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RESEARCH ARTICLE

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

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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 ammodramus*) in the semidesert and plains grasslands of southeastern Arizona, USA. The mean \pm 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. ammodramus*. The increased frequency of extreme storm events predicted for the region may result in reduced nest survival of *A. s. ammodramus*, but, conversely, lower seasonal precipitation prior to nesting may positively influence nest survival.

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

Respuesta reproductiva de *Ammodramus savannarum ammodramus* 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 ammodramus* en los pastizales semidesérticos y las planicies del sudeste de Arizona. La tasa de supervivencia diaria promedio \pm 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 ammodramus* 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.*

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. ammoregus*, y por el contrario, una menor precipitación estacional antes de la anidación puede influenciar positivamente la supervivencia del nido.

Palabras clave: *Ammodramus savannarum ammoregus*, 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 vesperilionid 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. ammoregus*). 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

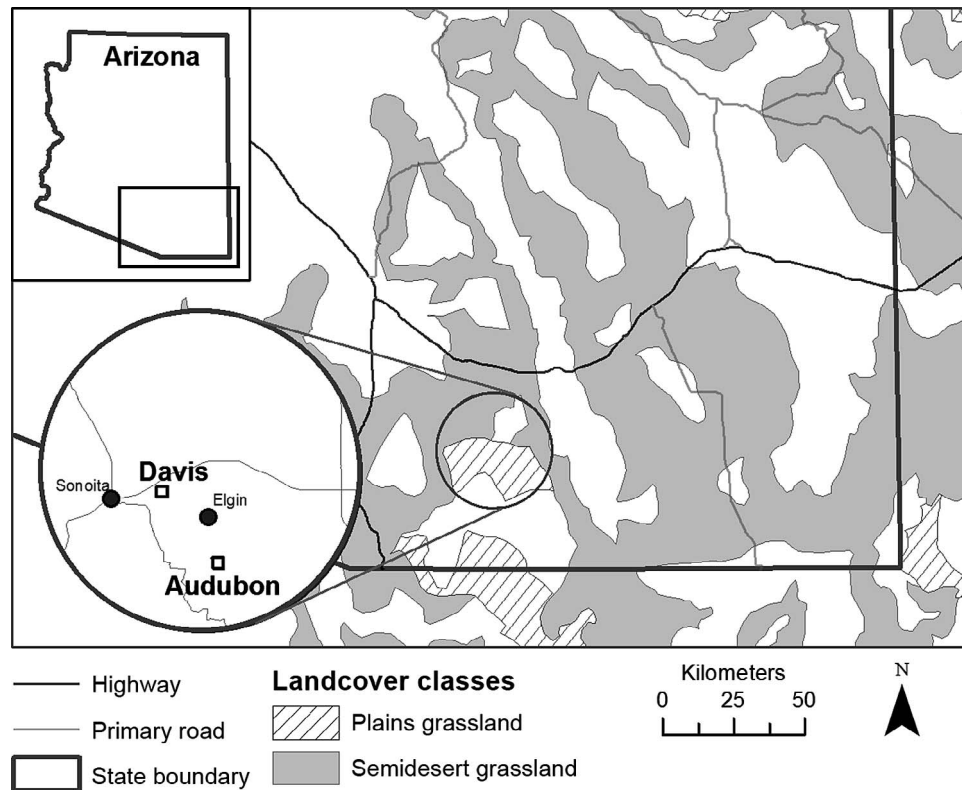


FIGURE 1. Location of study sites (Davis and Audubon) in the Sonoita Valley of southeastern Arizona, USA, where we examined how seasonal and daily weather conditions and habitat structure were associated with the nest survival of Arizona Grasshopper Sparrows in 2011–2013. Mapping of grassland biotic 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

