Association of Habitat Characteristics with Winter Survival of a Declining Grassland Bird in Chihuahuan Desert Grasslands of Mexico

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ASSOCIATION OF HABITAT CHARACTERISTICS WITH WINTER SURVIVAL OF A DECLINING GRASSLAND BIRD IN CHIHUAHUAN DESERT GRASSLANDS OF MEXICO

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Abstract.—Grassland bird populations have shown persistent declines over the past four decades in North America. Possible explanations for the declines include decreased winter survival because of habitat deterioration. To address this hypothesis, we evaluated the relationship between habitat structure and winter survival of Vesper Sparrows (*Pooecetes gramineus*) in Chihuahuan Desert grasslands of northern Mexico. We radiotagged and monitored the survival of 102 individuals during the winters of 2009 and 2010. We obtained visual estimates of vegetation structure and composition at every individual's radiotelemetry location. We used an exponential regression model to estimate daily survival rates and determine the association between habitat structure and survival. We estimated a daily winter survival probability of 99.1% (95% confidence interval: 97.4–99.7%) for Vesper Sparrows in both years. Our survival analysis suggests that habitat structure is an important predictor of winter survival. Average grass height and shrub height were positively related to Vesper Sparrow survival. Our results suggest that grassland bird populations may be negatively affected by poor grassland conditions during the winter and that low winter survival may be an important factor in population declines. Winter habitat conditions in the Chihuahuan Desert grasslands are shaped primarily by grazing and climate, highlighting the need to improve range management, especially in Mexico, as a means to reverse persistent population declines of grassland birds. *Received 17 March 2012, accepted 22 November 2012.*

Key words: Chihuahuan Desert, grassland birds, parametric survival analysis, *Pooecetes gramineus*, range management, Vesper Sparrow, winter survival.

Asociación de las Características del Hábitat con Supervivencia de Invierno de una Decreciente Aves de Pastizales en los Pastizales del Desierto Chihuahuense de México

Resumen.—Las poblaciones de aves de pastizal han disminuido persistentemente en las últimas cuatro décadas en América del Norte. Explicaciones posibles para estos descensos incluyen la disminución de la supervivencia invernal debido al deterioro del hábitat. Para abordar a esta hipótesis, estimamos la supervivencia invernal y se evaluó la influencia de la estructura del hábitat en la supervivencia invernal de Gorriones Cola Blanca (*Pooecetes gramineus*) en pastizales del Desierto Chihuahuense del norte de México. Instalamos radiotransmisores en 102 individuos y los monitoreamos durante los inviernos de 2009 y 2010. Obtuvimos estimaciones visuales de la estructura de la vegetación y composición en cada ubicación de detección de cada individuo. Utilizamos un modelo de regresión exponencial para estimar las tasas diarias de supervivencia y determinar la asociación entre la estructura del hábitat y la supervivencia. Estimamos una probabilidad de supervivencia diaria invernal de 99.1% (95% CI: 97.4–99.7%) para los Gorriones Cola Blanca en ambos años. Nuestro análisis paramétrico de supervivencia sugiere que la estructura del hábitat es un importante predictor de supervivencia durante el invierno. El promedio de la altura de los pastos y de la altura de los arbustos estuvieron relacionadas positivamente con la supervivencia de los Gorriones Cola Blanca. Nuestros resultados sugieren que las poblaciones de aves de pastizal pueden ser afectados negativamente por condiciones pobres de pastizales durante el invierno y que una baja supervivencia invernal puede ser un factor importante en la disminución de la población. Las condiciones invernales del hábitat en los pastizales del Desierto Chihuahuense están determinadas principalmente por el pastoreo y el clima, lo que destaca la necesidad de mejorar el manejo de los pastizales, especialmente en México, como un medio para revertir las disminuciones poblacionales persistentes de aves de pastizal.

Grassland birds have declined more than any other North American bird guild over the past four decades (Samson and Knopf 1994, Sauer et al. 2011). The factors driving these population declines are poorly understood but are likely related to the conversion of native grasslands to farmland and to habitat alteration by grazing throughout their breeding range (Peterjohn and Sauer 1999). Although the

role of winter habitat degradation in driving documented population declines in migratory grassland birds is hypothesized to be important (Rappole and McDonald 1994), it remains to be explored. Large numbers of North American grassland birds winter in the Chihuahuan desert and Sierra Madre foothills of northern Mexico (Peterson and Robbins 1999), where grasslands are highly threatened. Recent extensive conversion of grasslands to farmland (Macías-Duarte et al. 2009), overgrazing, encroachment by woody plants and invasive species, and increasing aridity (Seager et al. 2007) threaten the persistence of desert grasslands in northern Mexico. Determining habitat relationships of grassland birds in winter is crucial in designing conservation programs and targeting areas for management and protection. In this regard, there have been recent advances in our knowledge of the relationship between habitat structure and both presence and abundance of grassland birds in Mexico (Desmond et al. 2005, Macías-Duarte et al. 2009, Martinez et al. 2010, Panjabi et al. 2010a, Martínez-Guerrero et al. 2011) demonstrating the importance of grass for wintering grassland birds. However, no study has evaluated how patterns of habitat use are directly related to demographic parameters such as survival in wintering grassland birds in northern Mexico.

