



Canopy cover as the primary factor affecting habitat use by grassland-shrubland bird species in central Texas, USA

La cobertura de dosel como el factor principal que afecta el uso de hábitat por especies de aves de pastizales y arbustales en Texas central, EE. UU.

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ABSTRACT. Woody vegetation continues to encroach into grasslands in many regions of the world. It often leads to habitat loss for grassland birds. Habitat loss is one reason for the ongoing declines in abundance of many bird species that are grassland obligates. However, species that can tolerate and perhaps even prefer some amount of shrub and tree cover presumably would not be as negatively affected by woody encroachment. Using bird point-count data from the Oaks and Prairies Joint Venture, we examined the habitat associations of eight grassland-shrubland bird species in two ecoregions of central Texas USA. In particular, we focused on canopy cover, canopy height, and shrub species composition given that woody encroachment entails increases or other changes in these habitat characteristics. Further, as with many bird species, structural components of the vegetation often characterize habitat. We treated these habitat characteristics as predictor variables in logistic multiple regression models wherein the response variable was probability of species occurrence at 478 point-count locations. Overall, canopy cover was a better predictor of probability of species occurrence than was canopy height or canopy species composition. Thus, canopy cover was an important habitat characteristic for most of the species. Bewick's Wren (*Thryomanes bewickii*) exhibited its greatest probability of occurrence of approximately 0.63 at 40–60% canopy cover, Painted Bunting (*Passerina ciris*) approximately 0.74 at 15–45% canopy cover, and Rufous-crowned Sparrow (*Aimophila ruficeps*) approximately 0.09 at 50% canopy cover. The probability of occurrence of Field Sparrow (*Spizella pusilla*) consistently increased with increasing percent canopy cover, reaching a maximum value of 0.58 at 74% canopy cover. These results suggest that a limited amount of woody encroachment may actually benefit some grassland-shrubland bird species.

RESUMEN. La vegetación leñosa continúa invadiendo pastizales en muchas regiones del mundo. Ello a menudo conlleva la pérdida de hábitat para aves de pastizal. La pérdida de hábitat es una de las razones para el constante declive en la abundancia de muchas especies de aves que son especialistas de pastizales. Sin embargo, especies capaces de tolerar e incluso aun preferir cierta cantidad de cobertura arbustiva y arbórea presumiblemente no serán afectadas de manera negativa por la invasión leñosa. Utilizando datos de conteos de aves del programa Oaks and Prairies Joint Venture, examinamos las asociaciones de hábitat de ocho especies de aves especialistas de pastizales y arbustales en dos ecorregiones de Texas central, EE.UU. En particular, nos enfocamos en la cobertura y altura del dosel, y en la composición específica de arbustos dado que la invasión leñosa implica aumentos o cambios en estas características del hábitat. Además, como ocurre con muchas especies de aves, los componentes estructurales de la vegetación a menudo caracterizan el hábitat. Tratamos estas características del hábitat como variables predictoras en modelos de regresión logística múltiple, donde la variable respuesta fue la probabilidad de ocurrencia de especies en 478 sitios de puntos de conteo. En general, la cobertura del dosel fue mejor predictor de la probabilidad de ocurrencia de especies que la altura del dosel o la composición de especies del dosel. Así, la cobertura del dosel fue una característica importante del hábitat para la mayoría de las especies. La especie *Thryomanes bewickii* mostró su mayor probabilidad de ocurrencia, aproximadamente 0,63, con una cobertura del dosel del 40 -60%; *Passerina ciris* alcanzó aproximadamente 0,74 con una cobertura del dosel del 15-45%; y *Aimophila ruficeps* tuvo una probabilidad de ocurrencia de aproximadamente 0,09 con una cobertura del dosel del 50%. La probabilidad de ocurrencia *Spizella pusilla* aumentó consistentemente con el incremento en el porcentaje de cobertura del dosel, alcanzando un valor máximo de 0,58 con una cobertura del dosel del 74%. Estos resultados sugieren que una cantidad limitada de invasión leñosa podría beneficiar a algunas especies de aves de pastizales y matorrales.

Key Words: *Edwards Plateau; GIS; habitat association; juniper; mesquite; Northern Bobwhite*

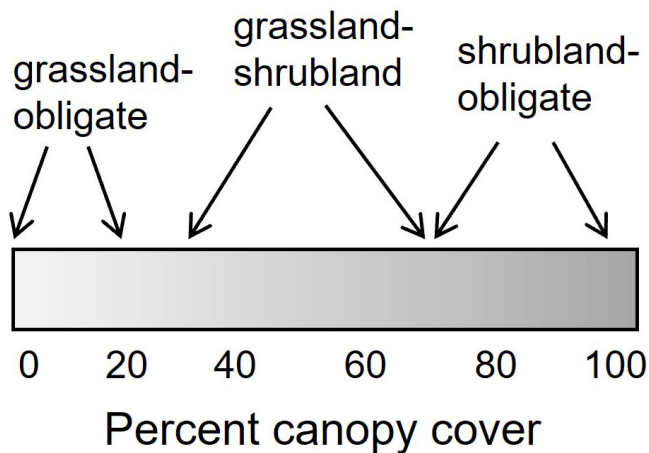
INTRODUCTION

The amount of woody canopy cover may be a distinguishing feature of the habitat of many grassland-shrubland bird species. These species are typically absent from or occur at very low densities in shrub thickets. They are also absent from the wide-open grassland habitat that is mostly devoid of woody vegetation and that is occupied by grassland-obligate species (Fig. 1). Avian ecologists are concerned about encroachment of woody vegetation into grassland areas because it leads to the loss of critical habitat for grassland-obligate species (Coppedge et al.

2001, Sirami et al. 2009, Lautenbach et al. 2020). Further, such habitat loss has been identified as a major driver in the ongoing declines of some grassland-obligate bird species (Coppedge et al. 2001, Chapman et al. 2004, Grant et al. 2004, Brennan and Kuvlesky 2005, Scholtz et al. 2017, Andersen and Steidl 2023, Silber et al. 2024). Contrary to the effect on grassland-obligate birds, woody plant encroachment may not be as detrimental to grassland-shrubland birds, those species that can tolerate and perhaps even seek out habitat with some amount of shrub and tree cover.

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Fig. 1. Schematic diagram indicating the differences among the three habitat-based groups of birds. Diagram shows the range of percent canopy cover, between the arrows, for which a species (in the group) would be expected to have its greatest probability of occurrence. Placement of arrows is not intended to indicate that individual birds of the given group would never occur in areas outside the indicated values of canopy cover.



