

Winter survival of North American grassland birds is driven by weather and grassland condition in the Chihuahuan Desert

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ABSTRACT. Populations of grassland birds that overwinter in the Chihuahuan Desert are declining more rapidly than other grassland birds, and survival during the non-breeding season may have a strong influence on population trends of these species. Habitat loss and deterioration due to desertification may be contributing to these declines, and the winter ecology of grassland birds under these changing environmental conditions remains relatively unexplored. To fill this information gap, we estimated the survival of two grassland-obligate sparrows, Baird's Sparrows (*Ammodramus bairdii*) and Grasshopper Sparrows (*A. savannarum*), on their wintering grounds in the Chihuahuan Desert, and investigated the role of habitat structure and weather on survival rates. We deployed radio-transmitters on Baird's ($N = 49$) and Grasshopper ($N = 126$) sparrows near Janos, Chihuahua, and tracked birds from November to March during the winters of 2012–2013 and 2013–2014. Causes of mortality included avian predators, mammals, and possibly weather. We estimated an overall weekly winter survival probability of $\hat{s} = 92.73\%$ (95% CI[s] = 88.63–95.44%) for Baird's Sparrows in 2012–2013. We estimated a weekly winter survival probability of $\hat{s} = 93.48\%$ (95% CI[s] = 90.29–96.67%) and $\hat{s} = 98.78\%$ (95% CI[s] = 97.88–99.68%) for Grasshopper Sparrow in 2012–2013 and 2013–2014, respectively. Weekly winter survival was lower with colder daily minimum temperatures for both species and in areas with taller shrubs for Grasshopper Sparrows, with the shrubs potentially increasing predation risk by providing perches for Loggerhead Shrikes (*Lanius ludovicianus*). Our results highlight the need to maintain healthy grass structure in wintering areas to provide birds with food, protection from predators, and adequate cover from inclement weather. Our results also demonstrate that the presence of shrubs can lower winter survival, and suggest that shrub encroachment into the winter habitat of these sparrows may be an important driver of their population declines. Shrub removal could increase survival of wintering sparrows in the Chihuahuan Desert by reducing availability of perches for avian predators, thus reducing predation risk.

RESUMEN. La supervivencia al invierno de aves en la pradera Norte Americana está determinada por el clima y las condiciones de la pradera en el desierto de Chihuahua

Las poblaciones de aves de la pradera que pasan el invierno en el desierto de Chihuahua están disminuyendo a una tasa más alta que otras aves de pradera y la supervivencia durante temporadas no reproductivas puede tener una influencia fuerte sobre las tendencias poblacionales de estas especies. La pérdida de hábitat y el deterioro por desertificación pueden contribuir a estas disminuciones y la ecología de invierno de las aves de pradera sujetas a estas condiciones ambientales cambiantes ha sido relativamente poco explorada. Con el fin de llenar este vacío de información, estimamos la supervivencia de dos especies obligatorias de sabana, *Ammodramus bairdii* y *Ammodramus savannarum* en sus territorios de invierno en el desierto de Chihuahua e investigamos el rol de la estructura del hábitat y del clima en las tasas de supervivencia. Utilizamos radio-transmisores en *A. bairdii* ($N = 49$) y *A. savannarum* ($N = 126$) cerca de Janos, Chihuahua y rastreamos las aves desde noviembre hasta marzo durante los inviernos de 2012–2013 y 2013–2014. Las causas de mortalidad incluyeron depredadores aviares, mamíferos y posiblemente el clima. Estimamos una supervivencia semanal durante el invierno de $\hat{s} = 92.73\%$ (95% CI[s] = 88.63–95.44%) para *A. bairdii* en 2012–2013. Estimamos una supervivencia semanal durante el invierno de $\hat{s} = 93.48\%$ (95% CI[s] = 90.29–96.67%) y $\hat{s} = 98.78\%$ (95% CI[s] = 97.88–99.68%) para *A. savannarum* en 2012–2013 y 2013–2014 respectivamente. La supervivencia semanal fue menor con menores temperaturas mínimas diarias para ambas especies y en áreas con arbustos más altos para *A. savannarum*. Los arbustos incrementan potencialmente el riesgo de depredación debido a que provee perchas para *Lanius ludovicianus*. Nuestros resultados resaltan la necesidad de mantener una estructura del pastizal saludable en las áreas de invierno para proveer comida para las aves, protección contra los depredadores y cubierta adecuada contra las inclemencias del clima. Nuestros

resultados demuestran también, que la presencia de arbustos puede disminuir la supervivencia al invierno y sugieren que la invasión de arbustos en estos hábitats puede ser un mecanismo importante para explicar la disminución en las poblaciones. La remoción de arbustos puede incrementar la supervivencia de aves que pasan el invierno en el desierto de Chihuahua reduciendo la disponibilidad de perchas para depredadores aviares y por consiguiente reduciendo el riesgo de depredación.