Population fluctuations in migratory grassland birds may be most influenced by annual fluctuations in mortality during the nonbreeding season (Sæther et al. 1996). Therefore, survival estimates are critical for assessing the long-term viability of populations and the design of conservation strategies. In this regard, we aimed to gather survival data from birds with radiotransmitters to model the association of grassland habitat structure with survival rates of a wintering grassland bird species in Mexico. The Vesper Sparrow (*Pooecetes gramineus*) is an appropriate species for examining the winter survival of small grassland passerines using current telemetry technology, because this species breeds in dry open habitats throughout western North America and winters in grasslands, shrublands, and similar habitats across the southwestern United States and Mexico (Jones and Cornely 2002). As with most grassland passerines, no estimate of winter survival is available for the species (Jones and Cornely 2002). Vesper Sparrows are one of the most common bird species in Chihuahuan Desert grasslands (Manzano-Fischer et al. 1999, Levandoski et al. 2009, Macías-Duarte et al. 2009, Martinez et al. 2010, Martínez-Guerrero et al. 2011), are captured relatively easily, and are large enough to carry a radiotransmitter that lasts ≤50 days. Vesper Sparrows also show the persistent population declines characteristic of their guild, having declined at an average rate of 0.9% annually since 1966 (Sauer et al. 2011).

Methods

Study species.—Several natural-history characteristics of the Vesper Sparrow are relevant to the species' survival on the wintering grounds of the Chihuahuan Desert. Vesper Sparrows feed primarily on grass and forb seeds during the winter (Desmond et al. 2008), the growth of which is directly influenced by summer precipitation (Gordon 2000, Macías-Duarte et al. 2009). Predatory birds kill Vesper Sparrows in desert grasslands (Lima and Valone 1991). Potential avian predators in our study area include Loggerhead Shrikes (*Lanius ludovicianus*), Northern Harriers (*Circus cyaneus*), American Kestrels (*Falco sparverius*), and Red-tailed Hawks (*Buteo jamaicensis*). In winter, Vesper Sparrows are found as solitary individuals and in small intra- and interspecific flocks (Pulliam and Mills 1977).

Study area.—We conducted our research at the Reserva Ecológica El Uno, in the municipality of Janos in the Mexican state of Chihuahua (Fig. 1). This property, owned and operated by The Nature Conservancy, spans 18,400 ha of Chihuahuan desert grasslands and shrublands within a 526,482-ha federally protected biosphere reserve. Grasslands in the area are dominated by Blue Grama (*Bouteloua gracilis*), three-awn grasses (*Aristida* spp.), and Tobosagrass (*Pleuraphis mutica*), with scattered woody plants such as Honey Mesquite (*Prosopis glandulosa*) and Mormon Tea (*Ephedra trifurca*). We trapped Vesper Sparrows
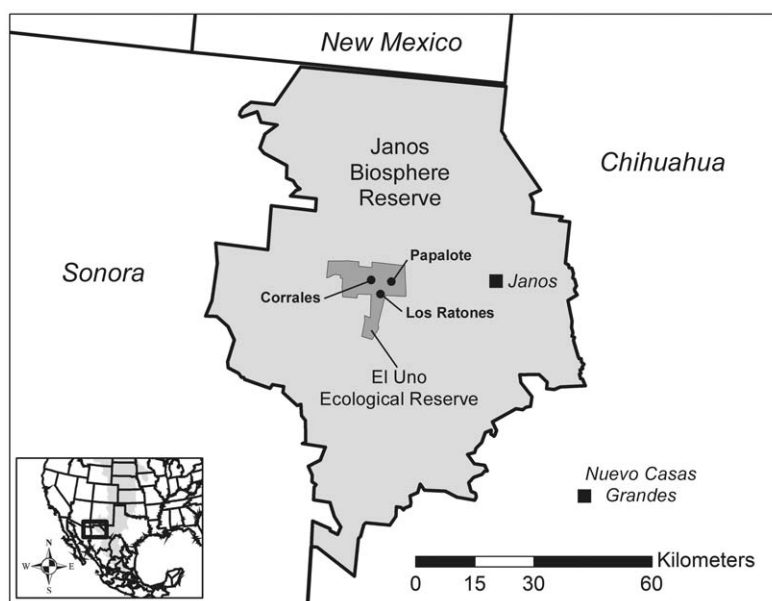

Fig. 1. Location of study sites within El Uno Ecological and Janos Biosphere Reserves in Chihuahua, Mexico.

at three study sites on El Uno that were ~2 km apart (Fig. 1). We chose these sites because they supported relatively high densities of Vesper Sparrows, particularly in 2010, when the species was scarce or absent from other available sites. Study sites varied, having little or no grazing to moderate grazing by American Bison (*Bison bison*). Climate is temperate semiarid, with 317 mm mean annual precipitation and 16.9°C mean annual temperature. Summer monsoons (July–September) and winter rainfall (December–February), frequently as snowfall, comprise 56.5% and 17.6% of the annual precipitation, respectively. Winter mean daily minimum temperature (December–February) is −0.1°C.

