HABITAT-CHARACTERISTIC PROFILES: AN INTUITIVE APPROACH TO EVALUATE SPECIES-HABITAT RELATIONSHIPS AS DEMONSTRATED ON SEVERAL TEXAS BIRD SPECIES

by

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LIST OF ABBREVIATIONS

Abbreviation	Description
ABC	American Bird Conservancy
AIC	Akaike information criterion
AUC	Area under curve
BEWR	Bewick's Wren
CASP	Cassin's Sparrow
FISP	Field Sparrow
FNR	False Negative Rate
FPR	False Positive Rate
GRIP	Grassland Restoration Incentive Program
GEDI	Global Ecosystem Dynamics Investigation
HCP	Habitat-Characteristic Profile
LASP	Lark Sparrow
LiDAR	Light Detection and Ranging
NAIP	National Agriculture Imagery Program
NOBO	Northern Bobwhite
OPJV	Oaks and Prairies Joint Venture
PABU	Painted Bunting
RCSP	Rufous-crowned Sparrow
ROC	Receiver operating characteristic (curve)
TNR	True Negative Rate
TPR	True Positive Rate
TPWD	Texas Parks and Wildlife Department
USFWS	United States Fish and Wildlife Service
YBCU	Yellow-billed Cuckoo

ABSTRACT

Identifying the habitat characteristics that matter most to a species is crucial to understanding its basic ecology and conservation needs. Although species-habitat relationships are often considered complex and best understood with large, multi-faceted models, a simpler approach may prove fast, cost-effective, and powerful. I used logistic regression models to generate habitat-characteristic profiles (HCPs), a graphical interpretation method wherein a single habitat variable is plotted on the x-axis and the probability of species occurrence is on the y-axis. For a group of eight bird species, I evaluated four habitat variables, all related to vegetation structure: canopy cover, contagion index (a measure of spatial heterogeneity), broadleaf:juniper ratio, and mean canopy height. All four variables were measured remotely with canopy cover, contagion index, and broadleaf:juniper ratio being generated from remote-sensing satellite imagery of the National Agricultural Imagery Program and mean canopy height coming from LiDAR data of the Global Ecosystem Dynamics Investigation. All eight bird species are "species of conservation concern", as identified by the Oaks and Prairies Joint Venture (OPJV). Model building was completed using seven years (2012-2019) of OPJV point count species presence-absence data. These data originate from 19 survey routes, in six Texas counties, for a total of 478 points. I used ArcGIS to circumscribe a 250 m radius circular buffer around each point and subsequently derive each of the four habitat variables within each buffer. Logistic regression models were developed to examine the effect of each habitat variable separately and in combination with the other variables. The models were compared using

AIC. Competitive models (ΔAIC < 3) were used to generate HCPs for each variable and species. HCPs proved to be an effective method for understanding and displaying species-habitat relationships and comparing among species. For most species, vegetation structure appeared to strongly influence species occurrence (habitat use) within the relatively small local area of the 250 m radius buffers. Furthermore, percent canopy cover alone was sufficient in explaining patterns of habitat use for the majority of focal species. This suggests that species-habitat relationships may be relatively simple, contrary to many habitat characterizations that sometimes include dozens of habitat variables. As a further assessment of the HCPs, I conducted model validation using two sets of independently collected species presence-absence data. I found that the models performed well at predicting probability of occurrence for all species (AUC > 0.5). In a time where many species are in steep decline, a quick method of evaluating species-habitat relationships could prove very beneficial. By utilizing HCPs, the habitat associations of any species could be quickly evaluated with minimal survey effort potentially resulting in better conservation outcomes.

I. INTRODUCTION

Avian abundance is decreasing in North America at an alarming rate (Rosenberg et al. 2019). While there are many influencing factors affecting global bird biodiversity such as climate change and anthropogenic mortality sources – window strikes, poaching, domestic cats – (Loss et al. 2015) the primary driving factor is habitat loss (Cunningham and Johnson 2019, Rosenberg et al. 2019, Li et al. 2021). Habitat comprises both the biotic and abiotic factors that influence whether a species will selectively identify, settle, and use a given geographic area (Forman and Godron 1986). With the rate of global environmental change continuing to increase (Visser et al. 2009, Erwin et al. 2011, Wu and Zhang 2015) there is an urgent need for simple and resource efficient solutions to evaluate species-habitat relationships. One major cause of habitat loss in grassland habitats is woody encroachment (Sirami et al. 2009, Lautenbach 2020). This problem is particularly evident within central Texas, where this research was conducted (Prather et al. 2017, Davis et al. 2018). Woody encroachment is driven, both directly and indirectly, through human actions. By transforming lowland prairies into pasture for livestock grazing, the habitats are made more permeable to woody encroachment (Van Auken 2000, Sharp and Whittaker 2003). Another major contribution has been years of fire suppression on the landscape (Higgens et al. 2000, Bond et al. 2003). North American grasslands are disturbance-driven ecosystems (Bragg 1995)—through periodic burns, native grasses and forbs are propagated, invasive species are removed (Grant and Murphy 2005), and aggressively growing woody plants, such as juniper, are reduced (Reemts and Hansen 2007). Due to their conspicuous nature, birds are excellent indicator species for evaluating habitat quality (Morrison 1986). As such, understanding the relationship between avian species and vegetation structure is crucial to proper grassland management.

For many organisms, the physical structure of vegetation can be an important factor in defining the habitat of a species, and also in determining the species' distribution and abundance. Canopy cover (or lack thereof) has been repeatedly identified as an influential factor in quantifying the habitat of shrubland and grassland bird species (Willson 1974, Wiens and Rotenberry 1980, Wiens 1989a, 1989b, Feichtinger and Veech 2013, Vasseur and Leberg 2015, Crouch et al. 2019). In fact, it is often the case that the physical structure of the vegetation, such as percent canopy cover and height, is a more important habitat requirement 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 shrubland and grassland species that build nests well off the ground, tree or shrub canopy also forms the requisite structure for nesting behavior.

The primary objective of my thesis is to better understand how structural habitat characteristics (canopy cover, canopy height, and canopy heterogeneity) influence species occurrence within a given area, and further to determine if a *single* characteristic (such as canopy cover) is sufficient in explaining patterns of species occurrence. A long-standing and implicit assumption in the study of habitat is that a species' habitat requirements are multi-faceted (Barrioz et al. 2013, Reidy et al. 2014, Roach et al. 2019, Veech 2021). As such, it is thought that meaningful species-habitat relationships can only be revealed by analyzing many different environmental variables or potential habitat characteristics (Korschgen and

Knutson 2005, Tokeshi and Arakaki 2012). For instance, a Habitat Needs Assessment of the Upper Mississippi River System conducted in 1999 relied on one to five spatial data layers containing five to 18 land cover classes in addition to habitat matrices for birds, fish, amphibians, reptiles, and aquatic invertebrates (Korschgen and Knutson 2005). While these complex, multifaceted analyses may be more thorough, many of the included factors may only explain a small fraction of a given species' relationship with its habitat. One problem with these complex analyses is that obtaining the habitat information or data can be difficult and time consuming. For species of conservation concern, this may cause unnecessary delays in the development of conservation management actions. In a time where many species, particularly birds, are in steep decline (Rosenberg 2019), such delays may be the difference between a species' survival or impending extinction. A simpler alternative, such as developing habitat characteristic profiles (see below), may be able to adequately explain a species' habitat associations. If so, the habitat requirements of a species could be quickly evaluated with minimal survey effort. This could result in both cost and time savings for implementing habitat management actions across a wide variety of taxa and ecosystems. In order to study species-habitat relationships, I examined the correlation of percent canopy cover, mean canopy height, spatial heterogeneity in canopy cover (as measured by a contagion index), and the ratio of broadleaf to juniper tree species (see Methods) with occurrence of eight focal species—Bewick's Wren, Cassin's Sparrow, Field Sparrow, Lark Sparrow, Northern Bobwhite, Painted Bunting, Rufous-crowned Sparrow, and Yellow-billed Cuckoo.

The focal species represent a wide array of habitat associations, from grassland species such as Field Sparrow to shrubland species such as Rufous-crowned Sparrow. Additionally, the focal species have been identified as indicators of grassland 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). For the last seven years, the Oaks and Prairies Joint Venture (OPJV), in association with Texas Parks and Wildlife Department (TPWD) and the American Bird Conservancy (ABC), have been conducting grassland bird monitoring throughout Texas and Oklahoma to assess the effectiveness of their Grassland Restoration Incentive Program, or GRIP (Giocomo et al. 2017). The eight focal species of my study are included in the group of 17 species that the OPJV has chosen as indicators of grassland health. To conserve grasslands and shrublands for these species and others, it is important to first gain a better understanding of their habitat requirements including whether any of the species require a certain amount of canopy cover. The National Land Cover Database (see below) defines grasslands as having > 80% grass or herbaceous ground cover (or < 20% canopy cover), while shrublands are defined as having > 20% canopy cover that is < 5 m tall.

Of the focal species, Painted Buntings tend to be associated with some form of shrublands (Parmelee 1959, Gates and Gysel 1978, Joos et al. 2014). In contrast, Lark Sparrows are more likely found within grasslands with sparse cover of woody vegetation (Walcheck 1970, McAdoo et al. 1989) Cassin's Sparrows fall somewhere in between, inhabiting arid grasslands with scattered shrubs or other relatively short vegetative cover (Williams and LeSarrier 1968, Wolf 1977). By including species with presumably different habitat requirements, my study examined a wide range of potential associations with canopy cover, from species that might tend to avoid canopy cover to those that have a strict requirement for substantial canopy cover. This allowed me to assess how relatively simple but important structural characteristics (canopy cover, canopy height, and canopy heterogeneity) define the habitat of several different grassland/shrubland bird species.

Understanding these relationships could have a broad impact on the way we manage habitat in the future.

In this study, I introduce the idea of a "habitat-characteristic profile" (HCP). These profiles are derived by quantifying a species' association (or lack thereof) with a particular measured habitat characteristic over a wide range of the characteristic. HCPs are curves in which probability of species occurrence is the dependent variable and a quantitative habitat characteristic is the independent variable (Figure 1). For each focal species, I developed a profile for each of the four habitat characteristics mentioned previously. Due to my survey design, all profiles were produced at a spatial extent of 250 m (see Methods). I predict that the species will differ from one another in their HCPs for a given habitat variable and that each species might have different HCPs for each of the four habitat variables. As an example, for Painted Bunting, I expect the HCP for canopy cover to peak around 30-40% (as in Species 3, Figure 1), because Painted Buntings have been known to associate with forest edges and mixed shrubland (Parmelee 1959, Kopachena and Crist 2000a, 2000b, Vasseur and Leberg 2015). I also expect a broad diffuse peak centered at about 50% canopy cover for Bewick's Wren. Because they are habitat generalists, Bewick's Wrens might associate with a wide range of canopy cover, indicating a weaker relationship between percent canopy cover and occurrence (Species 1, Figure 1) particularly in comparison to Painted Buntings. For the other focal species, I hypothesize HCPs with peaks centered around canopy cover percentages that correspond to the species' known habitat affinity (i.e., grassland vs. shrubland birds).

I predict associations with mean canopy height to be similar to associations with percent canopy cover, with species that strongly associate with dense canopy cover (e.g., Yellow-billed Cuckoo) also showing a strong association with increased mean canopy height. It is also possible that species that associate with forest edges (e.g., Painted Bunting), and thus expected to have a peak around 50 percent canopy cover, would also have a strong association with increasing mean canopy height. I expect species that associate with grasslands and shrublands (e.g., Field Sparrow and Cassin's Sparrow) to have a strong association with decreasing mean canopy height.

Both the contagion index and broadleaf:juniper ratio were used as measures of spatial heterogeneity (Li and Reynolds 1993, Ritters et al. 1995). For shrubland species that associate with intermittent canopy cover (e.g., Cassin's Sparrow), I expect the HCP to peak close to a contagion index value of zero. An area with near-zero contagion has a relatively well mixed and fine-grained (1 m^2) mosaic of canopy cover and canopy-less open spaces – see *Methods* section. For species that associate with grasslands (e.g., Field Sparrow), I predict the HCP to have a peak closer to a contagion value of 100 indicating an area that is a relatively homogeneous open space with no or very little canopy cover. For all eight focal species, I expect to see peaks centered around a higher broadleaf:juniper ratio as high concentrations of juniper would indicate poor habitat for the grassland, shrubland, and woodland species alike. The aggressive growth of juniper would crowd out any true grassland bird species via woody encroachment (Wang et al. 2018). I expect that the focal species that associate with shrublands are more likely to rely on broadleaf trees, rather than juniper, for food resources and nesting.

While there are benefits to exhaustive multifaceted analyses of species habitat, I predict individual HCPs to explain habitat-species relationships in a simple yet powerful way. By comparing the four HCPs within species, I expect to better understand species' habitat associations and how one might manage habitat to promote its population growth. By comparing HCPs between different species, I expect to better understand the differences in habitat associations and better understand how different habitat management strategies would affect the species composition of a given area. For example, while decreasing overall canopy cover may increase the populations of strictly grassland species, I would also expect an equivalent decrease in the species that associate with higher canopy cover values. Because there are active habitat modification projects, through programs like GRIP, in place for all the focal species in this study, understanding these relationships has practical and real-world conservation implications.

II. METHODS

I constructed profiles for each of four habitat characteristics for eight different bird species. These were (1) percent canopy cover, (2) spatial heterogeneity of canopy cover (measured by a contagion index), (3) ratio of broadleaf tree species to juniper species, and (4) canopy height. Each profile was based on a statistical model relating species presence-absence to the given habitat characteristic. I then compared these profiles (models) to identify the habitat characteristics that appeared to most strongly affect the species' probability of occurrence. This was followed by a model validation procedure applied to two datasets collected independently of the one used for building the models.