Key words: *Ammodramus bairdii*, *Ammodramus savannarum*, Baird's Sparrow, Grasshopper Sparrow, grasslands, overwinter survival, program MARK, telemetry

Long-term viability of wildlife populations is increasingly uncertain for a growing number of species. Given that a multitude of factors across the annual cycle may be driving population declines, biologists must identify limiting factors at every life stage to address the most relevant conservation concerns. Furthermore, numerous species of conservation concern cross international borders, posing unique challenges for wildlife agencies. In this regard, steep population declines of grassland bird populations in North America (Sauer et al. 2017) have become a continental conservation crisis for which the principal causes are still uncertain (Brennan and Kuvlesky 2005). Loss and deterioration of grassland habitat on the breeding grounds have been proposed as drivers of these population declines (Vickery et al. 1999) because almost 80% of grasslands in the Great Plains has been lost since the 19th century (White et al. 2000).

Increasing evidence suggests that survival during the non-breeding season also has a strong influence on population trends of migratory species (Calvert et al. 2009, Morrison et al. 2013). Populations of grassland bird species that winter in Chihuahuan Desert grasslands have suffered population declines twice as great as those wintering in other grasslands (North American Bird Conservation Initiative 2016). These declines may be due to habitat loss resulting from cropland expansion (Pool et al. 2014) and habitat deterioration by desertification (Agudelo et al. 2008). Despite these concerns, the winter ecology of grassland birds under changing environmental conditions remains relatively unexplored.

A study of Vesper Sparrows (*Pooecetes gramineus*) provided the first estimate of winter survival for a grassland passerine in the Chihuahuan Desert of Mexico (Macías-Duarte and Panjabi 2013). That research also

revealed an association between habitat characteristics and winter survival. However, different species may respond differently to the characteristics of winter habitat (Macías-Duarte et al. 2009, Panjabi et al. 2010, Pool et al. 2012). Therefore, functional relationships between survival and habitat structure must be determined for each species.

Estimates of winter survival are needed for full-annual-cycle (FAC) population models for migratory grassland birds. These models integrate the effects of both breeding and non-breeding season demographic rates on population dynamics (Hostetler et al. 2015) and can help elucidate where grassland birds are most limited during their annual cycles. Furthermore, FAC models can incorporate the effects on demographic rates at various life stages of variables amenable to management (e.g., vegetation structure) and/or affected by climate change (e.g., weather) and thus can be useful for guiding adaptive conservation. These models may help elucidate responses of species to key stressors in Chihuahuan Desert grasslands such as increased aridity (Seager et al. 2007), shrub encroachment (Archer et al. 2017), and habitat loss (Macías-Duarte et al. 2009, Pool et al. 2014).

Our objective was to use radio-telemetry to estimate, and identify environmental factors that drive, overwinter survival rates of Baird's Sparrows (*Ammodramus bairdii*) and Grasshopper Sparrows (*Ammodramus savannarum*). Grasshopper Sparrows have an extensive breeding range throughout southern Canada and the United States and winter in the southern United States and Mexico (Vickery 1996). Baird's Sparrows have a more restricted breeding range in the Northern Great Plains of Canada and the United States (Green et al. 2002) and a winter distribution limited to the grasslands of the Chihuahuan Desert and Sierra Madre Occidental in the southwestern United States and northern Mexico. Both species are grassland obligates undergoing severe population declines (2.6%

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and 2.8% annual declines, respectively) as revealed by North American Breeding Bird Survey data (Sauer et al. 2017). Both species prefer relatively tall and dense grasslands (Macías-Duarte et al. 2009), avoid shrubs (Macías-Duarte et al. 2009, Pool et al. 2012), and rely on grass for thermal cover at night and as source of food (Titulaer 2016). Because several avian predators of grassland sparrows, especially Loggerhead Shrikes (*Lanius ludovicianus*), prefer areas with more and taller shrubs (Macías-Duarte et al. 2004, Pool et al. 2012), shrub encroachment into these grasslands may increase predator densities and consequently predation on grassland sparrows. We hypothesized that winter survival would generally be low for these two species of sparrows and could be principal limiting factors for population growth. More specifically, we hypothesized that shrub cover and height would have a negative effect on survival, whereas grass cover and height would have a positive effect on survival. These habitat relationships would have implications for grassland conservation and management, especially in light of well-documented and widespread overgrazing that has resulted in woody-plant encroachment (Van Auken 2000, Archer et al. 2017) and loss of perennial grass cover (Estrada-Berg et al. 1999, Manzano et al. 2000) across the Chihuahuan Desert region.

METHODS

Study area. We conducted our study at Rancho El Uno in the municipality of Janos in the Mexican state of Chihuahua during the winters of 2012–2013 and 2013–2014 (Fig. 1). This property, owned by The Nature Conservancy, spans 18,400 ha of grasslands and shrublands within the 526,482-ha federally protected Janos Biosphere Reserve. We monitored Baird's and Grasshopper sparrows at three sites on El Uno located 2–6 km apart within a 999-ha polygon. Sites were characterized by native grass cover (*Bouteloua* sp., *Aristida* sp., *Bothriochloa* sp., *Panicum* sp., and *Pleuraphis mutica*) interspersed with patches of bare ground and forb cover. Shrub cover (*Prosopis glandulosa* and *Ephedra trifurca*) was low (< 5%) and patchy in most of the area. Our study sites had no to moderate grazing by American bison (*Bison bison*).

