipitation and temperature) were carried forward to identify the "base" model. For variable sets in which the constant model had $\Delta AIC_c = 0$, if there was a second-best model with $\Delta AIC_c < 0.10$, the variable in this model was carried forward to subsequent steps in the development of the base model. See Appendix Table 5 for all models used in subsequent steps to identify the final top model. Acronyms for variables are defined in Table 1. ΔAIC_c is the difference from the top model in Akaike's information criterion corrected for small sample sizes. Akaike model weights (w_i) in the context of the entire model set, the number of model parameters (K), and model deviance are presented in Appendix Table 5.

Variable set and univariate model	ΔAIC_c
Nest age	
Constant model	**0.00** [a]
Age	0.63
Age + Age^2	1.77
Age + Age^2 + Age^3	3.79
Time in season	
Constant model	**0.00** [b]
Time	0.44
Time + Time^2	2.12
Seasonal precipitation	
PGSPrec	**0.00** [c]
P12MPrec	1.18
P30DPrec	1.40
Constant model	1.93
PSpPrec	3.85
PWPrec	3.91
Daily precipitation	
Constant model	0.00 [d]
Over10mm2DP*	**0.05**
Over10mm1DP*	0.50
DaPrec1DP	1.56
DaPrec2DP	1.78
Daily temperature	
Constant model	**0.00** [e]
Over33°1DP*	1.58
Over33°2DP*	1.65
DaTMax1DP	1.84
DaTMax2DP	1.96
Over34°1DP*	1.99
Over34°2DP*	2.01

[a] Minimum $AIC_c = 298.70$.
[b] Minimum $AIC_c = 298.70$.
[c] Minimum $AIC_c = 296.77$.
[d] Minimum $AIC_c = 298.70$.
[e] Minimum $AIC_c = 298.70$.
* = binary variable.

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

APPENDIX TABLE 5. Nest survival models for Arizona Grasshopper Sparrows in southeastern Arizona, USA, 2011–2013. *K* is the number of model parameters, ΔAIC_c is the difference from the top model in Akaike's information criterion corrected for small sample sizes, w_i is the Akaike weight, and Dev is the model deviance. Models for the full nest dataset (2011–2013; 34 models) and for a subset of nests with measures of nest concealment (2012–2013; 21 models) were run in hierarchical fashion, including univariate models and consideration of closely competing variables to form a base model, and adding vegetation models to yield the top model. All models included an intercept. Acronyms for variables are defined in Table 1.

Model	ΔAIC_c	w_i	*K*	Dev
Full dataset ($n = 121$ nests)				
PGSPrec + Over10mm2DP	0.000 [a]	0.088	3	290.27
PGSPrec + Over10mm2DP + Time	0.276	0.077	4	288.53
PGSPrec	0.480	0.070	2	292.76
PGSPrec + Over10mm2DP + Age	0.636	0.064	4	288.89
PGSPrec + Over10mm2DP + NPlotBare	1.126	0.050	4	289.38
PGSPrec + Over10mm2DP + NPlotVVgDen	1.379	0.044	4	289.63
PGSPrec + Over10mm2DP + NestVO	1.442	0.043	4	289.69
PGSPrec + Over10mm1DP	1.469	0.042	3	291.74
PGSPrec + Over10mm2DP + DistNShrb1–2m	1.497	0.042	4	289.75
PGSPrec + Over10mm2DP + NPlantNative	1.518	0.041	4	289.77
PGSPrec + Over10mm2DP + NPlotVO	1.556	0.041	4	289.81
PGSPrec + Over10mm2DP + DistNShrb>2m	1.623	0.039	4	289.87
P12MPrec	1.662	0.039	2	293.94
P30DPrec	1.878	0.035	2	294.16
PGSPrec + Over10mm2DP + NestVVgDen	2.010	0.032	4	290.26
Constant model	2.410	0.027	1	296.69
Over10mm2DP	2.456	0.026	2	294.73
Time	2.849	0.021	2	295.13
Over10mm1DP	2.912	0.021	2	295.19
Age	3.037	0.019	2	295.31
DaPrec1DP	3.969	0.012	2	296.25
Over33°1DP	3.985	0.012	2	296.26
Over33°2DP	4.063	0.011	2	296.34
Age + Time	4.142	0.011	3	294.41
Age + Age^2	4.184	0.011	3	294.45
DaPrec2DP	4.193	0.011	2	296.47
DaTMax1DP	4.251	0.010	2	296.53
PSpPrec	4.315	0.010	2	296.59
DaTMax2DP	4.366	0.010	2	296.65
PWPrec	4.393	0.010	2	296.67
Over34°1DP	4.401	0.010	2	296.68
Over34°2DP	4.416	0.010	2	296.69
Time + $Time^2$	4.534	0.009	3	294.80
Age + Age^2 + Age^3	6.199	0.002	4	294.45
Partial dataset that included concealment variable ($n = 79$ nests)				
Conceal + Time + P12MPrec + Over10mm2DP + NPlotVO	0.000 [b]	0.147	6	172.49
Conceal + Time + P12MPrec + Over10mm2DP	0.098	0.140	5	174.62
Conceal + Time + P12MPrec + Over10mm2DP + NestVO	0.534	0.113	6	173.02
Conceal + Time + P12MPrec + Over10mm2DP + DistNShrb>2m	0.762	0.101	6	173.25
Conceal + Time + P12MPrec + Over10mm2DP + DistNShrb1–2m	1.258	0.079	6	173.75
Conceal + Time + P12MPrec + Over10mm2DP + NestVVgDen	1.496	0.070	6	173.99
Conceal + Time + P12MPrec + Over10mm2DP + NPlNat	1.872	0.058	6	174.36
Conceal + Time + P12MPrec + Over10mm2DP + NPlotBare	1.995	0.054	6	174.49
Conceal + Time + P12MPrec + Over10mm2DP + NPlotVVgDen	2.133	0.051	6	174.62
Conceal	2.750	0.037	2	183.34
Time + P12MPrec + Over10mm2DP	3.466	0.026	4	180.02
P12MPrec + Over10mm2DP	3.657	0.024	3	182.23
Time + P12MPrec	3.689	0.023	3	182.27
P12MPrec	3.717	0.023	2	184.31
Time + PGSPrec + Over10mm2DP	5.035	0.012	4	181.59
Time + Over10mm2DP	5.264	0.011	3	183.84
Time	5.333	0.010	2	185.93
PGSPrec	6.134	0.007	2	186.73
Constant model	6.521	0.006	1	189.13
Over10mm2DP	6.705	0.005	2	187.30
Age	8.433	0.002	2	189.03