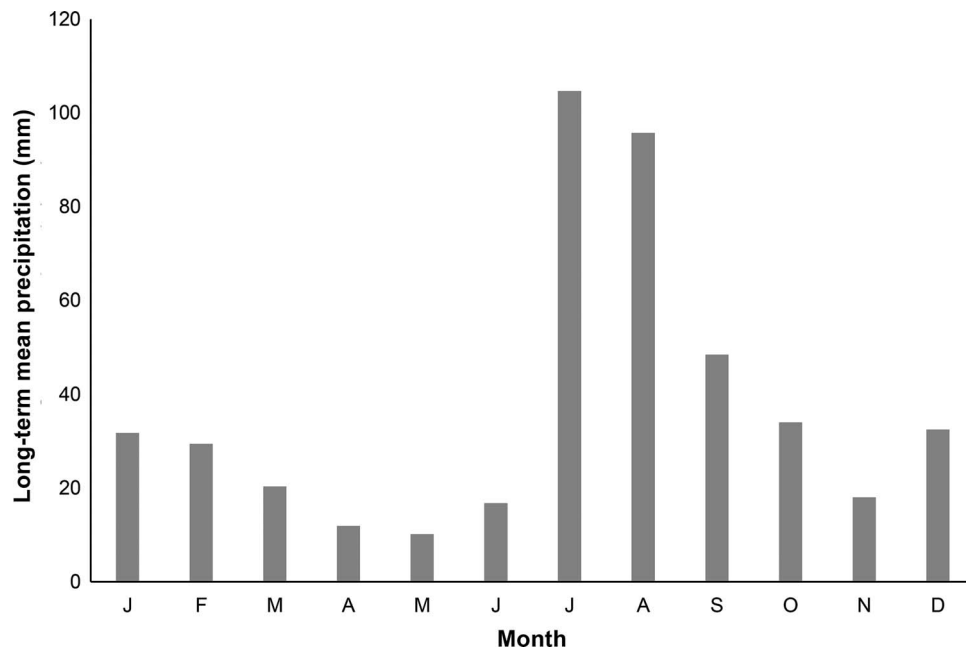


FIGURE 2. Long-term monthly precipitation averages for the Audubon Appleton-Whittell Research Ranch from NOAA 1981–2010 Normals (Arguez et al. 2012) taken from the Elgin 5S AZ station.

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

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 (NestVgDen) and in the 5-m radius nest plot (NPlotVgDen), 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 ≥ 10 mm (Skagen and Yackel Adams 2012, Öberg et al. 2015, Conrey

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 ≥ 10 mm 1 day prior (significant rain event, binary, 1 = yes)
Over10mm2DP	Precipitation ≥ 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 $\geq 33^{\circ}\text{C}$ 1 day prior (binary, 1 = yes)
Over33°2DP	Maximum temperature $\geq 33^{\circ}\text{C}$ 2 days prior (binary, 1 = yes)
Over34°1DP	Maximum temperature $\geq 34^{\circ}\text{C}$ 1 day prior (binary, 1 = yes)
Over34°2DP	Maximum temperature $\geq 34^{\circ}\text{C}$ 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)
NestPINat	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 $\geq 33^{\circ}\text{C}$ (Cunningham et al. 2013) and $\geq 34^{\circ}\text{C}$. We had insufficient data to test the daily maximum temperature threshold of $>35^{\circ}\text{C}$ (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 ≥ 10 mm 1 day prior (Over10mm1DP) and 2 days prior (Over10mm2DP), and the occurrence of daily maximum temperature events $\geq 33^{\circ}\text{C}$ and $\geq 34^{\circ}\text{C}$ 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

(PSPrec), 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, 2012b). 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

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.

Precipitation variable ^a	Abbreviation ^a	2011		2012		2013	
		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)	PWPPrec	29	70	82	103	86	104
Previous spring precipitation (mm)	PSPrec	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 \pm 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 \pm 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 $30^\circ\text{C} \pm 3^\circ\text{C}$ (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 \pm SD of the vegetation variables used in the DSR analyses (Table 1) were: percent bare ground on nest plot (NPlotBare) = $3\% \pm 5\%$ (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