Bird capture and radio-telemetry. We captured, banded, and attached radio-transmitters (PicoPip Ag379, Biotrack Ltd, Dorset, UK) to sparrows beginning on 12 November in 2012 and 4 December in 2013, and monitored birds through mid-March. Birds were captured using a flush-netting technique that involved a line of 3–5 12-m mist-nets. Using crews of 5–20 people, we formed semicircles up to 200 m away from nets and slowly walked toward nets to flush birds into them. After capture, birds were banded with United States Geological Survey aluminum bands and standard morphometrics were collected including mass (± 0.1 g). We collected one rectrix (r3) to determine sex genetically. We attached transmitters using a figure-eight leg-loop harness made of 1-mm-diameter nylon-coated elastic (Rappole and Tipton 1991). Total transmitter and harness weight was between 0.5 and 0.6 g and did not exceed 4% of bird mass $\bar{x} = 17.2$ g, range = 13.8–21.7 g).

We tracked birds using 3-element folding yagi antennas and receivers (Biotrack Ltd; Model R2000, Advanced Telemetry Systems, Isanti, MN). Observers searched daily for each radio-tagged bird between 07:00 and 19:00. Bird locations were determined by triangulation and, as observers approached triangulated locations, they maintained a visual on the location, making every effort to minimize bird movement. We confirmed that birds were dead or alive based on either observations (bird flushed or was observed running through the grass) or changes in signal location as birds moved through the grass. We marked triangulated locations with a GPS unit and recorded whether birds were detected visually or by signal only. If a transmitter or carcass was found, we looked for signs of predation such as blood, feathers, or bite marks on carcasses or transmitters. We also attempted to determine if the predator was a mammal (carcass cached underground), owl (transmitter in pellet), Loggerhead Shrike (body or transmitter impaled on a branch or cached in dense vegetation), or raptor (plucked feathers and transmitter). Basing predator type on the recovery of carcasses may not be accurate because birds that died from exposure to inclement weather could have later been scavenged and incorrectly identified as a predation event. However, this

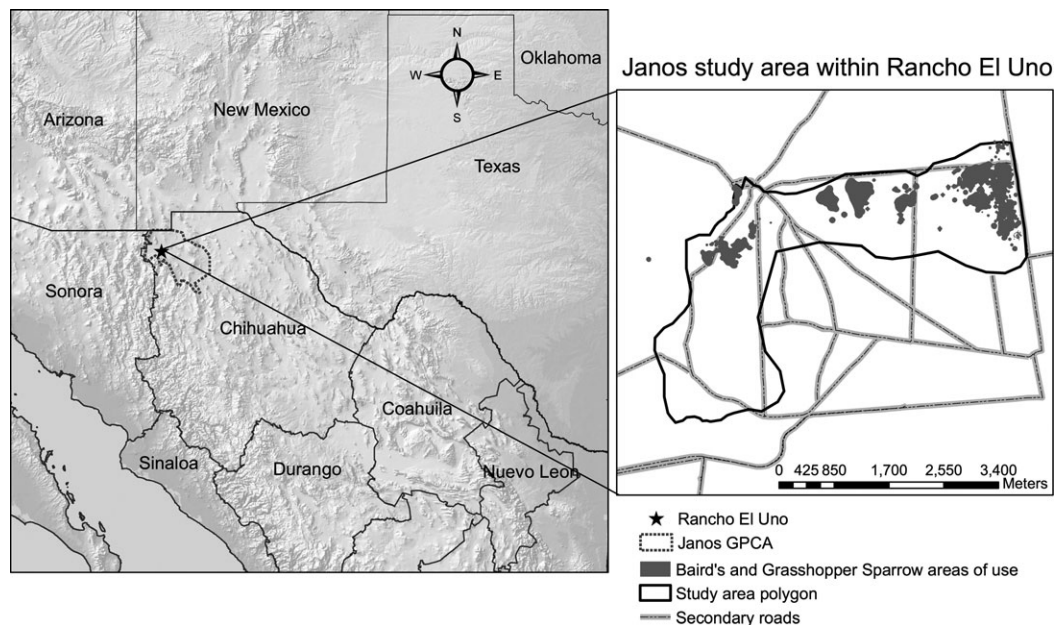


Fig. 1. Location of our study area in the municipality of Janos, Chihuahua, Mexico.

would primarily affect the few predation events attributed to mammals because most avian predators observed on El Uno are not known to scavenge to a significant degree. Additionally, we cannot rule out that birds were weakened by weather and were then predated. We attempted to locate missing individuals that either left the study area or were transported away by predators by walking through unsurveyed suitable habitat, climbing to high points, and driving roads within 10 km of the study area while using either a handheld Yagi or a truck-mounted omnidirectional antenna. This was done at least twice weekly every week until expected transmitter battery failure. These efforts led to the relocation of several birds outside of the study area as well as detection of birds that had left the area and subsequently returned to their territories. Relocated birds were monitored daily at the new locations until the end of the study period, or until they died or moved to another location.

Vegetation sampling and weather data. We conducted vegetation surveys at each triangulated or flushed-sparrow telemetry location within 1 mo of marking the location. We visually estimated percent cover of grasses, shrubs, forbs, tumbleweed, and other

cover (e.g., litter and animal excrement) within a 5-m radius around each location. Our visual ocular technique for grass and shrub cover produced estimates that were highly correlated to quantitative estimates of grass and shrub cover (Macías-Duarte and Panjabi 2013) and were strongly correlated ($r^2 > 0.8$) between observers (Bird Conservancy, unpubl. data). These habitat structure variables have previously been identified as factors influencing the abundance and distribution of wintering Baird's and Grasshopper sparrows in the Chihuahuan Desert (Macías-Duarte et al. 2009, Panjabi et al. 2010, Pool et al. 2012). We placed a Robel pole (Robel et al. 1970) marked at 2-cm intervals at a distance of 4 m from the plot's center in the four cardinal directions and recorded the height at which vegetation completely obstructed the pole and the maximum height at which vegetation obscured the pole as indices of visual obstruction. We used the Robel pole when estimating plot-level average grass, shrub, and forb heights.

