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Research Paper

The role of temperature and microclimate in the survival of wintering grassland birds

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ABSTRACT. Over the past 40 years, grassland birds have declined steeply in North America, necessitating the study of limiting factors throughout their full annual cycle to mitigate this decline. Here we explored factors that may influence winter survival of two grassland specialist birds with steep declines; Baird's Sparrow (*Centronyx bairdii*) and Grasshopper Sparrow (*Ammodramus savannarum*). We studied the relationship of broad-scale ambient temperature and vegetation structure with winter survival of these species and explored the role of vegetation structure in providing microclimatic refuges for these overwintering sparrows. During three winters from 2016-2019, we monitored these species in the Marfa grasslands, Texas, using radio-telemetry. We placed radio-transmitters on >200 individuals of both species combined, and tracked them daily from mid-December to mid-March. We estimated ground cover in a 5 m radius circular plot for ≥ 20 locations per individual. We also placed temperature loggers at 40 bird points (of both species combined) and 40 random points to measure microclimate used by these birds. We then estimated winter survival probability using logistic-exposure and used general linear models to evaluate the relationship of ambient temperature and habitat covariates with survival. Winter survival over an 85 day period was lower for Grasshopper Sparrow than Baird's Sparrow (three-year mean = 65.92% and 85.54%, respectively), and ranged from 47% to 100% for both species. We found that minimum ambient temperature was the main factor limiting survival of sparrows. Microclimate temperatures were higher in bird locations compared to random locations and were warmer in shrub cover and tall grass than short grass or litter. These results indicate that microclimate may be important to sparrows on the wintering grounds and highlight the value of habitat structure for providing thermal refuges. Our results emphasize the need to maintain vegetative cover for grassland birds to protect against harsh weather conditions that may limit their survival.

Le rôle de la température et du microclimat dans la survie des oiseaux de prairie hivernant

RÉSUMÉ. Au cours des 40 dernières années, les oiseaux de prairies ont connu une forte diminution en Amérique du Nord, justifiant l'étude des facteurs limitants tout au long de leur cycle annuel afin d'atténuer cette baisse. Dans le présent article, nous avons exploré les facteurs qui peuvent influencer sur la survie hivernale de deux oiseaux spécialistes de prairie dont la baisse est très marquée : le Bruant de Baird (*Centronyx bairdii*) et le Bruant sauterelle (*Ammodramus savannarum*). Nous avons étudié la relation entre la température ambiante à grande échelle et la structure de la végétation avec la survie hivernale de ces espèces et avons examiné le rôle de la structure de la végétation à fournir des refuges microclimatiques pour ces bruants hivernant. Pendant trois hivers de 2016 à 2019, nous avons suivi ces espèces dans les prairies de Marfa, au Texas, au moyen de la radiotélémetrie. Nous avons posé des radio-émetteurs sur > 200 individus des deux espèces, et les avons suivis quotidiennement de la mi-décembre à la mi-mars. Nous avons déterminé la couverture du sol dans un rayon de 5 m de rayon pour ≥ 20 sites par individu. Nous avons également installé des enregistreurs de température à 40 points d'oiseaux (des deux espèces combinées) et à 40 points aléatoires pour mesurer le microclimat utilisé par ces bruants. Nous avons ensuite calculé la probabilité de survie hivernale en utilisant la méthode d'exposition-logistique et des modèles linéaires généralisés pour évaluer la relation de la température ambiante et des covariables de l'habitat avec la survie. La survie hivernale sur une période de 85 jours était plus faible chez le Bruant sauterelle que chez le Bruant de Baird (moyenne sur trois ans = 65.92% et 85.54%, respectivement), et variait de 47 à 100% pour les deux espèces. Nous avons constaté que la température ambiante minimale était le principal facteur limitant la survie des bruants. Les températures du microclimat étaient plus élevées dans les endroits où se trouvaient les oiseaux par rapport aux endroits aléatoires et étaient plus chaudes dans le couvert arbustif et les hautes herbes que dans les herbes courtes ou la litière. Ces résultats indiquent que le microclimat est sans doute important pour les bruants sur les sites d'hivernage et soulignent la valeur de la structure de l'habitat à fournir des refuges thermiques. Nos résultats font ressortir la nécessité de maintenir un couvert végétal pour les oiseaux de prairies afin de les protéger contre les conditions climatiques sévères qui peuvent limiter leur survie.

Key Words: *Baird's Sparrow*; *Chihuahuan Desert*; *Grasshopper Sparrow*; *thermal refuge*; *winter survival*

INTRODUCTION

Grassland birds are experiencing some of the fastest population declines in North America (Rosenberg et al. 2019) as a result of long-term habitat loss and degradation across their annual cycle (e.g. Brennan and Kuvlesky 2005, Pool et al. 2014). In order to better understand what is driving population declines, it is necessary to study a species throughout its full annual cycle (Hostetler et al. 2015). Because the nonbreeding period is up to 8 months long, the effects of nonbreeding threats may influence populations more than those on the breeding grounds (Calvert et al. 2009). However, most studies on grassland birds have focused on breeding season demographics (Somershoe 2018), and comparatively little is known about winter survival.

The Chihuahuan Desert grasslands are an important wintering area for priority grassland birds such as Baird's Sparrow (*Centronyx bairdii*) and Grasshopper Sparrow (*Ammodramus savannarum*; NABCI 2016), two grassland specialist species that breed in the Great Plains of the U.S. and Canada. These grasslands have experienced habitat loss and degradation as a result of grazing mismanagement, drought, woody plant encroachment, and conversion of grasslands to irrigated agriculture (Pool et al. 2014). Population declines are steeper for migratory grassland birds wintering in the Chihuahuan Desert compared to migratory birds wintering elsewhere (NABCI 2016). For example, Baird's and Grasshopper Sparrows both inhabit the Chihuahuan Desert grasslands during the nonbreeding season and have declined by 75% since 1966 (Sauer et al. 2017), compared to an overall grassland bird population decline of 53% (Rosenberg et al. 2019).

Vegetation structure is likely an important driver of winter survival for these species. Population densities of wintering grassland birds have consistently been related to vegetation structure such as cover and height of grass and shrubs (e.g., Baldwin et al. 2007, Macías-Duarte et al. 2009, 2018, Henderson and Davis 2014, Ruth et al. 2014). Changes to vegetation structure could result in displacement or lower survival of wintering grassland birds (Grant et al. 2004, Sliwinski and Koper 2012), especially for specialists that have narrow ecological niches within the grassland ecosystem, making them more vulnerable to change (Correll et al. 2019). For example, Thatcher et al. (2006) directly related winter survival of Henslow's Sparrows (*Centronyx henslowii*) to fire management, presumably through the effects of fire on vegetation. In the Chihuahuan Desert, winter survival of Grasshopper Sparrows was negatively related to shrub height (Macías-Duarte et al. 2017), and winter survival of Vesper Sparrows (*Pooecetes gramineus*), a habitat generalist species, was positively associated with grass and shrub height (Macías-Duarte and Panjabi 2013a).

