

Fall vegetative cover and summer precipitation predict abundance of wintering grassland birds across the Chihuahuan desert

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ABSTRACT

Local winter abundance of grassland passerines is highly variable throughout the Chihuahuan Desert among years. The objective of this study is to determine if plant biomass in grasslands and precipitation are predictors of bird abundance in space and time through Chihuahuan Desert. We conducted avian surveys in 17 Grassland Priority Conservation Areas (GPCA) in northern Mexico and southwestern United States in the winters of 2007–2011. We used distance sampling on line transects to estimate annual winter bird density in all GPCAs. We used a hierarchical model of distance sampling to estimate the effect of summer precipitation and vegetative cover during the fall on bird density for 10 grassland species. We used the MODIS NDVI at a pixel resolution of 231.5 m as a measure of plant biomass. Grasshopper Sparrow, Baird's Sparrow, Savannah Sparrow, Vesper Sparrow, and Eastern Meadowlark showed a strict positive response to NDVI, while Horned Lark, Sprague's Pipit, Chestnut-collared Longspur and Lark Bunting did not show a strictly-positive response to NDVI. Our results provide a valuable tool for the conservation of declining migratory birds on their wintering grounds by identifying a wildlife-habitat relationship using a remotely-sensed and readily available index of vegetative growth.

1. Introduction

Deserts are by definition ecosystems where biological processes, including wildlife population dynamics, are ultimately limited by water. Relatively few Nearctic migratory birds overwinter in arid lands, preferring instead less water-limited tropical and subtropical environments. The overwintering of migratory grassland birds in arid lands warrants attention given that populations of North American grassland birds continue to decline at alarming rates (Sauer et al., 2017) and the drivers of these declines remain poorly understood for most species. The ongoing loss of grasslands throughout Canada and the United States since the 19th century (White et al., 2000) suggests that loss and deterioration of breeding habitat is a common factor. However, grassland birds that overwinter in the Chihuahuan Desert grasslands of Mexico and the southwestern USA have declined by twice as much as those wintering elsewhere (North American Bird Conservation Initiative, 2016). As in other guilds of migratory birds, increasing evidence suggests factors in the non-breeding (wintering) season can strongly influence population trends (Calvert et al., 2009). Grassland

birds that largely depend on Chihuahuan Desert grasslands are threatened by conversion of wintering habitat to farmland (Macías-Duarte et al., 2009; Pool et al., 2014), overgrazing (Curtin et al., 2002), invasive grasses (Sánchez-Muñoz, 2009) and woody plant encroachment (Van Auken, 2000). The extent to which grassland birds will be able to adapt to the loss and deterioration of wintering habitat depends on the suitability of the remaining habitat and the capability of these birds to track resources at a broad scale, especially in light of profound changes in temperature and precipitation projected in arid lands as a consequence of climate change (Seager et al., 2007).

Local winter abundance of grassland passerines is highly variable throughout the Chihuahuan Desert among years (Macías-Duarte et al., 2011). For instance, winter density of passerine birds can reach a 50-fold difference between two years (0.63 vs. 31.82 birds·ha⁻¹) in desert grasslands of central Chihuahua in a 9-year period (Macías-Duarte et al., 2009), and in some years a species may be completely absent from a region where it normally occurs (Macías-Duarte et al., 2011). This extreme temporal variation in local abundance of wintering grassland passerines in the Chihuahuan Desert may reflect the ability of

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populations to ‘shift’ their distributions to alternate locations with better conditions. More precisely, we hypothesize that spatio-temporal variation of abundance of wintering grassland birds in the Chihuahuan Desert follows the ideal free distribution model (Fretwell, 1972), i.e., grassland birds are able to track the spatial distribution of resources (ideal) and can move without constraints (free) throughout their winter range so that individual birds can maximize their intake rate of resources. This phenomenon has been documented in Palearctic migratory birds on their wintering grounds of the Sahel, a similarly arid environment, and has been called “itinerancy” (Kristensen et al., 2013) or nomadism (Andersson, 1980).

Quantifying the spatio-temporal covariation of bird abundance and environmental factors throughout the Chihuahuan Desert may reveal factors limiting winter survival. Because most grassland passerines are granivorous in winter, feeding on grass and forb seeds, it is likely that the annual production and availability of these foods affects winter distribution and survival. In addition, grass and forb biomass are important components of habitat quality, providing protection from low temperatures at night (Macías-Duarte et al. in review) and from predation (Macías-Duarte and Panjabi, 2013). Therefore, tracking changes in vegetation biomass in this desert environment may lead to being able to predict abundance, distribution and even survival of grassland birds in winter.

In this context, the objective of this study is to determine if plant biomass in grasslands is a predictor of wintering bird abundance in space and time in Chihuahuan Desert grasslands. Grass biomass production in the Chihuahuan Desert is driven by seasonal precipitation (Khumalo and Holechek, 2005) and herbaceous plant growth is particularly synchronized with monsoonal summer rainfall (Moreno-de-las-Heras et al., 2015). A positive relationship between abundance of grassland birds during the winter and precipitation in the preceding summer has been documented in the Chihuahuan Desert at the local scale (Dunning and Brown, 1982; Gordon, 2000; Macías-Duarte et al., 2009), suggesting a direct link between plant biomass and bird abundance at the local scale. If this relationship between plant biomass in grasslands and bird abundance is also true at the regional scale, the information generated by this study could help inform conservation strategies for grassland birds, especially in light of projected increases in aridity in the Chihuahuan Desert due to climate change (Seager et al., 2007).

