THRESHOLDS OF WOODY VEGETATION TOLERANCE AMONG BIRDS IN THE SOUTHERN GREAT PLAINS

By

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THRESHOLDS OF WOODY VEGETATION

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Abstract: Across the globe, grasslands are experiencing a loss of ecosystem services due to numerous threats, such as overgrazing, agriculture intensification, and woody plant encroachment. In North America, an estimated 20% of grasslands remain intact, but even these areas are threatened by encroaching woody vegetation. Degradation of grasslands are a primary reason that 73% of grassland birds in the Great Plains are experiencing population declines. Although the threat of woody plant encroachment is well known to conservationists, current management practices have not been successful in reversing the trend over broad areas. That is due in part to the treatment of all woody plants as encroaching and equally detrimental. A few studies have already linked the structural characteristics of woody plants to their impact on the landscape. In this study, we investigated how western Oklahoma birds are utilizing woody plants on the landscape, if the height of the woody plant alters their use, and identified the woody vegetation tolerance threshold of these bird species. We conducted point counts at four Wildlife Management Areas in western Oklahoma followed by vegetation sampling during the breeding season 2018–2020. We analyzed species habitat use and identified thresholds in species abundance and frequency using three different height classes of woody vegetation to determine if different woody plant structures on the landscape alter the responses of grassland birds. We sampled 1,129 points and had 3,639 detections from 87 bird species. Analysis showed that woody vegetation height, in particular the abundance of taller trees, was a primary driver of the bird community structure in western Oklahoma grasslands. We found a multitude of woody vegetation tolerance thresholds across our sampled species highlighting the need for heterogeneity in the southern Great Plains. In addition, we identified bird species that responded positively and negatively to increased woody vegetation on the landscape. These results suggest that not all woody vegetation is the same and should not be considered equal when developing management strategies. We recommend further threshold analysis be used to create regional conservation plans that take into consideration the positives and negatives of woody plants for bird and other wildlife communities and highlight the need for a heterogenous landscape.

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CHAPTER I

THRESHOLDS OF WOODY VEGETATION TOLERANCE AMONG BIRDS IN THE SOUTHERN GREAT PLAINS

ABSTRACT

Abstract: Across the globe, grasslands are experiencing a loss of ecosystem services due to numerous threats, such as overgrazing, agriculture intensification, and woody plant encroachment. In North America, an estimated 20% of grasslands remain intact, but even these areas are threatened by encroaching woody vegetation. Degradation of grasslands are a primary reason that 73% of grassland birds in the Great Plains are experiencing population declines. Although the threat of woody plant encroachment is well known to conservationists, current management practices have not been successful in reversing the trend over broad areas. That is due in part to the treatment of all woody plants as encroaching and equally detrimental. A few studies have already linked the structural characteristics of woody plants to their impact on the landscape. In this study, we investigated how western Oklahoma birds are utilizing woody plants on the landscape, if the height of the woody plant alters their use and identified the woody vegetation tolerance threshold of these bird species. We conducted point counts at four Wildlife Management Areas in western Oklahoma followed by vegetation sampling during the breeding season 2018–2020. We analyzed species habitat use and identified thresholds in species abundance and frequency using three different height classes of woody vegetation to determine if different woody plant structures on the landscape alter the responses of grassland birds.

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INTRODUCTION

Grasslands today are one of the most imperiled ecosystems worldwide due to anthropogenic landscape changes (e.g., land use change, overgrazing, alteration in fire regime, and introduction of non-native species) (Ceballos et al. 2010, Henwood 2010, Wilcox et al. 2018). In North America, grasslands are highly fragmented by this human activity, and only 20% of the grasslands remain undeveloped (Ceballos et al. 2010). One of the most notable concerns for these grasslands is the increase in woody plant encroachment (WPE) on the landscape. WPE began developing along the edges of the Great Plains as a result of widespread fire suppression (Knopf 1994), climate change (Archer et al. 2017), frequent use of trees as windbreaks by private landowners (Archer 1994), large scale decline in native browsers, and increased seed dispersal by livestock (Archer et al. 2017). In the Southern Great Plains (SGP), WPE has been particularly prevalent with an increase that is 5–7 fold greater than other grassland regions (Wilcox et al. 2018). This increase in woody plants is causing an ecosystem shift from grasslands and shrublands into woodlands (Scholtz et al. 2018, Eldridge et al. 2011). Therefore, WPE is a dominating concern in the Southern Great Plains due the rate of spread, the ineffectiveness of current management practices and the risk of irreversible changes to ecosystem function and services.