Local weather conditions could also influence winter survival of birds. Severe weather has been shown to negatively affect wintering abundance (Meehan et al. 2004), distributions (Zuckerberg et al. 2011), and survival (Salewski et al. 2013) of different landbird species. Low temperatures may be an important driver of mortality during winter (Robinson et al. 2007), especially in smaller-bodied birds with a higher thermoregulatory cost such as sparrows (Dawson and Connor 1989, King and Swanson 2013), and more so in harsh environments like the Chihuahuan Desert. Preliminary monitoring in northern Chihuahua, Mexico, found

that Baird's and Grasshopper Sparrow survival was lower on colder days (Macías-Duarte et al. 2017).

Vegetation structure can also interact with local weather conditions to impact winter survival. Grass or shrubs can provide thermal refuges for birds when local weather conditions are unfavorable (Carroll et al. 2015). Temperature measured at the microclimatic scale (small-scale surrounding a bird) can be very different from the broadscale ambient temperature (Tomecek et al. 2017) and could be more relevant to the survival of wintering birds and other animals (Suggitt et al. 2011). Microclimate can be defined as fine-scale climate variations based on local variation in habitat characteristics such as vegetation, litter, topography, and soil type (Bramer et al. 2018). Microclimate at this scale has been found to affect bird abundance (Rajpar and Zakaria 2015), selection of foraging patch (Villén-Pérez et al. 2013), and was a better predictor of grassland bird distributions in the Alps compared to broadscale ambient temperature (Jähnig et al. 2020). Ambient temperature can fluctuate widely during the Chihuahuan Desert winter, often dropping below freezing at night, and severe weather events, such as snow and rain storms, occur. Therefore, survival of birds wintering in this ecoregion could be limited by the availability of thermal cover provided by vegetation if local weather is poor (i.e., temperatures below freezing and/or rain or snow).

In this 3-year study, we investigated winter survival and its relationship with broadscale ambient temperature and vegetation structure for Baird's and Grasshopper Sparrows in the northern part of their winter distribution. We also explored the relationship between site-level ambient temperature, vegetation structure, and microclimate. Our study had three main objectives: 1) estimate winter survival probabilities of Baird's and Grasshopper Sparrows in the Marfa grasslands of Texas, 2) determine if vegetation structure and ambient temperature are drivers of winter survival of these two species, and 3) explore the thermal properties of vegetation that may provide thermal refuges for wintering grassland birds when conditions are unfavorable. We hypothesized that ambient temperature influences winter survival of Baird's and Grasshopper Sparrows, and that taller grass cover could provide thermal refuges for wintering sparrows. Therefore, we predicted that winter survival would be positively associated with minimum ambient temperature and grass height, and that minimum microclimate temperatures would be warmer in tall grass cover compared to bare ground or shorter vegetative cover.

METHODS

Study site

Our study site was located on the Mimms Ranch in west Texas, USA. The ranch, owned by Dixon Water Foundation, is located north of Marfa in Presidio County, Texas (30°19'10.3" N, 104°01'32.2" W), and is part of the Marfa Grassland Priority Conservation Area (GPCA; Pool and Panjabi 2011). The Mimms Ranch encompasses 4,390 ha divided into 30 rotationally grazed pastures of approximately 105 ha grazed by 180-190 cattle, and one 858.3 ha pasture that is continuously grazed by 30 cattle. We focused data collection and monitoring within two polygons. Polygons were created based on capture locations and tracking data from the first 3 weeks of bird monitoring in 2016-17 (rotational polygon) and 2017-18 (continuous polygon). The

Mimms Ranch is dominated by gramma grasses (*Bouteloua* spp.), threeawn grasses (*Aristida* spp.), Swallen's curly mesquite (*Hilaria swallenii*), and a low density (<1% cover) of mixed shrubs including yucca (*Yucca* spp.) and mesquite (*Prosopis* spp.). The study site is at an elevation of 1,450 m to 1,480 m, has an average annual precipitation of 390 mm, and an average annual minimum and maximum temperature of 5.4 °C and 24.3 °C, respectively. Average minimum and maximum temperatures from December to March (the study period) are -3.7 °C and 16.1 °C, respectively.

Capture

We captured Grasshopper and Baird's sparrows using an active mist-netting technique following Strasser et al. (2018). We placed between 2-4 mist nets (12 m each) in a straight line through open grassland habitat and we formed a semicircle around the nets with 7-15 people. From approximately 200 m away, the group slowly advanced towards the net array, flushing the birds toward the nets. We waved sticks or bamboo poles with bright flagging attached to flush the birds toward the nets and tossed brightly-colored fabric discs towards the net over the birds to deter them from escaping. We made an effort to capture an equal number of both species each year to the extent practical to given local abundance. Capture and recapture events occurred three times per season (December, January, March), however, we captured birds throughout the winter to supplement our sample size. In 2016-17 and 2018-19 we restricted captures to within the rotational pastures because both species were present there. In 2017-18 we captured birds in both the rotational and continuous grazing areas because in this year we found mostly Baird's Sparrows in the continuous pasture and mostly Grasshopper Sparrows in the rotational pasture.

Once captured, we banded all birds with a uniquely numbered aluminum band from the U.S. Geological Survey. We then deployed Very High Frequency (VHF) transmitters, PicoPip Ag379 (Biotrack Ltd, Dorset, UK), on the birds for tracking. We placed the transmitter on the birds' synsacrum using a harness of 1-mm nylon coated elastic that looped around the bird's legs (Rappole and Tipton 1991). The combined weight of the transmitter and harness did not exceed 4% of the bird's mass (Naef-Daenzer et al. 2001); birds not meeting the minimum weight requirements were processed and then released without a transmitter.

Because we observed that transmitter batteries lasted 40-65 days, we attempted to recapture birds halfway through the season (late January) to replace transmitters. At the end of the season (early-mid March), we attempted to recapture all birds in order to recover the transmitters and assess the condition of the birds (e.g. look for tattered feathers or skin irritation). To recapture the birds, we first radio-tracked an individual and then used one of two methods. The first method was similar to the original capture method but placing the mist nets as close as possible to the bird and then flushing it into the net by making a semicircle. For the second method, two technicians triangulated the bird, and then 2 groups of 2 people holding a mist net each slowly approached the bird's location with one net parallel to the other. Once both nets were close to the location, technicians placed the nets over the bird. All netting, banding, and sampling were performed under the requisite of Sul Ross State University (SRSU) Animal Care Committee, Texas Parks and Wildlife Department (permit number SPR-1216-286), and the USGS Bird Banding Laboratory (permit number 22415).