Bird capture and radiotelemetry.—We captured, banded with federal bands, and attached radiotransmitters to Vesper Sparrows at five study sites from 6 January to 29 January in 2009 (9 capture dates) and from 7 January to 16 January in 2010 (7 capture dates). Our study period encompassed the second half of an apparent 7-month (September–March) nonbreeding period of Vesper Sparrows in Chihuahua (A. B. Montoya unpubl. data). We set up a line of 4–10 mist nets with shrubs just in front of and behind the nets. Using ≤25 people, we slowly walked and drove birds from ≤500 m away toward the nets. We used Advanced Telemetry Systems (ATS; Isanti, Minnesota) transmitters on all monitored birds. Using a 0.08-g harness, we attached model A1035 (0.70 g) transmitters to Vesper Sparrows that weighed >21 g, and models A1015 (0.55 g) and A1025 (0.65 g) transmitters to Vesper Sparrows that weighed ≤21 g. Thus, the total mass of the transmitters and harness was ≤4% of each bird's body mass ($\bar{x}$ = 2.36 ± 0.76% [SD]). We placed transmitters over the rump with a leg-loop harness made of beading elastic (Rappole and Tipton 1991). The expected battery life of ATS transmitters was 45, 67, and 90 days for models A1015, A1025, and A1035, respectively, although actual battery life was substantially lower. We used four ATS radioreceivers (model R2000) with headphones (David Clark model H10-00-4) and antennae (three-element folding Yagi).

Twice a day, from early January to the end of February, two teams of two observers searched for the signal of radiotagged birds where birds were initially captured. Teams triangulated each bird's location by first scanning for the general location of the bird and then spreading out to track the origin of the signal from different directions. Once each team determined the direction to the transmittered bird, they walked toward the bird's signal until they met. If a tagged bird appeared to be flocking, both observers switched between all possible transmitter frequencies during triangulation to locate other radiotagged birds in the flock. Frequencies that exhibited the same signal strength and direction for both observers were determined to be at the same location. After estimating the bird's location, one observer conducted vegetation surveys while the other verified that the target bird(s) was (were) alive and well. Observers obtained coordinates of each location with a global positioning system (Garmin eTrex Legend). In general, we found almost all our radiotagged birds <1 km from their capture location. We then searched for any missing birds at increasing distances from the study sites (>1 km) and as we moved between study sites throughout the day. In addition, we scanned for every missing signal from the tops of the high hills once a day. This procedure allowed us to pick up signals from within 1 km, including a missing transmitter carried 1 km away by an avian predator. Prior to the end of the study in late February, we

searched for missing signals in areas far (≤10 km) from the study sites by car. After ~10 days of scanning for a missing signal daily, we searched for the signal once every 3 days within the circuit of our regular surveys for the duration of the project. When transmitters were recovered in the field, we examined the transmitter and immediate area for signs of predation such as blood on the transmitter and harness, Vesper Sparrow remains, predator feces, or transmitter damage.

Vegetation surveys.—We estimated vegetation structure at each Vesper Sparrow telemetry location to test for possible relationships between vegetation and survival. Trained field observers made visual estimates of shrub and grass heights and percent cover of shrubs, grasses, forbs, tumbleweed (*Salsola* spp.), and other groundcover (litter, rocks, animal excrement, woody vegetation <0.3 m in height, etc.) within a 5-m radius of each location. In 2009, forbs and tumbleweed were not estimated. We trained observers prior to field work by asking them to visually estimate these parameters in a given location and then compared their estimates with quantitative estimates obtained previously using line intersect techniques and total cover measurements of shrubs in the same location. This training produced visual estimates of grass and shrub cover that were highly correlated to quantitative estimates (r = 0.70 and r = 0.71, respectively) in a previous study in Colorado (A. O. Panjabi et al. unpubl. data), which suggests that trained observers can efficiently provide reasonably accurate estimates. In addition, field technicians frequently placed 30-cm rulers vertically on the ground when estimating grass height. Observers conducted vegetation surveys immediately after marking each Vesper Sparrow telemetry location, except for a few telemetry locations estimated at night that were surveyed the next day.

Statistical analysis.—We used parametric regression models of survival data (Hosmer and Lemeshow 1999) to determine the relationship between habitat structure and winter survival of radiotagged Vesper Sparrows and to provide an overall estimate of winter survival probability. To that end, we used a set of linear models that included shrub height, shrub cover, grass cover, grass height, year (with levels 2009 and 2010), and body mass as predictors. We also included Julian date of transmitter deployment (Julian date = 1 for 1 January, 2 for 2 January, etc.) to account for differences in survival and censoring times among sets of radiotagged birds released at different dates. Because parametric survival modeling requires the specification of a hazard function, we evaluated the fit of six distributions for survival time (exponential, Gaussian, logistic, log-normal, log-logistic, and Weibull) using Akaike's information criterion (AIC; Burnham and Anderson 2002) corrected for small sample size (AIC$_c$). The exponential, log-normal, log-logistic, and Weibull distributions were all equally efficient in explaining our survival data set (ΔAIC$_c$ < 2 for all 4 distributions) in the full model (all explanatory variables included). We chose one of these four hazard functions to evaluate a set of linear predictors within one hazard function by the means of ΔAIC$_c$ and to subsequently provide model-averaged regression parameter estimates that would allow us to provide quantitative statements on the strength of relationship between explanatory variables and survival time. We favored this approach over estimating model-averaged predictions across the top models with different hazard functions because the latter cannot provide regression parameter estimates. We chose to use the exponential