2. Methods

2.1. Study area

We conducted avian surveys in up to 17 Grassland Priority Conservation Areas (GPCA; CEC and TNC, 2005; Pool and Panjabi et al., 2010) in northern Mexico, southern Arizona, southern New Mexico and western Texas in winter from January 2007 to March 2011 (Levandoski et al., 2009; Macías-Duarte et al., 2011; Panjabi et al., 2010). GPCAs included in this study are Armendaris, Cuatro Ciénegas, Cuchillas de la Zarca, Janos, Lagunas del Este, Llano Las Amapolas, Malpaís, Mapimí, Marfa, New Mexico Bootheel, Otero Mesa, Sonoita, Sulphur Springs, El Tokio, Valles Centrales and Valle Colombia (Fig. 1).

2.2. Focal species

We focused this paper on winter abundance and distribution of the passerine component of the grassland bird guild, as defined by Sauer et al. (2011), whose winter distribution lies mostly in the Chihuahuan Desert and from which we had sufficient survey data to estimate model parameters (see 2.7. Hierarchical model). Our focal species included Horned Lark, Sprague's Pipit, Cassin's Sparrow, Vesper Sparrow, Lark Bunting, Savannah Sparrow, Grasshopper Sparrow, Baird's Sparrow, Chestnut-collared Longspur, and Eastern and Western meadowlark. We also included Brewer's Sparrow as a grassland facultative species, as it is

one of the most abundant bird species in Chihuahuan Desert grasslands (Desmond et al., 2005; Macías-Duarte et al., 2009; Manzano-Fischer et al., 2006). All these grassland species have undergone population declines on their breeding grounds in Canada and the USA (Sauer et al., 2011).

2.3. Sampling design

We overlaid a grid of roughly $18 \times 18 \text{ km}^2$ cell blocks across the Chihuahuan Desert and Sierra Madre Occidental Bird Conservation Regions to create a sampling frame for desert grasslands within GPCAs (Fig. 1). Eligible cells for sampling were those that intersected with GPCAs and had at least 5 km of road access to grasslands as identified using an intersect function and available GIS data (INEGI, 2003). Due to poor correspondence between some GPCA boundaries and actual locations of grassland in the vicinity of these GPCAs, we added additional cell blocks to the sampling pool that met the aforementioned criteria, but were outside the original GPCA boundaries. This sampling design is described in detail by Panjabi et al. (2007), with modifications by Levandoski et al. (2009). We added additional GPCAs to the sampling frame each year. In each sampling block we established randomly numbered points at 500 m intervals along roads intersecting grasslands. We chose the 3 lowest-numbered points that met habitat requirements for native grasslands with < 25% shrub cover, and established a pair of 1-km line transects at each of those 3 points. We used ArcGIS® 9.3 to implement the sampling design above.

2.4. Bird and vegetation surveys

We used distance sampling (Buckland et al., 2001) on line transects to estimate annual winter bird density in all GPCAs. We initiated surveys in early January and completed surveys by early March each winter. Each pair of 1-km line transects started from the road edge and headed in opposite directions perpendicular to the road. In a few instances (327 out of 3271 transects) where available grasslands were limited within the survey block, we split paired transects to start from different random points. Each pair of technicians surveyed the 6 transects in each block starting at sunrise and continuing until completion (273 out of 3271 before 13:00). Sometimes, due to weather, road conditions, and variability in the time needed to complete both bird and vegetation surveys, finishing all transects within 6 h was not possible. We did not conduct surveys during winds higher than category 4 in the Beaufort scale (20–28 kph) or during any precipitation greater than a drizzle.

From each starting point, technicians used Garmin E-trex Vista GPS units to walk towards the end point of the transect 1000 m away and maintain their position on the transect line while conducting the survey. Observers used a compass to select a point on the horizon that corresponded with the direction of the transect end point, and used this point and the bearing to it to visualize the transect line in front of them. Observers recorded the number of bird groups detected during each survey as well as group size (number of individuals) and perpendicular distance to the transect line for each bird group. Observers detected bird groups by detecting single individuals (group size of 1) or simultaneously detecting ≥ 2 individuals together. After an initial detection of a bird group, observers may have detected additional members of the group. Observers thus determined group size by adding all birds within a neighborhood of 25 m of an initial detection. Observers used both laser rangefinders and ocular estimates to obtain lateral distances from the transect line to each bird group. Birds can be detected as individuals or groups, the latter defined as 2 or more individuals of the same species occurring within 25 m of the first individual detected. In this context, we recorded the cluster size for each bird detection. If observers encountered a major obstacle (such as an international border, cliff or other impassable terrain) or if the transect would otherwise bisect a large area ($> 250 \text{ m}$) of non-grassland habitat,