Bird monitoring

We monitored all tagged birds from mid-December to mid-March once per day between 0730 to 1800 hrs. With one observer using a 3-element folding Yagi antenna and a Biotracker receiver (Lotek, Dorset, UK) we tracked birds quietly and efficiently, attempting to identify a bird's true location unbiased by human presence. To do so we triangulated the approximate location of the transmitter from ~ 50-200 m away and then took multiple mental bearings to hone our estimate as we walked in an arc or complete circle around the triangulated location. We attempted to confirm whether a bird was alive or dead by obtaining a visual of the bird or based upon detection of signal indicating movement through dense vegetation. We marked the locations with a Global Positioning System unit (GPS; Garmin Ltd., Olathe, KS) and aimed to mark locations when GPS accuracy was <5 m.

We were unable to assess location uncertainty for tagged birds because of factors beyond our control (influence of wind, vegetation, slope, bird movement, technician experience, bird sensitivity to disturbance). We recorded how the bird was detected (sight or by signal alone), and noted the status of the bird (alive or dead, unknown). When we found a transmitter with or without remains of a sparrow, we looked for signs of depredation or injury such as blood, feathers, visible hematomas, predator tracks, or a damaged transmitter. If we found any indication of mortality, we attempted to identify the direct cause of mortality (depredation, exposure to elements). We were vigilant of predators such as shrikes and did not track sparrows when they were in the vicinity.

Throughout the field season we made efforts to locate birds that went missing from our study polygons. We walked and drove roads transecting the entire ranch to scan for lost transmitter frequencies each day for a week, and then once every week thereafter until the expected life-span of the transmitter had passed (55 d).

Vegetation sampling

We measured ground cover at ≥ 20 radio telemetry locations for each bird using rapid assessment methods within a 5 m radius plot around the bird location following Strasser et al. (2018). Within each of these ~79 m² (845 ft²) plots we recorded a visual estimate of the percent cover of grass, forbs, Russian thistle (*Salsola* spp.), shrubs (including yucca), bare ground, and other cover (litter, rocks, animal excrement, burned grass). In addition, we recorded average height of grass, forbs, and shrubs using a ruler. Observers were trained to visually estimate cover and height and we calibrated these measurements at the start and throughout the season. Data comparing rapid assessment and quantitative sampling indicates that both methods provide similar results when observers are trained and then regularly calibrate their measurements (Macias-Duarte and Panjabi 2013a). Therefore, ocular sampling of vegetation cover parameters provides a reasonably accurate assessment of vegetation conditions without the associated time or expense of high-intensity sampling.

Microclimate sampling

To assess microclimate conditions, we placed 80 iButton® DS1921 temperature loggers, (Dallas Semiconductor, Sunnyvale, CA) accurate to 0.5 °C, in bird and random locations from 10 February to 3 March in 2018 and 2019. Loggers were placed into iButton fobs® (holders) that were mounted on orange pin flags. These flags were buried into the ground in such a way that the

logger was positioned 10 cm from the ground. All loggers were facing down where they measured microclimate temperature at the height of the bird and oriented west. We chose to face loggers down rather than exposing loggers directly by facing them upward, to obtain ambient microclimate temperatures that could be compared to ambient site-level temperatures. We programmed each logger to record temperature every 10 minutes. We calibrated loggers against a mercury thermometer and recorded ground cover type and height at the exact logger location.

During bird tracking, we set a temperature logger at the location where we detected the bird immediately after observing it (loggers were only placed when the bird was detected before it moved from its original location). In most cases, we placed a logger at one location per individual bird. However, because the number of individuals tracked was less than the total number of iButtons available to assess microclimate, for a small number of individual birds we placed loggers at two of their recorded locations. Because birds were almost exclusively observed in grass cover, of the 80 bird temperature logger locations (40 per year), 61 were placed in tall grass, 14 in short grass, 2 in litter (1-5 mm), 2 in bare ground, and one under a shrub.

We placed an equal number of loggers (40 per year) at randomly selected points from a grid of points spaced every 100 m throughout two study polygons within the rotational and continuous grazing areas. This grid of vegetation points was aimed at assessing the overall vegetation cover as part of the large scale study and followed the same protocol as the partner sites (Strasser et al. 2018). Random logger locations were selected randomly from the vegetation grid locations and, therefore, were not equally distributed over the vegetation types, but, rather, reflected that the shrub cover at this ranch was minimal (< 1%); of the 80 random temperature logger locations (40 per year), we placed 25 loggers in tall grass, 9 in short grass, 18 in litter, 26 in bare ground, and 2 under a shrub ($n = 80$).

We did not move loggers throughout the sampling period, but rather remained in the original location to be able to detect microclimate in different vegetation types over a prolonged period with variable climatic conditions. For most of the logger locations we collected 22 days of microclimate temperature data, from February 10 - March 3, 2018 and 2019, but programming mistakes resulted in 10 or 11 days of missing data for 2 bird locations and 6 random locations in 2018, and no temperature recordings at all for 4 bird locations and 7 random locations in 2019. Missing data for bird locations were almost all for tall grass (one bare ground) and missing data for random locations were equally distributed between tall grass, litter, and bare ground.

Data analysis

We estimated winter survival of Baird's and Grasshopper Sparrows using a general linear model with the `glm` function from package `lme4` (Bates et al. 2015) in program R 4.0.3 (R Core Team 2021). We used a logistic exposure link function to explicitly model survival as a function of covariates while accounting for differences in the start date and duration of monitoring (Shaffer 2004). We chose to use logistic exposure because it allowed us to account for birds that were tracked for different periods of time (i.e., the exposure period of the individual) and for birds that we started tracking at different days throughout the season (Shaffer

2004). We excluded data from the first 7 days after tagging to reduce the influence of capture stress or transmitter effects on survival as birds could be more vulnerable to physiological or behavioral responses that increase depredation or emigration from the site (Murray 2006).

First we estimated daily survival based on the null model (not including any covariates) and calculated the overall probability to survive the winter season by extrapolating daily estimates by the total number of days of our winter season (85 days). We then modeled daily survival probability as a function of minimum ambient temperature and vegetation cover estimates from bird locations as covariates (percent of grass cover, grass height, percent of shrub cover, shrub height, percent of forb cover, forb height, percent of Russian thistle, and percent of bare ground and other cover). Site-level (ambient) temperature data were obtained from a weather station (Weather Underground) at the Marfa Municipal Airport, which shares a border with the study site. We included an average of daily minimum temperature for the date of observation and also the previous 6 days, because we hypothesized that prolonged days of low temperatures would affect survival more than one single cold day. If a bird was found dead, it could have died the day it was found or the previous day after it was observed alive. We decided to use the day of observation and the previous 6 days to account for birds that died early in the morning due to a previous cold night or early morning depredation. We modeled daily survival as a function of this weekly average minimum temperature and as a function of the daily minimum temperature and found that the weekly average minimum temperature was a stronger predictor of survival ($\Delta AICc = 1.15$). Therefore, we included weekly average minimum temperature in all subsequent models and will refer to it hereafter as "minimum temperature".