The shift from grassland to woodland communities is an alteration of vegetation structure, and, in turn, changes light, nutrient, and habitat structure (Wilcox et al. 2018). This has resulted in major changes to ecosystem services including net primary productivity, biodiversity, pollination, and other services (Ratajczak et al. 2012, Wilcox et al. 2018). As a result, increased WPE has led to population declines among several species within multiple taxa (Ratajczak et al. 2012, Coppedge et al. 2004, Gibbons et al. 2000, Davidson et al. 2012, Rosenberg et al. 2019). This trend is especially apparent in many grassland bird species (Rosenberg et al. 2019). In fact, grassland birds in the Great Plains have experienced a 53% population loss since the 1970's, with 73% of those species still experiencing population declines (Rosenberg et al. 2019). These losses can be attributed to widespread changes in available habitat on the landscape as a result of WPE, including unfavorable changes in food resources, adequate nest sites, and roosting habitat (Archer et al. 2017). The increase in woody plants can also cause increased competition for food as woodland-associated species find suitable habitat due to the expansion of trees (Archer et al. 2017). As the landscape makes the transition to shrub or tree-dominated cover and herbaceous cover is lost, grassland species are lost, and biodiversity begins to decrease (Archer et al. 2017).

It is plausible that the influences of WPE on the grassland bird community are non-linear, that is, at a certain point the pressures created by WPE could disproportionately negative affect on the grassland bird community. However, it could provide additional habitat for shrubland and forest birds. Ecological thresholds can be useful in determining the impacts of these habitat changes on the bird community. A threshold is the inflection point at which an ecological process shows a rapid, non-linear response to an environmental gradient (Farwell et al. 2020, Duchardt et al. 2019, Ratajczak et al. 2014, Bestelmeyer et al. 2011, Briske et al. 2005). The landscape fragmentation and ecosystem changes occurring across the SGP can lead to these threshold type responses (Ratajczak et al. 2014, Briske et al. 2005), making thresholds identification increasingly more important for restoration and landscape ecology in this area because they provide quantifiable management targets (Bestelmeyer 2006, Turner 2005, Hobbs & Harris 2001). Multiple studies have identified tolerance threshold responses of avian communities to a variety of habitat characteristics including scale of available habitat and availability of nesting habitat (Zuckerberg & Porter 2010, Poulin et al. 2008, Betts et al. 2007). Quantifiable threshold points provide managers with more specific management targets and assist managers in prioritizing management efforts and developing success criteria for restoration (Bestelmeyer 2006, Suding et al. 2004, Hobbs & Harris 2001). For example, if one species has a threshold at 30% woody cover, we know to maintain that system at less than 30% woody cover to maintain that species.

Improving our understanding of the effects of WPE in the SGP on the bird community is increasingly important as areas make the transition to arid shrublands or woodlands with these changes only expected to intensify under climate change (Archer et al. 2017). Birds of the SGP are under threat from this expanding woody vegetation (Rosenberg et al. 2019), the temperature changes caused by climate change (Gorzo et al. 2016). By improving our understanding of the challenge faced by these bird species, we can preserve necessary habitat for the species. Ecological tolerance threshold identification can help us manage for these species by identifying accurate threshold points when bird species composition will change.

Most studies categorize all woody vegetation as WPE or focus on a singular expanding woody plant (e.g., eastern red cedar [*Juniperus virginiana*] or honey mesquite [*Prosopis glandulosa*]) when researching the effects of WPE on landscapes (e.g., Andersen & Steidl 2019, Ratajczak et al. 2014, Blaum et al. 2007, Coppedge et al. 2004). However, multiple studies support the idea that vegetative structure plays an important part in determining the effects of WPE (Eldredge & Ding 2021, Ding et al. 2020, Andersen & Steidl 2019). For avian species, the plant structure (density, height, and composition) can alter available nesting materials and habitat, change perching structure, and it could alter the visibility of call displays for species such as the Cassin's Sparrow (*Peucaea cassinii*). Therefore, it is important to continue researching the effects of WPE in order to make relevant and actionable management decisions. Identifying which structural characteristics are driving bird community response will help us better understand the impact WPE is having on the bird community in the Great Plains.

To determine how WPE is affecting the bird community, we used bird and vegetation surveys in a detrending correspondence analysis and identified tolerance thresholds of bird species and compared those with vegetation variables. Our primary objectives were to (1) determine which environmental variable (i.e., height of woody plants, cover of woody plants, herbaceous cover, canopy cover, or cover of bare ground) is driving the bird community composition in western Oklahoma and (2) identify each species tolerance threshold across to woody encroachment of varying heights.