distribution in our parametric survival analysis because the exponential distribution has a time-independent hazard function (Hosmer and Lemeshow 1999). This property is referred to as the "memoryless" property of the exponential distribution (Papoulis and Pillai 2002), resulting in the simplifying assumption that all Vesper Sparrows have the same probability of demise regardless of their survival time. In addition, this memoryless property allows us to provide an estimate of a time-independent daily survival probability (DSP). In this regard, we assumed that survival time t (i.e., time that a bird remained alive) had an exponential distribution, with parameter and hazard function equal to λ and probability density function $f(t) = \lambda e^{-\lambda t}$. Parametric regression models the effect of explanatory variables on survival by setting the logarithm of the inverse of the parameter λ equal to a linear combination of the explanatory variables ($x_1, x_2, \ldots, x_p$) as follows:

$$\log\frac{1}{\lambda} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_p x_p$$

The survival function (S), which gives the probability of survival at time t given the habitat explanatory variables, derived from the equation above (using the definition of hazard function; Hosmer and Lemeshow 1999), is given by

$$S(t|x_1, x_2, \ldots, x_p) = e^{-te^{-(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_p x_p)}}$$

Therefore, DSP, the proportion of birds surviving daily given the explanatory variables, is given by

$$DSP(x_1, x_2, \ldots, x_p) = e^{-te^{-(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_p x_p)}}$$

The exponential hazard rate function results in a multiplicative effect of explanatory variables on survival time. In this regard, the multiplicative effect of m units of increase in any given covariate x_i ($i = 1, 2, \ldots, p$) on Vesper Sparrow survival time is given by $e^{m\beta i}$, and we state the effects of habitat structure variables on survival in these terms. We used the package 'survival' (Therneau and Lumley 2009) in R, version 10.2.01, for Mac (R Development Core Team 2011) to obtain maximum-likelihood estimates for each β_i ($i = 0, 1, \ldots, p$) and its sampling variance $\sigma^2(\hat{\beta}_i)$

We used ΔAIC_c to evaluate the relative goodness-of-fit among survival models with different sets of explanatory variables. We built 19 models by including or excluding variables associated with grass vegetation (grass cover + grass height) and shrub vegetation (shrub cover + shrub height together), individual body mass, Julian date of radiotransmitter deployment, and year. We also included the intercept-only model in our set of models to evaluate the predictive value of all models (Anderson 2007). We recognized models with $\Delta AIC_c < 7$ as plausible (best models), and none could be dismissed on the basis of available evidence (Anderson 2007). In addition, we conducted a Grønnesby-Borgan test (Grønnesby and Borgan 1996, May and Hosmer 1998) for all best models to check their actual fit to our survival data set. We used 8 G-tile groups (*sensu* May and Hosmer 1998) for all Grønnesby-Borgan tests. We calculated the model-averaged estimates of regression coefficients, their unconditional variances, and their 95% unconditional confidence intervals (UCI; Burnham and Anderson 2002) across the best models to finally state the effect of the variables on Vesper Sparrow winter survival.

As mentioned above, we estimated additional habitat structure variables in 2010, including forb cover, *Salsola* cover, and other cover. We did not perform a separate model-selection procedure with ΔAIC_c including these variables. Instead, we estimated the effects of these variables on Vesper Sparrow winter survival by adding each of them to a full model that included all the explanatory variables mentioned in the paragraph above. We stated their effects in terms of their regression coefficient and 95% confidence intervals.

RESULTS

We radiotagged 33 and 69 Vesper Sparrows in 2009 and 2010, respectively, from which we confirmed 5 and 26 predator-related mortalities in 2009 and 2010, respectively. We found signs of avian and mammalian predation in recovered radiotransmitters, but we did not directly observe predation events on radiotagged birds. Avian predators removed feathers from radiotagged birds before consumption, such that transmitters from depredated birds were located among nonmasticated feathers. Specifically, Loggerhead Shrikes often impaled body parts or left the transmitters hanging on barbed-wire fences or spines of vegetation. We also found a transmitter in an owl pellet, presumably from a Short-eared Owl (*Asio flammeus*). Signs of mammalian predation included mastication marks on the transmitter and cached radiotransmitters underground (fox [*Vulpes* spp.] and Bobcat [*Lynx rufus*]). The rest of the birds were right-censored because we either lost track of their signals before the termination of the study or they survived to the end of the study period at the end of February (Fig. 2).