We tested for correlations among the covariates ($|r| > 0.6$) and found that bare ground was strongly correlated with the variables grass cover ($r = -0.85$) and other cover (-0.63), but grass cover and other cover were not correlated with one another. We therefore decided to remove bare ground from the analyses. Shrub cover and shrub height were also correlated ($r = 0.63$). We excluded shrub cover and included shrub height because this metric has been documented to influence grassland bird survival in other locations within the Chihuahuan Desert (Macías-Duarte et al. 2017). When a 5 m radius vegetation plot did not have any shrubs, we recorded a zero for shrub height.

We constructed 13 hypothesis-driven models (Table 1; Table A1.1) including a null model to explore which environmental variables influenced survival. We chose to use hypothesis-driven models to avoid the detection of spurious relationships by chance alone (Anderson et al. 2001). We chose the combination of covariates in the models based on literature on grassland bird-habitat relationships (eg. Macías-Duarte et al. 2009, 2017, Ruth et al. 2014) and experience in the field to test our hypotheses that certain vegetation characteristics and/or prolonged low minimum temperatures affect winter survival of grassland sparrows. We hypothesized based on previous studies (Macías-Duarte et al. 2017) that grass cover, grass height, shrub height, and temperature would be most important for winter survival. In models 2-5 (Table 1; Table A1.1) we test each of these variables individually. Model 6 tests the hypothesis that only grass structure (cover and height

Table 1. Model comparison results for 13 hypothesis-driven models to explain winter survival probability of Baird's and Grasshopper sparrows in the Marfa grasslands, Texas, as a function of temperature and habitat structure covariates using logistic exposure.

Model	loglik	Δ AICc	df(K)	AICc weight
Baird's Sparrow				
Model 2: Temperature	-39.65	0.00	2	0.321
Model 7: Temperature + Grass height	-39.32	1.33	3	0.165
Model 1: Null	-41.65	1.99	1	0.119
Model 9: Temperature * Grass height	-38.99	2.68	4	0.084
Model 4: Grass height	-41.14	2.96	2	0.073
Model 5: Shrub height	-41.14	2.98	2	0.072
Model 3: Grass cover	-41.44	3.58	2	0.054
Model 6: Grass height + Grass cover	-40.80	4.30	3	0.037
Model 10: Temperature * Grass height + Grass cover + Shrub height	-38.18	5.07	6	0.025
Model 12: Grass height + Forb height + Shrub height	-40.33	5.36	4	0.022
Model 8: Grass height + Grass cover + Shrub height	-40.36	5.42	4	0.021
Model 11: Grass cover + Forb cover + Salsola + Other	-40.62	7.94	5	0.006
Model 13: Temperature + Forb cover + Forb height + Shrub height + Grass cover + Grass height + Salsola + Other + Grass height*Temperature	-37.46	11.68	10	0.001
Grasshopper Sparrow				
Model 7: Temperature + Grass height	-84.48	0.00	3	0.330
Model 2: Temperature	-85.55	0.12	2	0.311
Model 9: Temperature * Grass Height	-84.35	1.74	4	0.138
Model 4: Grass height	-87.04	3.11	2	0.070
Model 6: Grass height + Grass cover	-86.73	4.49	3	0.035
Model 1: Null	-88.79	4.60	1	0.033
Model 3: Grass cover	-88.16	5.34	2	0.023
Model 10: Temperature * Grass height + Grass cover + Shrub height	-84.22	5.50	6	0.021
Model 8: Grass height + Grass cover + Shrub height	-86.68	6.41	4	0.013
Model 5: Shrub height	-88.76	6.56	2	0.012
Model 12: Grass height + Forb height + Shrub height	-86.90	6.83	4	0.011
Model 11: Grass cover + Forb cover + Salsola + Other	-88.00	11.06	5	0.001
Model 13: Temperature + Forb cover + Forb height + Shrub height + Grass cover + Grass height + Salsola + Other + Grass height*Temperature	-83.50	12.11	10	0.001

combined) explains winter survival. In model 7 we test the hypothesis that temperature and grass height are most important, but independent from each other. Model 8 tests the additive effects of grass height, grass cover, and shrub height. In model 9 we test the hypothesis that temperature and grass height interact in their effect on survival (i.e. grass height can mitigate the effect of low temps by providing thermal refuges). Model 10 tests the hypothesis that grass height and temperature interact but that the other two expected vegetation characteristics are also important (shrub height and grass cover). Model 11 tests the hypothesis that all ground cover variables affect survival. Model 12 tests the hypothesis that all vegetation height variables affect survival. Finally, model 13 represents our global model including all the vegetation covariates in previous models, temperature, and the interaction between grass height and temperature.

We standardized all variables to directly compare estimates of the regression coefficients within and across models. We used an information-theoretic approach and Akaike Information Criterion for small sample size (AICc) to compare model performance (Burnham and Anderson 2002). We used the model selection function from the MuMIn packages (Barton 2020) to build a

model selection table. We model-averaged the estimates and their 95% confidence intervals for the covariates in the top models (Δ AICc < 2), to determine which covariates were most important for survival (Burnham and Anderson 2002) using the modavg function of the AICcmodavg package (Mazarello 2020) which implements a natural based average method.

We ran two models to explore differences in microclimate at bird and random locations. We first tested if grass cover and height were higher at bird locations compared to grid locations in our study, as occurrence and abundance of Baird's and Grasshopper Sparrows have been related to grass cover and tall grass (Macias-Duarte et al. 2009, Ruth et al. 2014). We used a generalized linear mixed model with a beta distribution with location type (Baird's Sparrow, Grasshopper Sparrow, grid) as a fixed effect and grass cover as the dependent variable. A beta-regression is recommended for analyzing proportional data that is bounded between zero and one and therefore frequently violates model assumptions of normality and homoscedasticity (Douma and Weedon 2019). We included "year" as fixed effect in the model to control for variation among years that could be related to rainfall and/or management (grazing), and "ID" (bird band number for

Table 2. Number of birds by species (BAIS = Baird’s Sparrow, GRSP = Grasshopper Sparrow) that were banded, radio-tagged, and recaptured, and number of mortalities, missing birds, and confirmed survivals in three winter seasons in the Marfa grasslands of Texas.

	2016-2017			2017-2018			2018-2019		
	BAIS	GRSP	Total	BAIS	GRSP	Total	BAIS	GRSP	Total
# Banded [†]	46	30	76	55	35	90	51	53	106
# Tagged [‡]	40	26	66	48	30	78	35	37	73
# Recaptured [§]	2	2	4	4	12	16	6	14	20
# Dead	2	1	3	11	10	21	7	6	13
# Radio fell off [¶]	6	4	10	0	0	0	1	5	6
# Missing/unknown [#]	14	5	18	17	7	24	10	8	18
# Survived ^{††}	17	12	29	20	13	33	16	18	35

[†]Banded: Number of birds banded, including birds with and without transmitter. Recaptures not included.