[a] Minimum $AIC_c = 296.289$.
[b] Minimum $AIC_c = 184.611$.

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

APPENDIX TABLE 6. Comparison of Arizona Grasshopper Sparrow (*Ammodramus savannarum ammolegus*) nest success with the nest success of other Grasshopper Sparrow subspecies. To compare data for *A. s. ammolegus* with data for other Grasshopper Sparrow subspecies, decisions were required about which subspecies was represented in the Midwest where *A. s. pratensis* and *A. s. perpallidus* are thought to overlap (AOU 1957, Vickery 1996). For comparison purposes, we considered birds in Wisconsin, Iowa, Missouri, eastern Oklahoma, and northeastern Texas to be *A. s. pratensis*, and birds anywhere west of these areas to be *A. s. perpallidus*.

Subspecies and location	*n* (nests)	DSR (SE) [a]	Nesting period (days) [b]	Overall nest success (%)	Notes (grassland type, treatment)	Reference [c]
ammolegus						
Arizona	121	0.960 (0.006)	19	46	Desert grassland	This study [PM]
perpallidus						
Montana	123	0.948 (0.004)	20.6	39	Mixed-grass prairie, refuge	Jones et al. (2010) [PM]
Manitoba	48	unk	unk	23	Pasture and native mixed-grass prairie fragments	Davis (1994) [M]
North Dakota	14, 38	0.914, 0.950	25 [d]	11, 29	Waterfowl Production Area, Conservation Reserve Program (CRP) (separate values)	Koford (1999) [M]
Minnesota	13	0.918	25 [d]	12	CRP	Koford (1999) [M]
Minnesota	unk	0.908–0.947	unk	unk	Range from tallgrass prairie fragments	Johnson and Temple (1990) [M]
Texas	59	unk	22	44	Southern high plains, CRP	Berthelsen and Smith (1995) [M]
pratensis						
Maine	38	unk	unk	42	Sandplain grassland	Vickery et al. (1992) [M]
Kentucky and Tennessee	131	0.957 (0.006)	20.5	41	U.S. Department of Defense (DOD) grasslands	Giocomo et al. (2008) [M]
Kentucky	46	unk	19	31	DOD grasslands	Sutter and Ritchison (2005) [M]
Wisconsin	73	0.932 (0.157)	19	26	Remnant prairie, pasture and CRP	Ribic et al. (2012) [LE]
Iowa	62	0.957 (0.000), 0.937 (0.000) [e]	23 [d]	34	CRP	Patterson and Best (1996) [M]
Iowa	323	0.907–0.931	20	14–23	Range from pastures, patch-burn and graze-burn	Hovick et al. (2012) [PM]
New York	42	0.91, 0.95 [e]	unk	24	Grasslands, woodlots	Balent and Norment (2003) [M]
Missouri	38	unk	unk	42	CRP	McCoy et al. (1999) [M]
Pennsylvania	124	unk	21	44	Reclaimed mine lands	Stauffer et al. (2011) [PM]
West Virginia	94	unk	unk	35	Reclaimed mine lands	Ammer (2003) [M]
West Virginia	20, 18, 13	unk	unk	47, 8, 7	Reclaimed mine lands (separate values by year)	Wray et al. (1982) [M]
Indiana	41	0.961 (0.010)	21	43	Reclaimed mine lands	Galligan et al. (2006) [M], Stauffer et al. (2011)
Ohio	19	unk	unk	46	Reclaimed mine lands	Ingold (2002) [M]
Missouri	23	0.930 (0.018)	20	22	Tallgrass prairie fragments	Winter and Faaborg (1999) [M]
Oklahoma	38	unk	20	17	Tallgrass prairie, preserve	Rohrbaugh et al. (1999) [M], Stauffer et al. (2011)
floridanus						
Florida	74	0.90 (0.04)–0.95 (0.04)	21	10–33	Native dry prairie, range from 3 sites in 3 yr	Perkins et al. (2003) [M]

[a] DSR = Daily survival rate. 'unk' = unknown.
[b] The nesting period included the incubation and nestling stages unless otherwise noted.
[c] Daily survival rate (DSR) in these studies was calculated using a variety of methods and results are presented as in the cited paper. [PM] indicates the use of program MARK, [M] indicates use of the Mayfield method, citing various references (Mayfield 1961, 1975, Johnson 1979, Bart and Robson 1982), and [LE] indicates use of the logistic exposure method (Shaffer 2004).
[d] This study included the egg-laying stage in the nesting period; as a result, overall nest success calculations produced smaller values.
[e] DSR values for egg and nestling periods provided separately.

Downloaded From: https://complete.bioone.org/journals/The-Condor on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use