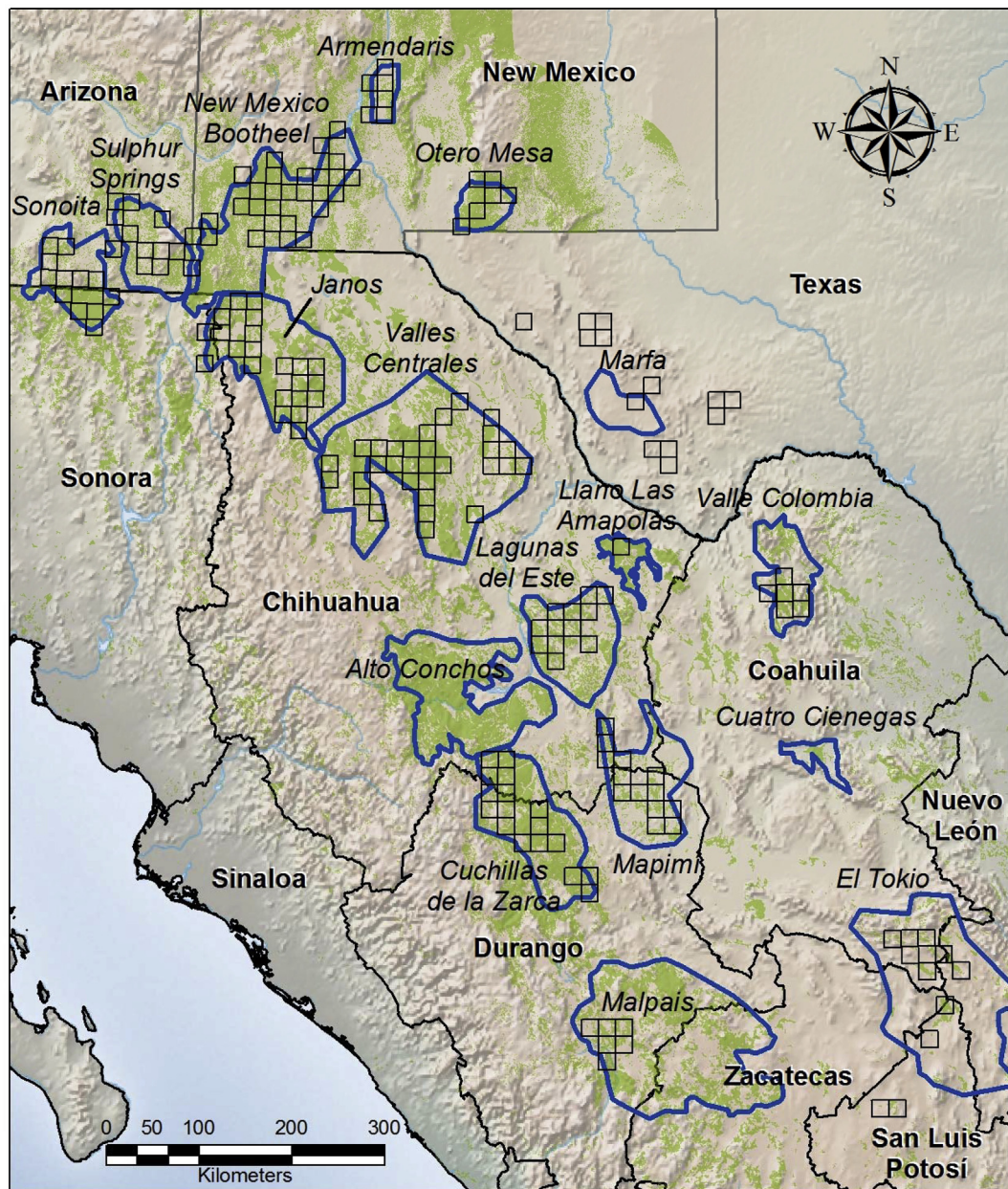


Fig. 1. Grassland Priority Conservation Areas in the Chihuahuan Desert (CEC and TNC, 2005; Pool and Panjabi et al., 2010) and wintering grassland bird sampling blocks surveyed in 2011. Green shading shows the extent of desert grasslands.

they turned the transect 90° in a randomly chosen direction to avoid the obstacle.

We estimated vegetation cover at 10 sub-sampling stations at 100 m intervals along each 1-km bird transect. We conducted these surveys immediately following each bird survey, while the observer was returning to the start point. At each sub-sampling station, we made ocular estimates of ground cover within 5-m radius circular plots. To estimate ground cover, technicians looked directly down to the ground out to 2 m in four cardinal directions, estimated the percent cover in each direction, averaged these, and then extrapolated the estimate out to 5 m, adjusting it for obvious variances. Ground cover estimates were broken down into woody vegetation, grass, and forbs. We trained observers in estimating vegetation cover on plots where all parameters had been either measured directly or estimated through quantitative sampling to minimize bias and calibrate observers' estimation skills. An analysis of grass-cover estimates from 2011 obtained through point-grid sampling of ground cover photos vs. ocular estimates on the same plots

showed a strong linear correlation between the two approaches ($r = 0.92$).

2.5. Remote sensing

We used the MODIS NDVI at a pixel resolution of 231.5 m (Pettorelli et al., 2005) as a measure of plant (particularly grass) biomass. NDVI is a measure of annual net primary productivity for herbaceous vegetation in Chihuahuan Desert grasslands (Moreno-de-las-Heras et al., 2015) and therefore, a likely measure of food and cover resources for grassland birds. Although other indexes, such as the EVI, may be more accurate predictor in other environments, it is noted that “for semiarid shrub and grassland biomes both indices were well correlated”, with NDVI showing a greater increase in values marking the peak growing season compared to EVI in the Chihuahuan Desert (Huete et al., 2002). NDVI is widely available and as a resource is specifically intended to maintain continuity with earlier satellite data which can be used with historic

wildlife survey data to replicate this study (Huete et al., 1999). NDVI is also available to researchers as an off-the-shelf remote sensing product that can be obtained from a wide range of sources. As a ratio based vegetation index there are no parameters to set with NDVI as compared to other enhanced vegetation indexes such as the Soil Adjusted Vegetative Index. Use of NDVI makes our approach accessible as a tool for land managers and planners with limited resources as is the case for many agencies and NGOs working in arid lands and predominately arid countries.

We measured vegetative cover for all bird transects under a single protocol from 2009 to 2011 and therefore we had the ability to test the assertion that NDVI is a predictor of vegetation biomass (see 2.6. Statistical analysis). We averaged herbaceous (grasses and forbs) ground cover estimates over all sub-sampling stations to yield a single value representative of the whole transect. We fitted a polynomial regression model (Kutner et al., 2005) with quadratic term ($y = \beta_0 + \beta_1 x + \beta_2 x^2$) for the predictor variable to determine if ocular estimates of herbaceous cover on the ground are a predictor of NDVI. We used an extra-sum-of-squares F test and the coefficient of determination (R^2) to assess the fit of the quadratic model.