[‡]Tagged: Number of birds with transmitter. Birds tagged more than one time count like one individual.

[§]Recaptured: Number of birds recaptured in January.

^{||}Dead: Birds found dead by depredation or other cause.

[¶]Radio fell off: Radio is found within the first week of capture.

[#]Missing/unknown: Birds not found after an extensive searching effort, or when it is not obvious if the bird is dead or the transmitter fell off.

^{††}Survived: Birds that were observed during the transmitter life-span (40-65 days), and birds that survived until the end of the season.

bird locations and grid point ID for grid locations) as a random effect to control for non-independence of multiple measurements for the same logger locations (Harrison et al. 2018). We ran the model using the function “glmmTMB” of the glmmTMB package (Brooks et al. 2017). Differences in grass height were analyzed with a linear mixed model with the same fixed and random effects as the model for grass cover, using the lmer function from package lme4 (Bates et al. 2015). We examined plots to ensure that we met model assumptions. For both models we obtained P values for the fixed effects with the joint_test function from the emmeans package (Lenth 2020), and performed pairwise comparisons with a Tukey test using pairs function in the same package.

We tested two different hypotheses with the microclimate data to explore if vegetation structure can create thermal refuges that may be used by grassland birds. Our first hypothesis was that the distribution of microclimate data was different at bird locations than at random locations. We therefore obtained a daily (24 h) temperature distribution with 10 min intervals for each logger location for the sampling period (22 d in 2018 and 2019, respectively). We then pooled the 24 h temperature distribution for all bird locations in both years, and all random locations in both years. We then compared these pooled distributions with a Kolmogorov-Smirnov test. Because we only placed temperature loggers during the daytime, and therefore did not know whether birds use the same locations at night, we also compared the pooled microclimate temperature distributions from 0800 to 1700 h to represent daytime microclimate.

Our second hypothesis was that mean, minimum, and maximum daily microclimate temperatures differed based on vegetative and ground cover. To test this, we used linear mixed models with cover type, location (bird/random), and their interaction as predictor variables. We characterized logger positions by assigning one of five categorical cover types to each logger location (recorded at

the exact location of the logger); bare ground, short grass (< 13 cm, usually grazed), tall grass (> 13 cm, not grazed), shrub, and litter. We assigned grass cover to one of two categories: 1) short and 2) medium to tall grass, because we predicted that taller grass, but not short grass, would provide thermal refuges for our birds, based on the association of our study species with tall grass (Macias-Duarte et al. 2009, Ruth et al. 2014). We included year as a fixed effect and logger ID as a random effect in the model of microclimate. Models were fitted with the lmer function from package lme4 (Bates et al. 2015). We checked model assumptions graphically and calculated P values for the fixed effects with the joint_test function from the emmeans package (Lenth 2020). We performed pairwise comparisons with a Tukey test to test for differences in microclimate temperature between individual vegetation types using pairs function from the emmeans package (Lenth 2020).

RESULTS

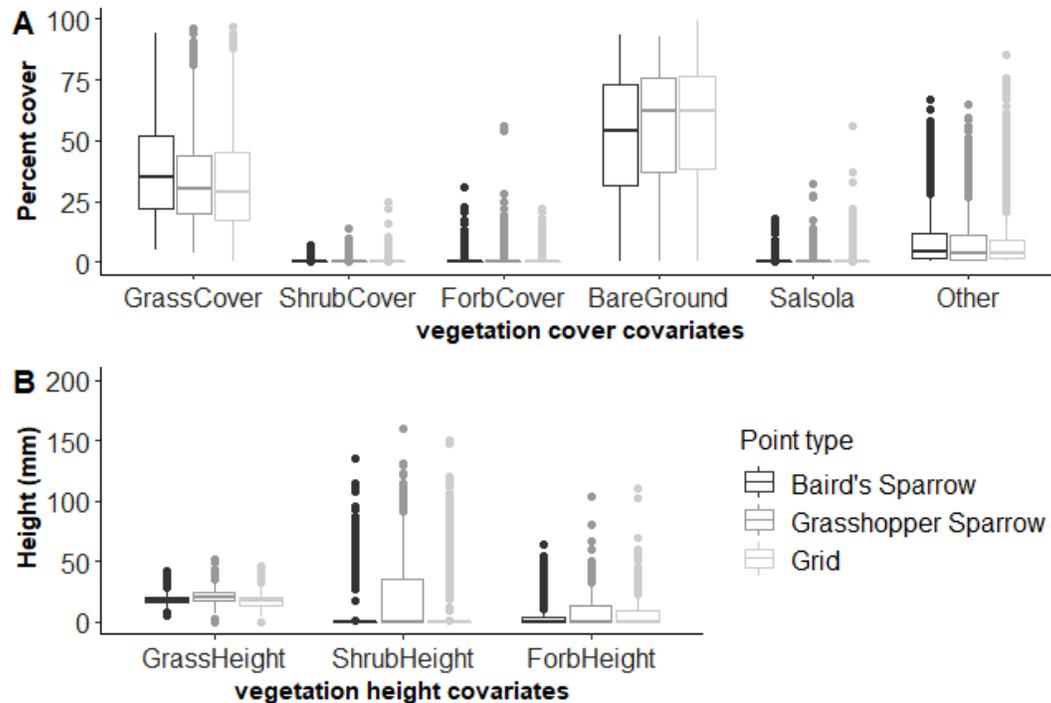
Bird monitoring

We radio tagged a total of 217 sparrows (123 Baird’s and 93 Grasshopper Sparrows) in three winters (Table 2) and obtained 6,486 locations for these tagged birds. We identified the main causes of direct mortality as depredation by the Loggerhead Shrike (*Lanius ludovicianus*; n = 16), and other diurnal raptors (n = 13) based on signs of depredation such as feathers and impaled birds or transmitters in case of depredation by Loggerhead Shrike. We also found expired birds without signs of depredation (n = 8), especially after cold nights, suggesting that these birds died from exposure.