Woody plant encroachment is often driven, both directly and indirectly, through human actions (Archer et al. 1995, Van Auken 2000, Briggs et al. 2002, Londe et al. 2022). By transforming prairies into pasture for livestock grazing, landscapes are made more permeable to woody encroachment (Van Auken 2000, Briggs et al. 2002, Sharp and Whittaker 2003). Another major factor has been years of fire suppression on the landscape (Higgins et al. 2000, Bond et al. 2003). North American grasslands are disturbance-driven ecosystems (Bragg 1995, Ratajczak et al. 2014). Through periodic burns, native grasses and forbs are propagated, invasive species are removed (Grant and Murphy 2005), and aggressively growing woody plants, such as mesquite and juniper, are reduced (Briggs et al. 2002, Reemts and Hansen 2007, Twidwell et al. 2013). Prior to fire suppression, near-eradication of grazing species such as bison and prairie dogs also initiated structural changes in landscapes of the Great Plains (Coppedge and Shaw 1997, Brennan and Kuvlesky 2005). Woody plant encroachment is particularly evident within central Texas where mesquite (*Prosopis glandulosa*) and ashe juniper (*Juniperus asheii*) have been spreading and causing increases in woody canopy density for at least a century (Murray et al. 2013, Rhodes et al. 2021). As such, the spread of woody vegetation into grassland areas provides greater physical structure (e.g., increased canopy cover and height) in the habitat perhaps making the habitat more amenable to grassland-shrubland bird species; i.e., those species that require a highly integrated mix or mosaic of dense shrub clusters interspersed with small open canopy-less areas. In this study, we examined the effect of canopy cover, canopy height, and shrub species composition on occurrence of eight grassland-shrubland bird species in central Texas.

Canopy cover has been repeatedly identified as an influential factor in the use of breeding and foraging habitat by various grassland-shrubland bird species (Willson 1974, Rotenberry and

Wiens 1980, Wiens 1989a, 1989b, Feichtinger and Veech 2013, Vasseur and Leberg 2015, Crouch et al. 2019). The physical structure of the vegetation, such as percent canopy cover and height, may be more important habitat requirements than species composition of the vegetation (Quine et al. 2007, Bahía and Zalba 2019, Hořák et al. 2019, Magnano et al. 2019). The amount of canopy cover influences the foraging and breeding (nesting) behavior of the species. For example, Scissor-tailed Flycatchers (*Tyrannus forficatus*) require shrubs or trees for perching while visually scanning for large insect prey in open spaces (Klopatek and Kitchings 1985, Teather 1992, Nolte and Fulbright 1996). Therefore, they are more likely to occupy landscapes that are generally open (lacking canopy cover) but with scattered trees and shrubs (Feichtinger and Veech 2013). For grassland-shrubland species that build nests well off the ground, tree and shrub canopy also forms the requisite structure for nesting. Canopy cover and height might both be important habitat characteristics. However, canopy cover is a more distinctive structural element in that it defines the horizontal dimension of the vegetation whereas canopy height forms the vertical dimension which is not as pronounced in the landscapes of central Texas where tall trees are generally absent except along rivers.

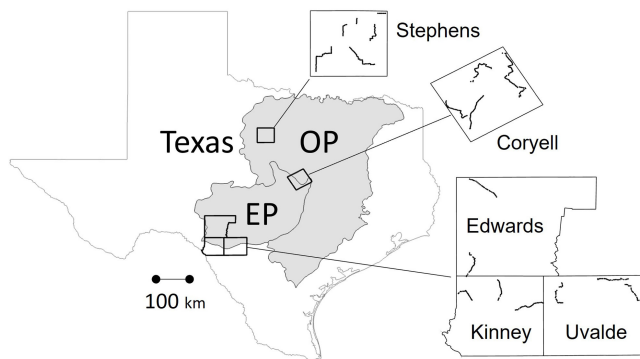
In this study we tested whether a suite of eight grassland-shrubland bird species differ in association with canopy cover, and whether canopy cover was a more important habitat characteristic in predicting species occurrence than either canopy height or species composition of the canopy. Our eight study species were Bewick's Wren (*Thryomanes bewickii*; BEWR), Cassin's Sparrow (*Peucaea cassinii*; CASP), Field Sparrow (*Spizella pusilla*; FISP), Lark Sparrow (*Chondestes grammacus*; LASP), Northern Bobwhite (*Colinus virginianus*; NOBO), Rufous-crowned Sparrow (*Aimophila ruficeps*; RCSP), Painted Bunting (*Passerina ciris*; PABU), and Yellow-billed Cuckoo (*Coccyzus americanus*; YBCU). All eight species have been identified as indicators of grassland and shrubland ecosystem health in certain regions of the United States such as the Oaks and Prairies and the Edwards Plateau bird conservation regions in Texas and Oklahoma (Giocomo et al. 2017, 2022). We predicted that each of these grassland-shrubland species would be most likely to occur at point-count locations ("Species data" section) having an intermediate amount (30 - 70%) of canopy cover (Fig. 1). Further, we expected that this maximum probability of occurrence for each species would be associated with different percentages of canopy cover depending on whether the species' habitat preferences leaned more toward grassland or shrubland vegetation. Based on the known general habitat of each species, we predicted that the species would be associated with increasing amounts of canopy cover in this order: CASP/LASP, BEWR/FISP/NOBO/PABU/RCSP, and YBCU, where "/" indicates nonresolvable order.

METHODS

Study region

The study region included areas within the Edwards Plateau and Oaks and Prairies regions of Texas, USA (Fig. 2). The landscapes in these areas consist of an interspersed mix of forest, shrubland, prairie, and agricultural land. The western and southwestern portions of the region (Edwards Plateau) have a varied topography of hills, canyons, and bottomlands along small rivers.

Fig. 2. Map of the study region, counties, and points along the survey routes. The study was confined to portions of 19 OPJV survey routes within the Edwards Plateau (EP) and Oaks and Prairies (OP) Bird Conservation Regions and five counties. Note that OP extends north into parts of Oklahoma and Kansas (not shown). The sinuous lines in each county represent survey routes.



Elevation ranges from 240–762 m (Griffith et al. 2007). The eastern and northern portions of the region (Oaks and Prairies) have a flatter topography; elevation ranges from 90–320 m (Griffith et al. 2007). Common native grasses are *Andropogon* and *Bouteloua* species. Canopy is mostly formed by mesquite (*Prosopis glandulosa*), juniper (*Juniperus sp.*), oaks (*Quercus sp.*), and cedar elm (*Ulmus crassifolia*), along with several other less common broadleaf species (Larkin and Bomar 1983).

Species data

Presence-absence data for the eight bird species were obtained from the Oaks and Prairies Joint Venture (OPJV, <https://www.opjv.org/>). Since 2013, the OPJV has been conducting a long-term grassland bird monitoring program to assess the efficacy of their Grassland Restoration Incentive Program (GRIP; Giocomo et al. 2022). The eight focal species of our study were included in the group of 17 species that the OPJV has chosen as indicators of grassland health. The nine species not included in our study either had insufficient amounts of data (occurrence at < 10% of survey points) or were considered *a priori* to be grassland-obligate species. We consider a low rate of species occurrence prevents a meaningful assessment of habitat associations. The OPJV monitoring program consisted of five-minute roadside point-counts along rural survey routes. All individuals of the focal species seen and heard within a presumed detection distance of approximately 250 m were recorded. For the species and survey points of our study, most detections (>90%) were by sound except for RCSP (85.8% sound) and LASP (70.8% sound). Each survey route consisted of 50 potential survey points, spaced roughly 800 m apart on public secondary and tertiary roads. Routes were typically surveyed once a year in May and June, with the goal of covering at least 30 points per route in a single one-day (morning) survey. Surveying was conducted by trained and paid staff of the OPJV. Most routes have been surveyed for the majority of years since the inception of the monitoring program; in this study we included data between 2013 and 2019. We used data from 17

survey routes located in five counties (Coryell, Edwards, Kinney, Stephens, and Uvalde; Fig. 2) that overlapped with the GIS databases used to obtain habitat variables (next section). Some survey routes were not located entirely within the bounds of the canopy cover GIS database. On those routes, points without canopy cover data were excluded. Points were also excluded if they were surveyed only one year of the seven-year time frame. Over the 17 survey routes, we had a total of 478 usable points, giving an average of about 28 points per route.