METHODS

Study Area

We conducted the study across four Wildlife Management Areas (WMAs) in Oklahoma, USA (Figure 1). Three of the study sites (Beaver, Packsaddle, and Sandy Sanders WMAs) located in western Oklahoma, while one (Cross Timbers WMA) is located in the south-central portion of the state. Mean annual rainfall in the area ranges from 60 cm in the western most portion of the state to 101 cm in the eastern portion (Kloesel et al. 2018). Rainfall during our sample years (2018-2020) ranged from 43-114 cm (Mesonet, 2021). In 2019, some sample locations, primarily in the southwest, had high rates of rainfall. For example, Sandy Sanders WMA, which means 50 cm annually, received 83 cm. These sites range from 4,200 to 12,000 hectares in size and encompass a large array of vegetation types from hardwood forest to short grass prairies (Table 1) (Tyrl et al. 2008). One area is dominated by mesquite or juniper woodlands and mixed prairies. Another is composed of medium structure woody plants including Shinnery Oak (*Quercus havardii*) stands, sand plum (*Prunus angustofolia*) or sumac (*Rhus* spp.) shublands, and mixed grasslands. The most northern site is dominated by short structured woody plants, sand sagebrush (*Artemisia filifolia* Torr.) and short grass prairie. Oak forest and savannas are found at our southernmost site. This range of vegetation was chosen to cover a large array of height classes of woody plants for our analysis. All sites are managed by the Oklahoma Department of Wildlife Conservation with techniques including disking, food plots, prescribed fire, and grazing (ODWC). Threats to our study sites include expanding hardwoods, encroaching junipers (*Juniperus* spp.) and encroaching mesquites (*Prospis* spp.) (Barger et al. 2011).

Sampling Design

Data were collected between May and July 2018-2020. Each summer, sample locations for point counts and vegetation surveys were created using a stratified random approach. These points were a minimum of 300 meters apart. The 300 points were grouped into 30 sections across the WMA to reduce travel time between points sampled each morning. Prior to sampling, we selected a random point and all points within the same quadrant were sampled the following day. No points were repeated to maximize coverage across the WMA. We attempted to maximize coverage by not repeating points to ensure that samples were taken across a gradient of vegetation composition and cover types. During the 3 years of the study, we sampled a total of 1,129 points (2018: 258, 2019: 709, and 2020: 162).

Avian Surveys

We conducted avian surveys using a fixed radius, point count that lasted 10 minutes. Point counts began at sunrise and continued for 4 hours after sunrise. Surveys were conducted by two observers with one observer identifying all birds seen or heard within 100 meters and measuring their distances using a rangefinder and the other observer recording the observations. Birds in flight were noted but not counted unless they landed within the survey point during the time allotted. Additional species were filtered out before analysis based on number of detections (<6).

Vegetation Sampling

Vegetation sampling was conducted at each point one week following completion of avian survey. To evaluate the influence of woody plants on the bird community, we measured multiple vegetation characteristics including canopy cover, shrub density, and basal cover of herbaceous vegetation, litter, bare ground, and woody plants. We used Daubenmire frame located 10 meters from each avian survey point in the 4 cardinal directions, to measure cover (Daubenmire 1959). Point-centered-quarter method was used to determining shrub density. This was done by dividing the area around the point into quarters along lines running in each cardinal direction. The distance to the nearest woody plant is then recorded and used in to determine the average density of woody plants in the area (Mitchell 2010). In the center of the point, spherical densitometer was used to measure canopy cover and an ocular estimation of woody plant cover within a 50-m radius was recorded. For the ocular estimation, percent cover was recorded in cover classes (0–5, 5–10, 10–25, 25–50, and >50) of woody plants in 3 height classes (<2 meters, 2–4 meters, and >4 meters) within 50 meters of the point. Measurements were averaged to obtain a single estimation of cover per point. Due to the measurement of understory and larger trees in some forested areas, estimated woody cover in each height class was combined to create an index of total woody cover ranging from 0–205%.