Vegetation sampling

We collected vegetation data at 3,019 locations of tagged birds and 1,557 grid locations (Table A1.2). Grass cover (beta-

Fig. 1. Vegetation cover (A) and height (B) covariates measured in 5 m radius circles at telemetry locations of Baird's Sparrow (n = 1,678) and Grasshopper Sparrow (n = 1,462), and grid locations (n = 1,557) in the Marfa grasslands, Texas, during the winters of 2016-17, 2017-18, and 2018-19.



regression, $F_{2,4690}=10.92$, $P < 0.001$) and height (linear mixed model, $F_{2,4690}=32.84$, $P < 0.001$) differed for bird and grid locations. Generally, we observed birds in areas of dense grass cover, tall grass and little shrub cover, although there was substantial variation in vegetation cover among locations, reflecting heterogeneity in habitat and bird-habitat preferences (Fig. 1, Table A1.2). Grass cover was denser at Baird's and Grasshopper Sparrow locations compared to grid locations (Tukey post-hoc test, $q_{4690} = 4.26$ and $q_{4690} = 2.64$, $P < 0.001$ and $P = 0.022$, respectively), but was not different between bird species (Tukey post-hoc test, $q_{4690} = 1.07$, $P = 0.531$). Grass was taller at Grasshopper Sparrow locations compared to Baird's Sparrow (Tukey post-hoc test, $q_{4690} = -4.62$, $P < 0.001$) and grid locations (Tukey post-hoc test, $q_{4690} = -8.06$, $P < 0.001$), and taller at Baird's Sparrow locations compared to grid locations (Tukey post-hoc test, $q_{4690} = 2.68$, $P = 0.021$).

Survival analysis

Of the 217 radio-tagged birds, we excluded 47 from analysis because during the first week after tagging they died (n = 8), lost their radio (n = 16), or went missing (n = 23). Therefore, our survival dataset consisted of 91 Baird's Sparrows and 79 Grasshopper Sparrows, distributed equally across the three field seasons. Estimation of daily survival probability (based on models not including covariates) extrapolated by the total number of days we monitored in winter (85 days) ranged from 0.77 (90% CI = [0.54, 0.89]) to 1 for Baird's Sparrow, and 0.47 (90% CI = [0.28, 0.64]) to 0.87 (90% CI = [0.63, 0.96]) for Grasshopper Sparrow (Fig. 2).

We identified three top models ($\Delta AICc < 2$) out of the 13 candidate models that best explained winter survival of Baird's Sparrow (Table 1). Two models included minimum temperature, and one of those models included grass height. The third top model was the null model (Table 1). Model averaged confidence intervals for both covariates included zero (temperature: $\beta = 0.82$, 95% CI = [-0.04, 1.68], grass height: $\beta = -0.31$, 95% CI = [-1.00, 0.39]). For Grasshopper Sparrow there were three top models ($\Delta AICc < 2$) that best explained daily winter survival (Table 1). All models included minimum temperature, and the other two the interaction and the additive effect of grass height; two models included grass cover, and one included grass height (Table 1). Model averaged confidence intervals of the covariates in the top models showed a positive relationship between the minimum temperature and survival probability for Grasshopper Sparrow ($\beta = 0.64$, 95% CI = [0.08, 1.21]). The predictors were standardized before analysis. Exponentiating the unstandardized model-averaged estimate ($e^{0.23} = 1.26$) indicates a 26% increase in the odds of Grasshopper Sparrow winter survival for every degree ($^{\circ}C$) increase in average minimum temperature. We did not find strong support for grass height ($\beta = -0.37$, 95% CI = [-0.84, 0.10]), or the interaction between minimum temperature and grass height ($\beta = -0.11$, 95% CI = [-0.52, 0.30]).

Microclimate

Microclimate temperatures were only moderately correlated with site-level temperature data (minimum daily temperature: $r = 0.463$, mean daily temperature: $r = 0.563$, maximum daily temperature: $r = 0.347$). The second winter was more severe than

the first and third winter of the study; average minimum ambient temperature was $-2.74\text{ }^{\circ}\text{C}$ ($\pm 4.08\text{ }^{\circ}\text{C}$) in 2017-18 compared to $-0.49\text{ }^{\circ}\text{C}$ ($\pm 3.95\text{ }^{\circ}\text{C}$) and $-0.32\text{ }^{\circ}\text{C}$ ($\pm 4.74\text{ }^{\circ}\text{C}$) in 2016-17 and 2018-19, respectively. Average daily microclimate temperatures ranged from $-3.5\text{ }^{\circ}\text{C}$ to $34.0\text{ }^{\circ}\text{C}$ and were, therefore, more extreme than average daily site-level temperature data that ranged from $-0.6\text{ }^{\circ}\text{C}$ to $20.5\text{ }^{\circ}\text{C}$ during the same period (Fig. 3, Table A1.3). This was to be expected because the temperature loggers are influenced by factors such as wind, radiant heat, and conduction, and therefore shows that ambient temperature might not be the best measure to represent the actual conditions to which birds are exposed in the field.

Fig. 2. Winter survival probabilities ($\pm 90\%$ CI) of Baird's Sparrow and Grasshopper Sparrow in three winters estimated over 85 days (from mid December - mid March) in the Marfa grasslands, Texas, USA.

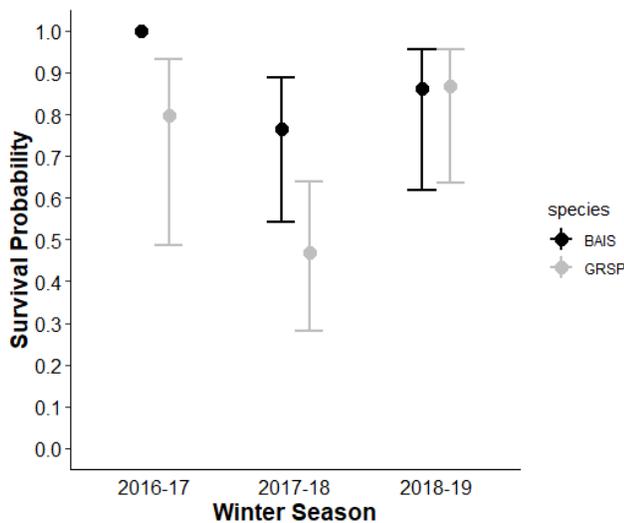
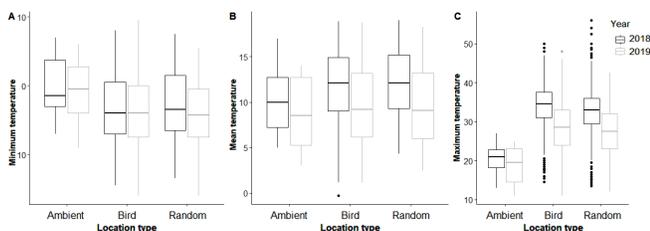


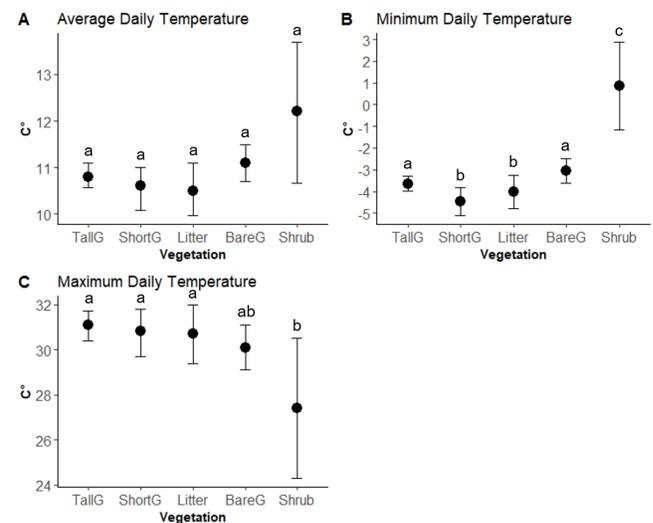
Fig. 3. Minimum ambient temperature ($^{\circ}\text{C}$) and minimum microclimate temperature ($^{\circ}\text{C}$) at bird ($n = 40$) and random ($n = 40$) locations measured from February 10 to March 3, 2018 and 2019, in the Marfa grasslands, Texas.