For each species, the probability of occurrence (i.e., naïve occupancy) was taken as the proportion of surveyed years that the species was recorded at the given point. Of the 478 points, 25 were surveyed 7 years, 182 for 6 years, 38 for 5 years, 179 for 4 years, 27 for 3 years, and 27 for 2 years, for a total of 2308 point-counts. The mean number of survey years per point was 4.8. Although the OPJV protocol collects repeat-survey data (i.e., survey units surveyed repeatedly over time) we did not use occupancy modeling in our statistical analysis. This was primarily because we did not consider the survey points to be closed between years and we did not have subsampling within a year (May to June) to allow for using occupancy models to estimate “extinction” and “colonization” rates. Thus, our measure for “probability” of species occurrence is atypical in that it derives from species occurrence over a range of years rather than occurrence over a range of days, week, or months representing temporally-repeated surveying within a closed survey season. Nonetheless, we believe our measure assesses the extent to which a species repeatedly uses the area (from year to year) around a survey point for breeding activities. That is, the measure is assessing habitat use. Also, despite not employing occupancy modeling, we were able to examine extraneous variables that might affect species detection probability.

We tested whether the following survey variables statistically influenced bird detections: anthropogenic noise, Julian date, percent cloud cover, survey start time, and wind speed (Table 1). Anthropogenic noise, percent cloud cover, and wind speed were estimated in the field by OPJV technicians at the time of a survey. For each species, we used a two-sample *t*-test to identify statistically significant ($P < 0.05$) differences in mean values of these variables, averaged for all survey years, between points where the species was detected and points where the species was not recorded (not detected). Variables that significantly affected detection were included in the logistic regression models in order to account for their effect on species probability of occurrence (i.e., proportion of years that a species was recorded; Table 1). RCSP was the only species in which detection was apparently unaffected by any of the survey variables.

Habitat data

We examined three environmental variables predicted to be important in forming the habitat of the eight species: percent canopy cover, mean canopy height, and canopy species composition. The latter variable was measured as the difference between percent cover of broadleaf tree/shrub species and juniper species. Data for the three variables came from different GIS databases, each of which were ultimately derived from remote sensing. For percent canopy cover, we utilized a canopy classification database developed by the United States Fish and Wildlife Service that incorporates 2016 National Agriculture Imagery Program (NAIP) data with a one-

Table 1. List of survey variables affecting bird detections. Refer to text for species abbreviations and for species scientific names.

| Variable | Description | Species detections affected |
|--------------------------|---------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------|
| Anthropogenic noise (AN) | 0-3 scale (0 = silent, 1 = distant noise, not interfering with detection, 2 = difficult to hear the birds at times, and 3 = constant noise) | BEWR, FISP, PABU, YBCU |
| Julian date (JD) | 0-365 days | CASP, FISP, LASP, NOBO, PABU, YBCU |
| Percent cloud cover (CC) | 0-100% (increments of 10%) | BEWR, FISP, LASP, NOBO, YBCU |
| Start time (ST) | Minutes before/after sunrise + 30 minutes | BEWR |
| Wind speed (WS) | 0-4 scale (0 = no wind, 1 = 1-3 mph sustained wind, 2 = 4-7 mph sustained wind, 3 = 8-12 mph sustained wind, and 4 > 12 mph sustained wind. | BEWR, NOBO, PABU, YBCU |

meter pixel resolution (Sesnie et al. 2016, Mueller et al. 2022). This database was originally developed to classify Golden-cheeked Warbler habitat (Mueller et al. 2022). As such, each pixel is assigned to one of three categories: juniper canopy cover, broadleaf canopy cover, or absence of woody canopy cover. The database was able to identify broadleaf species with 89% accuracy and juniper pixels with 95% accuracy (Sesnie et al. 2016). We considered any pixel categorized as either juniper or broadleaf to represent 100% canopy cover. Any pixel categorized as “absence” represented 0% canopy cover. With this information, we used ArcGIS Pro to determine the percent canopy cover (based on a count of all 100% canopy cover pixels) within a 250-m radius buffer centered on each OPJV survey point. For example, if 98,125 out of the 196,250 total possible 1-m² squared pixels in a 250-m radius circular buffer were assigned to 100% canopy cover, then the percent canopy cover for the buffer would be 50%. A buffer radius of 250 m matched the presumed maximum distance for detecting birds. However, this also entailed that our species-habitat models (next section) only apply to this spatial scale.

Canopy height was calculated using data from the Global Ecosystem Dynamics Investigation (GEDI) satellite. GEDI is a mission launched by NASA in December 2018 to study deforestation on a global scale and determine its impact on global CO₂ concentration in the atmosphere. The GEDI satellite uses LiDAR to generate canopy height data at a 30 m pixel resolution for the entire planet. In ArcGIS Pro, we calculated mean canopy height over all 218 pixels in each 250 m buffer. A 250 m buffer (196,349 m²) has 218 30 x 30 m pixels. Because mean canopy height was correlated with canopy cover ($r = 0.66$), we regressed height against cover to obtain the residuals to use as a “new” variable for canopy height. We thereby removed the correlation with canopy cover from the canopy height variable. The smallest residual value was -2.48, so we added +2.48 to all the residuals to rescale them so that they would all be > 0.

To calculate the difference between broadleaf and juniper cover (hereafter, B-J difference), we again used the USFWS-NAIP GIS database. We subtracted the number of juniper pixels within a 250 m buffer by the number of broadleaf pixels within the same buffer. Because this variable could take on negative values, we added 1 to each value so that all the observed values would be >

0. Thus, B-J difference could range between 0 and 2 with a value of 1 indicating equal canopy cover of broadleaf and juniper tree species. None of the three variables was substantially correlated with the other two: canopy cover vs. canopy height corrected ($r = 0.0005$), canopy cover vs. B-J difference ($r = -0.40$), and canopy height corrected vs. B-J difference ($r = 0.42$).

As described, we used 250 m radius circular buffers centered on the OPJV survey points to quantify and examine the effects of the habitat variables on each species. We chose buffers of this size because it was consistent with OPJV survey protocols, which did not record any bird observations that were greater than 250 m away from any given point. This was likely the maximum distance that any of these species could be detected acoustically. Most (86.3%) detections occurred within 150 m. Additionally, a 250-m buffer size was chosen to limit the chances of counting the same bird as present at two different points (as could occur if buffers were larger or closer together) on any given day and to prevent overlapping radii during both model building and testing. Lastly, the data for the three environmental variables derived from remote sensing imagery obtained in only a single year within the seven-year span covering the species data. Certainly, for some buffers, the amount of canopy cover and canopy height may have changed slightly during the seven-year period, although no buffers had major disturbances such as mechanical shrub clearing or fire. As such, any temporal change in canopy cover and height simply added measurement noise and made our estimates based on a single year slightly less representative of the entire seven-year period. The measurement error for the environmental variables was unbiased with regard to the species occurrence data.