Grassland birds wintering in the northern Chihuahua Desert are often subjected to freezing temperatures. Frequent exposure to intense cold nights (as low as -11°C) may have a negative effect on survival through

strong thermoregulation demands on small-bodied sparrows. We obtained temperature data from an automated weather station at Colonia Fernández Leal located 14 km from our study area and operated by Unión Agrícola Regional de Fruticultores del Estado de Chihuahua.

Statistical analysis. We used the known-fate model in program MARK (White and Burnham 1999) to provide estimates of weekly survival probability (s) for each species of sparrow. In this model, the response variable y_{ij} is the binary variable weekly survival status ($y_{ij} = 0$ if dead during the week, and $y_{ij} = 1$ if not dead during the week) of the i -th individual ($i = 1, 2, \dots, n$) in the j -th sampling occasion ($j = 1, 2, \dots, m$). Under this model, each y_{ij} is the realization of a Bernoulli random variable with parameter s_j (survival at the j -th sampling occasion). The known-fate model assumes perfect detection and, therefore, probability of detection (P) is not estimated ($P = 1$). Furthermore, a bird is censored from the analysis for any day it was not detected (ragged telemetry data) and its survival status does not contribute to the likelihood function even if the bird is known to be alive in subsequent weeks.

Our approach of modeling weekly survival (instead of daily survival) when we gathered survival and environmental data on a daily basis requires further explanation. Exploring the effect of habitat variables on daily survival in a telemetry study is difficult given that locations and their associated habitat characteristics where radio-tagged birds died may be unknown (e.g., predators move carcasses or transmitters are recovered after dead birds have gone undetected for several days). For this reason, we divided the study period into 17 weeks (7-d periods) and averaged values for each habitat structure variable by week, assuming that those averages reflected habitat use by each individual bird during the week.

We evaluated the effects of time-independent and time-dependent covariables on weekly survival probability using the logit link function with a linear predictor. The factor winter (with levels 2012–2013 and 2013–2014) was the only time-independent covariable. We did not include winter for Baird's Sparrows because we only captured two individuals during the winter of 2013–2014 and were unable to generate reliable survival

estimates. Time-dependent covariables were the weekly average of minimum daily temperature ($^{\circ}\text{C}$) and weekly averages of habitat structure variables grass cover (%), grass height (cm), shrub cover (%), shrub height (m), forb cover (%), forb height (cm), and visual obstruction of vegetation. We removed one covariable per pair of highly correlated covariables ($|\tau| > 0.7$) to avoid multicollinearity in our models. This procedure eliminated the covariable visual obstruction that was highly correlated with grass cover. In addition, we fit the intercept-only model to provide overall estimates of weekly survival probability for the winter of 2012–2013 for Baird's Sparrows and a pooled estimate of weekly survival for both winters for Grasshopper Sparrows. We also fit a model that included only winter for Grasshopper Sparrows to provide estimates of weekly survival probability per winter.

We model-averaged estimates (sensu Anderson 2007) of regression coefficients in (2) overall possible additive models (Doherty et al. 2012, but see Cade 2015) with the constraint that cover and height were entered together for each vegetation type (grass, forbs, and shrubs) when building the model set. This process generated 16 and 32 models for Baird's and Grasshopper sparrows, respectively (the former lacked winter). We expressed the effects of habitat structure variables on weekly survival by stating the multiplicative effect ($e^{\beta_i m}$) on the odds of survival ($\omega = s/(1-s)$) by m units of increase in any given covariate x_i ($i = 1, 2, \dots, P$). We used the delta method (Powell 2007) to estimate sampling variances of derived parameters from sampling variances of regression coefficients estimated by program MARK, such as survival estimates and odds ratios. We used Wald tests (Kutner et al. 2005) for ad hoc hypothesis tests on regression coefficients using standard errors derived from the delta method.

RESULTS

Baird's and Grasshopper sparrows occurred at grassy locations in our study area, with an average grass cover of 31.0% and 45.5%, respectively. Baird's and Grasshopper sparrows also occurred most often at locations with fewer ($\bar{x} \approx 1\%$ shrub cover) and shorter

shrubs ($\bar{x} < 50$ cm). However, Grasshopper Sparrows showed a wider tolerance to habitat conditions, with higher standard deviations for grass cover, forb height, and visual obstruction (Table 1).

Average body masses at first encounter for Baird's and Grasshopper sparrows were 18.4 g (SD = 1.2 g) and 17.0 g (SD = 0.9 g), respectively. We found that Baird's and Grasshopper sparrows did not reach their maximum daily body mass prior to roosting; mass of banded sparrows did not steadily increase with time of day, but instead peaked at ~13:38 and declined temporally (extra-sum-of-squares F -test for quadratic vs. linear regression, $F_{1,388} = 6.4$, $P = 0.01$).