We did not find support for different distributions of microclimate temperature data in bird and random locations measured over 24 hours (Kolmogorov-Smirnov test, $D = 0.02$, $P = 0.109$). However, when we compared the distributions during daytime (0800 to 1700 h) they did differ significantly (Kolmogorov-Smirnov test, $D = 0.05$, $P = 0.007$), with higher maximum microclimate temperatures at bird locations vs random locations (linear mixed

model, $F_{1,78} = 7.27$, $P = 0.008$). We also found that cover type influenced the mean, minimum, and maximum microclimate temperature (linear mixed model, $F_{4,3110} = 16.70$, 16.33 , and 45.28 for mean, minimum, and maximum temperature, respectively, all $P < 0.001$, Fig. 4), but there was no interaction with point type (linear mixed model; $F_{4,3106} = 1.24$, 0.59 , and 0.57 for mean, minimum, and maximum temperature, respectively, all $P > 0.2$). Minimum temperature was significantly lower in short grass and litter compared to tall grass and bare ground (Tukey post-hoc test, all $P < 0.05$; Fig. 4.B). Minimum temperature under shrub cover was significantly higher than other vegetation types (Tukey post-hoc test, $P < 0.05$; Fig. 4.B). In contrast, the maximum temperature was significantly lower for shrubs compared to all other cover types (Tukey post-hoc test, all $P < 0.05$) except for bare ground ($P = 0.089$; Fig. 4.C).

Fig. 4. Average, minimum, and maximum daily temperature (least-square means $\pm 95\%$ CI) in different ground cover types, measured 10 cm above the ground in the Marfa grasslands, Texas, USA. Letters indicate significant differences ($P < 0.05$).



DISCUSSION

Grassland bird populations are plummeting across North America, necessitating intensive study across their full annual life cycle to understand these declines. We found that survival of Baird's and Grasshopper Sparrows wintering in Chihuahuan Desert grasslands of west Texas was driven by broadscale ambient temperature; survival probability decreased with prolonged low temperatures. We also found that, at least during the day, microclimate temperature was higher at bird locations, suggesting that grassland birds could be selecting specific microclimate on their wintering grounds. These combined findings contribute to a growing body of evidence highlighting the relationship of temperature with wintering grassland bird populations. Our research provides the first estimates of both winter survival and microclimate characteristics for Baird's and Grasshopper Sparrows in the U.S. These results are consistent with winter survival rates documented for these species in northern Mexico (Macías-Duarte et al. 2017).

Our results indicate that certain types of vegetative cover could provide microclimate refuges for grassland birds, particularly on their wintering grounds. Minimum microclimate temperatures were lower in short grass compared to tall grass. Tall grass may provide better protection against unfavorable thermal conditions (e.g. Tomecek et al. 2017, Milling et al. 2018) than short grass cover because taller vegetation could shelter birds from wind, precipitation, intense solar radiation, or frost. We also found that minimum daily temperature was higher in shrubs than in the other cover categories. Although shrubs were sparse on this landscape and our sample size for shrub microclimate was small, our results are in agreement with other studies finding warmer nighttime temperatures (D'Odorico et al. 2010, He et al. 2010, Shelef and Groner 2011), and lower daytime temperatures under shrub canopy (Shelef and Groner 2011, Tracol et al. 2011, Ruth et al. 2020).

Thermal refuges are undoubtedly important for Baird's and Grasshopper Sparrows given the negative association of winter survival with minimum daily temperature. Because of their small body size, the energetic cost of thermoregulation during cold stress is high for these birds (Scholander et al. 1950, McNab 1983). The lower critical temperature of birds the size of these sparrows is 20+ °C (Bakken 1991). Therefore, the need for metabolic heat production can result in energetic stress that could explain a higher mortality rate at low ambient temperatures (Olson and Kendeigh 1980, Porter and Kearney 2009). Furthermore, birds may need to adopt thermoregulatory postures that could increase predation risk (Carr and Lima 2011). The bill can also play a role in thermoregulation and heat loss through the bill when temperatures are low could incur an additional thermoregulatory cost (Greenberg et al. 2012, Tattersall et al. 2018). In general, Grasshopper Sparrows weigh less and have larger bills than Baird's Sparrows (Titulaer et al. 2018) and, therefore, may experience a higher thermoregulatory cost (Tattersall et al. 2017). This could explain why we found higher mortality rates for Grasshopper than Baird's Sparrows, especially in the second winter season which had the lowest minimum temperatures.

The need for thermal refuge can also restrict movement and foraging behavior generally in avifauna and other species (Villén-Pérez et al. 2013, Carroll et al. 2015, Levy et al. 2016, Haase et al. 2019) and could indirectly influence survival. Furthermore, cold-stressed birds that face the risk of starvation may find the need to replenish their energy reserves by foraging for longer periods, reducing vigilance, or foraging away from protective cover, increasing the risk of predation (Rogers 1987, Cresswell and Whitfield 2008). Foraging can also be less efficient when the ground is covered by frost, increasing searching and handling time and, therefore, lowering energy intake over time (Spencer 1982), requiring birds to forage for more extended periods under exposed conditions. Microclimate refuges provided by optimal vegetation conditions could possibly buffer this effect (Tomecek et al. 2017). Because these sparrows almost exclusively consume seeds during winter (Titulaer et al. 2017), tall grass could provide food and cover against predators and unfavorable climate.