Vesper Sparrows varied considerably in their individual patterns of habitat use (multivariate analysis of variance for differences in mean grass cover, grass height, shrub cover, and shrub height between individuals, Wilks' $\lambda = 0.4487$, $F = 6.65$, df = 392 and 11,748, $P < 0.001$), and individual variation in habitat use accounted for significant variation in winter survival of marked individuals. Five of our seven best models ($\Delta AIC_c < 7$) included
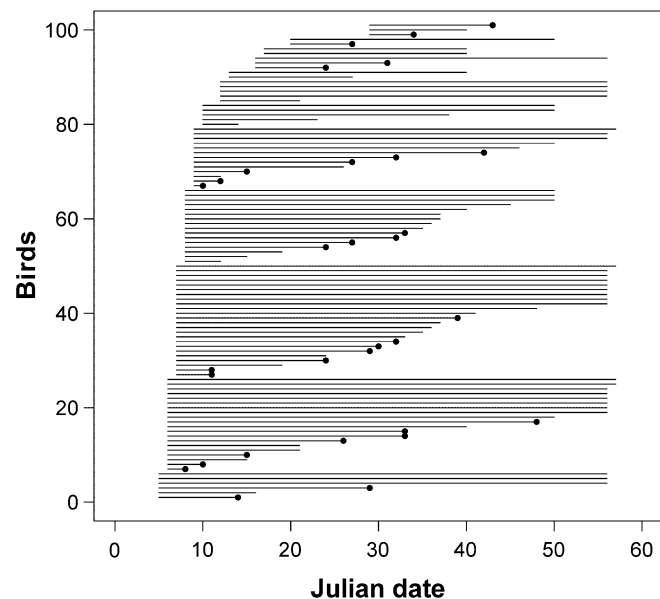

FIG. 2. Tracking history of radiotagged Vesper Sparrows in desert grasslands of Chihuahua, Mexico, 2009–2010. Each line represents an individual Vesper Sparrow, from the date of radiotransmitter deployment to the date of demise (black dot) or the date of censoring (last sighting).

Table 1. Ranking of parametric survival models (exponential hazard function) for wintering Vesper Sparrows in the Chihuahuan Desert grasslands of Mexico. K denotes the number of parameters in the model, and w_i denotes the Akaike weight. Explanatory variables include average grass height (GH), average grass cover (GC), average shrub height (SH), average shrub cover (SC), categorical variable for year, bird body mass (mass), and Julian date of radiotransmitter deployment (date).

Model	K	logL	AIC_c	ΔAIC_c	w_i
GC + GH + SC + SH + date	6	–152.3	317.54	0.00	0.4238
GC + GH + SC + SH + year + date + mass	7	–151.6	318.47	0.93	0.2663
GC + GH + date	4	–155.8	320.04	2.50	0.1217
SC + SH + date	4	–156.4	321.24	3.70	0.0668
date	2	–159.9	323.93	6.39	0.0174
GC + GH + year + date + mass	6	–155.6	324.14	6.60	0.0156
Year + date + mass	4	–157.9	324.24	6.70	0.0149
GC + GH + SC + SH	5	–157.0	324.67	7.12	0.0120
SC + SH + year + date + mass	6	–156.0	324.94	7.40	0.0105
Intercept only	1	–161.5	325.04	7.50	0.0100
GC + GH	3	–159.6	325.46	7.92	0.0081
Year	2	–160.9	325.93	8.39	0.0064
SC + SH	3	–160.0	326.26	8.72	0.0054
GC + GH + SC + SH + year	6	–156.8	326.54	9.00	0.0047
GC + GH + SC + SH + mass	6	–157.0	326.94	9.40	0.0039
Mass	2	–161.5	327.13	9.59	0.0035
GC + GH + year	4	–159.6	327.64	10.10	0.0027
GC + GH + mass	4	–159.6	327.64	10.10	0.0027
SC + SH + year	4	–160.0	328.44	10.90	0.0018
SC + SH + mass	4	–160.0	328.44	10.90	0.0018

habitat structure variables and were all better at explaining our survival data than the intercept-only model (Table 1). In addition, the five top models (as well as the other two best models) fit our survival data set, as shown by the Grønnesby-Borgan test (likelihood ratios from 2.02 to 11.71, df = 7, $P > 0.10$ for all models). However, only grass height, shrub height, and date of radiotransmitter deployment had 95% UCIs that did not include zero (Table 2). We estimated that survival time increased by a factor of 4.09 (95% UCI: 1.19–14.04) for every 10-cm increase in grass height and increased by a factor of 1.48 (95% UCI: 1.01–2.19) for every 10-cm increase in shrub height. In terms of DSP, the largest evident effects occurred when shrub height was <0.75 m and when grass height was <20 cm (Fig. 3). Grass cover, however, had a marginal negative effect on Vesper Sparrow survival, given that the 95% UCI upper limit barely included zero (Table 2). Forb vegetation cover was positively associated with survival of Vesper Sparrows. For the 2010 data set only, survival time increased by a factor of 4.07 (95% CI: 1.33–12.49) for each 10% increase in forb cover, whereas *Salsola* cover and other cover were not associated with Vesper Sparrow winter survival, given that the 95% CI of their multiplicative effects on survival time included 1.0 (95% CI: 0.74–1.88 and 0.85–1.25, respectively). The categorical variable

Table 2. Model averages of regression coefficients and their unconditional SE computed across the best exponential hazard survival models ($\Delta AIC_c < 7$ in Table 1) that model the relationship between Vesper Sparrow survival and explanatory variables in the Chihuahuan Desert grasslands of Janos, Mexico. The reference level for the categorical variable "year" is 2009. Variables marked with an asterisk denote parameters whose unconditional confidence intervals (UCI) do not include zero.