Statistical analysis

Given that our response variable, proportion of years that the species was recorded at a given point-count location, was constrained between 0 and 1, we used logistic regression to analyze species-habitat associations. Although logistic regression is more often applied to data that are strictly binary, it can be used on a response variable that derives from a binary process (e.g., at a given point-count location in a given year, species X either was or was not detected). Further, “proportion of years recorded” provided more detailed information about a species’ frequency of using the habitat at a point-count location than did simple presence-absence.

For each species, we first conducted a full model that had all three habitat variables as both linear and quadratic terms and the relevant survey variables identified as affecting detection probability. We then performed a single-factor model for any of the habitat variables whose linear or quadratic terms had $P \leq 0.1$ in the full model. The more permissive alpha level of 0.1 (rather than 0.05) was used so as to not discard predictor variables that could possibly be statistically significant ($P \leq 0.05$) when examined in isolation from the other variables. As is common practice with logistic regression, we calculated the null and residual deviance to assess model fit. Null deviance quantifies how well a model with just an intercept term fits the data, whereas residual deviance quantifies model fit when the predictor variables are also included. Thus, a good measure of model performance is simply the percent reduction in deviance that comes from having predictor variables in the model. To further measure the performance of models relative to each other, we calculated the AIC value of each model.

Table 2. Species prevalence among the point-count locations depicted in Fig. 2 and as accumulated from 2013 to 2019. N_{total} is the total number (out of 478) of point-count locations where the species was recorded in at least one out of the 2 to 7 survey years. $N_{p=0}$ is the number of point-count locations at which the species was never recorded, $P(\text{occurrence}) = 0$. $N_{p=1}$ is the number of point-count locations where species was recorded in every survey year, $P(\text{occurrence}) = 1$. Mean naïve probability of occurrence is the mean proportion of years that the species was recorded at each point-count location. Maximum probability of occurrence is the maximum predicted probability of occurrence from the full model.

| Species | N_{total} | $N_{p=0}$ | $N_{p=1}$ | Mean naïve $P(\text{occur.})$ | Max. $P(\text{occur.})$ canopy | Total number of detections |
|---------------------------------------------------|-------------|-----------|-----------|-------------------------------|--------------------------------|----------------------------|
| Bewick's Wren, <i>Thryomanes bewickii</i> | 419 | 59 | 47 | 0.4532 | 0.6229 | 992 |
| Cassin's Sparrow, <i>Peucaea cassinii</i> | 73 | 405 | 19 | 0.0846 | 0.1509 | 157 |
| Field Sparrow, <i>Spizella pusilla</i> | 149 | 329 | 17 | 0.1629 | 0.5847 | 313 |
| Lark Sparrow, <i>Chondestes grammacus</i> | 305 | 173 | 9 | 0.2313 | 0.2656 | 519 |
| Northern Bobwhite, <i>Colinus virginianus</i> | 198 | 280 | 13 | 0.1784 | 0.2123 | 386 |
| Painted Bunting, <i>Passerina ciris</i> | 451 | 27 | 105 | 0.6404 | 0.7376 | 1510 |
| Rufous-crowned Sparrow, <i>Aimophila ruficeps</i> | 78 | 400 | 0 | 0.0465 | 0.0852 | 91 |
| Yellow-billed Cuckoo, <i>Coccyzus americanus</i> | 206 | 272 | 1 | 0.1238 | — | 301 |

Logistic regression modeling and calculation of deviance and AIC values were conducted in R using the glm() function with family = binomial.

Lastly, as a check on the performance of the models when using “proportion years recorded” as a response variable, we also conducted logistic regression models with presence-absence (coded as 1,0) as the response variable. For these models, a species being recorded in at least one survey year of a point-count location was considered as “present.” Further, our species data derived from a stratified sampling design in that point-count locations were associated to a route. Therefore, we also applied conditional logistic regression using route as the stratum. We used the clogit () function in the “survival” R package; conditional logistic regression can also be conducted using the clogistic() function in the “Epi” R package. For both functions, the response variable must be binary, hence we used our 0,1-coded response variable. We then compared the mean residuals of these three logistic regression techniques as applied to the full models.

RESULTS

Over the 478 point-count locations and two to seven survey years, the probability of species occurrence (proportion of years a species was recorded) ranged from 0–1 for all species except RCSP. That is, each species was always absent from at least one point-count location and always present at one or more locations. The maximum proportion of surveys where RCSP was observed was 0.75 at only a single point-count location. By far, the most often detected species was PABU, which was detected at 451 of 478 (94.4%) survey points, followed by BEWR (87.7%) and LASP (63.8%) respectively (Table 2). Thus, these three species were relatively common and widespread. The remaining species were detected at less than half of the survey points: YBCU (43.1%), NOBO (41.4%), FISP (31.2%), RCSP (16.3%), and CASP (15.3%; Table 2). As such, they were less common but still common enough for a meaningful analysis of habitat associations.

As expected, canopy cover, height, and relative amounts of broadleaf and juniper cover varied among the survey points. Within the 250 m-radius circular buffers surrounding the survey points, canopy cover values ranged from 0.01–73.6%, with a mean of 23.95% over all 478 survey points. Mean canopy height in raw form ranged from 0 to 6.90 m, in corrected and rescaled form the

range was 0.003 - 5.88. B-J difference ranged from 0.60 (juniper dominant canopy) to 1.4 (broadleaf dominant canopy). Recall that B-J difference = 1.0 represents equal proportions (50:50) of broadleaf and juniper in the canopy. Of the 478 survey points, 316 (66%) had a B-J difference value between 0.9 and 1.1 indicating relatively equal proportions of broadleaf and juniper in the canopy contained within the 250-m radius circular buffers.

The initial comparison of regression techniques indicated that logistic regression with “proportion years recorded” was appropriate for revealing meaningful effects ($P \leq 0.1$) of the habitat variables. These models revealed 17 instances of such effects or relationships between the response variable and a predictor habitat variable (Appendix 1). In addition, these models had the smallest mean residual for 6 out of 8 species (Appendix 1). Logistic regression with presence-absence as the response variable revealed 19 meaningful relationships but never had the smallest mean residual. Conditional logistic regression revealed only 11 meaningful relationships. For some species, there was fairly good agreement between the three techniques (e.g., FISP) whereas for others (e.g., NOBO) there was not (Appendix 1). To streamline our analysis, we decided to do all further modeling using “proportion years recorded” as the response variable.