It is important to note that we placed the temperature loggers in bird locations that were observed during telemetry, which was conducted during the daytime. Therefore, we were unable to measure microclimate conditions at bird locations during the night and predawn, when temperatures are at their lowest. Baird's

and Grasshopper Sparrows generally avoid shrub cover during the day (Desmond et al. 2005, Ruth et al. 2014), which can negatively affect survival in some cases (Macías-Duarte et al. 2017). We did not find a negative relationship between shrub cover and survival, but shrubs were so sparse in our study site (<0.5%) that birds would rarely encounter them. While these sparrows may select daytime foraging locations based on seed resources (Titulaer et al. 2017) and avoidance of diurnal predators that use shrubs for perching and hunting (eg. Loggerhead Shrike; Yosef 2020), shrub avoidance may be less critical at night, when birds more likely select for thermal cover and protection from nocturnal predators. Selection of vegetative cover at roosting locations may therefore differ from foraging locations (Ginter and Desmond 2005, Macías-Duarte and Panjabi 2013b). In fact, some birds entirely move outside of their daytime range to roost in favorable habitat (Jirinec et al. 2016). Possibly, some amount of shrub cover could be helpful to wintering birds by providing thermal refuges, but more research on nocturnal site selection in relation to microclimate conditions is needed.

Despite the microclimate buffering of tall grass, we did not find a direct effect of grass cover or height on survival. Grass cover was in top models for both species and grass height in one top model for Grasshopper Sparrow, however neither variable was considered competitive. It should be noted that this does not mean that grass cover is not important for winter survival. Baird's and Grasshopper Sparrows are strongly associated with grass cover and height in the Chihuahuan Desert (Panjabi et al. 2010, Ruth et al. 2014, Macías-Duarte et al. 2017). If birds are strongly selecting for grass cover and height, minimal variability among telemetry locations could explain the lack of relationship. Furthermore, grass cover in our study site was relatively high. It is also possible that a direct relationship of grass cover and height with survival can only be detected when roosting locations are taken into consideration, emphasizing the need for future studies that consider nighttime microclimate. Finally, habitat represents fine-scale heterogeneity, and it is possible that birds may have been moving during tracking. Thus, our estimates of vegetation are under the assumption that a bird was at the recorded location by choice. However, we believe that the use of triangulation of bird locations and highly trained technicians minimized the error in obtaining true bird locations, whereas the use of fairly large vegetation plots (5 m radius) accounted for fine-scale heterogeneity in vegetation cover.

The need for microclimate refuges may increase with climate change and the continuing fragmentation of grasslands because the effects of temperature on survival could be inversely related to patch size (Zuckerberg et al. 2018). Furthermore, widespread livestock overgrazing could exacerbate these effects by reducing vegetative cover. Therefore, we suggest additional study on grassland microclimates that records more detailed measurements on vegetation structure and species composition within open grassland patches where grassland specialist birds are found. Small-scale variations in microclimate within grassy patches are likely as important for open grassland specialists such as Baird's and Grasshopper Sparrows as the larger-scale variation between cover types measured in this study, especially in the Marfa grasslands where grass cover represents the dominant cover type. Ideally, future studies would also move temperature loggers daily to be able to incorporate microclimate measurements into analysis of survival.

CONCLUSION

We found that winter survival of Baird's Sparrow and Grasshopper Sparrow fluctuated across years ranging from 47 to 100%, and that the main driver of this variation was broadscale ambient temperature; prolonged days of low broadscale minimum temperatures negatively influenced winter survival. We also found that microclimate temperatures were warmer 1) at bird locations when compared to random locations and 2) within/under shrub and tall grass vegetation cover types and were lower in short grass when compared to tall grass. Based on our findings, we conclude that temperature is a key driver of overwintering survival of grassland birds and that the presence of thermal cover and refuges are likely important for their persistence. We suggest additional study on 1) the assessment of habitat conditions at night roost locations for grassland birds, and 2) fine-scale measurement of microclimate conditions across the full 24-hour day to advance knowledge of how grassland birds select and benefit from microclimate conditions on the wintering grounds. In addition to temperature, future studies could measure wind velocity and relative humidity.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/2010>

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Appendix 1. Supplementary tables from “The role of ambient temperature and microclimate refuges in the survival of grassland birds overwintering in the Chihuahuan Desert”.

Table A1.1. Candidate model set for winter survival analysis of Baird’s and Grasshopper sparrows in the Marfa grassland of Texas, 2016-2019. Temperature is ambient average weekly minimum temperature (°C).

Model	Model Structure
(Null) 1	Survive/trials ~ 1
2	Survive/trials ~ Temperature
3	Survive/trials ~ Grass cover
4	Survive/trials ~ Grass height
5	Survive/trials ~ Shrub height
6	Survive/trials ~ Grass height + Grass cover
7	Survive/trials ~ Temperature + Grass height
8	Survive/trials ~ Grass height + Grass cover + Shrub height
9	Survive/trials ~ Temperature * Grass height
10	Survive/trials ~ Temperature* Grass height + Grass cover+Shrub height
11	Survive/trials ~ Grass cover + Forb cover + Salsola + Other
12	Survive/trials ~ Grass height + Forb height + Shrub height Survive/trials ~ Temperature + Forb cover + Forb height + Shrub height
(Global) 13	+ Grass cover + Grass height + Russian thistle + Other + Grass height*Temperature

Table A1.2. Vegetation structure measured in 5 m radius circles at telemetry locations of Baird’s Sparrow (n = 1,678) and Grasshopper Sparrow (n = 1,462), and grid locations (n = 1,557) in the Marfa grasslands, Texas, during the winters of 2016-17, 2017-18, and 2018-19.

	Baird’s Sparrow		Grasshopper Sparrow		Grid	
	Mean	SD	Mean	SD	Mean	SD
Grass cover (%)	38.2	19.7	34.2	18.5	33.0	20.7
Grass height (mm)	18.7	5.3	20.7	6.3	17.9	5.7
Shrub cover (%)	0.2	0.6	0.3	1.0	0.3	1.2
Shrub height (mm)	6.2	17.5	11.3	25.6	9.7	22.5
Forb cover (%)	0.5	1.7	0.7	2.8	0.8	2.2
Forb height (mm)	5.1	10.2	5.4	11.4	6.1	11.0
Bare ground (%)	51.4	24.5	55.7	23.3	56.6	24.6
Salsola (%)	0.3	1.1	0.7	2.3	0.6	2.7
Other cover (%)	9.5	11.9	8.3	10.8	8.7	12.8

Table A1.3. Average minimum, mean, and maximum daily temperature ($^{\circ}\text{C} \pm \text{SD}$) from February 10 to March 3, 2018 and 2019, for broad scale (ambient) data and microclimate measurements in bird ($n = 40$) and random ($n = 40$) locations in the Marfa grasslands, Texas.

	Minimum		Mean		Maximum	
	2018	2019	2018	2019	2018	2019
Ambient (broad scale)	-0.05 (4.47)	-0.60 (4.18)	10.05 (3.47)	8.82 (3.91)	20.50 (3.99)	19.05 (4.82)
Bird (microclimate)	-3.48 (4.86)	-3.97 (4.56)	11.88 (3.58)	9.64 (4.06)	34.00 (5.58)	28.10 (7.13)
Random (microclimate)	-2.84 (7.48)	-4.19 (4.40)	12.07 (3.45)	9.50 (3.98)	32.84 (5.70)	27.07 (6.70)