Ordination Analysis

We used vegetation means and bird abundance at each point to establish the primary vegetation characteristics driving the change in bird community composition. Vegetation characteristics used in this analysis included mean cover of forbs, litter, bare ground, grass, total cover of woody plants, cover of woody plants in each height class, and canopy cover. WMA was recorded and used in analysis to account for vegetation differences across sites. To qualitatively characterize the relationship between vegetation structure and bird community composition, we used Detrending Correspondence Analysis (DCA) in RStudio with the default settings of the "decorana" function in package "vegan" (Oksanen et al. 2008). This method is useful for datasets containing multiple environmental gradients and has been used to summarize similarities in the bird community and determine primary ecosystem drives of bird community changes. (Fuhlendorf et al. 2006, Collins 2000, Peet et al. 1988). We determined the most influential environmental variables and bird species in the DCA by species scores and site scores. These scores estimate the influence of each variable on the DCA. Higher scores indicate a more substantial impact on the DCA and assist in interpreting the gradient on each of the DCA axes.

Threshold Analysis

We used Threshold Indicator Taxa Analysis (TITAN; Baker & King 2010) to identify species-specific change-points or thresholds along a gradient of WPE. TITAN uses a combination of change-point analysis (King & Richardson 2003) and indicator species analysis (Dufrene & Legendre 1997) to identify change points in species abundance and frequency of occurrence. These change points, which are considered thresholds, are the point at which a species habitat use is decreased due to the measured habitat characteristic. TITAN assesses the strength of the association with the environmental gradient by using taxon-specific indicator scores (Farwell et al. 2020). These indicator value scores are normalized to allow comparison across taxon and are represented as the z-score.

TITAN uses 500 bootstrap resampling to estimate purity/reliability and describe uncertainty in the analysis. With each bootstrapped replication, the threshold point is altered to identify the upper and lower possible change point. The narrower the margin between the change points, the sharper the change in species frequency and abundance. The purity measurement provides a measure of the number of bootstrap replications that result in the same response direction (positive or negative). The reliability measure indicates the consistency of the bootstrap resampling that provides a p-value equal or lower than 0.05. For this study, only species with purity and reliability measures greater or equal to 95% were included (Baker & King 2010). This analysis was performed for overall woody cover at the 50-meter spatial scale and for woody cover of individual height classes.

RESULTS

Bird Community

During the study, we surveyed 1,129 points and detected a total of 87 species and 3,639 individual birds. Of these 87 species detected, 46 had at least 5 occurrences to use in our analysis. Using the Partners in Flight Conservation Assessment Database, we classified these species into four habitat guilds: forest (22 species), open mosaic (10 species), grassland (8 species), and shrubland (6 species) (Table 3). Avian species occurred on 85% of all point counts with up to 14 individuals per point count. Our most common species were the Dickcissel (*Spiza americana*), Painted Bunting (*Passerina ciris*), Northern Cardinal (*Cardinalis cardinalis*), Great Crested Flycatcher (*Myiarchus crinitus*), and Blue-gray Gnatcatcher (*Polioptila caerulea*) with 577, 366, 325, 288, and 149 detections, respectively, across the three sampling years (Table 3). The lowest number of detections included in the analysis (6) belonged to Orchard Oriole (*Icterus spurius*), Ladder-backed Woodpecker (*Dryobates scalaris*), Greater Roadrunner (*Geococcyx californianus*), and Blue Jay (*Cyanocitta cristata*). The WMA with the highest species richness was Packsaddle WMA with 37 species across the 3 years. Beaver River, Sandy Sanders and Cross Timbers all had comparable species richness totals with 32-33 species. Cross Timbers had the highest count of birds with a total of 1,201 individuals across 256-point counts. Beaver River WMA had the lowest count of birds with only 609 individuals across 285-point counts.

Vegetation Characteristics

The mean total woody cover (the sum of cover at all height classes) from our broad scale estimation across all sites was 72%. The mean woody cover across all WMAs of short shrubs (0-2 meters), mid-height shrubs (2-4 meters) and trees (>4 meters) was 38%, 18%, and 15%, respectively. Some points had 0% woody cover but were relatively uncommon only occurring on 3% of all points. Short shrubs were the most common vegetation height class across sites (highest frequency of occurrence), occurring on 93% of points followed by mid-height shrubs (62%) and trees (51%). Canopy cover of trees across all points ranged from ~0% to 100%, but averaged 11% across all points. Estimated shrubs per ha also had a large range spanning from 0 to 1,600 woody plants per ha, but averaged 277 shrubs per ha across the study sites. Herbaceous cover of grass and forbs ranged from 0-98%, but averaged 35% an 16%, respectively. Cover of bare ground and litter also ranged 0-98% and both averaged 14% across all points.