We constructed a total of 20 logistic regression models to test for habitat associations of the eight species. A full model including all three habitat variables was examined for each species, followed by single-factor models for those variables that were statistically significant ($P \leq 0.1$) in the full model. The full models showed a deviance reduction between 10 and 50% (Table 3), indicating that addition of the habitat variables into the logistic regression model (equation) substantially improved the fit of the model to the data, in comparison to the null model that included only the y-intercept. There was substantial deviance reduction (> 10%) for 8 of the 12 single-factor models, however none of the single-factor models had a greater deviance reduction than their counterpart full model (Table 3). In addition, with one exception (RCSP), the full models always had lower AIC values than the single-factor models, with ΔAIC often > 20 (Table 3). There were five instances where a given habitat variable in either linear or quadratic form was statistically significant ($P < 0.05$) in both the full model and the single-factor model. These were BEWR - canopy cover, FISP - canopy cover,

Table 3. Results from the logistic regression models applied to probability of occurrence of eight grassland-shrubland bird species in central Texas. Refer to text for species abbreviations and for species scientific names.

| Species | Full model [†] | | | | | Single factor model | | | | Significant in both models? | |
|---------|-----------------------------|-------------|---------|---------------------------------|-------|---------------------|---------|---------------------------------|-------|-----------------------------|----------------|
| | Habitat variables | Coefficient | P-value | Deviance reduction [‡] | AIC | Coefficient | P-value | Deviance reduction [‡] | AIC | <i>P</i> < 0.05 | <i>P</i> < 0.1 |
| BEWR | Canopy cover | 0.062 | 0.0013 | 14.74% | 612.0 | 0.057 | 0.0021 | 10.14% | 612.9 | yes | yes |
| | Canopy cover ² | -0.0005 | 0.0765 | — | — | -0.0006 | 0.0320 | — | — | no | yes |
| | B-J difference | 16.45 | 0.0956 | — | — | -1.14 | 0.88 | 5.71% | 632.3 | no | no |
| | B-J difference ² | -8.83 | 0.0801 | — | — | -0.555 | 0.90 | — | — | no | no |
| CASP | Canopy cover | -0.018 | 0.77 | 49.49% | 141.4 | 0.065 | 0.0851 | 9.09% | 218.4 | no | no |
| | Canopy cover ² | -0.003 | 0.0291 | — | — | -0.0012 | 0.0692 | — | — | no | yes |
| | Canopy height | -4.54 | 0.0365 | — | — | 0.616 | 0.53 | 31.08% | 167.8 | no | no |
| | Canopy height ² | 0.418 | 0.46 | — | — | -0.587 | 0.0585 | — | — | no | no |
| FISP | Canopy cover | 0.107 | 0.0010 | 36.88% | 293.7 | 0.085 | 0.0036 | 19.96% | 323.5 | yes | yes |
| | Canopy cover ² | -0.0005 | 0.24 | — | — | -0.0008 | 0.0582 | — | — | no | no |
| | Canopy height | 1.58 | 0.0428 | — | — | -0.396 | 0.42 | 19.01% | 320.8 | no | no |
| | Canopy height ² | -0.502 | 0.0045 | — | — | -0.047 | 0.68 | — | — | no | no |
| | B-J difference | 57.46 | 0.0018 | — | — | 32.47 | 0.0571 | 15.50% | 329.2 | no | yes |
| | B-J difference ² | -29.69 | 0.0029 | — | — | -19.54 | 0.0394 | — | — | yes | yes |
| LASP | Canopy cover | 0.028 | 0.24 | 10.09% | 354.0 | 0.023 | 0.32 | 9.04% | 347.4 | no | no |
| | Canopy cover ² | -0.0007 | 0.0897 | — | — | -0.0008 | 0.0563 | — | — | no | yes |
| NOBO | Canopy cover | 0.015 | 0.56 | 17.57% | 312.8 | 0.012 | 0.62 | 8.22% | 321.8 | no | no |
| | Canopy cover ² | -0.0008 | 0.0882 | — | — | -0.0004 | 0.40 | — | — | no | no |
| | Canopy height | -1.51 | 0.0511 | — | — | -0.193 | 0.68 | 13.57% | 316.0 | no | no |
| | Canopy height ² | 0.191 | 0.22 | — | — | -0.074 | 0.50 | — | — | no | no |
| PABU | Canopy cover | 0.067 | 0.0004 | 18.11% | 587.7 | 0.068 | 0.0003 | 11.93% | 610.1 | yes | yes |
| | Canopy cover ² | -0.001 | 0.0001 | — | — | -0.001 | 0.0003 | — | — | yes | yes |
| RCSP | Canopy cover | 0.126 | 0.0367 | 18.67% | 71.8 | 0.129 | 0.0297 | 12.65% | 62.27 | yes | yes |
| | Canopy cover ² | -0.001 | 0.11 | — | — | -0.001 | 0.0960 | — | — | no | yes |
| YBCU | — | — | — | — | — | — | — | — | — | — | — |

[†] Results for the full models only show the habitat variables that had *P* ≤ 0.1. These variables were then examined in the single factor regression models.

[‡] Percent deviance reduction pertains to a model having all three habitat variables (for the full model) and relevant survey variables (for full and single-factor models), not just the variables shown in the table.

FISP - B-J difference, PABU - canopy cover, and RCSP - canopy cover (Table 3). BEWR and FISP were most likely to be present at point-count locations with 50–70% canopy cover (Figs. 3, 4) whereas greatest probability of occurrence for PABU and RCSP was at about 30 and 50% canopy cover respectively (Fig. 3).

Percent canopy cover in either linear or quadratic form was significant (*P* < 0.05) in the full model for each species except LASP, NOBO, and YBCU (for this species, none of the three habitat variables were significant). The model-predicted maximum probability of occurrence as based on canopy cover was greater than the naïve probability of occurrence (Table 2). For four species (BEWR, FISP, PABU, and RCSP), significance (*P* < 0.05) of either the linear or quadratic term for percent canopy cover was also retained in the single-factor models. These models revealed that deviance was reduced by 10–20% based solely on including percent canopy cover as a predictor variable (Table 3). Probability of species occurrence for BEWR, PABU, and RCSP was a curvilinear function of percent canopy cover based on both the full model and the single-factor model. Indeed, for a given species, the full and single-factor models agreed very well regarding the form of the relationship (Fig. 3). This result indicates that for these species, habitat can be characterized by a relatively narrow range of canopy cover. This was not the case for FISP; the full model and single-factor model did not agree on the form of the relationship (Fig. 4). The full model revealed that species probability of occurrence increased with increasing percent canopy cover whereas the single-factor model revealed a flat relationship with a negligible (extremely restricted) peak in