Study species

Bewick's Wren (BEWR)

Bewick's Wrens are medium-sized members of the family Troglodytidae. The adults are characterized by a white eye stripe, gray-white belly and side, brown and sometimes muted upperparts, and barring on the middle tail feathers and some wing feathers. The adults of the species are not sexually dimorphic. Bewick's wrens are commonly found year-round along the west coast of North America from southwest British Columbia to southern Mexico and in the south-central United States and Mexico. Model building and training data originate within the eastern half of the species' range.

Cassin's Sparrow (CASP)

Cassin's Sparrows are small members of the family Passerellidae. They are drab and non-descript in appearance with adults possessing light underparts and mottled brown, black, and gray upperparts. They have a faint brown eye stripe, a large bill, and a long, rounded tail. Adults are not sexually dimorphic. Cassin's Sparrows are primarily identified by their unique song which has been described as an "exquisitely sweet, haunting song. Two low, soft notes (seldom heard) followed by long, loud, high, liquid trill and two shorter, descending notes" (Williams and LeSarrier, 1968). Cassin's Sparrows are found year-round in south-central United States and north-central Mexico, with a breeding range that extends as far north as Nebraska. Some model building data originate within the year-round range of the species (parts of Edwards, Kinney, and Uvalde counties). The rest of the model building and validation data originate within the breeding range of the species. Notably, data from Stephens and Coryell counties as well as the Freeman Center originate from the eastern edge of Cassin's Sparrows' breeding range.

Field Sparrow (FISP)

Field Sparrows are small members of the Passerellidae family. The adults have a characteristic pink bill and legs, a rusty-brown crown and back, a white eye ring, pale underparts and typical sparrow markings on the wings accented by two faint, white wing bars. Field Sparrows are not sexually dimorphic. They can be found year-round across the eastern United States with a breeding range extending further north to around the US-Canada border and a nonbreeding range that extends down to the US-Mexico border. The model building and validation data originate within the southern extents of the species' year-round and breeding ranges.

Lark Sparrow (LASP)

Lark Sparrows are large-bodied, long-tailed members of the family Passerellidae. The adults of this species have striking facial patterns consisting of multiple chestnut, black, and white stripes that cover the entire head and throat areas. Lark Sparrows are not sexually dimorphic. They breed in a large range covering most of the western and central United States and can be found year-round throughout most of Texas, excluding the panhandle. The model building and validation data originate within the southern half of the breeding range and cover a large portion of the year-round range for this species.

Northern Bobwhite (NOBO)

Northern Bobwhites are one of the two game species of interest in this research project and a small-medium sized member of the family Odontophoridae. Males have a slight crest with a white forehead and throat separated by a black supraciliary stripe. The body is a chestnut brown, mottled with white, brown, gray, and black markings. Underparts tend to be lighter on average and the upperparts tend to be darker. Females look similar, although they lack the black and white markings on the face and instead have a brown supraciliary stripe and a buff-colored forehead and throat. Northern Bobwhites have a contiguous range throughout the eastern United States and south into central Mexico. The model building and validation data originate within the southwestern quadrant of the species' range.

Painted Bunting (PABU)

Painted Buntings are small, colorful passerines in the family Cardinalidae. Males are multicolored with a red body, yellow-green back, and a blue head, while females are a uniform yellow-green. They are 13 – 14 cm long and feed primarily on grass seeds during the winter and insects in the summer (Lowther et al. 1999). Painted Buntings have two distinct and separate ranges in the United States. There is an eastern range located along the Atlantic coast, which is separated from the main breeding range by a 500 km gap (Shipley et al. 2013). The main breeding range is located in the south-central United States, stretching from the western tip of Texas to the eastern panhandle of Florida. The model building and validation data originate within the center of the main breeding range of this species.

Rufous-crowned Sparrow (RCSP)

Rufous-crowned Sparrows an average-sized member of the family Passerellidae. Adults have a characteristic rufous or rust colored crown and eye stripe. They have a grey body overall with some mottled brown markings on the back and wings, the belly is a buff color. Males are slightly larger than females. Rufous-crowned Sparrows have a discontinuous range but can be found year-round throughout central Texas and west through Arizona and south through central Mexico, there is also a small range along the west coast of California. The model and building data originate within the northeastern portion of the species' range. Notably, data from Coryell, Kinney, and Uvalde counties, as well as the Freeman Center originate along the eastern edge of the species' range.

Yellow-billed Cuckoo (YBCU)

Yellow-billed Cuckoos are a medium-sized member of the family Cuculidae. Interestingly, despite the name, Yellow-billed Cuckoos are not obligate brood parasites and build their own nests. They are known to be occasional intraspecific and interspecific brood parasites, but the exact frequency has not been quantified (Hughes 1997). Yellow-billed Cuckoos are zygodactyl, and they have grey-brown upperparts contrasting against white underparts, and the tail is long and graduated with white tipped outer retries. The bill is long and decurved with a black upper mandible and a characteristic bright yellow lower mandible with a dark tip. Females are slightly larger than males. Yellow-billed Cuckoos breed in the temperate United States and in some parts of Mexico and the Greater Antilles, migration occurs throughout most of Mexico, and the wintering range is almost entirely in South

America, east of the Andes Mountains. Model building and validation data originate within the western half of the species' breeding range.

Study region

My study included parts of central Texas, notably areas within the Edwards Plateau and Oaks and Prairie regions (Figure 2). The landscapes in these regions consist of a mix of forest, shrubland, and meadow, ideal for examining the effect of canopy cover and related habitat variables on the occurrence of the selected bird species. The Edwards Plateau has a varied topography of hills, canyons, and bottomland grasslands with interspersed agricultural land, particularly pastureland and orchards. Elevation across the Edwards Plateau ranges from 100 – 1000 m. Temperatures in the region varied from lows of about 16°C and highs of about 32°C during the months encompassing the survey period. Climate is categorized as subtropical to semiarid although with high relative humidity year-round (Toomey et al., 1993). Annual rainfall is between 38 cm in the west and 84 cm in the east (Larkin and Bomar 1983). Common grasses in the area consist of bluestems in the genus *Andropogon* and grama grasses in the genus *Bouteloua*, with canopy cover provided by juniper (*Juniperus ii*), oaks (*Quercus sp.*), and cedar elm (*Ulmus crassifolia*), along with several other broadleaf species (Larkin and Bomar 1983). The Oaks and Prairies region has a flatter topography and a more mesic climate, but is otherwise similar to the Edwards Plateau in the mix of land cover types.

Species data for model building

Species presence-absence data for building models were obtained from the Oaks and Prairie Joint Venture (OPJV, https://www.opjv.org/). The OPJV has been conducting a long-term grassland bird monitoring program to assess the efficacy of their Grassland Restoration Incentive Program (GRIP). This monitoring program consists of five-minute roadside point counts consistent with the protocol used by the North American Breeding Bird Survey (except that the BBS uses three-minute point counts). When the grassland bird monitoring program was first initiated, survey routes were established as 50 points, spaced roughly 800 m apart on public secondary and tertiary roads, avoiding primary highways. Survey routes began at a randomly selected point and continued in a randomly selected direction until the 50th point was reached. Routes are typically surveyed only once a year, with the goal being to cover at least 30 points per route in a single survey. Surveying is conducted by trained and paid staff of the OPJV. The first OPJV surveys were conducted from May to June of 2013 and have been conducted during those months every year since. Most routes have been surveyed most years since the inception of the monitoring program, although the majority of routes have been surveyed by different observers over the years. I used data from 19 survey routes located in six counties (Coryell, Edwards, Kinney, Real, Stephens, and Uvalde; Figure 2) that overlapped with the habitat databases. For the 19 survey routes, there was a mean of 38.3 points surveyed per route for 727 total points. Some survey routes were not located entirely within the bounds of the canopy cover classification database (see next section). On those routes, points without canopy cover data were excluded. Points were also excluded if they were surveyed only one year. As a result, my species datasets included 478 points. For each species and each point, the probability of species occurrence (i.e., occupancy) was taken as the proportion of surveyed years that the species was recorded. 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. The mean number of survey years per point was 4.8.

Habitat data for model building

Data for the four habitat variables came from different GIS databases, each of which were ultimately derived from remote sensing. For percent canopy cover and contagion of canopy cover, I 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-meter pixel resolution (Sesnie et al. 2016). This database was originally developed to classify Golden-cheeked Warbler habitat. 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). I 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, I 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 (see below). For example, if 98,125 out of 196,250 one-meter squared pixels were assigned to 100% canopy cover, then the percent canopy cover for the buffer would be 50%. Spatial heterogeneity in canopy cover was determined by calculating the landscape contagion index (Li and Reynolds 1993, Riitters et al. 1995). The equation used to calculate this index is CONTAG = 100 × $(1+[\sum_{q=1}^{N}(p_q \ln(p_q))/2\ln(t)]$, wherein p_q is the proportion of pixel pairs of a given type of adjacency q, N is the number of adjacency types, and t is the total number of classes in the landscape (Riitters et al. 1996). In my study t = 3 cover types and thus there are nine types of adjacencies: 11, 12, 13, 21, 22, 23, 31, 32, and 33. CONTAG quantifies the extent to which all three classes— juniper, broadleaf, and no cover pixels—are spatially intermixed. A contagion value near zero means that the spatial distribution of pixels of the three classes is evenly mixed, which represents diffuse or heterogeneous canopy cover. "Diffuse" cover indicates the extent to which the canopy is "thinned out" based upon the intermixing of either or both juniper and broadleaf canopy pixels with 0% cover pixels. "Heterogeneous" cover indicates the intermixing of juniper and broadleaf pixels with each other. Low contagion values are most likely to arise from buffers that have intermediate canopy cover values (40 – 70%). Greater contagion values mean that the pixels of each type are contiguous (maximally aggregated) which represents less intermixing of the two canopy types (if each is present) with each other and with pixels of 0% canopy cover. CONTAG can approach 100 but only when a single cover type dominates the landscape. High contagion values could arise from buffers that have relatively high overall percent canopy cover or relatively low percent canopy cover. The contagion index was calculated using 'landscapemetrics', 'raster', 'rasterVis', and 'rgdal' packages in R.

Although the contagion index allowed me to examine spatial heterogeneity and diffuseness of canopy cover, it did not provide information on the relative proportions of broadleaf and juniper canopy types. To calculate the ratio of broadleaf to juniper I simply divided the number of broadleaf pixels within a 250 m buffer by the number of juniper pixels within the same buffer.

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 CO_2 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, I calculated mean canopy height for each 250 m buffer.

Model building

As described above, I 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. As such, the models also apply to this spatial scale. I 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. Additionally, this 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.

For each species, I constructed logistic regression models that included the four habitat variables as well as several abiotic survey covariates that could potentially influence bird detection (Table 1). With the exception of Julian date and start time, all of the survey covariates were estimated in the field by OPJV grassland bird survey technicians. Rather than automatically include every covariate in each habitat model, I first examined which covariates might have the greatest influence on species detection. I used a two-sample *t*-test to identify statistically significant ($p<0.05$) differences in mean survey covariates, averaged for all survey years, between points where the species was detected and points where the species was not recorded (not detected). Any survey covariate that had a statistically significant difference was included in each of the models run for a given species.

The response variable for each model was the proportion of surveys (out of 2 – 7 years) in which the species was observed at the given location (again, N = 478). Because this response variable is constrained between 0 and 1, logistic regression is an appropriate method of analysis in that it is widely used for analyzing species habitat associations (Veech 2021). Further, the predicted value of the response variable ($\hat{y}$) can be interpreted as the probability that the species could use the particular location as habitat given the set of habitat characteristics at the location (Veech 2021). The formula for multiple logistic regression is $\hat{y} = \exp(\beta_0 + \beta_1 X_1 + \beta_p X_p)/[\exp(\beta_0 + \beta_1 X_1 + \beta_p X_p) + 1]$, wherein β_0 is the *y*-intercept and X_1 to X_p are the independent (predictor) variables. For each species, a total of five habitat models were examined: a complete model with all four habitat variables and four reduced models, one each for canopy cover, contagion index, mean canopy height, and the ratio of broadleaf to juniper. In addition, each model included a squared factor for each habitat variable. This squared factor allowed me to identify the peak value (in the habitat profile) that represents the "ideal" habitat condition where a species was most likely to occur. Thus, the complete model included all habitat variables and their squared counterparts along with any abiotic site covariates that were found to be statistically significant as described above. Reduced models included only one habitat variable, its squared counterpart, and statistically significant site covariates.

For each species, I conducted an AIC model comparison to determine which models best predicted species occurrence. If the complete model was competitive (ΔAIC ≤ 3), then it was retained and used to generate habitat profiles and undergo model validation; this occurred for five species. In cases where the complete model had a ΔAIC > 3, then the reduced models with a ΔAIC ≤ 3 were retained and used to construct the habitat-characteristic profiles (see next section); this occurred for three species. However, among these latter three species there were two reduced models in which ΔAIC was much > 3, these were the models for ratio of broadleaf tree species to juniper and canopy height for Lark Sparrow. These variables were not further analyzed for this species.

Habitat-characteristic profiles

Using the selected habitat model for each species, profiles were generated by setting one of four possible habitat variables (canopy cover, mean canopy height, contagion, and broadleaf:juniper ratio) as the independent variable and using predicted probability of occurrence as the dependent variable. The peak of a habitat profile curve represents the "ideal" value for the particular focal habitat variable plotted along the x-axis. This is the value (or range of values if the peak is broad) for the habitat variable for which the species probability of occurrence is highest. That is, the habitat value on the x-axis at the peak provides relevant information about the species' habitat associations. When the complete model was selected (or retained) then it was used to generate habitat profiles for all four habitat variables. Otherwise, when the reduced model was selected, then only the single habitat variable (corresponding to the model) was used to generate the profile.