We radio-tagged 175 sparrows (49 Baird's Sparrows in 2012–2013 and 54 and 72 Grasshopper Sparrows in 2012–2013 and 2013–2014, respectively). In 2012–2013, 10 Baird's Sparrows and 13 Grasshopper Sparrows disappeared from the study area and, in 2013–2014, 15 Grasshopper Sparrows went missing. These missing birds could have left the study area, been predated, or had their transmitters fail. We confirmed 39 mortalities (17 Baird's Sparrows in 2012–2013 and 15 and 7 Grasshopper Sparrows in 2012–2013 and 2013–2014, respectively), all apparently the result of predation. The number of mortalities differed between winters, with 32 in the winter of 2012–2013 and seven in 2013–2014 (Fig. 2A). We suspect that 16 birds were predated by diurnal raptors, including Northern Harriers (*Circus cyaneus*), Merlins (*Falco columbarius*), Prairie Falcons (*F. mexicanus*), and American Kestrels (*F. sparverius*), 12 by Loggerhead Shrikes, three by Short-eared Owls (*Asio flammeus*), and two by

mammals (*Lynx rufus* or *Vulpes* spp.). We were unable to identify predator type for six carcasses.

We estimated a weekly winter survival probabilities of $\hat{s} = 92.73\%$ (95% CI_[s] = 88.63–95.44%) for Baird's Sparrows in the winter of 2012–2013, and of $\hat{s} = 93.48\%$ (95% CI_[s] = 90.29–96.67%) and $\hat{s} = 98.78\%$ (95% CI_[s] = 97.88–99.68%) for Grasshopper Sparrows in the winters of 2012–2013 and 2013–2014, respectively, with a pooled estimate of $\hat{s} = 97.26\%$ (95% CI_[s] = 95.88–98.19%) for both winters. We found no difference in weekly survival probability between Baird's and Grasshopper sparrows, with their 95% CI(s) overlapping in the winter of 2012–2013 when we had estimates of weekly survival for both species. We found that winter survival was associated with habitat structure and minimum daily temperatures. Minimum daily temperatures decreased during the study period from mid-November to their lowest levels (about -10°C) by mid-January in both winters, and then increased afterward, although minimum temperatures remained lower for the winter of 2012–2013 (Fig. 2B). Confidence intervals (95%) of model-averaged effects suggest that weekly winter survival was positively associated with minimum temperature (Table 2, Fig. 3A) for Grasshopper Sparrows. The odds of surviving a week increased 1.27 times (95% CI = 1.09–1.46) for every 1°C increase in the weekly average of minimum temperature.

Shrub height was negatively associated with weekly winter survival of Grasshopper Sparrows (Table 2, Fig. 3B). The odds of surviving a week increased 1.49 times (95% CI 1.17–1.81) for every 10 cm decrease in

Table 1. Habitat structure variables at telemetry locations of Baird's and Grasshopper sparrows in desert grasslands of Chihuahua, Mexico, during the winters of 2012–2013 and 2013–2014.

Variable	Baird's Sparrow				Grasshopper Sparrow			
	\bar{x}	SD	Min	Max	\bar{x}	SD	Min	Max
Grass cover (%)	31.0	13.0	9.5	71.0	45.5	23.6	7.5	94.8
Grass height (cm)	24.6	4.8	13.8	41.0	24.0	4.0	15.0	49.5
Forb cover (%)	1.0	1.1	0	10.0	2.4	2.6	0	19.0
Forb height (cm)	13.4	6.6	0	45.0	15.5	13.7	0	83.0
Shrub cover (%)	1.0	1.3	0	11.0	1.2	1.5	0	11.6
Shrub height (cm)	49.9	26.6	0	105.7	36.9	26.7	0	126.3
Visual obstruction (cm)	4.1	2.5	0.3	15.0	8.6	5.5	0	27.9