Ordination Analysis

The first two axes of our ordination explain 58% of the variance in the grassland bird community data. DCA axis 1 and 2 had eigenvalues of 0.657 and 0.570, respectively, meaning that DCA1 explained slightly more of the variance in the bird community than DCA2. DCA axis 1 represents a gradient ranging from tall, closed canopy forest to open grassland/savanna habitats. Specifically, Axis 1 low scores indicate areas with closed canopy, high cover of litter, woody cover >4m, and high scores indicate areas with low canopy cover, few instances of tall trees and high percent grass cover. Several bird species appeared to sort along DCA1. Specifically, Turkey Vulture (*Cathartes aura*) and Red-winged Blackbird (*Agelaius phoeniceus*) were associated with open savannah areas with high % grass cover (strongly positive DCA1) and sparse tall trees.

Whereas, Summer Tanager (*Piranga rubra*), Red-eyed Vireo (*Vireo olivaceus*) and Tufted Titmouse (*Baeolophus bicolor*) were strongly associated with closed canopy and tall (>4m) woody cover (strongly negative DCA1). Axis 2 represents a gradient ranging from shrublands to open grasslands with bare ground present. Axis 2 low scores indicate areas containing higher density of shrubs per hectare and woody cover in the 0-2m range and high scores indicate areas containing few shrubs per hectare and a higher cover of bare ground. Multiple species sorted along DCA2 including House Wren (*Troglodytes aedon*) and Bell's Vireo (*Vireo bellii*) which were associated with areas of higher shrub cover (negative DCA2). Whereas, Cassin's Sparrow, Ring-necked Pheasant (*Phasianus colchicus*), and Western Meadowlark (*Sturnella neglecta*) were associated with areas of few shrubs and increased cover of bare ground (positive DCA2). Location or WMA showed little impact though our study covered a large portion of Oklahoma with a variety of dominating vegetation types.

<u>Threshold Response of Birds to Woody Plant Cover</u>

Sampling across the 4 WMAs resulted in 47 avian species with sufficient detections for inclusion in TITAN analysis (n >6), 18 of which had a significant response to increasing total woody cover. Of these, 3 species responded negatively (Grasshopper Sparrow, Western Meadowlark, and Eastern Meadowlark), meaning they showed a decrease in abundance and frequency at a specific change point between 5–50% woody cover (Figure 3). There were 15 species that responded positively (e.g. Northern Cardinal, Blue-gray Gnatcatcher, and Tufted Titmouse; Figure 3), meaning they showed an increase after a specified change point between 30-125% woody cover. All negative responding species fell within the grassland habitat guild; however, the group of positive responding species was made up of 11 individuals from the forest guild, 2 from the arid shrubland guild, and 1 each from the grassland and open country mosaic guild (Table 3 and Figure 3).

When we further examined woody cover by vegetation height, we found that 26 species exhibited significant responses to woody plant cover at a particular vegetation height. Additionally, it is worth mentioning that when comparing the total estimated cover analysis to that of the height classes, there is a difference in the reliability of the threshold responses, meaning that the height classes had higher z-scores than the total woody cover. Z-scores indicate how consistent the threshold identification was across all 500 bootstrapped samples. Species found to have a threshold response in each height class had narrower margins than those of the total estimated woody cover, indicating that the height of vegetation is an important driver (Figures 3 and 4).

There were 16 total species that showed a threshold type response to higher woody vegetation cover that were less than 2-meters tall (Figure 4). All negative responding species (Western Meadowlark, Grasshopper Sparrow, and Cassin's Sparrow) fell within the grassland habitat guild and had a threshold point of 5% woody cover. Similar to the total woody cover responses, the positive responding species in this height class also showed more range in the threshold point and guild assignment. There were 13 species that responded positively with threshold points between 5–25% woody cover. Of the species that responded positively, 6 belonged to the forest guild, 4 belonged to the open country mosaic guild and 3 belonged to the arid shrubland guild (Table 3 and Figure 4).

Species responses to woody vegetation cover in the 2–4-meter height category was identical to that of the less than 2-meter height class (Figure 5). Negative and positive responding species were the same and had the same threshold points. Based on our analysis, shorter height classes do have an influence, however, we cannot separate the impacts between these two height classes.

Woody vegetation in the >4-meter height class had the most species with significant threshold type responses. There were 22 total species with responses, 7 negative and 15 positive responders to an increase in woody vegetation within this height class (Figure 6). Of the 7 species that responded negatively, 6 belonged to the grassland habitat guild and 1 belonged to the forest guild. The threshold points of these species varied between 5–25%. Again, the positive responding group had more range in threshold point and species guild assignment. There were 10 species within the forest guild, 4 in the open country mosaic guild and 2 within the arid shrubland guild (Table 3). The threshold point ranged between 5–50% woody cover greater than 4 meters tall.