Model validation

I conducted a model validation exercise to assess performance of each model in predicting species occurrence. This required data that were independent of (although collected in a similar way as) the OPJV model building data. Within the 35 counties included in the GIS canopy-cover database, I selected two study sites that were known to have populations of the focal species. These study sites were the Freeman Center and Kerr Wildlife Management Area (WMA). The Freeman Center is a 1,410-hectare research property managed by Texas State University in San Marcos, Texas. Kerr WMA, which was established by the Texas Parks and Wildlife Department as a base for ecological research in the Edwards Plateau region, covers 2,628 hectares in Hunt, Texas (Figure 3).

I conducted point counts for the eight focal species at the Kerr WMA from May 12 – June 30, 2020, and at the Freeman Center from May 17 – June 21, 2021. At each study site, there were a total 40 point count locations, each spaced at least 200 m from the nearest adjacent point count location. The 40 point count locations were randomly generated using ArcGIS Pro and were at least 200 m from a navigable road or trail. The points were then divided into groups of 10 points to be surveyed on any given day. Each point in a group was at least 400 m from the nearest point in the group to reduce the odds of double-counting the same bird at two points on any given day. To increase the probability of detecting a species at least once (assuming it was present at a given location), I visited each survey point three times within the 2020 survey season. Due to excessive rain during the 2021 survey season each point was only visited at least two times. There was a minimum of two days and a maximum of seven days between visits. Surveys were conducted between civil twilight (30 minutes before sunrise) and 11:00 AM. Upon arrival to a point, I allowed for a minute-long adjustment period before beginning the five-minute observation period. Each individual bird (of any of the eight focal species) seen or heard within the five-minute survey window and within 250 m of my position was tallied and its position relative to myself was noted. Utilizing a laser range finder, I determined the distance to the bird in meters. If a bird was not visible, I used a combination of known distance to certain landmarks and made an estimate of the bird's distance. For each point count location at the Kerr WMA and Freeman Center, I used ArcGIS to derive the four habitat variables within 250 m radius buffers, as previously described for the OPJV point count locations. For each point count location, this allowed me to determine the predicted probability of occurrence for each species by inserting the values of the habitat variables into the models or more precisely into the multiple logistic regression equations representing the models.

For each model, I calculated the true negative rate (TNR), true positive rate (TPR), false negative rate (FNR), and false positive rate (FPR) for different threshold values of predicted probability of occurrence. The threshold value is the predicted probability of occurrence at which the researcher considers the model to be indicating a species to be present at a given location. The true negative rate indicates field survey sites where the model correctly predicted a species would *not* occur and the true positive rate indicates field sites where the model correctly predicted a species *would* occur. The false negative rate indicates field sites where the model incorrectly predicted that a species would be *absent,* and the false positive rate indicates field sites where the model incorrectly predicted that a species would be *present*.

I also calculated the area under curve (AUC) values for the receiver operating characteristics (ROC) curve for each model applied to the Kerr and Freeman validation datasets. The ROC curve is a graph of the TPR over the FPR across the entire range of possible threshold values (0 – 1). For a model to be considered successful, it should have a TPR that substantially exceeds its FPR across most threshold values. Thus, the area under the ROC curve (AUC value) indicates how well the model is predicting species occurrence over the entire range of threshold values. An AUC value that is close to one indicates a model is performing very well. An AUC of 0.5, otherwise known as the line of no discrimination, indicates a model that is performing no better than randomly predicting presence or absence. In other words, TPR and FPR are equal across all threshold values. Any AUC value less than 0.5 indicates a model that is actively performing worse than random guessing and should therefore not be used to predict species occurrence.

III. RESULTS

Species detection data from the OPJV were used to calculate a probability of occurrence (proportion of the two to seven survey years in which the species was recorded) for each species at each survey point. Over the 478 point count locations and two to seven survey years, the probability of species occurrence ranged from 0 – 1 for all species except Rufous-crowned Sparrow. The maximum proportion of surveys where this species was observed was 0.75. By far the most abundantly detected species in the model building data was Painted Bunting, followed by Bewick's Wren and Lark Sparrow respectively, which was detected at a majority of survey points (Table 2). Yellow-billed Cuckoo, Northern Bobwhite, and Field Sparrow were all fairly abundant, detected at > 30% of the survey points (Table 2). Rufous-crowned Sparrow and Cassin's Sparrow were both detected at less than 17% of survey sites, making them the least abundantly detected of the focal species (Table 2).

As expected, habitat conditions varied among the OPJV survey points. Within the 250 m-radius circular buffers surrounding the survey points, canopy cover values for the OPJV point count locations ranged from 0.01 – 73.64%, with a mean of 23.95%. Contagion, as a measure of spatial aggregation of juniper, broadleaf trees, and open space, ranged from 9.22 – 99.89, with a mean of 51.11. Broadleaf:juniper ratio ranged from 0.05 – 69.27, with a mean of 1.93. Note that ratios less than 1 represent a greater amount of juniper than broadleaf trees and a ratio of 0.05 is equivalent to a broadleaf:juniper ratio of 20. Lastly, canopy height ranged from 0 – 6.90 m, with a mean of 1.27 m.

Model selection

Models were selected for building habitat-characteristic profiles using Akaike information criterion (AIC). For Cassin's Sparrow, Field Sparrow, and Painted Bunting, the complete model (all four habitat variables included) had the lowest AIC (i.e., $\Delta AIC = 0$) and was therefore selected for constructing profiles (Table 3). Two additional species, Bewick's Wren and Northern Bobwhite, had ΔAIC values < 3 for the complete model, and thus they were used to construct the habitat profiles even though it was not the top model for these species (Table 3). For the remaining three species (Lark Sparrow, Rufous-crowned Sparrow, and Yellow-billed Cuckoo), the complete models had ΔAIC values much greater than 3. Therefore, the complete model was not used for these species. Instead, the single-factor reduced models were selected to use in constructing the habitat profiles when such models had $\Delta AIC < 3$. (Table 3). For Rufous-crowned Sparrow and Yellow-billed Cuckoo, all four reduced models had ΔAIC values < 2, meaning each reduced model explained the variation present in the data as well as any other reduced model (Table 3). For Lark Sparrow, the reduced models for canopy cover and contagion were the only two models with ΔAIC values < 3, thus HCPs were not generated for tree species ratio or mean canopy height (Table 3). Finally, for most of the species, the selected models also included one or more of the survey covariates (Table 3) which allowed me to account for the effects of those additional factors on species detection. Of the survey covariates, Julian date was significant for seven species, cloud cover for six species, anthropogenic noise for five species, wind speed for four species, and start time for one species (Table 3).

Habitat-characteristic profiles

Based upon the beta coefficients of the logistic multiple regression models that were selected as described above, habitat-characteristic profiles were generated for each species and each of the four habitat characteristics. Recall from Table 3 that each model has additional variables other than just the habitat characteristic of interest (e.g., the complete model has four habitat variables and one or more survey covariates and most of the reduced models include survey covariates). Therefore, in using the regression equation for each model to calculate predicted probability of species occurrence, the other variables were held constant at their mean values. The variable or habitat characteristic of interest was allowed to vary between its minimum and maximum values as observed in the OPJV data; for example, canopy cover percentage ranged from near 0 to 73.4%.

Among the eight species and four habitat characteristics, the HCPs varied considerably in form (see below). This prevented me from being able to use simple numeric descriptors (such as location of the peak along the x-axis) to quantitatively assess the HCPs. To aid in interpreting and understanding the various forms of the HCPs, I categorized them into one of four qualitative types (Figure 4). A Type 1 curve is characterized by a species reaching a peak probability of occurrence near a habitat characteristic value of zero. A Type 2 curve is characterized by a species reaching a peak probability of occurrence near the maximum habitat characteristic value. A Type 3 curve is characterized by a species reaching a peak probability of occurrence near the median habitat characteristic value. A Type 4 curve is characterized by a species having no distinct peak probability of occurrence; i.e., the HCP is relatively flat. To be categorized into Types 1 – 3, and thus have a distinct peak, I required there to be a difference between minimum and maximum probability of occurrence ≥ 0.08.

Any HCP that had a difference in minimum and maximum probability of occurrence < 0.08 was categorized as a Type 4 curve. All four types of HCP were represented among the 8 species and four habitat variables, although Type 1 curves were most common, with 15 out of 30 instances (Table 4). Type 2 occurred six times, Type 3 occurred three times (although one was an inverted Type 3), and Type 4 occurred six times. Even apart from this general framework of classifying HCPs, the actual HCPs exhibited substantial variation in form (Figures 5 – 8).

The HCPs indicate how the species probability of occurrence varies with a particular habitat characteristic. Even when the HCP has a distinct peak (Types 1 – 3), the height of the peak, or the maximum probability of occurrence, may be much less than 1 (e.g., canopy cover for Rufous-crowned Sparrow; Figure 5). The probability of occurrence (as scaled on the y-axis) may be influenced by the habitat characteristic as well as the species relative abundance in the surrounding landscape or region. Even the species' inherent detectability, which is not directly assessed, could influence the estimated values of probability of occurrence. As another example, Bewick's Wren has a peak probability of occurrence of 0.92 at its highest canopy cover value, compared to a value of 0.09 for Rufous-crowned Sparrow at its peak canopy cover value (Figure 5). This difference is in part due to Bewick's Wrens being far more common in the model building dataset. Bewick's Wrens were recorded at 87.8% of OPJV survey points while Rufous-crowned Sparrows were recorded at only 16.3% (Tables 5 and 6).

P-values for each HCP were derived from the logistic regression models. Canopy cover had a significant effect ($P \leq 0.05$) on probability of occurrence for five species, Bewick's Wren, Field Sparrow, Lark Sparrow, Northern Bobwhite, and Rufous-crowned

Sparrow (Figure 5). Contagion had statistically significant p-values for four species, Bewick's Wren, Field Sparrow, Lark Sparrow, and Northern Bobwhite (Figure 6). Broadleaf:juniper ratio had statistically significant p-values for two species, Cassin's Sparrow and Rufous-crowned Sparrow (Figure 7). Lastly, mean canopy height had a statistically significant effect on probability of occurrence for two species, Cassin's Sparrow and Northern Bobwhite (Figure 8).

The r^2 value indicated how well the models explained the variation in probability of occurrence values. This ranged from 0.09 for Lark Sparrow and 0.48 for Cassin's Sparrow. The complete model had higher overall r^2 values (0.19 – 0.48) than the reduced models (0.09 – 0.15). While these r^2 values are considered low overall, indicating the models are not completely explaining probability of occurrence for these species, the amount of variation explained is not insignificant when considering the simplicity of the logistic regression models (i.e., models only contained at most four habitat variables).

Model Validation

Recall that model validation involved using the habitat data collected at each point count location at Kerr WMA and the Freeman Center and the multiple logistic regression equations to generate a predicted probability of occurrence for each species. Validation was conducted on the complete models (all four habitat variables in the model) for Bewick's Wren, Cassin's Sparrow, Field Sparrow, Northern Bobwhite, and Painted Bunting given that those models had $\Delta AIC < 3$. For the other three species, I performed a model validation on the best reduced model, i.e., the one that had $\Delta AIC = 0$ (Table 3). These models were as follows: Lark Sparrow – canopy cover, Rufous-crowned Sparrow – canopy cover, and Yellow-billed Cuckoo – canopy cover.

There were 40 point count locations surveyed at Kerr WMA during late spring/early summer 2020. Within a 250-meter radius of the survey points, canopy cover ranged from 31.05 – 72.78%, with a mean of 53.44%. Contagion values ranged from 16.38 – 38.97, with a mean of 24.96. Broadleaf to juniper ratio ranged from 0.13 – 2.47, with a mean of 0.53. Mean canopy height ranged from 1.15 – 5.93 m, with a mean of 3.63 m. At the Freeman Center, 40 points were surveyed in late spring/early summer 2021. Within a 250-meter radius of the survey points, canopy cover ranged from 28.43 – 75.48 percent, with a mean of 57.42 percent. Contagion ranged from 7.38 – 40.86, with a mean of 17.08. Broadleaf to juniper ratio ranged from 0.79 – 1.89, with a mean of 1.29. Lastly, mean canopy height ranged from 1.28 – 8.33, with a mean of 5.28. The two validation datasets exhibited a range of variation in the habitat characteristics that was similar to that for the model-building OPJV dataset except that the validation datasets did not contain any survey points that were relatively devoid of woody vegetation, and as a consequence the validation datasets also had a relatively higher mean canopy height. These were minor differences, and both validation datasets were suitable for testing the performance of the models and accuracy of the HCPs. In addition, each species was common enough to provide enough instances of observed presences at point count locations except for Cassin's Sparrow and Field Sparrow at the Freeman Center, although some species had relatively low incidence rates (around 10% or less) at Kerr and/or Freeman (Tables 5 and 6).

Several metrics were calculated to validate the models built on OPJV data. These include the true negative rate (TNR), true positive rate (TPR), false negative rate (FNR), and false positive rate (FPR) as determined for a threshold value that simultaneously minimizes FNR and FPR (and as a corollary, maximizes TNR and TPR). I also used ROC curves to calculate AUC values (Tables 5 and 6). AUC is a metric of model performance across the *entire range* of threshold values, which in this case was 0 to 1. Models that are performing well (i.e., high sensitivity and specificity) at a given threshold value will have substantially higher TPR and TNR values than their respective FPR and FNR values. For example, the model for Field Sparrow had a TPR of 0.786 which is considerably greater than its FPR of 0.167 at a threshold value of 0.04 for the Kerr WMA dataset (Table 5). Similarly, the TNR of 0.833 for Field Sparrow at Kerr WMA was also greater than the FNR of 0.214 (Table 5). Yellow-billed Cuckoo provided an example of an inaccurate model. At the Freeman Center the model for Yellow-billed Cuckoo had a TPR of 0.416 which closely matched its FPR of 0.393 and a TNR of 0.607 closely matching the FNR of 0.583, at a threshold value of 0.038 (Table 6). For the Kerr WMA dataset, 6 out of eight species had a greater TPR than FPR and greater TNR than FNR (Table 5). At the Freeman Center, 4 out of 7 species had greater TPR than FPR and greater TNR than FNR (Table 6). Additionally, for 5 out of 7 species at Kerr WMA and 5 out of 7 at the Freeman Center, the TNR was higher than the TPR indicating that models were better at predicting species absence than presence (Tables 5 and 6). Lastly, note that many of the threshold values are very low (< 0.1) (Tables 5 and 6); this is partly due to the rather low incidence rates for some species at Kerr WMA and the Freeman Center.