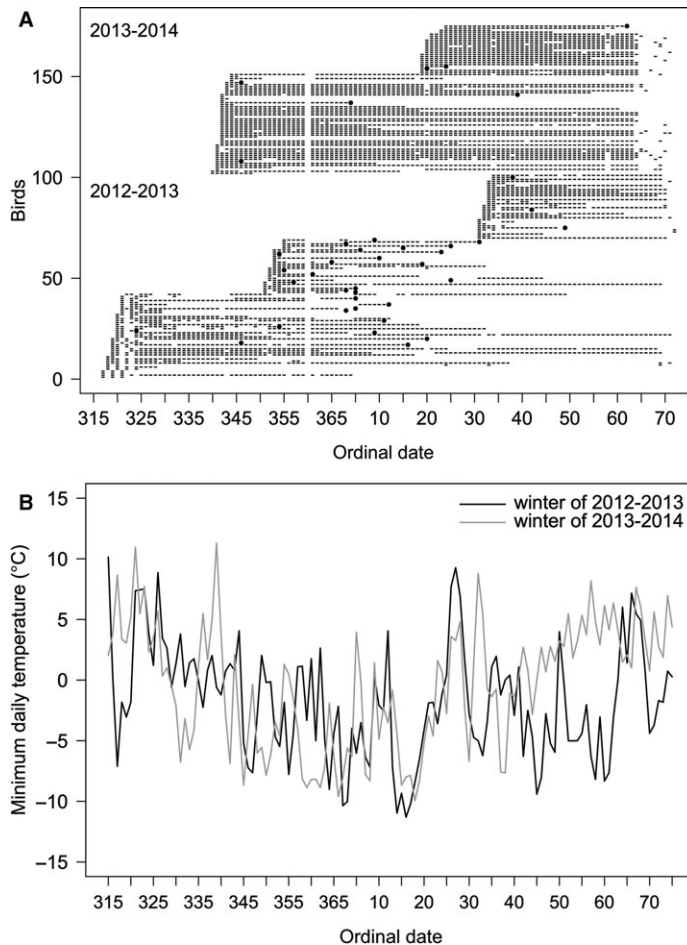


Fig. 2. (A) Survival histories of 175 Baird's and Grasshopper sparrows in the Chihuahuan Desert grasslands of Janos, Mexico, during the winters of 2012–2013 and 2013–2014. Each horizontal set of line segments represents an individual radio-tagged sparrow. Dates when radio-transmitters were recovered from dead birds are shown as a black dot. (B) Trajectories of minimum daily temperatures during the winters of 2012–2013 and 2013–2014. Ordinal date 315 = 11 November, and ordinal date 70 = 11 March.

average shrub height. We found no evidence that weekly survival differed between winters of 2012–2013 and 2013–2014 (Wald test on regression coefficient, $z = 0.8$, $P = 0.42$) for Grasshopper Sparrows, suggesting that differences in the number of mortalities between winters (see above) were due to differences in minimum temperatures and habitat use. All variables related to grass and forb vegetation were uninformative for Grasshopper Sparrows because their confidence intervals overlapped zero (Table 2). Weekly winter survival of Baird's Sparrows was also associated with

minimum temperature, but not habitat structure covariables (Table 3). The odds of surviving a week increased 1.23 times (95% CI = 1.02–1.45) for every 1°C increase in the weekly average minimum temperature. The effect of minimum temperature on weekly winter survival was similar for Baird's and Grasshopper sparrows (Wald test on the difference of regression coefficients, $z = 0.3$, $P = 0.78$). We found no evidence of sex-related differences in mortality in a subset of molecularly sexed birds (Pearson's test of independence, $\chi^2_1 = 0.2$, $P = 0.69$, $N = 165$).

Table 2. Effect of environmental and habitat structure variables on winter weekly survival (with logit link) of Grasshopper Sparrows in desert grasslands of Chihuahua, Mexico.

Explanatory variables	Estimate	SE	LCI	UCI
Intercept*	5.365	1.057	3.292	7.437
Grass cover	-0.003	0.011	-0.023	0.018
Grass height	-0.006	0.025	-0.055	0.042
Forb cover	0.204	0.199	-0.185	0.594
Forb height	0.032	0.028	-0.023	0.087
Shrub cover	0.063	0.134	-0.199	0.326
Shrub height*	-0.040	0.011	-0.061	-0.018
Minimum temperature*	0.241	0.075	0.095	0.387
Winter (2013–2014)	0.527	0.657	-0.760	1.814

Estimates are model-averaged regression coefficient estimates across all additive models (see text). The reference level for winter is 2012–2013. Asterisk (*) denotes effects different from zero at $P < 0.05$. LCI and UCI denote the lower and upper limits of the 95% confidence intervals.

DISCUSSION

Our estimates of winter weekly survival probability yielded overall winter survival rates (i.e., extrapolated to a 17-week monitoring period) of 27.7% (95% CI = 10.8–44.7%) and 31.8% (95% CI = 13.3–50.2%) for Baird's and Grasshopper sparrows, respectively, during the winter of 2012–2013. Even with the most optimistic scenario of ~50% of the birds surviving through a winter (i.e., the upper limit of the 95% CI of winter survival), these low winter survival rates may have a strong influence on annual survival and population growth rates for both species. However, our estimates of survival should not be extrapolated to all wintering populations in the Chihuahuan Desert. Differences in sparrow abundance between winters suggest that these sparrows may track resource abundance and habitat conditions at large scales and occupy locations that maximize survival (ideal free distribution, Fretwell 1972). Baird's Sparrows, which were virtually absent from our study area during the winter of 2013–2014, may have occupied higher-quality locations outside our study areas, resulting in higher winter survival. Further study of the relationship between bird abundance and survival across the Chihuahuan Desert is needed to fully understand this phenomenon. For instance, Panjabi et al. (2013) found that average bird densities of both species of sparrows were often higher further south in Durango and winter survival rates could have been higher there.

For comparison purposes, our estimates of weekly winter survival (s) can be transformed to daily winter survival, resulting in a daily winter survival of 98.93% (95% CI 98.42–99.43%) for Baird's Sparrows in the winter of 2012–2013, and 99.04% (95% CI 98.56–99.52%) and 99.82% (95% CI = 99.69–99.95%) for Grasshopper Sparrows during the winters of 2012–2013 and 2013–2014, respectively. Vesper Sparrows wintering in the Chihuahuan Desert had a similar estimate of daily survival probability of 99.1% (95% CI = 97.4–99.7%; Macías-Duarte and Panjabi 2013). Winter survival probabilities for congeneric Henslow's Sparrows (*Ammodramus henslowii*) ranged from 92.3% to 99.9% (Thatcher et al. 2006) in the coastal pine savannas of Mississippi. These relatively low and variable rates suggest that population limitation may at times be occurring in wintering areas and highlight again the need for spatially and temporally robust integrated population monitoring and modeling to understand how seasonal demographic rates interact and influence overall population trends of grassland birds.