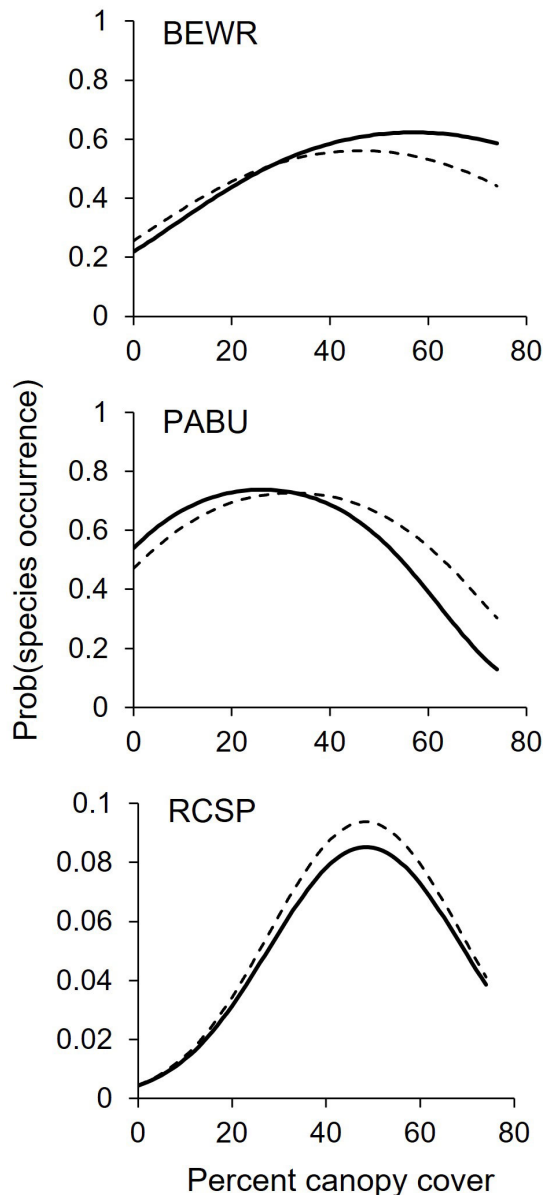
probability of occurrence (Fig. 4) even though the linear term (*P* = 0.0036) and quadratic term (*P* = 0.0582) were significant in the single-factor model. Based on the full model, FISP was most likely to be present at point-count locations having the maximum observed canopy cover of 70–74% (Fig. 4).

Mean canopy height in either linear or quadratic form was significant (*P* < 0.1) in the full model for only three species (CASP, FISP, and NOBO; Table 3), thus revealing that this habitat characteristic does not influence species probability of occurrence as much as canopy cover does. The only instance of canopy height being significant in the single-factor models was the quadratic term in the model for CASP (*P* = 0.0585). B-J difference in either linear or quadratic form was significant (*P* < 0.01) for only BEWR and FISP (Table 3). However, this significance was not retained in the single-factor model for BEWR and the percent deviance reduction (5.71%) of that model was the lowest of all models examined. Contrary to this result for BEWR, B-J difference did retain its significance in the single-factor model for FISP (Table 3). Probability of occurrence of FISP was curvilinearly related to B-J difference, although the form of the relationship differed somewhat between the full model and the single-factor model (Fig. 5).

DISCUSSION

In landscapes of central Texas, the eight bird species that we examined exist in a tight mosaic of dense clusters of shrubs and small trees (e.g., areas of 0.1 to 0.5 ha with 90–100% canopy cover) interspersed with open grassy meadows (e.g., areas of the same

Fig. 3. Relationship between species probability of occurrence and percent canopy cover for Bewick's Wren (BEWR, *Thryomanes bewickii*), Painted Bunting (PABU, *Passerina ciris*), and Rufous-crowned Sparrow (RCSP, *Aimophila ruficeps*). Species not shown did not have a statistically significant relationship with percent canopy cover. Solid line depicts the full model with all variables, other than percent canopy cover, held constant at the mean observed over the 478 point-count locations. Dashed line depicts the single-factor model that includes only percent canopy cover and the survey variables that affected detection of the given species, as indicated in Table 1. Confidence intervals (not shown) are large given that the standard errors of the beta-coefficients for many of the non-significant variables were large. Note that the y-axis for RCSP is scaled differently from BEWR and PABU. X-axes are scaled from 0% to 74%, the maximum value observed for percent canopy cover.

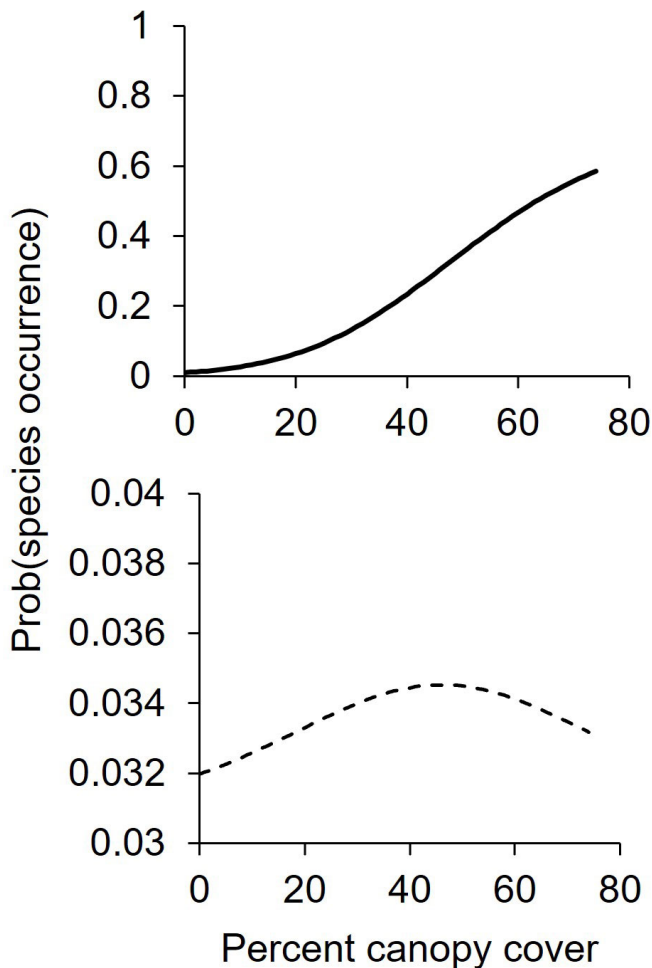


size but with 0% canopy cover). Canopy height is much more uniform. At each survey location, spatial variation in canopy cover is much more visually apparent (to humans and possibly birds as well) than variation in canopy height or shrub species composition. Perhaps, grassland-shrubland birds use canopy cover as a cue in selecting breeding habitat. For this reason, we expected that canopy cover would be an important factor in determining the distribution (or probability of occurrence) of each species. The logistic regression models revealed percent canopy cover to have a greater influence on species probability of occurrence than did mean canopy height or B-J difference (canopy species composition). That is, most of the eight bird species were more strongly associated with canopy cover than the other two habitat characteristics. Canopy cover was a statistically significant predictor (in either linear or quadratic form, $P < 0.05$) in the full and single-factor models for Bewick's Wren, Field Sparrow, Painted Bunting, and Rufous-crowned Sparrow but not for Cassin's Sparrow, Lark Sparrow, and Northern Bobwhite (Table 3).