2.6. Precipitation data

We used monthly precipitation data for Mexican GPCAs from 2006 to 2010 gridded at a spatial resolution of 0.5° longitude \times 0.5° latitude (Maurer et al., 2002; Wood et al., 2002). The dataset is a global downscale of CMIP3 GCM output. Finer resolution downscaled data were not available for the southern portion of the Chihuahuan Desert. The scientific data set files were obtained from the University of South Carolina Engineering web site which hosts the data portal (http://www.engr.scu.edu/%7Eemaurer/global_data/).

2.7. Hierarchical model

We used a hierarchical model (Royle and Dorazio, 2008) of distance sampling (Buckland et al., 2001) to estimate the effect of vegetative cover on bird density for our focal grassland species, while accounting for both imperfect detection and random spatial variation in bird counts. A hierarchical model describes how data is generated (observation process) conditional on an underlying ecological process (state process). In distance sampling, bird density (D , number of individuals per unit of area) for line transects is estimated from the equation (Buckland et al., 2001):

$$D = \frac{E(n)f(0)E(s)}{2L} \quad (1)$$

where $E(n)$ is the mean number of groups detected, $E(s)$ is the mean number of individuals per detection (group size), L is the total transect length and $f(0)$ is the probability density function of perpendicular distances evaluated at zero distance. In the context of a hierarchical model, $E(n)$, $f(0)$ and $E(s)$ are components of the observation model whereas D is a component of the process model. Each of these components is usually modeled as a function of covariates of interest. Our sampling units for this study were transects and therefore the random variables D , $E(n)$ and L are indexed over all transects surveyed ($i = 1, 2, \dots, 4509$).

2.7.1. Observation model

Data generated in distance sampling consists in number of detections (n) and their respective detection distances (y) and group sizes (s). We assumed that the random variable number of detections for the i -th transect (n_i) followed a Poisson distribution with parameter $E(n_i)$. From equation (1), the Poisson parameter $E(n_i)$ relates to density, our state variable of interest, by

$$E(n_i) = \frac{2L_i D_i}{E(s)f(0)}$$

where L_i and D_i are the length of and the density at the i -th transect. We used a half-normal detection function to model the distribution of perpendicular detection distances, whose probability density function ($f(y)$) is given by

$$f(y) = \frac{1}{\sigma} \left(\frac{2}{\pi} \right)^{\frac{1}{2}} e^{-y^2/2\sigma^2}$$

where y is the perpendicular distance of detection and σ is a model parameter. To improve our estimation of parameter σ , we used right-truncated distance data (Buckland et al., 2001), with truncation determined for optimum maximum likelihood estimates using program Distance 6.0, as described in Panjabi et al. (2010).

Ocular estimates of detection distance are widely used in distance sampling of bird populations (e.g. Fuller et al., 2009; Loss et al., 2009; Walker and Shochat, 2010). However, the inherent error associated an ocular estimation of distances, including the variation in estimation abilities between observers (Nadeau and Conway, 2012), may reduce the precision of bird density estimates. We did not model the effect of observers on parameter σ (fall in detection capability as distance increases) of the detection function $f(y)$ to avoid overparameterization of the model as we had 44 observers. Our approach to reduce the error associated to ocular estimates of detection distances was to train field technicians to obtain reasonably-accurate ocular estimates of lateral distance from transects before the start of each field season.

2.7.2. State model

We modeled bird density, our state variable, as generalized linear model with a logarithmic link function to the linear predictor. The linear predictor included the explanatory variable Normalized Difference Vegetation Index (NDVI) during the fall months after summer precipitations ($ndvi$). Vegetative cover in the autumn is likely to be associated with precipitation and it may be argued that including precipitation in the linear predictor may be redundant. However, we found moderate simple linear correlation ($95\%CI(r) = 0.336\text{--}0.404$, $n = 2403$) between NDVI in the fall and summer precipitation (total precipitation from July–September). Therefore, we included a variable for summer precipitation ($precipitation$) in the linear predictor to account for the effects of rainfall on bird habitat quality beyond the effects of vegetative cover. We also included factor $YEAR$ (5 levels: 2007–2011) to account for differences in the number of birds coming from the breeding grounds due to yearly variation in recruitment and survival. Then, bird density at the i -th transect in the j -th year (D_{ij}) becomes:

$$\log(D_{ij}) = \beta_0 + \beta_1 ndvi + \beta_2 precipitation + \beta_3 ndvi \times precipitation + \beta_4 YEAR$$

where each β is a regression parameter.

2.7.3. Parameter estimation and model evaluation

We used the Bayesian estimation paradigm to compute model parameters. We used BUGS language (Spiegelhalter et al., 1996) to construct the likelihood function for each of study species and to specify a prior distribution for each parameter in the model. We specified standard normal prior distributions for all regression parameter $\beta \sim \text{Normal}(0,1)$ for standardized $ndvi$ and $precipitation$ values. We implemented the BUGS language using WinBUGS 1.4 (Lunn et al., 2000) through program R (R Development Core Team, 2015) with package R2WinBUGS (Sturtz et al., 2005). Markov Chain Monte Carlo runs consisted of 3 chains of 50,000 samples, with a burn-in of 25,000 samples and a posterior distribution based on 25,000 samples for each chain. MCMC chains for all model parameters reached stationarity (Gelman-Rubin statistics > 1.01 ; (Gelman et al., 2004), except for the

Cassin's Sparrow, which was excluded from the analysis. We conducted a model selection procedure (sensu Burnham and Anderson, 2002) on a nested model set including the reduced, intercept-only model $\log(D) = \beta_0$ up to the full model $\log(D) = \beta_1 \text{ ndvi} + \beta_2 \text{ precipitation} + \beta_3 \text{ ndvi} \times \text{precipitation} + \beta_j \text{ YEAR}$ using the deviance information criterion (DIC, Spiegelhalter et al., 2002). The best (most plausible) model is the model with the lowest DIC. Models with a DIC within a difference of 5 ($\Delta\text{DIC} < 5$) from the DIC of best model were regarded to have equal empirical support from the data (Spiegelhalter et al., 2002). In this regard, we used the full model for our inferences whenever the full model was the best model or had a $\Delta\text{DIC} < 5$. We used the 95% credible intervals (from the 2.5th and 97.5th percentile of the posterior distribution, 95%CrI) for each regression coefficient (β) to assess the predictive value of variables in the model. We produced contour plots for the bird density model using the package *graphics* of program R (R Development Core Team, 2015).