Although we cannot rule out a negative effect of radio-transmitters on sparrow survival in our study, the results of numerous studies have revealed no negative effects of radio-transmitters on non-breeding passerines (Powell et al. 1998, Davis et al. 2008, Rae et al. 2009, Townsend et al. 2012). Additionally, we were able to recapture birds to remove tags prior to migration and noticed no apparent physical impacts from the tags or

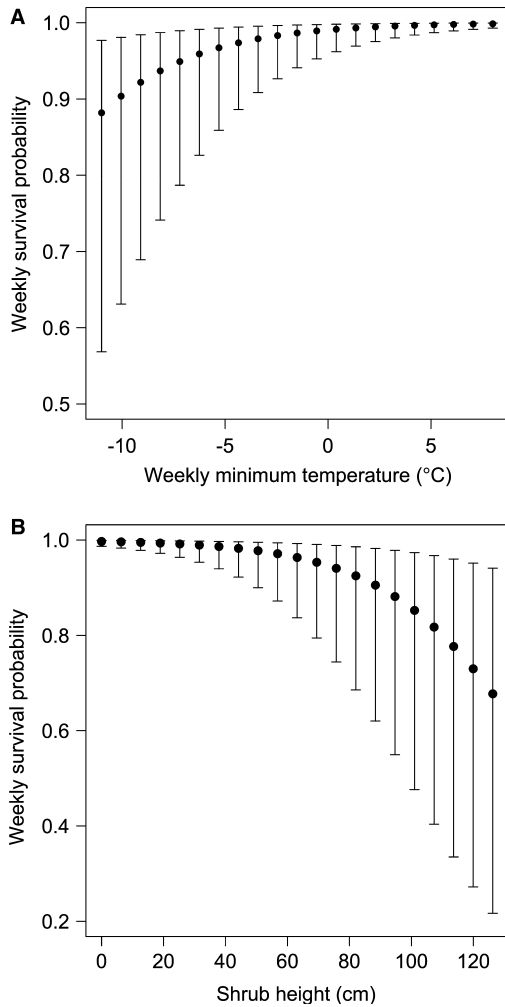


Fig. 3. (A) Association of weekly averages of minimum daily temperature and (B) shrub cover with weekly survival probability (s) of Grasshopper Sparrow in Chihuahuan Desert grasslands of Janos, Mexico, during the winters of 2012–2013 and 2013–2014 as predicted by an averaged model over 32 additive models (Table 1). Bars are estimates of $SE(s)$; upper and lower limits of bars are the expit-transformed values of $\text{logit}(s) \pm SE(\text{logit}[s])$.

harnesses. We also found no difference in mass gain or loss between recaptured birds that were or were not radio-tagged (E. H. Strasser, unpubl. data), suggesting that the extra weight did not limit the ability of radio-tagged birds to forage effectively.

Our results suggest that temperature and habitat characteristics, specifically shrub height, influenced the winter survival of

Table 3. Effect of environmental and habitat structure variables on winter weekly survival (with logit link) of Baird's Sparrows in desert grasslands of Chihuahua, Mexico.

Explanatory variables	Estimate	SE	LCI	UCI
Intercept	2.863	1.475	-0.027	5.754
Grass cover	-0.012	0.016	-0.043	0.020
Grass height	0.026	0.053	-0.078	0.131
Forb cover	-0.117	0.175	-0.459	0.226
Forb height	0.013	0.028	-0.041	0.067
Shrub cover	0.003	0.138	-0.267	0.274
Shrub height	0.002	0.006	-0.011	0.015
Minimum temperature*	0.209	0.088	0.036	0.382

Estimates are model-averaged regression coefficient estimates across all additive models (see text). LCI and UCI denote the lower and upper limits of the 95% confidence intervals.

*Effects different from zero at $P < 0.05$.

Baird's and Grasshopper sparrows. Model-averaged estimates of effects show a positive association between weekly average daily minimum temperature and weekly survival of both sparrows, suggesting that cold weather may limit their populations in winter, especially during prolonged periods of below-freezing temperatures often associated with storms. Energetic stress is likely a major process responsible for mortality of birds wintering in temperate climates (Krams et al. 2011). Thermoregulation when temperatures fall below the thermoneutral zone imposes high energetic costs through metabolic heat production, particularly for small-bodied animals that lose heat at a faster rate (Hill et al. 2012). Wintering birds must replenish their fat reserves by foraging intensively during the day (Lehikoinen 1987). Our banding data suggest that Baird's and Grasshopper sparrows are constrained (either physiologically, by food supply, or by availability of thermal refuges) in their ability to build body mass to face low nocturnal temperatures because body mass did not steadily increase throughout the day. Although the ability of birds to withstand extreme low temperature may vary with sex and age (Krams et al. 2011), we found no difference between the sexes in the number of mortalities.