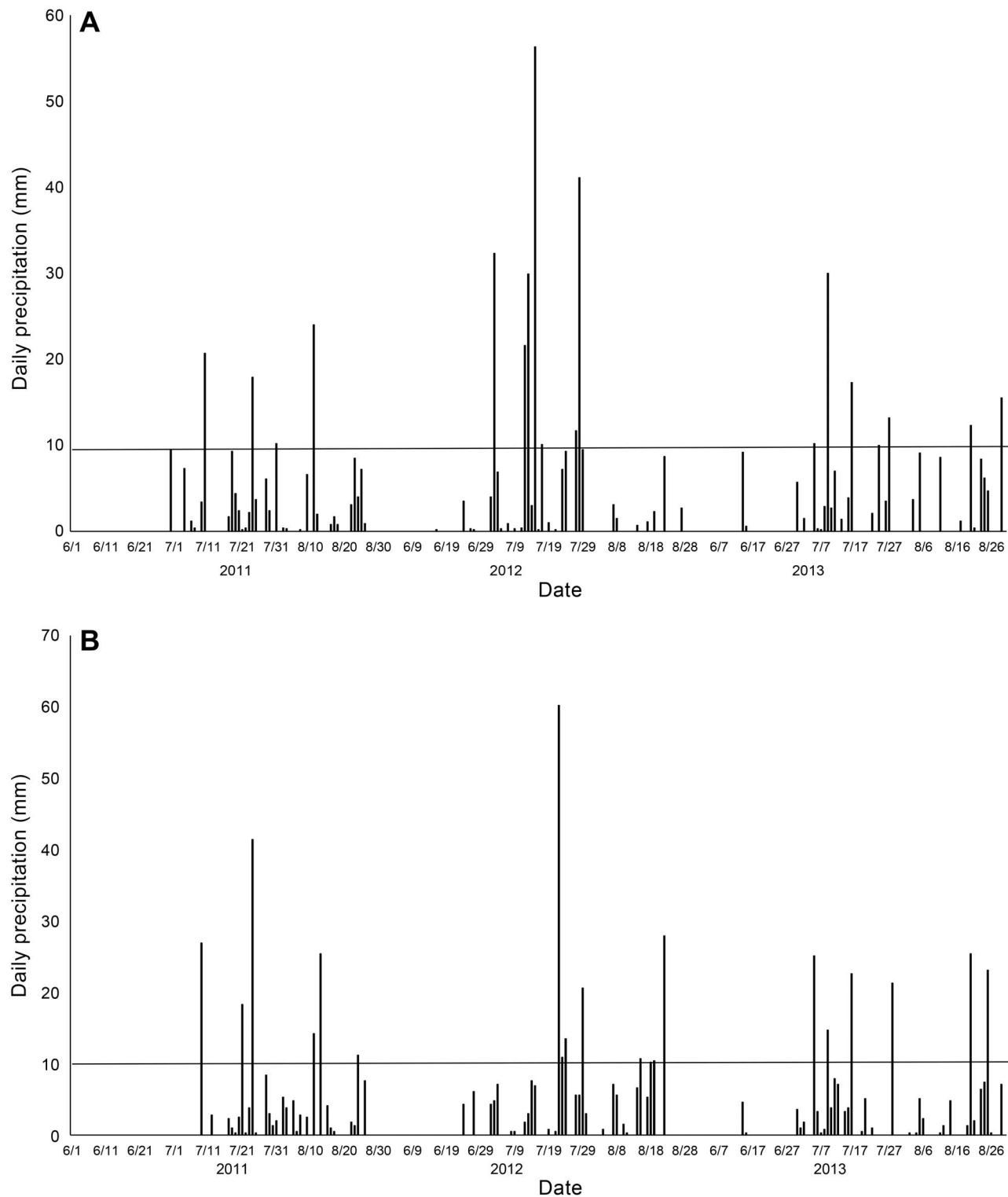


FIGURE 3. Daily precipitation for June 1 through August 30 in 2011–2013 for our 2 study sites: **(A)** Audubon, and **(B)** Davis. The heavy horizontal line indicates the threshold for an extreme daily rain event (≥ 10 mm).