Given that all focal species showed non-zero responses to precipitation and NDVI (i.e. $\beta_1 > 0$, $\beta_2 > 0$, and $\beta_3 > 0$), we simulated a random Grasshopper Sparrow (a widespread species in the Chihuahuan Desert) distribution through all transects (i.e. a Poisson distribution though transects where Grasshopper Sparrows were present) and ran the analyses to determine if the significant effects were an artifact of a large sample size. We found no effect of either summer precipitation nor NDVI (Table 1).

3. Results

We found that NDVI values reflect plant biomass levels at bird transects in Chihuahuan Desert grasslands (Fig. 2). We found evidence that ocular estimates of herbaceous cover are a predictor of NDVI

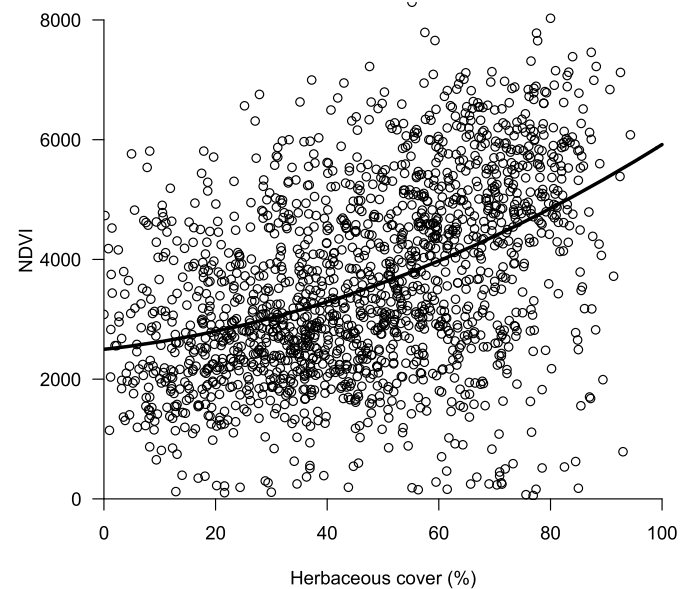


Fig. 2. Relationship between ocular estimates of herbaceous cover and values of the Normalized Differential Vegetation Index (NDVI) on bird survey transects in the Chihuahuan Desert. The curve represent the quadratic regression model for the mean NDVI.

values at the bird transect level through a quadratic regression model (extra-sum-of-squares F test, $F = 11.40$, d.f. = 1, 1715, $P < 0.001$). However, we also observed a relatively large unexplained variance

Table 1

Posterior distribution of the effect of summer precipitation (*precipitation*) and the Normalized Difference Vegetation Index (*ndvi*) and their interaction (*precipitation* \times *ndvi*) on density of 10 grassland bird species during the winters of 2007–2011. Parameters of the linear predictor (β) are computed over standardized *precipitation* (mean = 224 mm, SD = 75 mm) and standardized *ndvi* (mean = 3603, SD = 1552). The term e^{β} is the factor by which baseline annual density is increased or decreased with an increase of one standard deviation of each variable.

Species	Parameter	$\bar{\beta}$	$SD(\bar{\beta})$	95% CrI		$e^{\bar{\beta}}$
Baird's Sparrow	<i>precipitation</i>	0.49	0.07	0.36	0.62	1.63
	<i>ndvi</i>	0.71	0.06	0.60	0.83	2.04
	<i>precipitation</i> \times <i>ndvi</i>	-0.15	0.05	-0.25	-0.05	0.86
Brewer's Sparrow	<i>precipitation</i>	0.04	0.03	0.00	0.09	1.05
	<i>ndvi</i>	0.12	0.02	0.08	0.17	1.13
	<i>precipitation</i> \times <i>ndvi</i>	-0.11	0.02	-0.15	-0.06	0.90
Chestnut-collared Longspur	<i>precipitation</i>	0.20	0.03	0.15	0.26	1.23
	<i>ndvi</i>	-0.12	0.03	-0.18	-0.07	0.88
	<i>precipitation</i> \times <i>ndvi</i>	-0.38	0.03	-0.43	-0.33	0.69
Eastern Meadowlark	<i>precipitation</i>	-0.11	0.04	-0.18	-0.04	0.90
	<i>ndvi</i>	0.38	0.03	0.33	0.44	1.46
	<i>precipitation</i> \times <i>ndvi</i>	0.01	0.03	-0.04	0.06	1.01
Grasshopper Sparrow	<i>precipitation</i>	0.42	0.03	0.36	0.48	1.52
	<i>ndvi</i>	0.53	0.03	0.47	0.59	1.70
	<i>precipitation</i> \times <i>ndvi</i>	-0.18	0.02	-0.23	-0.13	0.83
Grasshopper Sparrow (random)	<i>precipitation</i>	-0.02	0.04	-0.09	0.06	0.98
	<i>ndvi</i>	-0.02	0.03	-0.08	0.05	0.98
	<i>precipitation</i> \times <i>ndvi</i>	0.01	0.03	-0.05	0.07	1.01
Horned Lark	<i>precipitation</i>	-0.68	0.03	-0.74	-0.62	0.51
	<i>ndvi</i>	-0.29	0.02	-0.34	-0.24	0.75
	<i>precipitation</i> \times <i>ndvi</i>	0.07	0.02	0.03	0.11	1.07
Lark Bunting	<i>precipitation</i>	-0.16	0.04	-0.25	-0.08	0.85
	<i>ndvi</i>	-0.29	0.04	-0.38	-0.20	0.75
	<i>precipitation</i> \times <i>ndvi</i>	-0.08	0.04	-0.16	0.00	0.92
Savannah Sparrow	<i>precipitation</i>	0.01	0.03	-0.05	0.07	1.01
	<i>ndvi</i>	0.61	0.02	0.56	0.66	1.84
	<i>precipitation</i> \times <i>ndvi</i>	0.11	0.02	0.07	0.15	1.12
Sprague's Pipit	<i>precipitation</i>	-0.06	0.07	-0.21	0.07	0.94
	<i>ndvi</i>	0.12	0.06	0.00	0.25	1.13
	<i>precipitation</i> \times <i>ndvi</i>	0.15	0.05	0.04	0.25	1.16
Vesper Sparrow	<i>precipitation</i>	0.37	0.01	0.34	0.39	1.44
	<i>ndvi</i>	0.35	0.01	0.32	0.37	1.41
	<i>precipitation</i> \times <i>ndvi</i>	-0.03	0.01	-0.05	-0.01	0.97