There were 18 species that had no significant response across all sites and vegetation height. Of these species, 9 belonged to the forest guild, 5 belonged to the open country mosaic guild, 3 belonged to the arid shrubland guild, and 1 belonged to the grassland guild (Table 3). The lack of significant response in the analysis of this study does not rule out the avoidance of shrub or tree cover for these species because some species may be responding in a more linear way rather than showing thresholds. For example, the Bell's Vireo belongs to the arid shrubland guild and was most often recorded in dense stands of shrubs. However, the change in frequency and abundance was not abrupt and did not meet the requirements for a threshold response.

DISCUSSION

Woody plant encroachment in the North American Great Plains has become a significant conservation issue, especially when you consider that WPE rates are up to 7 times greater than other regions in North America (Barger et al. 2011, Willcox et al. 2018). WPE changes the landscape structure and function by altering light, nutrients, and water availability (Ratajczak et al. 2012). The change of grasslands to woodlands in this region of the Great Plains is leading to the decline of multiple taxa, especially bird species (Rosenberg et al. 2019, Ratajczak et al. 2012, Davidson et al. 2012, Coppedge et al. 2004, Gibbons et al. 2000). Though WPE is causing significant, negative changes, this study shows that this issue may not be entirely straightforward since bird species of the region have variable responses to woody cover. These results show that the height and amount of cover of WPE are major drivers of population trends in the bird community; however, not all WPE is equally impactful on these bird communities.

Across our sample sites in the SGP, our data showed a relatively high frequency of woody plant cover with 98.6% of sample points containing woody vegetation. This was to be expected, considering findings by other studies such as Wilcox et al. (2018) which found large pieces of the Great Plains in Oklahoma and Texas to be covered by trees and shrubs with only small pockets of intact grasslands remaining. Furthermore, other studies have found that structural traits of woody plants (e.g., root type and length, height) alter the woody plants' impact on grassland ecosystems (Edridge & Ding 2021, Grant et al. 2019). We found a similar result when looking at above ground structure of WPE. Our results showed that woody plant cover had distinct effects on the bird abundance when separated into height classes. Additionally, the most impactful height class on the bird community was woody plants greater than 4 meters. This could be due to the transition from grassland habitat type to woodlands habitat type, subsequently causing a community shift from grassland guild species to species that fall within the forest guild. Nonetheless, the importance of this impact is still important to note. The second most impactful height class was short shrubs less than 2 meters. This height class is representative of areas that contain expanding shrubs or trees in an early successional stage. For instance, taller tree species, such as Eastern Red Cedar, are comparable to shorter shrub species during their early stages of growth. Grassland obligate birds, such as Grasshopper Sparrow and Western Meadowlark, may be less tolerant of this expansion, even in early stages; however, shrubland guild species, such as the Bewick's Wren (*Thryomanes bewickii*), may prefer new growth at this stage and will utilize the area. Though we focused on how height affects species abundance, other studies have also found that distance to the edge of shrubs or tree patches can also causes increases in nest parasitism and predation rates (Grant et al. 2019). This is an example of the varied habitat requirements of bird species within the Great Plains that complicates management decisions to control WPE because all management will have negative and positive impacts to consider.

Threshold identification in birds is becoming an increasingly popular way of informing management for bird species (Gutzwiller et al. 2015, Bestelmeyer 2006, Suding et al. 2004). For birds, and many other wildlife species, it is most often the extremes (weather, temperature, vegetation density) within their habitat that drives their habitat use (e.g., Carroll et al. 2018). Thresholds allow us to focus on these extremes, rather than the mean, and determine how they affect individual species. Our threshold analysis identified 55% of species having a threshold response, which falls within previously found ranges of 30–80% of species showing threshold responses in human altered landscapes (Gutzwiller et al. 2015). In addition, we found the type and structure of woody plant cover does shape species responses to WPE. This is indicated by the identification of narrower, more reliable, threshold points in response to woody cover when broken into height classes rather than treated as total woody cover. This could be an artifact of the cover range (0–100%) for each height class versus the larger range (0–200%) of the total woody cover class; however, we believe that this is an accurate representation of vegetation impact based on the DCA which provided that woody cover categorized by height classes had a stronger impact on bird community composition than that of other vegetation characteristics, including total woody cover.