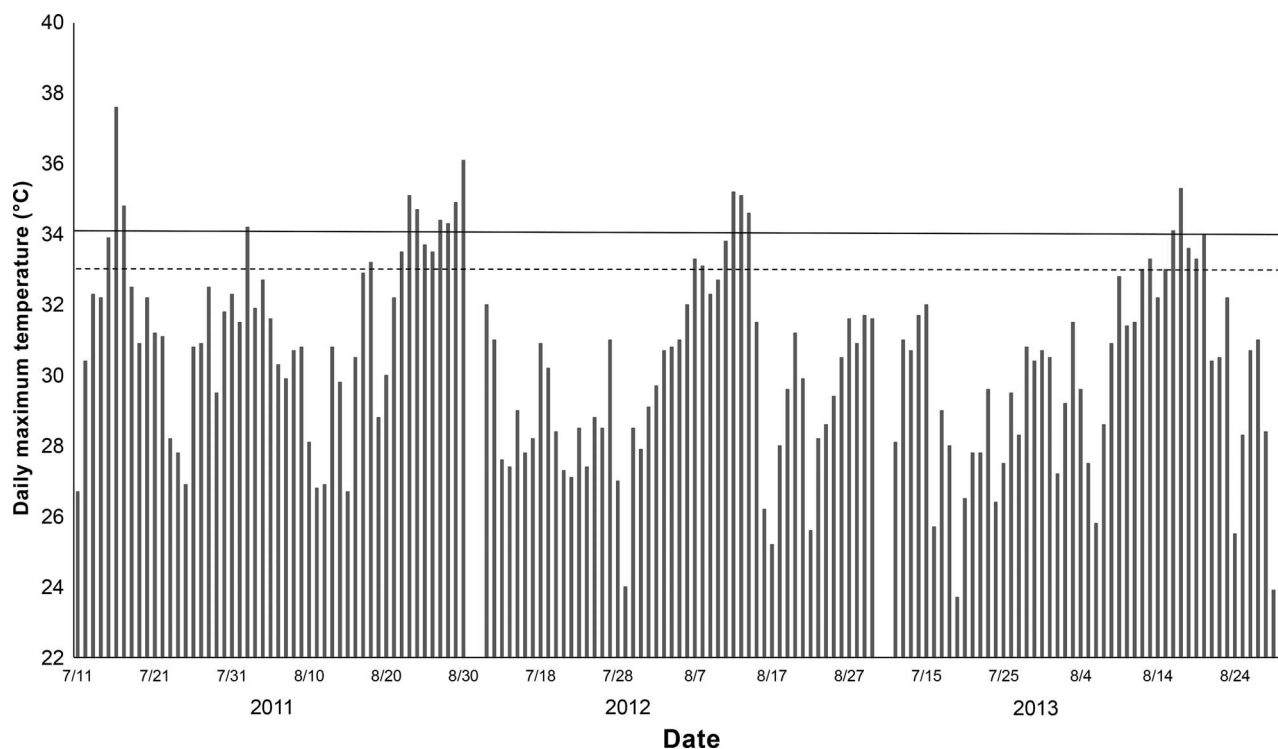


FIGURE 4. Daily maximum temperatures during the nesting period (July 11 through August 30) in 2011–2013 at the Audubon study site. Dotted and heavy horizontal lines indicate thresholds for extreme daily maximum temperature events identified from the literature ($\geq 33^{\circ}\text{C}$ and $\geq 34^{\circ}\text{C}$).

(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 ($\text{DistNShrb}>2\text{m}$) = 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 \pm SD nest concealment for 2012–2013 was $88\% \pm 8\%$ (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 \pm 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

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 \pm 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	$-0.197, 0.083$	$-0.175, 0.061$
NestPINat	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 >2 m (DistShrb >2 m) 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