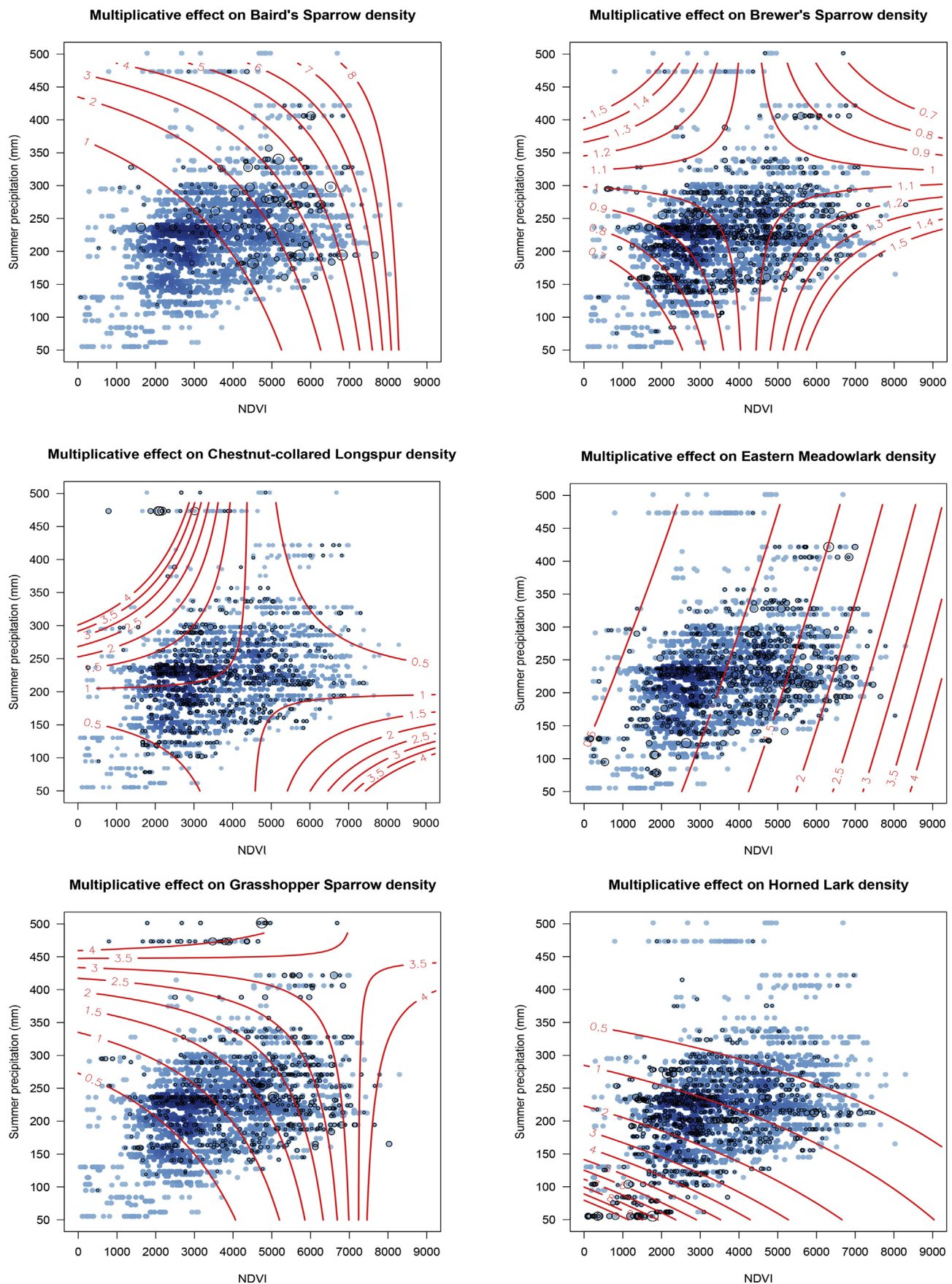


Fig. 3. Effect of summer precipitation (*precipitation*) and the Normalized Difference Vegetation Index (*ndvi*) on density of 10 grassland bird species during the winters of 2007–2011. Level curves denote combination of NDVI and summer precipitation values that produce the same multiplicative effect on bird density. Each blue dot represents a bird transect in a given winter. Empty black circles represent birds transects where the species was detected; the size of these empty circles is proportional to the number of bird detections.