During the winter of 2012–2013, we observed spikes in the numbers of birds

predated following colder weather and snowstorms during the period from mid-December to mid-January, as supported by the high proportion of mortality events during the coldest part of the winter (Fig. 2). Birds are more visible following snowfall on cold days and, especially for grassland birds that seek refuge from predators in dense grass and other near-ground vegetation like Grasshopper and Baird's sparrows (A. O. Panjabi, pers. observ.), predation risk appears to increase sharply after snow events. The effect of cold weather may also reflect the relationship between predation risk and risk of starvation (Lima and Dill 1990, Cresswell and Whitfield 2008). Birds attempting to compensate for energy loss after cold winter nights may be less vigilant and are predated at higher rates. Similarly, as risk of starvation increases, birds may forage farther from protective cover (Lima 1986). Finally, cold weather and snow may also reduce availability of other types of prey, such as grasshoppers, small mammals, and lizards, leaving birds as the most accessible prey for avian predators.

We found evidence of an association between shrub height and winter weekly survival of Grasshopper Sparrows. The negative effect of shrub height on survival, especially as shrubs exceed 50 cm in height, is likely related to increased predation pressure in areas with taller shrubs. Tall shrubs (above the grass stand or > 1 m in height) are perching, hunting, and nesting sites for Loggerhead Shrikes, one of the most widespread bird species in the Chihuahuan Desert whose abundance is positively associated with shrub height in Chihuahuan Desert grasslands (Macías-Duarte et al. 2004, Pool et al. 2012). Tall shrubs are also used for hunting and perching by a variety of diurnal raptors in Chihuahuan Desert grasslands, including falcons and *Accipiter* hawks (A. O. Panjabi and E. H. Strasser, pers. observ.). In our study area, Loggerhead Shrikes accounted for 30% of the predation events of radio-tagged birds. Further study of predator movements and other behaviors may provide insight into the relationship between shrubs, predators, and survival of grassland birds. Nonetheless, evidence of this relationship provides guidance for grassland bird conservation on the wintering grounds through habitat management. Shrub encroachment, possibly due to grazing

mismanagement and increased atmospheric CO₂ (Van Auken 2000), is a widespread and primary driver of grassland loss in the Chihuahuan Desert (Archer et al. 2017). Shrub removal has been a frequent focus in grassland restoration (Rango et al. 2005) and may increase wintering densities of species of grassland sparrows (De León Mata et al. 2013). Previous research has demonstrated that more shrub cover and taller shrubs can limit abundance of some wintering grassland species of birds in Chihuahuan Desert grasslands (Pool et al. 2012). Our results demonstrate that the presence of shrubs also can lower winter survival, and suggest that shrub encroachment into wintering habitat may be a driver of population declines in these migratory species, given the widespread nature of this phenomenon in their wintering areas (Archer et al. 2017). As such, shrub removal could increase survival of wintering sparrows in the Chihuahuan Desert by reducing availability of perches, nest sites, and ladders for Loggerhead Shrikes and perches for raptors, thus reducing predation risk. The relationship between survival of Baird's Sparrows and shrubs may not be apparent in our study because these sparrows avoid using areas with greater shrub cover (Pool et al. 2012, Ruth et al. 2014). However, shrub characteristics examined at larger spatial scales (e.g., a scale that accounts for shrub cover on the edges of areas used by Baird's Sparrows) could help explain the low winter survival rates we observed.

The density and presence of *Ammodramus* sparrows in Chihuahuan Desert grasslands are strongly associated with grass cover, grass height, and grass volume (Macías-Duarte 2002, Macías-Duarte et al. 2004, 2009, Panjabi et al. 2010, Pool et al. 2012). In addition, daily winter survival of Vesper Sparrows in Chihuahuan Desert grasslands was found to be related to grass height (Macías-Duarte and Panjabi 2013). Although Baird's and Grasshopper sparrows are considered grassland specialists, we found that grass cover and grass height were not associated with winter survival for either species. However, this does not necessarily imply that grass conditions are not important to these species because a strong preference for a given habitat condition may lead to relatively low variation in that condition when measured only where the species is detected (i.e., telemetry locations),

and this may explain the lack of relationship between survival and grass characteristics. Alternatively, this lack of relationship may be related to a wider tolerance of grass conditions during the winter within the range of suitability. However, because Chihuahuan Desert grasslands continue to disappear at alarming rates (Pool et al. 2014), birds and predators may become more concentrated in remaining patches, increasing competition for winter microhabitats that provide better cover and reduce predation risk. Another possibility is that greater grass volume may be more important for roosting locations, which we did not sample, because denser grass may provide improved nighttime thermal refuges for sparrows. Finally, the value of dense grass may only be apparent during harsh weather events (Janke et al. 2015), a relationship that may be elucidated with more data across years of varying weather and grassland conditions.

Our results suggest that habitat management for wintering Baird's and Grasshopper sparrows should focus on maintaining or improving grassland vegetation to provide sufficient grass seed and cover (for food and for refuge from both predators and inclement weather), and controlling and reversing shrub encroachment. This recipe for enhancing grassland bird habitat is well known, but its implementation requires new range management paradigms in the grasslands of northern Mexico and southwestern United States because overgrazing is still the norm and shrub encroachment continues (De León Mata et al. 2013, Archer et al. 2017). In addition, protection of high-quality grassland bird habitat from conversion to farmland in northern Mexico remains a top priority affecting Canada, Mexico, and the United States, as this unfettered and illegal conversion continues to reduce habitat availability for migratory grassland birds shared among these countries (Macías-Duarte et al. 2009, Pool et al. 2014).

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