Of the four species for which canopy cover seemed to be an important habitat component (significant in full and single-factor models), the species' response to canopy cover varied. The probability of occurrence for Bewick's Wren displayed a broad peak at probability ≈ 0.6 between about 40 and 60% canopy cover. Painted Buntings had a more defined peak at probability ≈ 0.7 between about 18 and 22% canopy cover. These results are expected given that both species are known to occupy habitat that is a diffuse and heterogeneous mix of small trees, shrubs, and open grassy areas (Miller 1941, Bent 1948, Parmelee 1959, Oberholser 1974, Gates and Gysel 1978, Joos et al. 2014) as would occur in landscapes and breeding territories that have 20–60% canopy cover on average. Rufous-crowned Sparrows had a very well-defined peak at about 48–50% canopy cover but at a very low probability of occurrence < 0.1 (Fig. 3). The habitat of Rufous-crowned Sparrows has previously been defined as semiarid grassy shrublands, with patches of open area such as grass, rock outcrops, or bare ground (Wolf 1977, Howell 1995, Collins 1999). Probability of occurrence of Field Sparrows increased consistently with an increase in percent canopy cover, as revealed by the full model; the single-factor model showed virtually no relationship of probability of occurrence to canopy cover (Fig. 4). In a study conducted in the Missouri Ozarks, Reidy et al. (2014) found the density of Field Sparrows to peak at 70–80% forest cover. In central Texas, Field Sparrows are known to occur in juniper-oak scrub habitat that has been disturbed and recovered to an early or mid-successional stage having many small shrubs but also open grassy areas (Oberholser 1974); a similar habitat is occupied by the species in Illinois (Best 1977). Therefore, unlike some sparrow species, Rufous-crowned and Field Sparrows will occur in landscapes and utilize breeding territories that have some amount of woody vegetation.

The importance of vegetation structure in forming the habitats of species (particularly birds) is not surprising or a new discovery (James 1971, Rotenberry and Wiens 1980, Cody 1981). The amount of canopy cover and possibly canopy height might serve as visual cues to an individual bird for whether to establish a territory (or not). Although habitat selection is a complex ecological process, with numerous factors (e.g., conspecific attraction, predator avoidance, food availability) determining

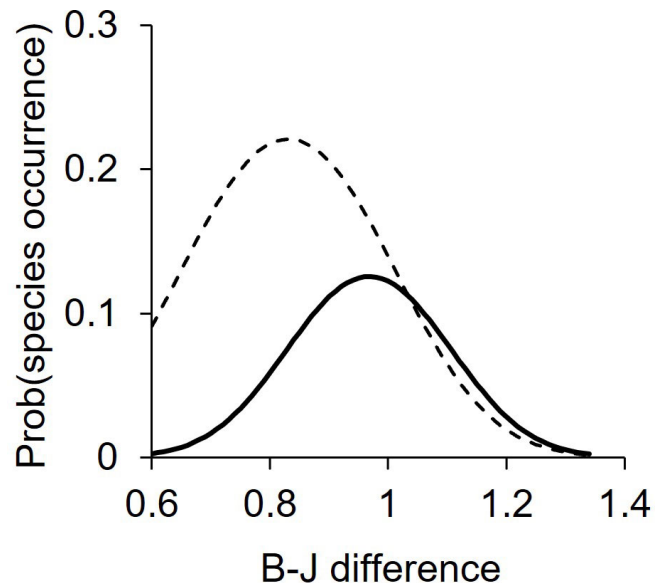
Fig. 4. Relationship between species probability of occurrence and percent canopy cover for Field Sparrow (*Spizella pusilla*). Top panel depicts the full model with all variables, other than percent canopy cover, held constant at the mean observed over the 478 point-count locations. Bottom panel depicts the single-factor model that includes only percent canopy cover and the survey variables that affected detection of FISP, as indicated in Table 1. Confidence intervals (not shown) are large given that the standard errors of the beta-coefficients for many of the non-significant variables were large. Note that the y-axis on the bottom panel is scaled differently. X-axes are scaled from 0 to 74%, the maximum value observed for percent canopy cover.



how an individual selects and uses habitat, one or a few very prominent features of a habitat may serve as the main cue for attracting and retaining a dispersing individual (Veech 2021:53–57).

Why does canopy cover characterize the breeding habitat of these grassland-shrubland species? Canopy cover has long been identified as an important habitat characteristic for characterizing and classifying habitats of birds (Igl and Ballard 1999, Brawn 2006, Au et al. 2008, Barrioz et al. 2013, Feichtinger and Veech 2013, Reidy et al. 2014, Crouch et al. 2019, Roach et al. 2019).

Fig. 5. Relationship between species probability of occurrence and B-J difference for Field Sparrow (*Spizella pusilla*). Solid line depicts the full model with all variables, other than B-J difference, held constant at the mean observed over the 478 point-count locations. Dashed line depicts the single-factor model that includes only B-J difference and the survey variables that affected detection of FISP, as indicated in Table 1. Confidence intervals (not shown) are large given that the standard errors of the beta-coefficients for many of the non-significant variables were large. X-axis is scaled from 0.6 to 1.4, the minimum and maximum values observed at the 478 point-count locations.



The correlation between bird communities and canopy cover is evident at both local and landscape scales (Au et al. 2008, Mabry et al. 2010). There are several hypotheses that may explain the importance of this single factor. First, canopy cover has a large effect on the overall characteristics of a habitat. Grass cover (Barrioz et al. 2013), forb cover (Peterson et al. 2007), and woody understory plant cover have been shown to negatively correlate with percent canopy cover (Brudvig and Asbjornsen 2009), whereas canopy cover positively correlated with oak regeneration (Barrioz et al. 2013). Second, the plants that make up the canopy can provide many potential benefits for birds including, but not limited to, sites for perching, displaying, foraging (Fitch 1950, Regosin and Pruett-Jones 1995) and socializing (Grzybowski 1983), all activities that relate to breeding. In grassland-obligate species, it is thought that scattered canopy cover may provide protection from predators in landscapes that are otherwise devoid of overhead cover (Pulliam and Mills 1977, Lima and Dill 1990, Igl and Ballard 1999). For tree-nesting species, canopy cover provides the necessary structure and materials for nest building, and even ground-nesting species are known to nest near trees and shrubs (Johnston 1947, Lanyon 1981). Indeed, this last explanation may be most pertinent to our study as we were examining breeding habitat. Outside the breeding season, canopy cover might not be as influential in characterizing habitat of these species.

Although our models performed fairly well in identifying the habitat characteristics of most of the species, there were two notable exceptions. First, for Northern Bobwhite, canopy cover and canopy height (quadratic and linear terms respectively) were not significant in either the full model or the single-factor models. Thus, our study does not add significant novel insight into the decades-old pursuit to obtain detailed knowledge of this species' habitat requirements (Stoddard 1931, Johnson and Guthery 1988, Spears et al. 1993, Guthery 1997, Kopp et al. 1998, Lusk et al. 2006, Janke et al. 2015, Mosloff et al. 2021). Northern Bobwhite are an important species for recreational harvesting (hunting) and their populations are declining in many parts of their geographic range for a multitude of reasons (Brennan 1991, Church et al. 1993, Lusk et al. 2002, Veech 2006, Twedt et al. 2007, Hernández et al. 2013, Olsen et al. 2016). Elucidation of the exact habitat requirements of Northern Bobwhite is likely better accomplished by in-depth studies that precisely measure habitat features in the field. Second, none of the three habitat variables were significant in the full model for Yellow-billed Cuckoo. For this species, there are likely other habitat variables that are more important than those examined here. For example, Yellow-billed Cuckoos are known to associate with densely wooded riparian areas (Laymon and Halterman 1989) and open woodlands that have trees greater than 7 m height (Nolan 1963, Eastman 1991). Their probability of colonizing habitat also greatly increases with increasing canopy cover becoming close to 1.0 when canopy cover exceeds 70% (Johnson and Benson 2023). Tall trees were relatively scarce at most of our survey locations. However, we note that mean canopy height for a given buffer might not adequately capture the presence of tall trees (i.e., 30×30 m pixels with canopy height > 7 m). Future habitat studies for this species could be conducted in areas that include potentially important habitat variables such as proximity to creeks and rivers and density of tall trees.