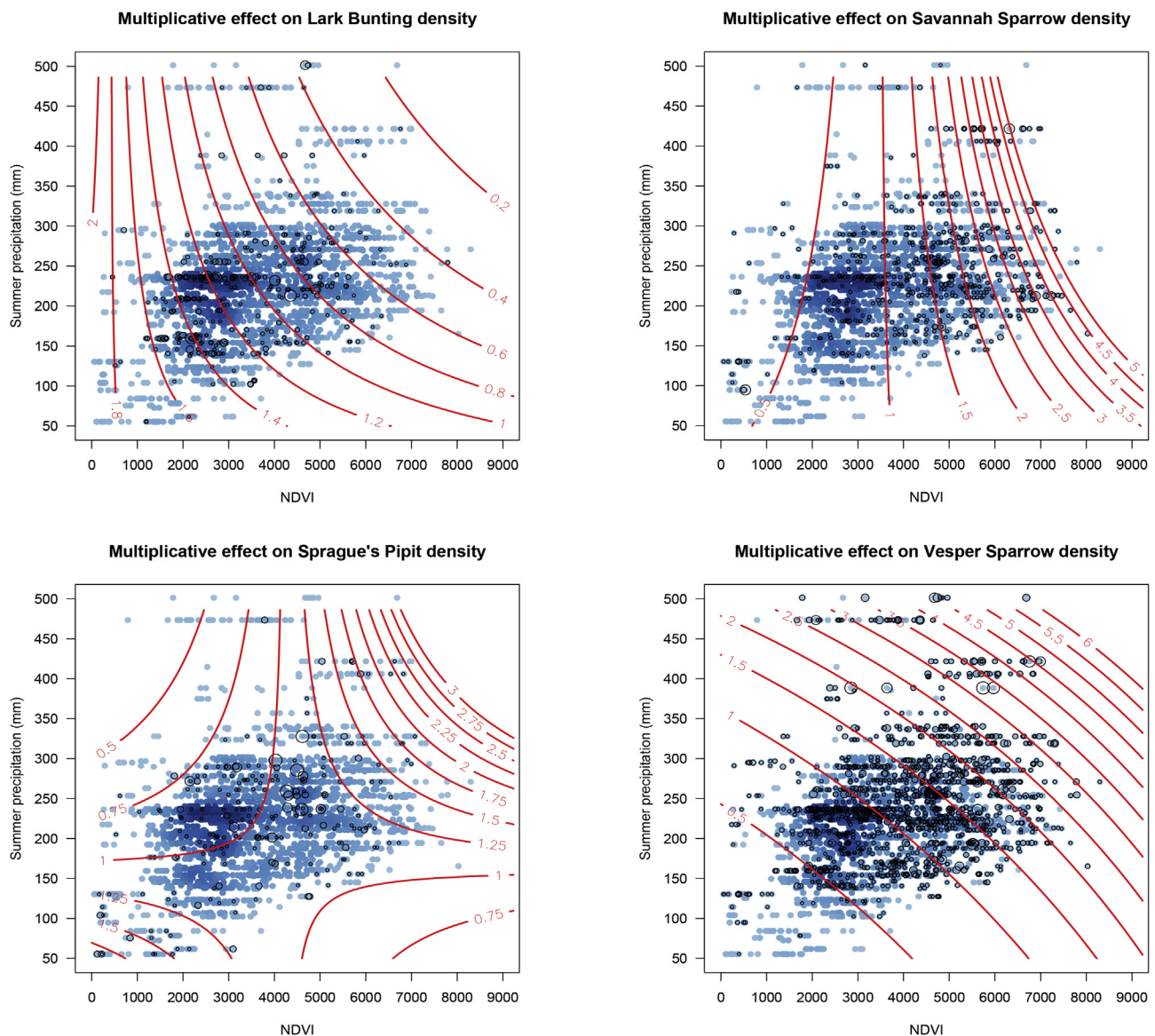


Fig. 3. (continued)

($R^2 = 0.20$), likely associated to the additive effects of observers' variation in ocular estimation and sampling error in vegetation surveys.

Mean density across GPCAs and years (2007–2011) was 7.20 birds·km⁻² (95%CrI(D) = 5.05–9.78 birds·km⁻²) for Baird's Sparrow, 93.80 birds·km⁻² (95%CrI(D) = 82.35–106.34 birds·km⁻²) for Brewer's Sparrow, 143.23 birds·km⁻² (95%CrI(D) = 125.24–162.71 birds·km⁻²) for Chestnut-collared Longspur, 8.83 birds·km⁻² (95%CrI(D) = 7.55–10.31 birds·km⁻²) for Eastern Meadowlark, 31.63 birds·km⁻² (95%CrI(D) = 27.05–36.81 birds·km⁻²) for Grasshopper Sparrow, 41.41 birds·km⁻² (95%CrI(D) = 37.01–46.17 birds·km⁻²) for Horned Lark, 72.07 birds·km⁻² (95%CrI(D) = 58.56–87.72 birds·km⁻²) for Lark Bunting, 37.52 birds·km⁻² (95%CrI(D) = 33.27–42.22 birds·km⁻²) for Savannah Sparrow, 2.78 birds·km⁻² (95%CrI(D) = 2.07–3.73 birds·km⁻²) for Sprague's Pipit, 114.89 birds·km⁻² (95%CrI(D) = 107.43–122.88 birds·km⁻²) for Vesper Sparrow, and 1.18 birds·km⁻² (95%CrI(D) = 0.87–1.56 birds·km⁻²) for Western Meadowlark.

The response of bird density to annual and regional variation in summer precipitation and vegetation growth (i.e. NDVI) differed between species (Table 1 and Fig. 3). For all species but the Western Meadowlark, the full model that included precipitation, NDVI and their interaction was the best model or had a $\Delta\text{DIC} < 5$ (table of ΔDIC

omitted) and we then use the full model for inferences. For the Western Meadowlark, all models in the model set (including $\log(D) = \text{YEAR}$) had a $\Delta\text{DIC} < 5$ and we did not claim effects of NDVI or precipitation on bird density. For all species, at least one effect of the explanatory variables differed from zero (i.e., the 95%CrI for the regression coefficient β did not include zero). Baird's Sparrow density had a strong response to both variables although the effect of precipitation on Baird's Sparrow density was lower when vegetation was relatively denser. The negative effect of NDVI on Brewer's Sparrow and Chestnut-collared Sparrow density was in general negligible for most of its joint range of variation with precipitation, although both variables showed a negative interaction on these species' density. Eastern Meadowlark showed a positive response to vegetation volume but a slight negative response to precipitation. Grasshopper Sparrow showed a strong positive response to both variables; precipitation lessened the response of Grasshopper Sparrow density to vegetative growth. Horned Lark density had a negative response to both summer precipitation and vegetation growth with negligible interaction effect between the two explanatory variables.