The diversity of the bird community habitat requirements were clear within this study with species having varied responses across height classes and within guild. Moreover, there were instances of species within the same guild having different threshold points or responses to each height class. For example, Blue-gray Gnatcatcher showed an increase in abundance in only 15% cover of tall trees, while Tufted Titmouse did not show an increase in abundance until 30% cover of tall trees. Another example is the grassland species Cassin's Sparrow showing a decreasing in abundance at only 5% cover of tall trees, and Dicksissel did not show a decrease in abundance until 25% tall tree cover. Dickcissels also showed no response to increasing woody plants less than 4 meters tall while Cassin's Sparrow showed a negative response to an increase in woody plants in all height classes. These inconsistent results have been considered an issue with threshold identification because they could complicate management decisions (Bestelmeyer 2006). However, these inconsistencies highlight the complexity of habitat requirements and oversimplify a complicated issue. This does not make threshold identification irrelevant or inaccurate. Nor does it negate the need for further threshold identification for all species on the landscape in order to come to a more comprehensive understanding of the impact of WPE.

Often management decisions are made with species of conservation concern in mind. Managers try to make decisions that will benefit those species that are experiencing declines to prevent further decline. To determine what species included in our study might be most important to consider while making management decisions, we identified the conservation status and habitat guilds of species included in this study using Partners in Flight Conservation Assessment Database. Information including breeding and non-breeding habitat, current population size, threats to breeding and non-breeding habitat and more are combined to give species a PIF, score. Higher PIF scores denote a higher cause for concern. Species of concern are then placed into a variety of categories dependent on the variables impacting their decline. Four of the species in this study had PIF scores high enough to be considered a species of concern. One species, the Grasshopper Sparrow, belongs to the grassland guild, and is considered a common bird in steep decline. The Northern Bobwhite (*Colinus virginianus*), belonging to the open country mosaic guild, is also considered a common bird in steep decline. The last two species, the Red-headed Woodpecker (*Melanerpes erythrocephalus*), and the Yellow-billed Cuckoo, both belong to the forest guild. The Yellow-billed Cuckoo is also considered a common bird in steep decline. The

Red-headed Woodpecker is the only species considered to be on a watch list. It is on the Yellow D watch list, meaning it is experiencing steep declines and major threats. These birds may be targeted for management in this region, it is important to understand the impact that woody plant encroachment will have on them.

Of the species identified as species of concern using PIF, only 2 showed threshold type responses to our vegetation characteristics, the Yellow-billed Cuckoo (*Coccyzus americanus*) and the Grasshopper Sparrow. The Grasshopper Sparrow was negatively affected by the increase in woody plants in all height classes with a threshold point of 5% across all height classes, while the Yellow-billed Cuckoo was positively affected by an increase in woody plants greater than 5% in all height classes. This contradiction becomes an issue when determining the extent of woody plant removal and necessary management practices on the landscape because what benefits one species of concern may harm another. With bird populations in all guilds experiencing population declines (Rosenberg et al. 2019), the removal of WPE on the landscape will always have advantages and disadvantages.

CONCLUSION AND MANAGEMENT IMPLICATIONS

Woody plant encroachment is a multifaceted, dynamic issue that is continuously altering habitat structure and complicating land management decisions in the southern Great Plains (e.g. Eldridge and Ding 2021, Bestelmeyer et al. 2006, Weins et al. 2002,). This study adds nuance to our understanding of the impacts of WPE on bird communities. We found evidence of a wide spectrum of threshold points as well as positive and negative species responses to WPE, though WPE is often viewed in the literature as only having negative effects (Archer et al. 2017, Hoekstra et al. 2004). However, a multitude of species responded positively to the increase in woody plants to some degree. For example, species such as the Painted Bunting, which is a focus species for the Oaks and Prairies Joint Venture 2020, responded positively to the increase in woody plants. Similarly, the Northern Bobwhite, a species of considerable management focus and conservation concern, requires shrubs on the landscape and may also benefit from WPE (Duquette et al. 2019, Carroll et al. 2018). That being said, we still need to focus on maintaining our grasslands in order to provide habitat for less shrub tolerant species (Grasshopper Sparrow) and increasing heterogeneity. Understanding the positive and negative impacts of WPE can help managers determine what areas need to be managed to prevent WPE and what areas can be maintained at the current state (Ding et al. 2020) by understanding the tradeoffs of management decisions. Therefore, there is a need for a balanced view of WPE in the Great Plains by increasing studies that focus on multiple species to gather information that will accurately determine the winners and losers of management decisions.