For all species and both model validation datasets, the AUC values were greater than 0.5 (Tables 5 and 6). This indicates that, across the board, the models perform better than could be predicted at random. The best performing model for the Kerr WMA dataset was Field Sparrow with an AUC of 0.911, while the worst performing model was for Yellow-billed Cuckoo with an AUC of 0.527 (Table 5). At the Freeman Center, the best performing model was Lark Sparrow with an AUC of 0.726, and the worst performing was again Yellow-billed Cuckoo (Table 6). Of the six species that had models validated at Kerr and Freeman, those for Painted Bunting had the highest consistent AUC values at 0.790 and 0.724 respectively.

IV. DISCUSSION

Structural habitat characteristics related to vegetation (canopy cover, canopy heterogeneity, and canopy height) appear to strongly influence avian species occurrence within a relatively small local area (i.e., a circular extent of 250 m radius). Furthermore, a single habitat characteristic, namely percent canopy cover, was sufficient in explaining patterns of habitat use for most of the eight focal species. The contagion index, which assesses spatial heterogeneity in canopy cover, was also notable in this regard. Canopy cover was the best performing habitat variable in model selection, it was present in the complete model and had the lowest ΔAIC of the 3 reduced models (Table 3). P-values for canopy cover were significant for 5 of 8 species, more than any other habitat variable. Contagion performed almost as well with significant p-values for half of the species tested. Additionally, HCPs for canopy cover and contagion were more distinctive than those for canopy height and the ratio of broadleaf to juniper cover. The importance of vegetation structure in defining the habitats of species (particularly birds) is not a new discovery (see James 1971, Rotenberry and Wiens 1980, Cody 1981). However, the results of my study suggest that just a *single* characteristic or feature of the habitat may have disproportionate influence in determining whether an individual of a given species selects and uses a particular area. The amount of canopy cover and its spatial dispersion might serve as a visual cue to an individual bird for whether to establish a territory (or not). This is a reductionist perspective on the evolutionarily—and ecologically—complex processes of habitat selection and use. Many different factors influence habitat selection and subsequent use (occupancy) of the habitat, but one or a few very prominent features of a habitat might serve as the main cue for attracting and retaining a dispersing individual (Veech 2021).

Why does canopy cover explain habitat so well for these grassland-shrubland species? Canopy cover has long been identified as an important habitat characteristic for defining and classifying a habitat, particularly with 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). The correlation between bird communities and canopy cover is evident at both point and landscape scales (Au 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 avian species including, but not limited to, sites for perching, displaying, foraging (Fitch 1950, Regosin and Pruett-Jones 1995) and socializing (Grzybowski 1983). In grassland species, it is thought that canopy cover may provide protection from predators (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 woody structures (Johnston 1947, Lanyon 1981).

My study demonstrates that the use of HCPs as a method for displaying and interpreting species-habitat relationships is effective. HCPs could largely be identified to one of four distinct types. The ecological meaning of a type will vary depending on the habitat variable. For instance, a Type 1 curve for canopy cover means the species is more strongly associated with grasslands, shrublands, or forest edge where overall canopy cover will be limited. In contrast, a Type 1 curve for broadleaf:juniper ratio (or juniper:broadleaf ratio) simply means that tree species composition matters to the bird species. There are two major ways to glean useful ecological knowledge from studying HCPs. First, by comparing all HCPs of the analyzed habitat variables for a single species, we can better understand and identify those habitat characteristics that best predict habitat associations. This then motivates and allows us to explore multiple facets of the species' ecology and address the follow-up question of why a particular characteristic is important. Second, by comparing the HCPs for one habitat variable among multiple species we obtain a better understanding of how different species use their habitats in unique ways or even may occupy unique niches or conversely how two or more species may have similar habitat requirements and yet still be able to coexist. Below, I selectively interpret some of the 36 HCPs that were generated so as to demonstrate their ability to describe a given species' habitat and to facilitate comparisons among species.

Bewick's Wren has a Type 1 curve for all four HCPs (Table 4). For canopy cover, this indicates that the species becomes more common in areas of grassland with sparse canopy cover, such as forest edges or mixed shrublands (Figure 5). A Type 1 curve for contagion indicates that Bewick's Wrens occur more frequently in habitat with greater intermixing of non-canopy, broadleaf, and juniper cover as opposed to habitat that has a uniform and homogenous canopy layer (Figure 6). Ecologically, this again suggests a species that is more commonly found in forest edges or mixed shrublands. The Type 1 curve for the broadleaf:juniper HCP reveals that Bewick's Wrens tend to be found in areas with greater cover of juniper than broadleaf tree species (Figure 7). The Type 1 curve for the mean canopy height HCP indicates that Bewick's Wrens are more commonly found in areas where canopy height is shorter (Figure 8). Compared to canopy cover and contagion, the Type 1 curves for broadleaf:juniper ratio and canopy height are not as pronounced. They cover a smaller range of occurrence probabilities (0.05 – 0.5) than do the HCPs for canopy cover and contagion; compare Figures 7 and 8 to 5 and 6. Altogether, the HCPs for Bewick's Wren describe a species that is most commonly found in a diffuse, heterogenous habitat, with sparse canopy cover, that, at least in the Edwards Plateau, is typically dominated by juniper. These results are consistent with previous studies and well established knowledge of Bewick's Wren habitat (Miller 1941, Bent 1948, Shuford 1993).

For Cassin's Sparrow, the curve for canopy cover spanned the largest range of probability of occurrence values, indicating that of the four HCPs, canopy cover best discriminates species occurrence. The Type 2 curve for canopy cover indicates a species that associates with canopy dominant areas. Note that probability of occurrence value begins to increase around 40% canopy cover (Figure 5). None of the eight focal species were forest birds, but if they were, I would expect a sharp, rapid increase in probability of occurrence starting around 70-80% canopy cover. Also, Cassin's Sparrow has a slight Type 1 curve for canopy height and notably a zero probability of occurrence when *mean* canopy height exceeds about 1 m (Figure 8). The combination of relatively high percent canopy cover but low canopy height represents a habitat of low-lying shrubs and grassy areas with only scattered tall shrubs or trees. This is consistent with previous descriptions of the species' habitat (Simmons 1925, Williams and LeSarrier 1968, Wolf 1977).

Bewick's Wren and Field Sparrow present another useful comparison of differences between species for a given HCP. Both species have Type 1 curves for canopy cover in which probability of occurrence is greatest near 0% canopy cover. However, the curve for Bewick's Wren is far more gradual in slope, reaching a minimum value around 60% canopy cover, whereas the Type 1 curve for Field Sparrow has a steeper slope, reaching zero probability of occurrence around 20% canopy cover (Figure 5). This indicates that the Field Sparrow is more of a true grassland species than is Bewick's Wren. The two species also have Type 1 curves for contagion although the HCPs reveal subtle differences (Figure 6). Bewick's Wren has a non-zero probability of occurrence across the entire range of possible contagion values. However, for Field Sparrow, probability of occurrence goes to zero above a contagion value around 60 (Figure 6). This indicates that Bewick's Wrens are slightly less selective with respect to canopy cover and its spatial heterogeneity than are Field Sparrows. Field Sparrows do not occur in landscapes completely devoid of woody vegetation. They require some tree cover for nest building and predator avoidance. While they are ground nesting species early in the season and transition into shrubs later in the breeding season (Best 1978), their nests are typically found within 40 m of woody vegetation, indicating that its presence is an important habitat characteristic during the breeding season (Johnston 1947, Lanyon 1981). This characterization of Field Sparrow habitat is consistent with established scientific consensus, mostly open grasslands with scattered woody cover to provide perches and nesting sites (Stewart 1975, Reidy et al. 2014).

I found that Northern Bobwhite also strongly associate with grassland-shrubland habitat. HCPs for canopy cover and contagion index are nearly identical to that of Field Sparrow (Figures 5 and 6). The HCP for mean canopy height is particularly interesting, as it is the only one to have an inverted Type 3 curve (Figure 8). This suggests that Northern Bobwhites are about equally likely to occur in habitats relatively devoid of tall shrubs and trees as well as areas having tall trees albeit not dense forest. These habitat associations likely reflect the species' requirement for habitat heterogeneity, meaning that while they had the highest probability of occurrence in grasslands where canopy cover and thus height would be lower, they also associate with a variety of tall woodland habitats (Leopold 1959, Lehmann 1984), particularly on the edges of clearings in early successional stages (Spears et. al. 1993).

The Lark Sparrow was similar to Bewick's Wren, Field Sparrow, and Northern Bobwhites in having a Type 1 curve for canopy cover, although the curve was not as pronounced (Figure 5). However, unlike those three species, Lark Sparrows had a Type 2 curve for contagion, meaning that they had a higher probability of occurrence in areas that were more homogenous, that is, less mixing of juniper, broadleaf, and non-canopy (Figure 6). This result is supported by the known habitat of Lark Sparrows, which is characterized as structurally open habitat with scattered trees or shrubs (Walcheck 1970, McAdoo et al. 1989, Knopf 1996).

Painted Buntings were notable in being the most common species recorded in both the model building (Table 2) and validating datasets (Tables 5 and 6). The HCPs were unique in that they were all broad and diffuse, with no clearly defined peak. This indicates a habitat generalist that is abundant across a wide arrange of habitats and ecotones. However, there is still meaningful habitat associations indicated by the HCPs. Painted Buntings are more strongly associated with lower canopy cover values (Figure 5), but they are also tolerant of small to moderate amounts of woody plant encroachment. Given that they have a Type 3 curve for contagion, Painted Buntings would seem to favor forest edges or grasslands with areas of dense shrubs where in a GIS depiction, canopy pixels are neither uniform nor perfectly diffuse (Figure 6). They have a slight preference for juniper over broadleaf cover and lastly seem to slightly favor areas of greater canopy height over areas with lower canopy height (Figures 7 and 8). This is consistent with Painted Buntings being nearly always absent from locations in central Texas that are completely forested or entirely devoid of woody plants (*pers. obs.*). This also aligns with current knowledge of Painted Bunting habitat. While not specifically well defined, possibly due to its generalist niche, the habitat of Painted Buntings is broadly understood to be semi-open areas within shrub thickets or forest edges/patches (Parmelee 1959, Oberholser 1974).

Rufous-crowned Sparrow represented the best example of a shrubland species. It was the only species with a Type 3 curve for canopy cover. Further, the curve was very symmetrical with a peak in probability of occurrence at about 48% canopy cover (Figure 5). When combined with the Type 1 curves for contagion index and broadleaf:juniper ratio (Figures 6 and 7), I interpret this to mean that Rufous-crowned Sparrow habitat in the Edwards Plateau consists of a predominance of juniper mixed fairly evenly with grasses and otherwise open space. The habitat of this species has previously been defined as semiarid grassy shrublands, with patches of open area such as grass, rock outcrops or bare ground (Wolf 1977, Shuford 1993, Howell 1995, Collins 1999).

The models only produced two ecologically meaningful HCPs for Yellow-billed Cuckoo. This likely indicated that the specific habitat-characteristics examined in my study do not have a major impact on the species' habitat use, meaning that Yellow-billed Cuckoos select habitat based on at least one other habitat characteristic that I did not examine in my study. One possible characteristic to investigate in future would be proximity to water resources, given Yellow-billed Cuckoos known association with riparian areas (Laymen and Halterman 1989). Yellow-billed Cuckoo had a Type 4 curve for canopy cover and contagion index and Type 2 curves for broadleaf:juniper ratio and mean canopy height. The remaining two HCPs, broadleaf:juniper ratio and mean canopy height, did seem to have a meaningful effect on probability of occurrence for Yellow-billed Cuckoo. The Type 2 curve for both

HCPs suggests a species that associates with taller, broadleaf tree species (Figures 7 and 8). This agrees somewhat with Yellow-billed Cuckoos' reported use of open woodlands and trees greater than 7 m tall (Nolan 1963, Eastman 1991), but fails to capture its apparent affinity for successional shrublands and dense riparian thickets (Johnsgard 1979, Stevenson and Anderson 1994).

HCPs are a simple yet powerful tool for understanding species-habitat relationships. Each HCP was constructed based on either a single-factor or multiple logistic regression model. In general, except for Yellow-billed Cuckoo, the models were well validated by two independent datasets. Of the four habitat characteristics modeled, canopy cover and contagion index seem to perform the best at describing a species' habitat. Using these two HCPs alone, I was able to broadly define a given species' habitat into categories such as open grassland or mixed shrubland. However, contagion index cannot be meaningfully interpreted without context since a value near 100 could represent continuous forest, grassland, or any other spatially homogenous landscape. By considering contagion index with canopy cover, context is provided, and the meaning of the value can be interpreted.

A species with a Type 1 curve for canopy cover has vastly different habitat requirements than a species with at Type 2 or Type 3 curve. Canopy cover alone allows us to broadly place species into categories such as "grassland species", "shrubland species", and "forest species". The slope of the curve allows us to distinguish between habitat "specialists" and "generalists". Although a single habitat characteristic (e.g., canopy cover) may go a long way in characterizing a species habitat, by considering more HCPs for each species, we could potentially learn even more about their habitat associations. Thus, HCPs should not be thought of as fully describing a species' habitat requirements or as a replacement for comprehensive, multi-faceted habitat analyses that might examine dozens of variables. Rather, they serve as a first step in understanding a species-habitat relationship. Neither a single HCP nor several will describe 100% of a species' relationship with its habitat. However, with only a couple HCPs we can sometimes gain a general understanding of a species most basic habitat requirements. Furthermore, the methodology used in creating HCPs could provide a useful framework for visualizing the individual habitat characteristics of complex species-habitat models as HCPs are both simple to construct and intuitive.