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

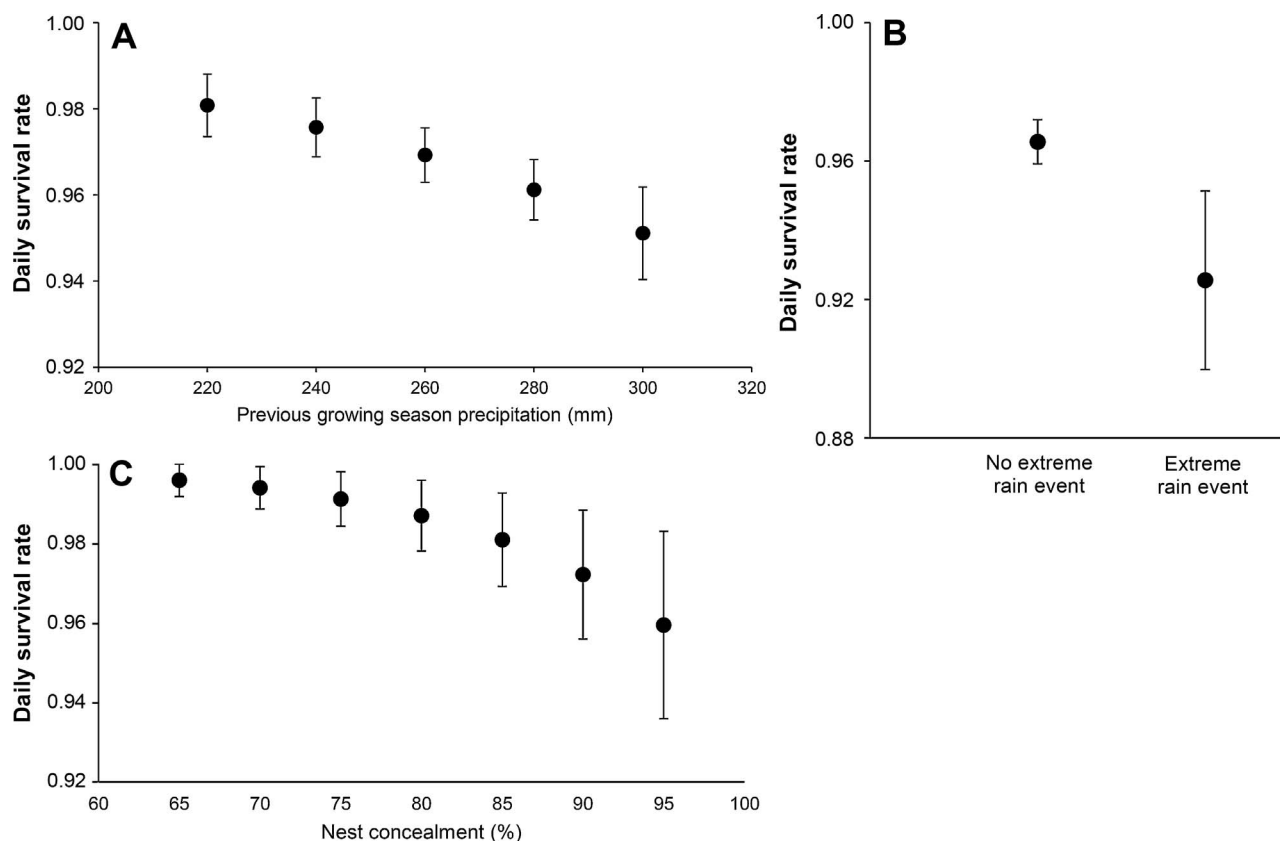


FIGURE 5. Daily survival rates (mean \pm SE) of Grasshopper Sparrow nests predicted in relation to important variables based on best models (Appendix Table 4); predictions were made at specific values for the variable using its best model, while controlling for other variables in that model. **(A)** 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

(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).

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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>

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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
PSPrec	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.

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
PSPrec	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 + NPINat	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 $AIC_c = 184.611$.

APPENDIX TABLE 6. Comparison of Arizona Grasshopper Sparrow (*Ammodramus savannarum ammodramus*) nest success with the nest success of other Grasshopper Sparrow subspecies. To compare data for *A. s. ammodramus* 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	<i>n</i> (nests)	DSR (SE) ^a	Nesting period (days) ^b	Overall nest success (%)	Notes (grassland type, treatment)	Reference ^c
<i>ammodramus</i>						
Arizona	121	0.960 (0.006)	19	46	Desert grassland	This study ^{PM}
<i>perpallidus</i>						
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
<i>pratensis</i>						
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)
<i>floridanus</i>						
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.