Parameter	Model-averaged $\hat{\beta}$	Unconditional SE($\hat{\beta}$)	Lower limit of 95% UCI	Upper limit of 95% UCI
Intercept	4.0036	1.5279	1.0089	6.9984
Grass cover (%)	–0.0569	0.0313	–0.1182	0.0044
Grass height (cm)*	0.1408	0.0630	0.0174	0.2642
Shrub cover (%)	–0.1131	0.0754	–0.2609	0.0347
Shrub height (m)*	3.9400	1.9992	0.0217	7.8584
Julian date deployed*	–0.1466	0.0457	–0.2362	–0.0570
Mass (g)	0.0276	0.0392	–0.0492	0.1044
Year (2010)	–1.0932	0.6263	–2.3207	0.1343

"year" was not an informative variable for Vesper Sparrow survival (Table 2) despite the evidently better habitat conditions observed in 2009; mean grass height and grass cover were 9.7 cm (95% CI: 8.3–11.1 cm) and 8.6% (95% CI: 5.5–11.7%) higher in 2009 than in 2010. These differences in standing grass crop were likely caused by higher precipitation prior to the winter of 2009 (274 mm, December 2007–September 2008) than prior to the winter of 2010 (167 mm, December 2008–September 2009).

Our analyses identified Julian date of radiotransmitter deployment as a relevant predictor of survival time (95% UCI of its regression parameter did not include zero; Table 2). Survival time decreased for birds entering our study later in the study period by a factor of 0.30 week^{-1} (95% UCI: 0.28–0.35 week^{-1}). That is, birds that entered into our survival study later in the study period either died or became censored after shorter periods of time (Fig. 2). This result was not apparently related to a decreasing trend in survival probability as winter progressed (Fig. 4).

We estimated a DSP (at average levels of explanatory variables) equal to 99.1% (95% UCI: 97.4–99.7%) to provide a rough estimate of DSP during the study period. Extrapolation of this estimate of DSP throughout the study period (January–February, ~60 days) yielded a survival estimate of 56.6% (95% UCI: 20.5–81.5%).

Discussion

The present study presents novel research that helps to fill gaps in our knowledge of the winter ecology of a migratory grassland bird species. Our estimates of Vesper Sparrow survival are needed to help identify factors that may be limiting and contributing to this species' population decline. No previous survival estimate exists for Vesper Sparrows (Jones and Cornely 2002) or for any grassland bird species wintering in the Chihuahuan Desert. Survival estimates for other grassland emberizid species include 60% annual survival for the resident Florida subspecies of the Grasshopper Sparrow (*Ammodramus savannarum floridanus*; Delany et al. 1993) and 37–73% annual survival for the Savannah Sparrow (*Passerculus sandwichensis*; Wheelwright et al. 1992). Our estimate of winter daily survival rate for the Vesper Sparrow (99.1%) is comparable to estimates of winter daily survival rate for Henslow's
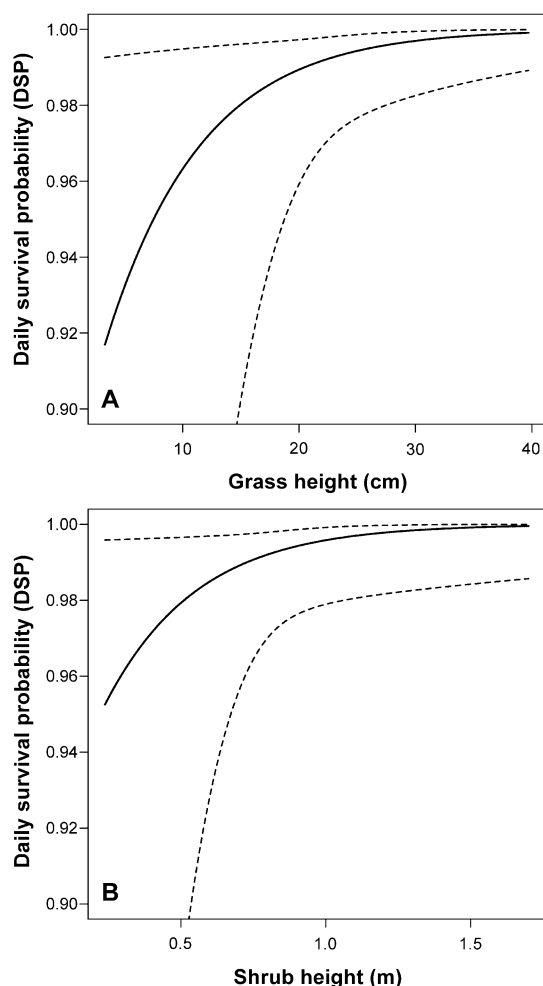
FIG. 3. Relationship of Vesper Sparrow winter daily survival probability to (A) grass height and (B) shrub height, obtained by averaging predictions across the best parametric survival models ($\Delta AIC_c < 7$; Table 2). Dashed lines denote 95% unconditional confidence intervals for model-averaged predicted values.