HCPs could become a powerful tool in identifying species with conflicting habitat management needs. A relevant example would be the conflict in managing habitat for both Black-capped Vireos and Golden-cheeked Warblers. While both species overlap in breeding season geographic range in central Texas, their habitat associations are very different. Black-capped Vireos associate with recently fire-disturbed areas, dominated by early successional, broadleaf shrubs such as young shin oak, *Quercus sinuate* (Grabber 1958, Grzybowski et. al. 1994), whereas Golden-cheeked Warblers associate with old-growth Ashe juniper (Ladd 1985, DeBoer and Diamond 2006, Sesnie et al. 2016). It is reasonable to assume that such a conflict would be immediately apparent via the inspection of HCPs. A relevant example of conflicting requirement needs from this research is evident when examining the canopy cover HCPs for Field Sparrow and Rufous-crowned Sparrow (Figure 5). If a hypothetical habitat was managed for Field Sparrows, the canopy cover would likely be too low for Rufous-crowned Sparrows and vice versa.

Species-habitat relationships may often be far simpler than is commonly thought within ecology. This project demonstrated that by utilizing HCPs for only a few habitat variables, the habitat associations of many species can be generally defined. In my study, all four HCPs were generated using remotely sensed habitat variables which are broadly applicable and accessible to land managers everywhere. As such, the majority of survey effort can be spent on gathering reliable presence/absence data for the species of interest. It is also possible that HCPs could be built upon species data from existing databases such as eBird or the North American Breeding Bird Survey. In such a scenario, evaluating species' habitat relationships would require little, if any, field surveying. Thus, HCPs have the potential to drastically reduce the time between habitat evaluation and management action, particularly for species of conservation concern. Even if a more in-depth analysis of a species' habitat is desired, initial management decisions can still be made based upon the HCPs while the more complex and time-consuming analysis is being conducted.

V. TABLES AND FIGURES

Table 1. List of abiotic variables that could affect detection of birds

Variable	Description
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)
Julian date (JD)	0-365 days
Percent cloud cover (CC)	0-100% (increments of 10%)
Start time (ST)	Minutes before/after sunrise + 30 minutes
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.

Table 2. Species prevalence in the OPJV data. 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*(*occurrence*) = 0. $N_{p=1}$ is the number of point count locations where species was recorded in every survey year, *P*(*occurrence*) = 1.

Species	N_{total}	$N_{p=0}$	$N_{p=1}$	Mean *P*(*occurrence*)	Overall number of detections
Bewick's Wren	419	59	47	0.4532	992
Cassin's Sparrow	73	405	19	0.0846	157
Field Sparrow	149	329	17	0.1629	313
Lark Sparrow	305	173	9	0.2313	519
Northern Bobwhite	198	280	13	0.1784	386
Painted Bunting	451	27	105	0.6404	1510
Rufous-crowned Sparrow	78	400	0	0.0465	91
Yellow-billed Cuckoo	206	272	1	0.1238	301

Table 3. Results of the model selection process for each bird species. ΔAIC values are shown for the complete model (all four habitat variables included) and each of the reduced models corresponding to percent canopy cover, spatial heterogeneity of canopy cover as measured by the contagion index, ratio of broadleaf tree species to juniper species (tree sp. ratio), and canopy height. The last column indicates the abiotic survey covariates that were included in the models for each species (abbreviations given in Table 1).

Species	ΔAIC values					Survey covariates included
	Complete Model	Canopy Cover	Contagion	Tree sp. Ratio	Canopy Height	
Bewick's Wren	1.13*	5.31	0	19.64	30.01	AN, CC, ST, WS
Cassin's Sparrow	0*	75.17	74.53	61.40	30.76	JD
Field Sparrow	0*	22.01	15.63	17.43	29.81	AN, CC, JD
Lark Sparrow	11.49	0*	0.48*	10.78	8.26	CC, JD
Northern Bobwhite	2.76*	10.13	11.99	13.12	0	CC, JD, WS
Painted Bunting	0*	20.42	7.30	39.68	22.79	AN, JD, WS
Rufous-crowned Sparrow	13.78	0*	0.23*	1.66*	0.56*	None
Yellow-billed Cuckoo	13.64	0*	0.06*	0.85*	1.22*	AN, CC, JD, WS

* - indicates that the corresponding model was selected and used to construct habitat-characteristic profiles. Note that for Lark Sparrow the models for tree species ratio and canopy height had ΔAIC values much > 3 and hence they were not retained for further use.

Table 4. The shape of habitat-characteristic profile curves described as one of four types (as depicted in Figure 4). The HCPs for tree species ratio and canopy height were not generated for Lark Sparrow because the models had ΔAIC values > 3 (broadleaf:juniper ratio = 10.78, canopy height = 4.99).

Species	Canopy Cover	Contagion	Tree sp. Ratio	Canopy Height
Bewick's Wren	1	1	1	1
Cassin's Sparrow	2	4	4	1
Field Sparrow	1	1	1	4
Lark Sparrow	1	2	–	–
Northern Bobwhite	1	1	2	3*
Painted Bunting	1	3	1	2
Rufous-crowned Sparrow	3	1	1	4
Yellow-billed Cuckoo	4	4	2	2

* I consider the canopy height HCP for Northern Bobwhite the shape to be an *inverted* type 3 curve.

Table 5. Model validation based upon the species presence/absence data collected at Kerr WMA. Metrics are true positive rate (TPR), true negative rate (TNR), false positive rate (FPR), and false negative rate (FNR) for the given threshold value†. Table also shows area under curve (AUC) values, R^2 value for the logistic regression model, percent of OPJV study sites (n=478) where the species was recorded during at least one of the survey years, and percent of Kerr study sites (n=40) where the species was recorded at least once.

Species	Threshold Value	TPR	TNR	FPR	FNR	AUC	% OPJV	% Kerr
Bewick's Wren	0.4500	0.400	0.400	0.600	0.600	0.557	87.7	75.0
Cassin's Sparrow	0.0015	0.600	0.629	0.371	0.400	0.697	15.3	12.5
Field Sparrow	0.0400	0.786	0.833	0.167	0.214	0.911	31.2	70.0
Lark Sparrow	0.1100	0.546	0.621	0.379	0.455	0.640	63.8	27.5
Northern Bobwhite	0.0500	0.750	0.719	0.281	0.250	0.801	41.4	20.0
Painted Bunting	0.6700	0.790	0.500	0.500	0.211	0.790	94.4	95.0
Rufous-crowned Sparrow	0.0900	0.133	0.680	0.320	0.867	0.643	16.3	37.5
Yellow-billed Cuckoo	0.0980	0.417	0.607	0.393	0.583	0.527	43.1	30.0

† For each species the threshold value was taken as the value of predicted *P*(occurrence) in which FPR and FNR are simultaneously minimized, though neither is at its absolute minimum.

Table 6. Model validation based upon the species presence/absence data collected at the Freeman Center. Metrics are true positive rate (TPR), true negative rate (TNR), false positive rate (FPR), and false negative rate (FNR) for the given threshold value[†]. Table also shows area under curve (AUC) values, R^2 value for the logistic regression model, percent of OPJV study sites (n=478) where the species was recorded during at least one of the survey years, and percent of Freeman study sites (n=40) where the species was recorded at least once.

Species	Threshold Value	TPR	TNR	FPR	FNR	AUC	% OPJV	% Freeman
Bewick's Wren	0.5300	0.600	0.700	0.300	0.400	0.647	87.7	75.0
Lark Sparrow	0.1200	0.667	0.919	0.088	0.333	0.726	63.8	15.0
Northern Bobwhite	0.2900	0.572	0.818	0.182	0.429	0.619	41.4	17.5
Painted Bunting	0.4000	0.500	0.500	0.500	0.500	0.724	94.4	95.0
Rufous-crowned Sparrow	0.0700	0.400	0.429	0.571	0.600	0.611	16.3	12.5
Yellow-billed Cuckoo	0.0380	0.292	0.750	0.250	0.708	0.513	43.1	6.0

[†] For each species the threshold value was taken as the value of predicted *P*(occurrence) in which FPR and FNR are simultaneously minimized, though neither is at its absolute minimum.

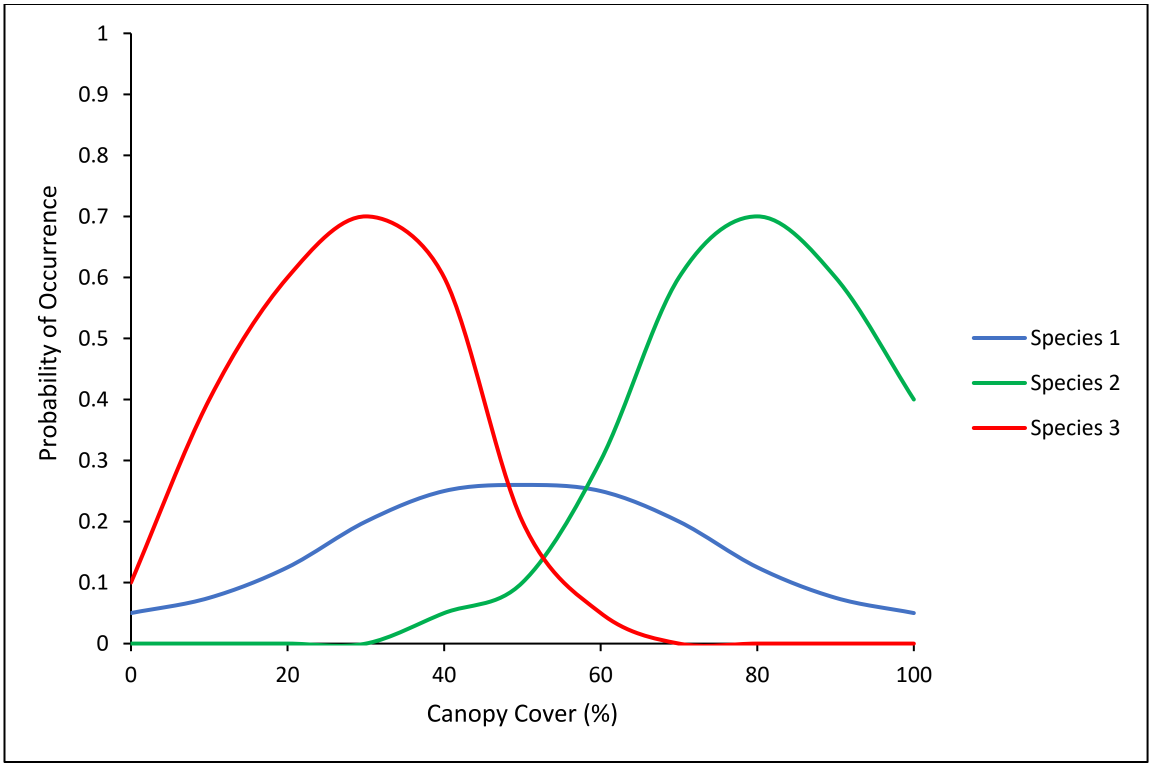


Figure 1. Relationship between canopy cover and probability of occurrence for three different hypothetical species. Species 1 does not have a strong association with canopy cover and could be thought of as a habitat generalist with regard to canopy cover. Species 2 associates strongly with areas of high canopy cover. Species 3 associates strongly with areas of low canopy cover.

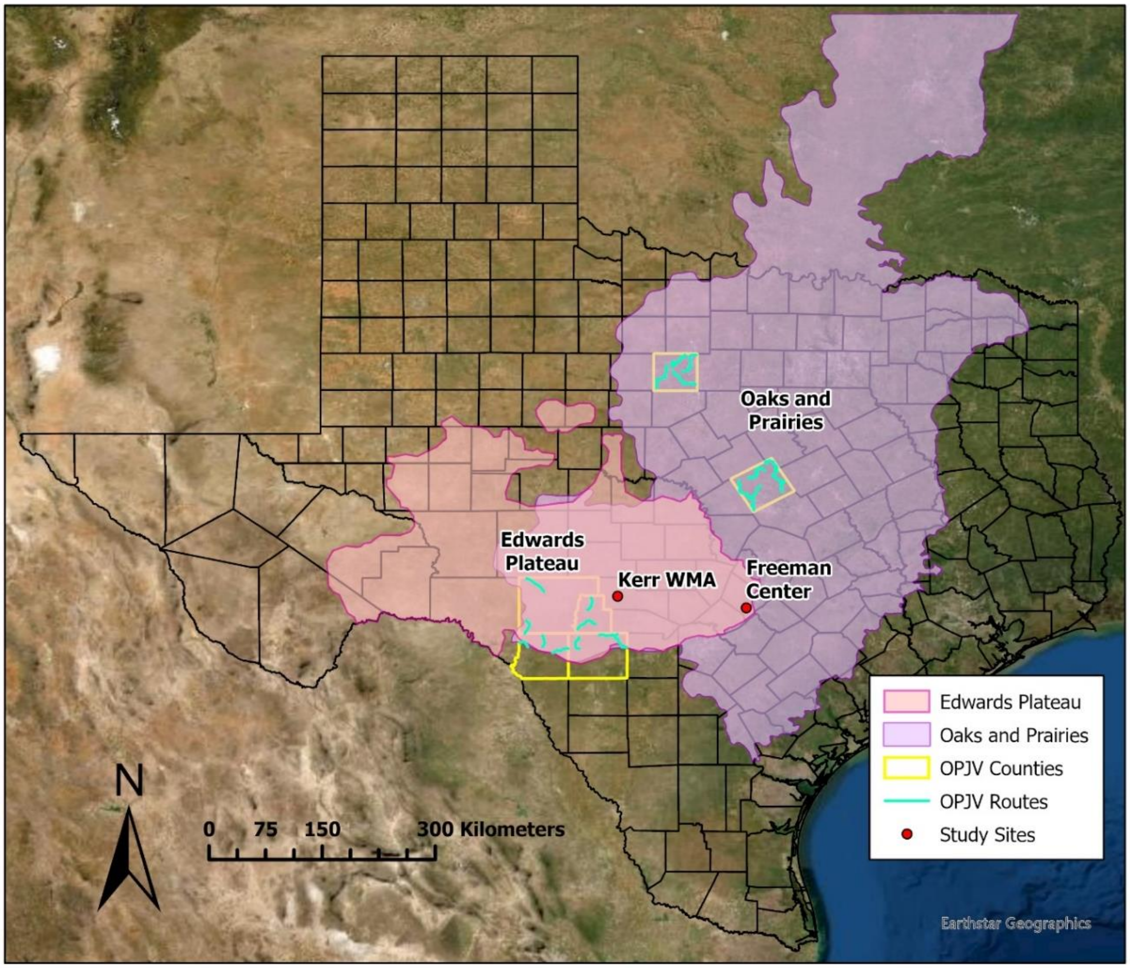


Figure 2. Map showing an overview of locations used in this research. The area shown in pink represents the Edwards Plateau. The Oaks and Prairies region, shown in purple is not geologically defined (as is the Edwards Plateau) but rather consists of the expanse of land immediately to the northeast of the Edwards Plateau and extending into Oklahoma. Counties outlined in yellow represent the six counties from which OPJV data were used for model building. Teal lines represent the OPJV survey routes within these counties. Red dots represent the two study areas used for model validation, Kerr WMA (2020) and the Freeman Center (2021).