Lark Buntings favored grasslands with low vegetative growth and this response was enhanced during years of relatively high summer precipitation. Savannah Sparrows were more abundant in grasslands

with relatively high vegetative growth and their response to this variable was higher when precipitation was relatively high. Sprague's Pipit response to both summer precipitation and NDVI was relatively weak but with a noticeable positive response in both variables for high values in both. Vesper Sparrows had a strong and clear positive and additive response to both increased vegetation growth and summer precipitation. The response of Western Meadowlarks to vegetation growth and precipitation differed from that of its congeneric species the Eastern Meadowlark. Our model selection procedure showed that the full model of density (including the additive effects of *YEAR*, *NDVI* and precipitation plus the interaction between the latter two) for Western Meadowlarks had equal support as the reduced density model (only factor *YEAR*), providing weak support to the effect of vegetative cover and precipitation.

4. Discussion

The mechanism for habitat selection in migratory land birds has been hypothesized to be a hierarchical scale-dependent process (Hutto, 1985): at the broadest scale, birds are programmed to head along a certain migratory route to a wintering ground, whereas at the local scale, wintering habitat selection involves exploratory assessment and habitat use primarily determined by ecological factors. This hierarchical decision-making process, in theory, may sometimes limit the ability of birds to exploit the best winter habitats. In contrast, our results suggest that wintering grassland passerines follow the ideal free distribution and are capable of selecting habitat across the entire Chihuahuan Desert based on vegetation condition and therefore can optimally exploit resources in the wintering grounds. However, aridity may not imply limited resources. Abundance of granivorous birds in Monte Desert, Argentina, are the highest when seed abundance is the lowest (Marone, 1992).

The relationship between NDVI and winter bird density in the Chihuahuan Desert inferred in this study is supported by habitat relationships at a local scale obtained in central Chihuahua by Macías-Duarte et al. (2009). The similarities in response to vegetation between these two studies are conspicuous. For instance, species whose density showed a strict positive response to NDVI (i.e., Baird's Sparrow, Savannah Sparrow, Vesper Sparrow, and Eastern and Western Meadowlark) also showed a positive response (presence) to grass cover and grass height in central Chihuahua. In addition, Horned Lark, Sprague's Pipit, Chestnut-collared Longspur, and Lark Bunting, which did not show a strictly-positive response to NDVI in this study, showed either no response or a negative response to grass cover or grass height (or their interaction) at the local scale in central Chihuahua (Macías-Duarte et al., 2009). This lack of response to NDVI is probably related to the frequent occurrence of these species in open grasslands of low height with a high proportion of bare ground. The lack of a strictly-positive response in Brewer's Sparrows to NDVI may be related to the species' frequent use of shrubbier vegetation with lower NDVI response to the summer growing season (Moreno-de-las-Heras et al., 2015). In addition, it is remarkable that we found associations between vegetation and bird density in spite of the variation in plant species composition across the Chihuahuan Desert grasslands.

Besides the correspondence of our results to smaller, local scales in the Chihuahuan Desert, our results also correspond with grassland bird species on their breeding grounds. In this regard, Gorzo et al. (2016) found that the abundance of Baird's and Grasshopper sparrows during the breeding season are also positively associated with precipitation during the previous spring, which in turn is positively related to vegetative condition. In contrast, Vesper Sparrow's abundance was negatively related to spring precipitation and precipitation in the previous summer and Horned Larks did not show any significant response. These results highlight the global importance of vegetation cover in grassland habitat as a measure of habitat quality and support the idea that grassland birds are habitat specialists (Igl and Ballard, 1999; Wiens,

1974).

Our results provide a valuable tool for the conservation of declining migratory birds on their wintering grounds by identifying a wildlife-habitat relationship, a functional relationship between animal abundance and a habitat variable, using a remotely-sensed and readily available index of vegetative growth. Wildlife-habitat relationships allow the management of wildlife population parameters (such as winter survival), and hence population trajectories, through the management of habitat components. When a remotely-sensed measure such as NDVI (as opposed to measures taken directly on the ground) is a proven indicator of animal abundance, rapid large-scale assessments of habitat suitability are possible. Such assessments could be used to determine annual habitat capacity for grassland bird species and inform conservation and management objectives at various spatial and temporal scales, from individual ranches to GPCAs to the entire Chihuahuan Desert region, both within years and long-term. It is also possible to project population trajectories under future scenarios of increased aridity on the wintering grounds (Seager et al., 2007) and delayed summer precipitation (Cook and Seager, 2013).

This study demonstrates the importance of healthy grassland vegetation in determining wintering grassland bird abundance and distribution throughout the Chihuahuan Desert (Macías-Duarte et al., 2009; Macías-Duarte and Panjabi, 2013). In this regard, population declines in the grassland bird guild (Sauer et al., 2017) may result from decreasing quality in grassland cover caused by decades of inadequate grazing management (Curtin et al., 2002) and, more currently, accelerated loss of grasslands (Macías-Duarte et al., 2009; Pool et al., 2014). Nevertheless, if the ideal free distribution holds for the wintering grassland bird system, then it is possible that grassland birds may be able to adapt better to the effects of climate change provided that suitable grasslands are maintained across the full geographic scope of their wintering grounds.

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