Sparrow (*A. henslowii*) (92.3–99.9%; Thatcher et al. 2006). Overall survival estimated from the extrapolation of our daily survival rate to the study period is 56.6% (95% CI: 20.5–81.5%), which is seemingly low for only one-third of a potential 7-month nonbreeding potential in Chihuahua. This estimate must be viewed with caution because we estimated overall DSP under average levels of explanatory variables and there is large sampling variation associated with the extrapolation. Nevertheless, this estimate represents our best knowledge of winter survival of Vesper Sparrows in northern Mexico. Because reduced winter survival rates may be a major contributor to population declines inferred from the North American Breeding Bird Survey (Saracco et al. 2010), low winter survival of Vesper Sparrows suggests that winter mortality may be an important factor in the species' ongoing population declines (−0.9% annually; Sauer et al. 2011). Therefore, efforts to reverse the persistent population declines of Vesper Sparrows should attempt to increase survival during the nonbreeding season (Sæther et al. 1996) in Mexico.
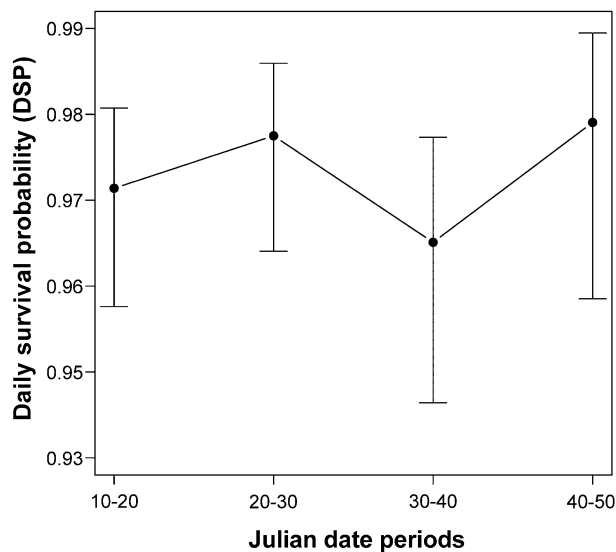

FIG. 4. Variation in daily survival probability of wintering Vesper Sparrows in the Chihuahuan Desert grasslands of Mexico, January–February, 2009–2010. Estimates of DSP were computed using intercept-only regression model with an exponential hazard function on our data set divided over 10-day periods of Julian dates.

Our parametric survival analysis relied on critical assumptions, and therefore our results must be viewed with caution. Values of habitat variables assigned to each radiotagged bird in this analysis were the averages of vegetation measurements across all telemetry locations where the bird was sighted. Therefore, this analysis assumes that an individual's average use of habitat structure variables reflects the overall habitat characteristics used by each individual. Hence, estimates of individual averages of habitat structure variables may be more accurate for birds that survived for longer periods (i.e., larger sample sizes to calculate averages). We favored this approach over the use of an analysis that included time-dependent explanatory variables because of the uncertainty in the exact locations where mortality events occurred (and, hence, the location's habitat characteristics) because predators may move Vesper Sparrow carcasses and radiotransmitters. In addition, we included censored individuals in our survival data set, which may introduce bias to survival estimates (Williams et al. 2002). Censoring occurred when we could not determine survival times, either because a radio signal disappeared for an unknown reason before the termination of monitoring or because an individual was still alive at the termination of our monitoring. In this regard, all censored birds were right-censored at the time of last sighting, regardless of their detection history since the time of radiotransmitter deployment. Thirty-four percent and 35% of our radiotagged Vesper Sparrows were censored prior to the end and at the end of the study period, respectively. Nevertheless, censored individuals provide useful information on minimum survival time (Murray 2006), and their exclusion may also highly bias survival estimates (Fox 2001). The parametric regression used here assumes that censoring is independent of survival time (noninformative censoring; Kleinbaum and Klein 2005), but this

assumption may also be challenged (Murray 2006). However, the presence of informative censoring is not easily testable (Williams et al. 2002). In this regard, if all birds that were censored before the end of the study period were classified as dead birds at the time of censoring, the estimated DSP would be reduced from 99.1% to 97.9% (95% UCI: 95.6–99.0%) and the survival rate for the study period would be reduced from 56.6% to 28.6% (95% UCI: 6.9–55.6%). These results show that estimates of winter survival rates largely depend on the assumptions regarding the final fate of censored birds, and also that winter survival could be alarmingly low. We also trapped birds in areas with high relative abundance, and our inferences of survival probability may be biased if survival holds a functional relationship with winter population density, which is a possibility (Marra 2000). Finally, we cannot account for any possible effect of radiotransmitters on bird survival.