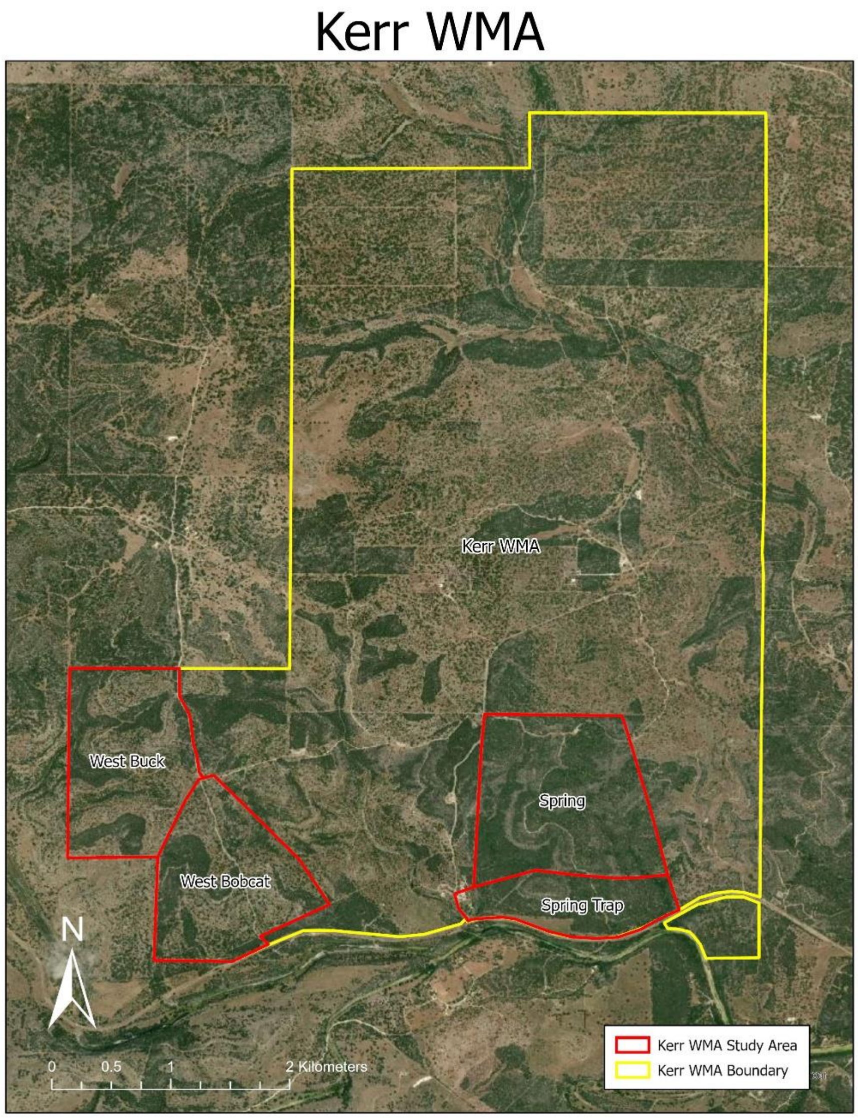


Figure 3. Map showing Kerr Wildlife Management Area. The area outlined in yellow represents the entirety of the property while the areas outlined in red represent tracts that were available for surveying in Spring 2020 (due to safety concerns associated with the COVID-19 pandemic).

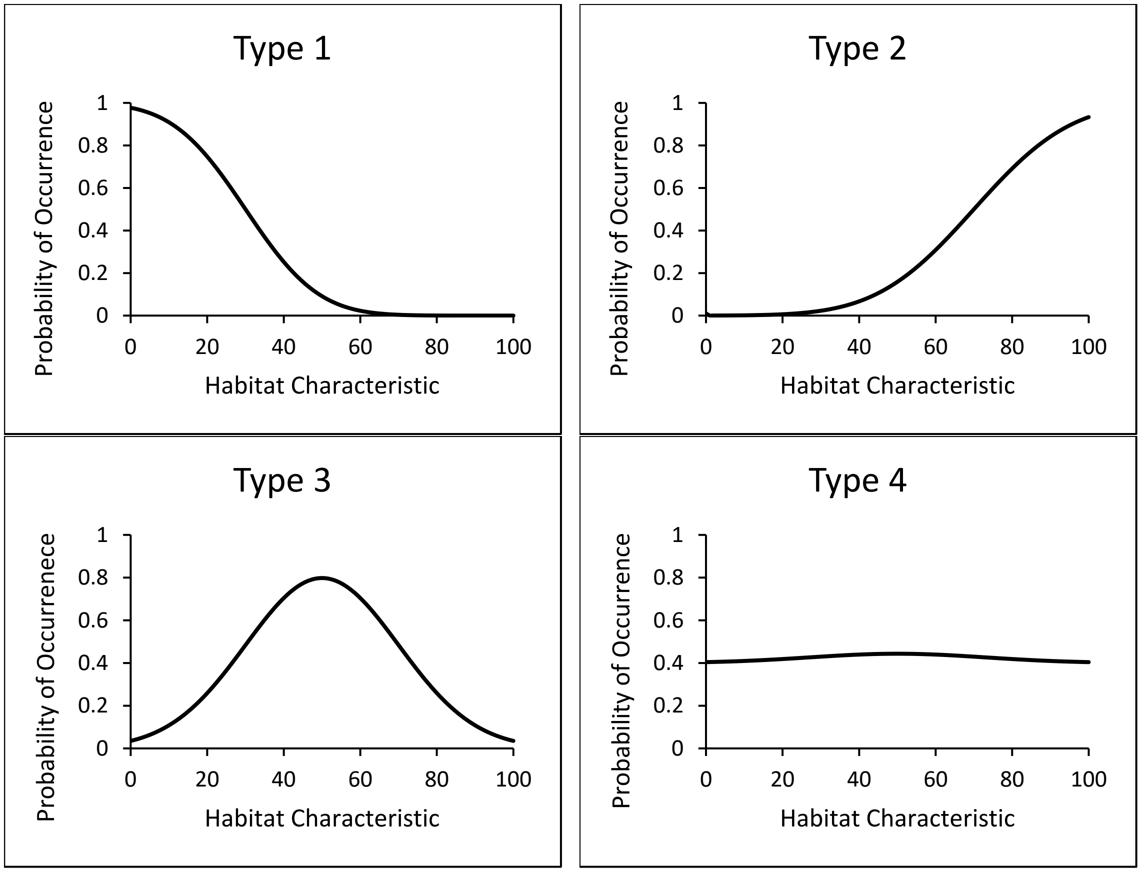


Figure 4. Four hypothetical curves used to qualitatively categorize the actual HCP curves derived from the multiple logistic regression models. A Type 1 curve is characterized by a species reaching a peak probability of occurrence near a habitat characteristic value near zero. A Type 2 curve is characterized by a species reaching a peak probability of occurrence near the maximum habitat characteristic value, in this case 100. A Type 3 curve is characterized by a species reaching a peak probability of occurrence near the median habitat characteristic value. A Type 4 curve is characterized by a species having no distinct peak probability of occurrence, which I define as the deviation between minimum and maximum probability of occurrence < 0.08.

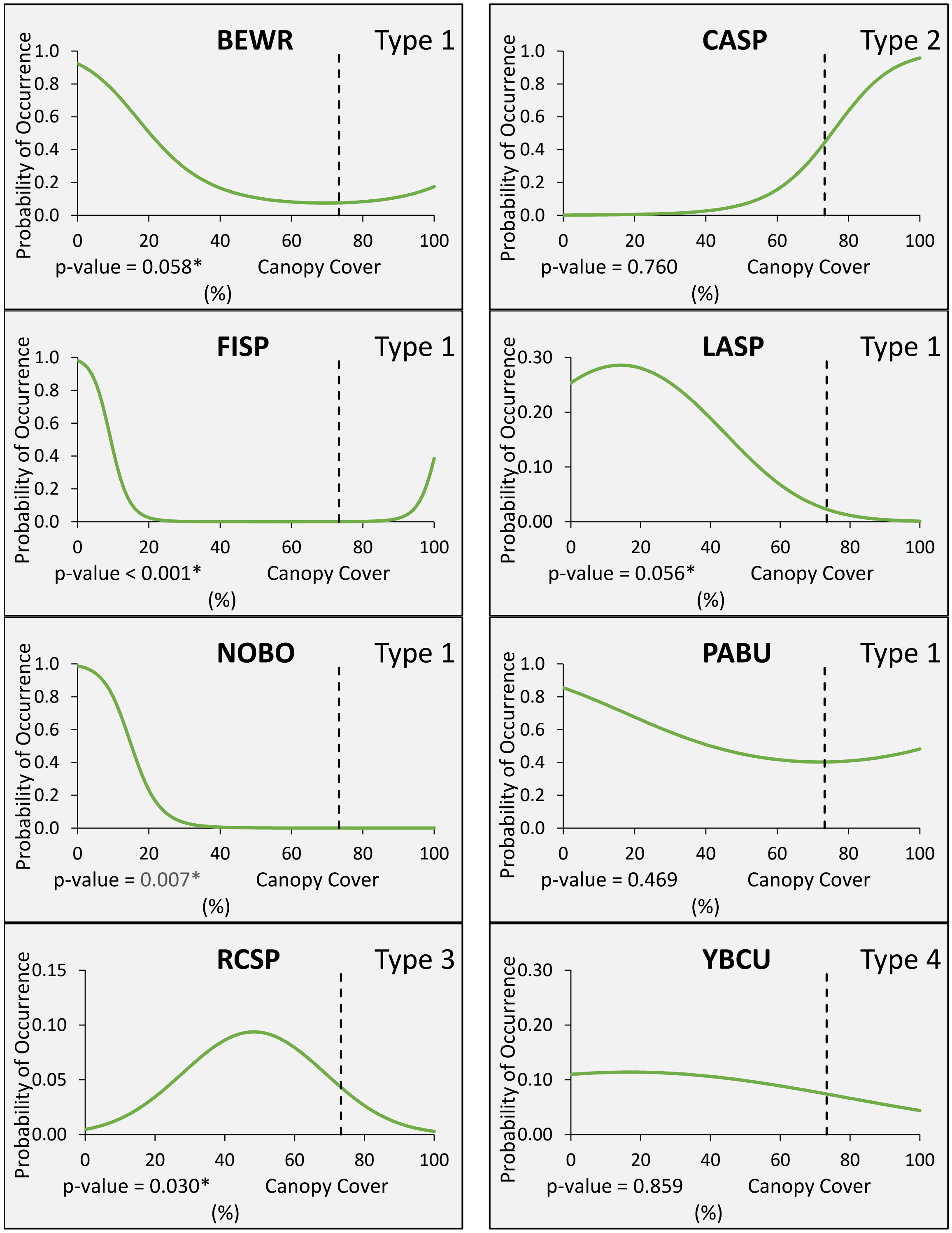


Figure 5. The relationship between canopy cover and probability of occurrence for all eight species. Stippled vertical line at 73.29% represents the maximum observed canopy cover. P-values were derived from logistic regression models (* = values considered to be statistically significant).