At the survey locations of our study, spatial variation in canopy height is not as pronounced as spatial variation in canopy cover. Nonetheless, analysis of additional variables such as the standard deviation of canopy height (to assess heterogeneity) and maximum canopy height within a buffer might have identified these two variables as important habitat characteristics for some of the species. We also did not analyze heterogeneity in canopy cover given that the 1×1 m pixels were binary. Thus, our analyses were based solely on habitat variables representing central tendencies (means). More detailed habitat studies could be conducted to take into account fine-scale spatial heterogeneity in characteristics such as canopy cover, height, and shrub species composition.

In addition to analyzing the breeding habitat associations of the eight species, two additional goals of our study were to assess the singularity of canopy cover (or either of the two other variables) in explaining habitat use and evaluate whether shrub encroachment could potentially have a negative effect on the species. Canopy cover alone was not sufficient in explaining a substantial proportion of the variation in whether a given species was recorded at a survey point. The percent deviance reduction of the single-factor canopy cover models was $< 20\%$ for all species and $< 10\%$ for some species. As such, there are other unexamined factors that may determine habitat use for these eight species and more specifically, determine whether a given species occurs and is detected at a survey point. One of these factors, that is neither related to the habitat nor the broader environment, is recruitment

limitation. In nature, most species do not saturate their habitat due to limits on the number of dispersing individuals and possible geographic/spatial isolation of some habitat patches (Veech 2021:22). If species were to saturate habitat, then identifying all of the important habitat characteristics would theoretically be easier (Mitchell 2005).

Encroachment of woody vegetation into grassland areas is likely to continue given that current management practices may not be adequately controlling the encroachment (Ratajczak et al. 2016, Scholtz et al. 2021, Londe et al. 2022). Some amount of woody vegetation is a required habitat characteristic for grassland-shrubland bird species. Nonetheless, some species will be negatively affected by excessive and intensive encroachment of woody vegetation that alters a landscape toward having greater amounts of closed-canopy vegetation and fewer open, non-canopied areas. For example, Painted Bunting, Rufous-crowned Sparrow, and to a lesser extent Bewick's Wren show a statistically significant decline in probability of occurrence when canopy cover exceeds 50% (Fig. 3). These species, and perhaps others, likely will not be able to persist in shrubland ecosystems that are on a trajectory to become more enclosed with woody vegetation both in a horizontal (canopy cover) and vertical (canopy height) dimension. As such, habitat management for these species should involve removal and control of woody vegetation to promote a tight mosaic of open grassland and shrubland patches. This is particularly important in areas that traditionally had minimal canopy coverage and where woody encroachment is often driven by anthropogenic alterations to historic fire regimes and overgrazing. Future research on the habitat requirements of grassland-shrubland birds could focus on the role of canopy cover (and other habitat variables) on nesting success as well as the extent that species' populations can endure over time in grassland-shrubland ecosystems that are naturally dynamic.

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Data Availability:

Data available from the corresponding author upon request.

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Appendix 1.

Table A1. Comparison of different logistic regression techniques on revealing meaningful habitat variables (β_x having $P \leq 0.1$) as they affect probability of occurrence eight grassland-shrubland bird species in central Texas. Table also shows AIC values and the means of the absolute values of the deviance residuals. The conditional logistic regression algorithm did not converge on a solution for YBCU.

| Species | Parameter | Regression technique [†] | | |
|---------|-----------------------------|-----------------------------------|-----------------|-----------------------------|
| | | Logistic on prop. years | Logistic on p/a | Conditional logistic on p/a |
| BEWR | Canopy cover | yes | yes | yes |
| | Canopy cover ² | yes | no | yes |
| | Canopy height | no | no | no |
| | Canopy height ² | no | no | no |
| | B-J difference | yes | yes | no |
| | B-J difference ² | yes | yes | no |
| | AIC | 612.0 | 339.9 | 260.7 |
| | Mean residual | 0.485 | 0.632 | 0.751 |
| CASP | Canopy cover | no | no | no |
| | Canopy cover ² | yes | yes | no |
| | Canopy height | yes | yes | no |
| | Canopy height ² | no | yes | no |
| | B-J difference | no | no | no |
| | B-J difference ² | no | no | no |
| | AIC | 141.4 | 291.7 | 166.3 |
| | Mean residual | 0.312 | 0.544 | 0.322 |
| FISP | Canopy cover | yes | yes | yes |
| | Canopy cover ² | no | no | no |
| | Canopy height | yes | yes | no |
| | Canopy height ² | yes | yes | yes |
| | B-J difference | yes | yes | yes |
| | B-J difference ² | yes | yes | no |
| | AIC | 293.7 | 418.9 | 271.4 |
| | Mean residual | 0.462 | 0.757 | 0.461 |
| LASP | Canopy cover | no | no | no |
| | Canopy cover ² | yes | no | no |
| | Canopy height | no | no | no |
| | Canopy height ² | no | no | no |
| | B-J difference | no | no | no |
| | B-J difference ² | no | no | no |
| | AIC | 354.0 | 587.3 | 486.9 |
| | Mean residual | 0.466 | 1.033 | 0.618 |
| NOBO | Canopy cover | no | no | yes |
| | Canopy cover ² | yes | no | yes |

| | | | | |
|------|-----------------------------|-------|-------|-------|
| | Canopy height | yes | yes | yes |
| | Canopy height ² | no | yes | yes |
| | B-J difference | no | yes | no |
| | B-J difference ² | no | yes | no |
| | AIC | 312.8 | 564.9 | 310.7 |
| | Mean residual | 0.531 | 0.992 | 0.612 |
| PABU | Canopy cover | yes | no | no |
| | Canopy cover ² | yes | yes | no |
| | Canopy height | no | no | no |
| | Canopy height ² | no | no | no |
| | B-J difference | no | no | no |
| | B-J difference ² | no | no | no |
| | AIC | 587.7 | 215.5 | 149.1 |
| | Mean residual | 0.496 | 0.432 | 0.582 |
| RCSP | Canopy cover | yes | yes | yes |
| | Canopy cover ² | no | yes | yes |
| | Canopy height | no | no | no |
| | Canopy height ² | no | no | no |
| | B-J difference | no | no | no |
| | B-J difference ² | no | no | no |
| | AIC | 71.8 | 377.0 | 289.7 |
| | Mean residual | 0.322 | 0.705 | 0.506 |
| YBCU | Canopy cover | no | no | — |
| | Canopy cover ² | no | no | — |
| | Canopy height | no | no | — |
| | Canopy height ² | no | no | — |
| | B-J difference | no | no | — |
| | B-J difference ² | no | yes | — |
| | AIC | 184.9 | 562.5 | — |
| | Mean residual | 0.415 | 0.988 | — |

† For each regression technique as applied to the full models, “yes” and “no” refer to whether the habitat variable had a regression coefficient (β_x) with $P \leq 0.1$.