Our analyses provide a direct link between Vesper Sparrow winter survival and habitat characteristics, demonstrating that patterns of habitat use during winter have fitness consequences that explain the associations between abundance and presence with vegetation attributes previously documented for the species in the Chihuahuan Desert grasslands of Mexico (Macías-Duarte et al. 2009, Panjabi et al. 2010a, Martínez-Guerrero et al. 2011). Vesper Sparrow winter survival was positively associated with grass and shrub height (Fig. 3), as well as with forb cover (2010 data set only). In addition, the negative association between grass cover and survival was marginally informative, given that the 95% UCI of its regression parameter barely included zero. Hence, we conclude that Vesper Sparrows survive longer in desert grassland locations with tall and relatively sparse grasses, tall shrubs, and abundant forbs, possibly as a result of both predation avoidance strategies and food availability. Predation is a major contributor to the organization of avian communities in North American desert grasslands and influences the response of grassland birds to vegetation structure (Lima and Valone 1991). Vesper Sparrows wintering in the desert grasslands of southeastern Arizona usually forage <4 m from shrubs and fly to shrubs for cover at the appearance of a predator, and only seek shelter from predators in herbaceous vegetation when shrubs are far (Pulliam and Mills 1977). Our result that Vesper Sparrows survive longer when foraging in areas with taller shrubs may indicate that taller shrubs offer better protective cover for escaping predatory attacks, while also offering better vantage points for detecting predators before they attack. This habitat use and predation avoidance strategy predicts that food for Vesper Sparrows will become more depleted near shrubs and birds may be forced to forage far from shrub cover. Thus, the positive association between survival and grass height and forb cover may be explained by the increased concealment from predators that taller grasses and more forbs provide to Vesper Sparrows when they are forced to forage far from shrub cover. In addition, greater forb cover may also be correlated to the amount of other seeds available, given that Chihuahuan Desert forb seeds may comprise ~20% of the winter diet of Vesper Sparrows (Desmond et al. 2008).

From a management perspective, the strong inferred relationship between Vesper Sparrow winter survival and habitat characteristics suggests that habitat conditions on the wintering grounds may influence population trends measured on the breeding grounds. The association between Vesper Sparrow survival and grass height is of particular interest because annual variation in grass height is related to grass use by cattle across the Chihuahuan Desert. Our results (Fig. 3) suggest that Vesper Sparrows that use moderately grazed locations with average grass height of 40 cm have a high probability (~90%) of surviving through the winter ($S[t = 150$ days]). The greatest predicted average increase in winter survival probability occurs between 20 and 30 cm grass height, increasing from 15% to 61%. These results suggest that an average minimum grass height threshold of ~30 cm is required to promote Vesper Sparrow winter survival. However, average winter grass height in Chihuahuan Desert grasslands in Mexico is ~25 cm (Panjabi et al. 2010b), evidence of the need for better range-management practices to increase Vesper Sparrow winter survival.

Our results also suggest negative consequences of climate change in the Chihuahuan Desert on Vesper Sparrow population viability. Grass productivity in the Chihuahuan Desert is under strong control by precipitation (McClaran 1996, Khumalo and Holechek 2005), as is grass height. In this regard, the higher grass cover and height observed in late winter 2009 were likely related to higher precipitation from December 2007 to September 2008 (the period most strongly related to perennial grass production; Khumalo and Holechek 2005) than in the same period prior to late winter 2010. Therefore, summer precipitation may ultimately drive Vesper Sparrow winter survival in the Chihuahuan Desert by its effects on grass vegetation. However, our proxy for modeling the effect of precipitation on winter habitat quality, categorical variable "year," was not an important predictor of survival (Table 2). The effect of year on survival was confounded by the difference in grass height between 2009 and 2010 (9.7 cm taller in 2009) and prevented the identification of year as an important predictor variable. Given that grass vegetation is severely reduced under heavy grazing during drought periods in the Chihuahuan Desert (Holechek et al. 2003), the increased aridity projected for the region in the coming decades (Seager et al. 2007) and persistence of overgrazing in northern Mexico will likely reduce the extent and height of the winter standing grass crop in the Chihuahuan Desert. If so, the strong relationship between grass height and Vesper Sparrow survival suggests that these climate-related changes would exacerbate the species' ongoing population declines.

In summary, conservation of grassland birds in western North America must focus on strategies that promote high annual survival (Faaborg et al. 2010) and, especially, winter survival (Sæther et al. 1996). Our results demonstrate that winter survival of grassland birds may be enhanced through habitat management on the wintering grounds. However, the ongoing destruction of winter habitat by an unprecedented rate of land-use change (Macías-Duarte et al. 2009) in Chihuahua (where the most extensive desert grasslands in Mexico remain) threaten to overshadow any conservation benefits gained from our improved knowledge of grassland-bird winter ecology in northern Mexico. If sustained, the current rate of land-use change may lead to the virtual disappearance of the desert grassland ecosystem in Chihuahua and the primary winter habitat for Vesper Sparrows and other grassland bird species of conservation concern (Macías-Duarte et al. 2011).

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