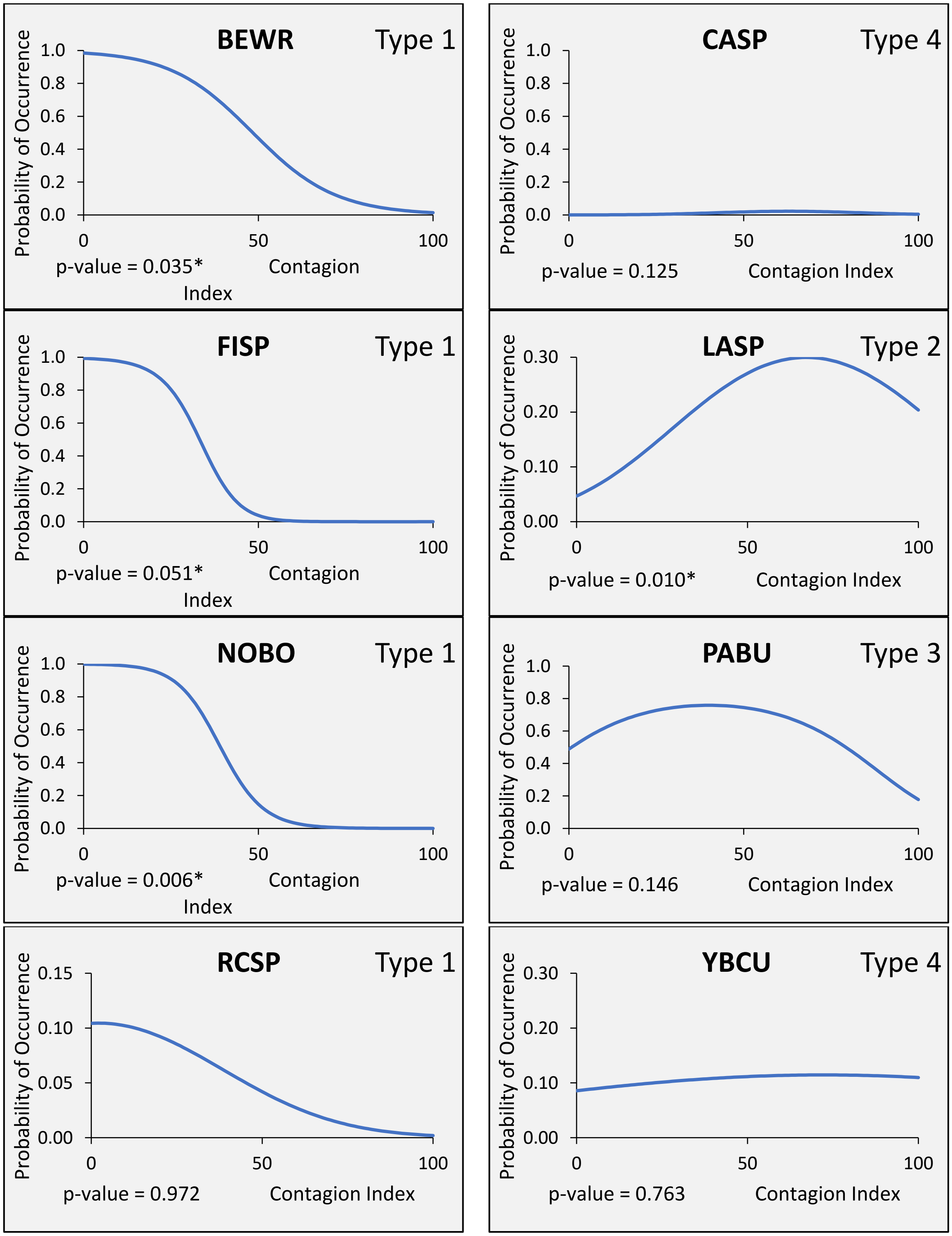


Figure 6. The relationship between the contagion index (a measure of the spatial heterogeneity of canopy cover) and probability of occurrence for all eight species. P-values were derived from logistic regression models (* = values considered to be statistically significant).

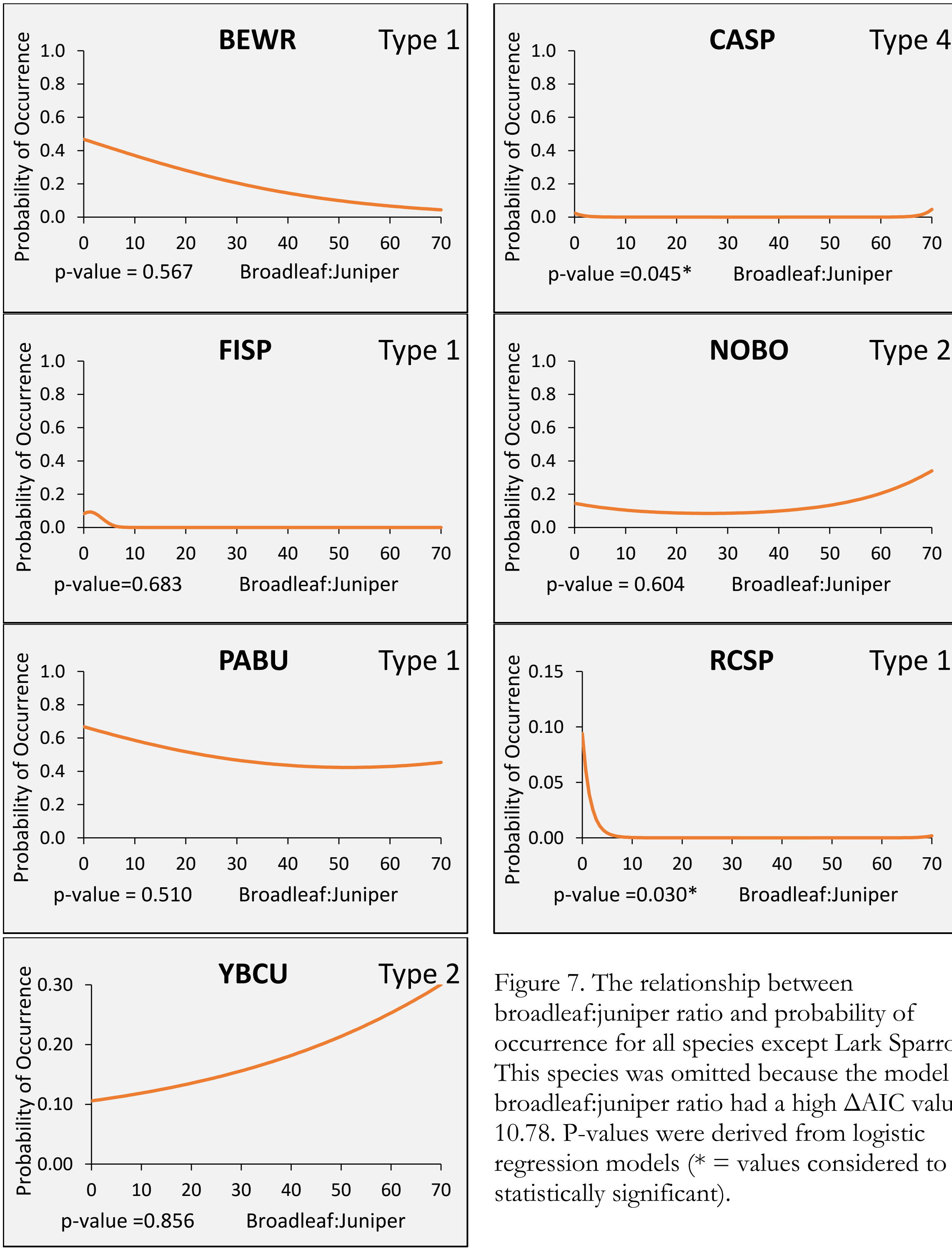
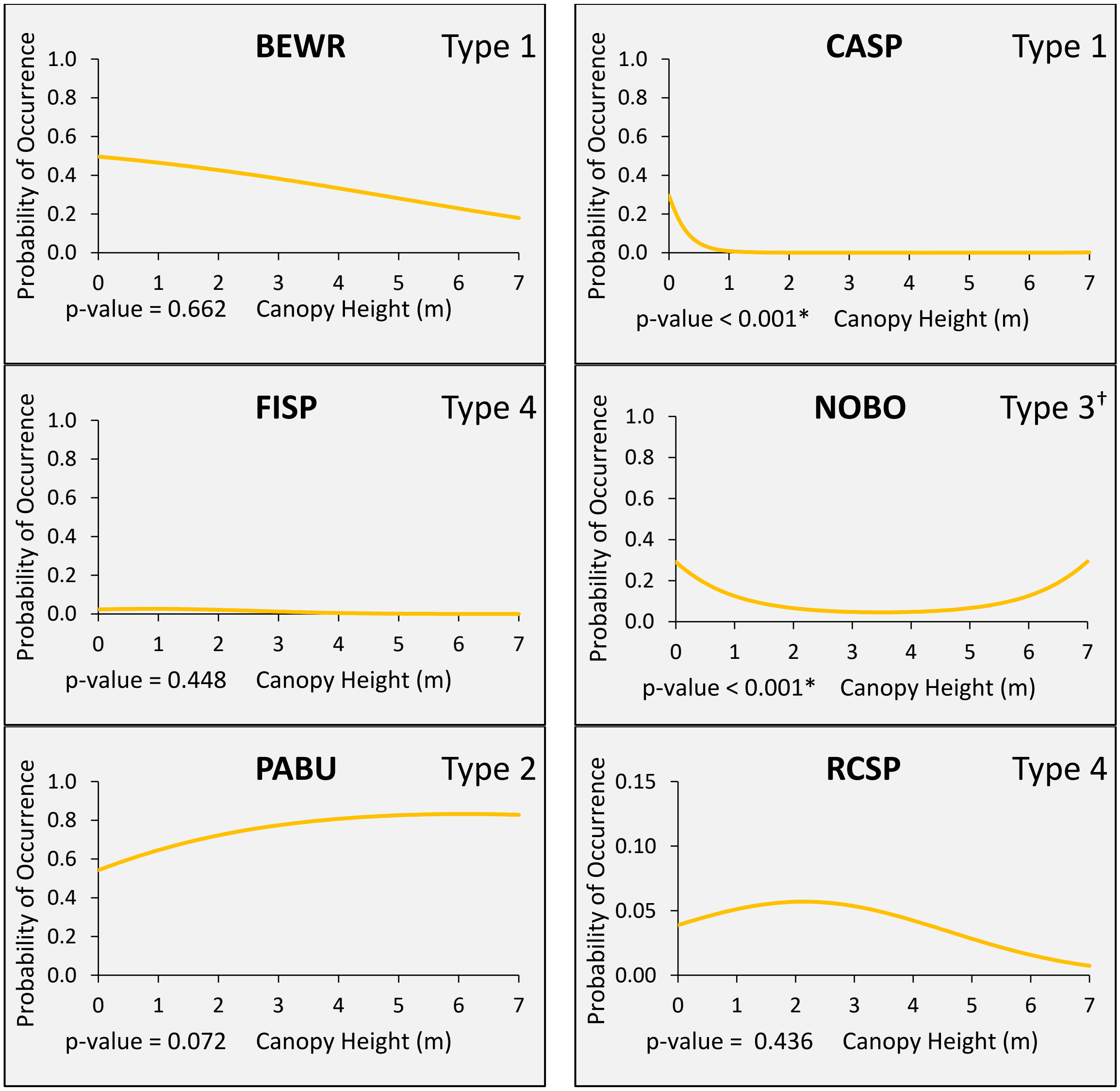


Figure 7. The relationship between broadleaf:juniper ratio and probability of occurrence for all species except Lark Sparrow. This species was omitted because the model for broadleaf:juniper ratio had a high ΔAIC value = 10.78. P-values were derived from logistic regression models (* = values considered to be statistically significant).



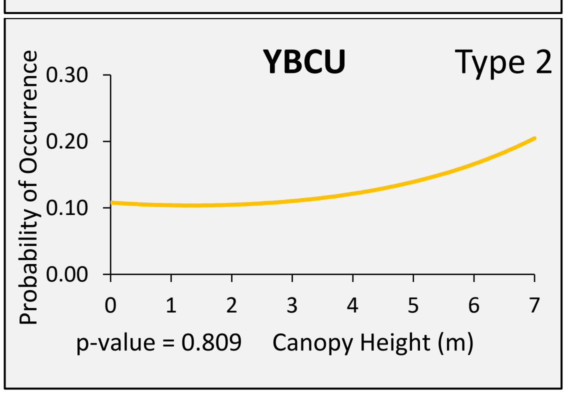


Figure 8. The relationship between mean canopy height and probability of occurrence for all species except Lark Sparrow. This species was omitted because the model for mean canopy height had a high ΔAIC value = 4.99. †The Type 3 curve for Northern Bobwhite is inverted (see Discussion). P-values were derived from logistic regression models (* - indicates values considered to be statistically significant).

REFERENCES

Au, L., D. E. Andersen, and M. Davis. 2008. Patterns in bird community structure related to restoration of Minnesota dry oak savannas and across a prairie to oak woodland ecological gradient. Natural Areas Journal 28:330–341.

Bahía, R., and S. Zalba. 2019. Changes in grassland bird communities and breeding success after a fire in the Argentinian Pampas. Biodiversity and Conservation 28:3767–3786.

Barrioz, S., P. Keyser, D. Buckley, D. Buehler, and C. Harper. 2013. Vegetation and avian response to oak savanna restoration in the mid-South USA. American Midland Naturalist 169:194–213.

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrrs, and their allies. United States National Museum Bulletin 195.

Best, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95:9-22.

Binford, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. Ornithological Monographs 43. American Ornithologists' Union, Washington, DC, USA.

Bond, W.J., G. F. Midgley, and F. I. Woodward. 2003. The importance of low atmospheric CO2 and fire in promoting the spread of grasslands and savannas. Global Change Biology 9:973–982

Bragg, T. B. 1995. The physical environment of Great Plains grasslands. Pages 49–81 in the changing prairie. Oxford University Press, New York, New York, USA.

Brawn, J. D. 2006. Effects of restoring oak savannas on bird communities and populations. Conservation Biology 20:460–469.

Cody, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. BioScience 31:107–113.

Collins, P. W. 1999. Species account on Rufous-crowned Sparrow (Aimophila ruficeps). Pages 99 150 in Distribution and habitat associations of six bird species of special concern at Vandenberg Air Force Base, Santa Barbara County, California.. Santa Barbara Museum of Natural History, Santa Barbara, CA

Crouch, C. G., A. J. Flores, A. Krainyk, L. A. Brennan, D. B. Wester, E. D. Grahmann, R. H. Benson, F. Hernández, and J. F. Kelly. 2019. Comparative habitat use of wintering American Kestrels and Loggerhead Shrikes along south Texas roadways. Southeastern Naturalist 18:240.

Cunningham, M. A., and D. H. Johnson. 2019. Narrowness of habitat selection in woodland and grassland birds. Avian Conservation and Ecology 14.

Davis, H. T., A. M. Long, J. A. Baumgardt, T. A. Campbell, and M. L. Morrison. 2018. Factors affecting nest success and predator assemblage of breeding birds in semiarid grasslands. Rangeland Ecology and Management, 72:385-395

DeBoer, T. S., and D. D. Diamond. 2006. Predicting presence-absence of the endangered Golden-cheeked Warbler (Dendroica chrysoparia). Southwestern Naturalist 51:181–190.

Dechant, J. A., M. L. Sondreal, D. H. Johnson, L. D. Igl, C. M. Goldade, B. D. Parkin and B. R. Euliss. (1999). Effects of management practices on grassland birds: Lark Sparrow. Jamestown, ND: U.S. Dept. of Interior, Geological Survey, Northern Prairie Wildlife Research Center.

Eastman, J. 1991. Yellow-billed Cuckoo. In The atlas of breeding birds of Michigan., edited by R. Brewer, G. A. McPeek and Jr R. J. Adams, 234-245. East Lansing: Michigan State Univ. Press.

Erwin, R. M., D. F. Brinker, B. D. Watts, G. R. Costanzo, and D. D. Morton. 2011. Islands at bay: rising seas, eroding islands, and waterbird habitat loss in Chesapeake Bay (USA). Journal of Coastal Conservation 15:51–60

Feichtinger, E. E., and J. A. Veech. 2013. Association of Scissor-Tailed Flycatchers (*Tyrannus forficatus*) with specific land-cover types in south-central Texas. The Wilson Journal of Ornithology 125:314–321.

Fitch, F. W. 1950. Life history and ecology of the Scissor-tailed Flycatcher, *Muscivora forficata.* The Auk 67:145–168.

Forman, R.T.T. and M. Godron. 1986. Landscape Ecology. Wiley, New York, New York, USA.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.

Giocomo, J., J. Hayes, K. Gee, J. Raasch, and R. Perez. 2017. Strategic habitat conservation for declining grassland wildlife populations in the Oaks and Prairies Joint Venture. National Quail Symposium Proceedings 8:57–64.

Graber, J. W. 1957. A Bioecological study of the Black-Capped Vireo (Vireo atricapillus) Approved By. The University of Oklahoma.

Grant, T. A., and R. K. Murphy. 2005. Changes in woodland cover on prairie refuges in North Dakota, USA. Natural Areas Journal 25:359– 368.

Grzybowski, J. A. 1983. Patterns of space use in grassland bird communities during winter. The Wilson Bulletin 95:591–602.

Grzybowski, J. A., D. J. Tazik, and G. D. Schnell. 1994. Regional analysis of Black-Capped Vireo breeding habitats. The Condor 96:512–544.

Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88:213-229.

Hořák, D., M. Ferenc, O. Sedláček, F. N. Motombi, M. Svoboda, J. Altman, T. Albrecht, E. D. Nana, Š. Janeček, M. Dančák, Ľ. Majeský, E. N. Lltonga, and J. Doležal. 2019. Forest structure determines spatial changes in avian communities along an elevational gradient in tropical Africa. Journal of Biogeography 00:1–13.

Howell, S. N. G., and S. Webb. 1995. A guide to the birds of Mexico and Northern Central America. Oxford University Press, New York, NY, USA.

Hughes, J. M. 1997. Taxonomic significance of host-egg mimicry by facultative brood parasites of the avian genus Coccyzus (Cuculidae). Canadian Journal of Zoology 75:1380–1386.

Igl, L. D., and B. M. Ballard. 1999. Habitat associations of migrating and overwintering grassland birds in Southern Texas. The Condor 101:771–782.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. The Wilson Bulletin 83:215–236.

Johnsgard, P. A. 1979. Birds of the Great Plains: breeding species and their distribution. University of Nebraska Press, Lincoln, NE, USA.

Johnston, V. R. 1947. Breeding birds of the forest edge in Illinois. Condor 49:45-53.

Joos, C. J., F. R. Thompson III, and J. Faaborg. 2014. The role of territory settlement, individual quality, and nesting initiation on productivity of Bell's Vireos *Vireo bellii bellii*. Journal of Avian Biology 45:584–590.

Klopatek, J. M., and J. T. Kitchings. 1985. A regional technique to address land-use changes and animal habitats. Environmental Conservation 12:343–350.

Knopf, F. L. 1996. Prairie legacies-birds. Pages 135-148 in Prairie conservation: preserving North America's most endangered ecosystem. Island Press. Covelo, CA.

Kopachena, J. G., and C. J. Crist. 2000a. Macro-habitat features associated with Painted and Indigo Buntings in Northeast Texas. The Wilson Bulletin 112:108–114.

Kopachena, J. G., and C. J. Crist. 2000b. Microhabitat features associated with the song perches of Painted and Indigo Buntings (Passeriformes: Cardinalidae) in Northeast Texas. Texas Journal of Science 52:133–144.

Korschgen, C., M. Knutson, T. J. Fox, L. Holland-Bartels, H. C. Dehaan, C. H. Theiling, J. J. Rohweder, K. Kenow, L. E. Leake, and T. Will. 2005. Natural resource assessment and decision support tools for bird conservation planning. USDA Forest Service General Technical Report.

Ladd, C. 1985. Nesting habitat requirements of the Golden-cheeked Warbler. Approved By. Texas State University.

Lanyon, W. E. 1981. Breeding birds and old field succession on fallow Long Island farmland. Bulletin of the American Museum of Natural History 168:1-60.

Larkin, T. J., and G. W. Bomar. 1983. Climatic atlas of Texas. Texas Department of Water Resources. Austin, TX, USA.

Lautenbach, J. M., N. Stricker, M. Ervin, A. Hershner, R. Harris, C. Smith. 2020. Woody vegetation removal benefits grassland birds on reclaimed surface mines. Journal of Fish and Wildlife Management 11:89-98

Laymon, S. A. and M. D. Halterman. (1989). A proposed habitat management plan for Yellow-billed Cuckoos in California. USDA Forrest Service. Gen. Tech. Rep. PSW-110:272-277.

Leopold, A. S. 1959. Wildlife of Mexico: The game birds and mammals. University of California Press, Berkeley, CA, USA.

Lehmann, V. W. 1984. Bobwhites in the Rio Grande Plain of Texas. College Station: Texas A&M University Press. College Station, TX, USA.

Li, H., and J. F. Reynolds. 1993. A new contagion index to quantify spatial patterns of landscapes. Landscape Ecology 8:155–162.

Li, Y., Z. Chen, C. Peng, G. Huang, H. Niu, and H. Zhang. 2021. Assessment of habitat change on bird diversity and bird–habitat network of a Coral Island, South China Sea. BMC Ecology and Evolution. 21:137

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lowther, P. E., S. M. Lanyon, and C. W. Thompson. 1999. Painted Bunting (Passerina ciris). In The birds of north america, No. 398. The Birds of North America, Inc., Philadelphia, PA.

Loss, S. R., T. Will, P. P. Marra. 2015. Direct mortality of birds from anthropogenic causes. Annual Review of Ecology, Evolution, and Systematics 46:99–120

Mabry, C. M., L. A. Brudvig, and R. C. Atwell. 2010. The confluence of landscape context and site-level management in determining Midwestern savanna and woodland breeding bird communities. Forest Ecology and Management 260:42–51.

Magnano, A. L., N. G. Fracassi, A. S. Nanni, and R. D. Quintana. 2019. Changes in bird assemblages in an afforestation landscape in the lower delta of the Paraná River, Argentina. Emu 119:346–354.

McAdoo, J. K., W. S. Longland, and R. A. Evans. 1989. Nongame bird community responses to sagebrush invasion of crested wheatgrass seedings. The Journal of Wildlife Management 53:494–502.

Miller, E. V. 1941. Behavior of the Bewick Wren. The Condor 43:81–99.

Morrison, M. L.. 1986. Pages 429–451 in Current Ornithology. Springer US, Boston, Massachusetts, USA.

Nolte, K. R., and T. E. Fulbright. 1996. Nesting ecology of Scissor-Tailed Flycatchers in south Texas. The Wilson Bulletin 108:302–316.

Nolan, V., Jr.. 1963. Reproductive success of birds in a deciduous scrub habitat. Ecology 44: 305–313.

Oberholser, H. C. 1974. The bird life of Texas. University of Texas Press, Austin, TX, USA.

Parmelee, B. D. F. 1959. The breeding behavior of the Painted Bunting in Southern Oklahoma. Bird-Banding 30:1–18.

Peterson, D. W., P. B. Reich, and K. J. Wrage. 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. Journal of Vegetation Science 18:3.

Prather, C. M., A. Huynh, S. C. Pennings. 2017. Woody structure facilitates invasion of woody plants by providing perches for birds. Ecology and Evolution 7:8032–8039.

Pulliam, H. R., and G. S. Mills. 1977. The use of space by wintering sparrows. Ecology 58:1393-1399.

Quine, C. P., R. J. Fuller, K. W. Smith, and P. V. Grice. 2007. Stand management: A threat or opportunity for birds in British woodland? Ibis 149:161–174.

Reemts, C. M. and L. L. Hansen. 2007. Slow recolonization of burned oak–juniper woodlands by juniper (Juniperus i): Ten years of succession after crown fire. Forest Ecology and Management 255:1057–1066

Regosin, J. V, and S. Pruett-jones. 1995. Aspects of breeding biology and social organization in the Scissor-Tailed Flycatcher. The Condor 97:154–164.

Reidy, J. L., F. R. Thompson, and S. W. Kendrick. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. Forest Ecology and Management 313:34–46.

Riitters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. A factor analysis of landscape pattern and structure metrics. Landscape Ecology 10:23–39.

Roach, M. C., F. R. Thompson, and T. Jones-Farrand. 2019. Effects of pine-oak woodland restoration on breeding bird densities in the Ozark-Ouachita Interior Highlands. Forest Ecology and Management 437:443–459.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. Science 366:120–124.

Sesnie, S. E., J. M. Mueller, S. E. Lehnen, S. M. Rowin, J. L. Reidy, and F. R. Thompson. 2016. Airborne laser altimetry and multispectral imagery for modeling Golden-cheeked Warbler (*Setophaga chrysoparia*) density. Ecosphere 7:1–30.

Sharp, B. R., and R. J. Whittaker. 2003. The irreversible cattle-driven transformation of a seasonally flooded Australian savanna. Journal of Biogeography 30:783–802

Shipley, J. R., A. Contina, N. Batbayar, E. S. Bridge, A. T. Peterson, J. F. Kelly, J. R. Shipley, A. Contina, N. Batbayar, E. S. Bridge, A. T. Peterson, and J. F. Kelly. 2013. Niche conservatism and disjunct populations. The Auk 130:476–486.

Shuford, D. W. 1993. The Marin County breeding bird atlas: a distributional and natural history of coastal California birds. Bushtit Books, Bolinas, CA, USA.

Simmons, G. F. 1925. Birds of the Austin region. University of Texas Press, Austin, TX, USA.

Sirami, C., C. Seymour, G. Midgley, and P. Barnard. 2009. The impact of shrub encroachment on savanna bird diversity from local to regional scale. Diversity and Distributions 15:948–957

Spears, G. S., F. S. Guthery, S. M. Rice, S. J. DeMaso and B. Zaiglin. 1993. Optimum seral stage for northern bobwhites as influenced by site productivity. Journal of Wildlife Management 57:805-811.

Stewart, R. E. 1975. Breeding birds of North Dakota. Tri-College Center for Environmental Studies, Fargo, ND, USA.

Stevenson, H. M., and B. H. Anderson. 1994. The birdlife of Florida. University Press of Florida, Gainesville, FL, USA.

Teather, K. 1992. Foraging patterns of male and female Scissor-Tailed Flycatchers. Journal of Field Ornithology 63:318–323.

Tokeshi, M., and S. Arakaki. 2012. Habitat complexity in aquatic systems : fractals and beyond. Hydrobiologia 685:27–47.

Toomey, R. S., M. D. Blum, and S. Valastro. 1993. Late quaternary climates and environments of the Edwards Plateau, Texas. Global and Planetary Change 7:299–320.

Van Auken, O. W. 2000 Shrub invasions of North American semiarid grasslands. Annu. Rev. Ecol. Syst. 31:197–215

Vasseur, P. L., and P. L. Leberg. 2015. Effects of habitat edges and nest-site characteristics on Painted Bunting nest success. Journal of Field Ornithology 86:27–40.

Veech, J.A. 2021. Chapter 3 The primacy of habitat. Pages 39 – 71 in Habitat Ecology and Analysis. Oxford University Press, Oxford, UK.

Visser, M. E., A.C. Perdeck, J. H. Van Balen, and C. Both. 2009. Climate change leads to decreasing bird migration distances. Global Change Biology 15:1859–1865.

Walcheck, K. C. 1970. Nesting bird ecology of four plant communities in the Missouri River breaks, Montana. Wilson Bulletin 82:370-382.

Wang, J., X. Xiao, Y. Qin, R. B. Doughty, J. Dong, and Z. Zou. 2018. Characterizing the encroachment of juniper forests into sub-humid and semi-arid prairies from 1984 to 2010 using PALSAR and Landsat data. Remote Sensing of Environment 205:166–179.

Wiens, J. A. 1989a. The ecology of bird communities, volume 1. Cambridge University Press, Cambridge, UK.

Wiens, J. A. 1989b. The ecology of bird communities, volume 2. Cambridge University Press, Cambridge, UK

Wiens, J. A., and J. T. Rotenberry. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. Ecological Monographs 50:287–308.

Williams, F. C. and A. L. LeSarrier. (1968). Aimophila cassinii (Woodhouse) Cassin's Sparrow. Pages 981-990 in Life histories of North American towhees, sparrows and buntings. Bulletin of the American Museum of Natural History.

Willson, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017–1029.

Wolf, L. L. 1977. Species relationships in the avian genus Aimophila. Ornithological Monographs 23.

Wu, J. and G. Zhang. 2015. Can changes in the distributions of resident birds in China over the past 50 years be attributed to climate change?. Ecology and Evolution 5:2215–2233.