The multitude of threshold points highlights a need for heterogeneity, diversity in woody plant density and size across the SGP. The Oaks and Prairies Joint Venture and many research papers highlight this need and advise land management practices such as prescribed fire at a variety of return intervals and herbicide and/or mechanical treatment to slow the spread of WPE where occurring. In order to reduce time and cost of removing woody plants, land managers have emphasized disruption of WPE before trees, such as Eastern Redcedar, reach mature size and areas become unrestorable (Fuhlendorf et al. 2017). We found that tall woody plants were the most impactful to the bird community. This means that current management practices, such as prescribed fire, brush hogging, and grazing are a good step and decrease the land area that will be converted to forested land. It also indicates though, a need for management that targets areas already transitioned to woodlands for restorations, though these areas may present more barriers to restoration by requiring more time-consuming management practices (Scholtz et al. 2018). Our research provides quantifiable thresholds on a multitude of bird species that can be used to inform management by identifying species that will benefit and lose as a result of management actions across the Southern Great Plains. These threshold points can provide important targets for restoration and by providing specific management targets and assist managers in prioritizing management efforts and developing success criteria for restoration (Bestelmeyer 2006, Suding et al. 2004, Hobbs & Harris 2001). Therefore, we believe species specific management practices are best informed by threshold identification and threshold identification should continue to be used moving forward.

In conclusion, many studies have been done on the issue of WPE, however, there are still areas to improve our understanding of the structural characteristics that shape the impacts of WPE, and what species are significantly impacted by its spread. We need to recognize that woody plants on the landscape are not only negative and some bird species could benefit from their spread. The creation and implication of regional management plans could reduce the confusion on woody plant encroachment by identifying specific problem woody species and areas, and targeting management for regional species of conservation concern. These conservation plans could benefit from identifying thresholds of more species to provide quantifiable targets and allowing for customizing WPE management to the species and bird community as a whole.

FIGURES

Figure 1: Map of North American Great Plains. Wildlife Management Areas in western Oklahoma used in study marked by black points.

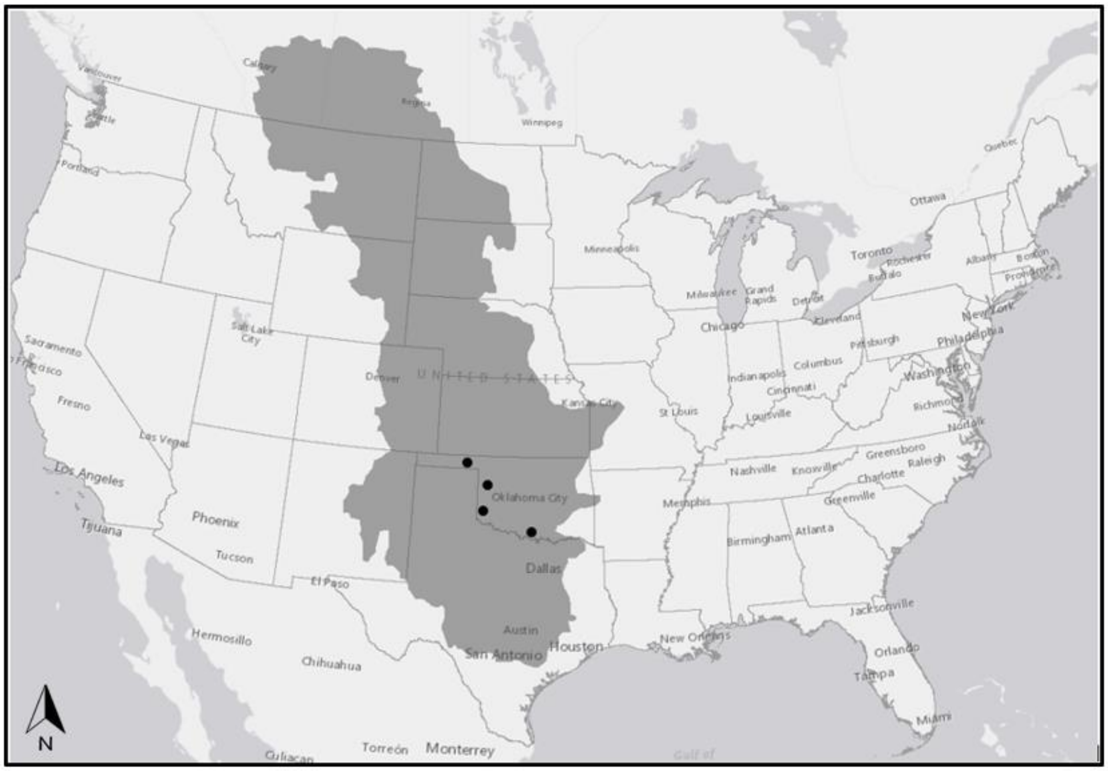
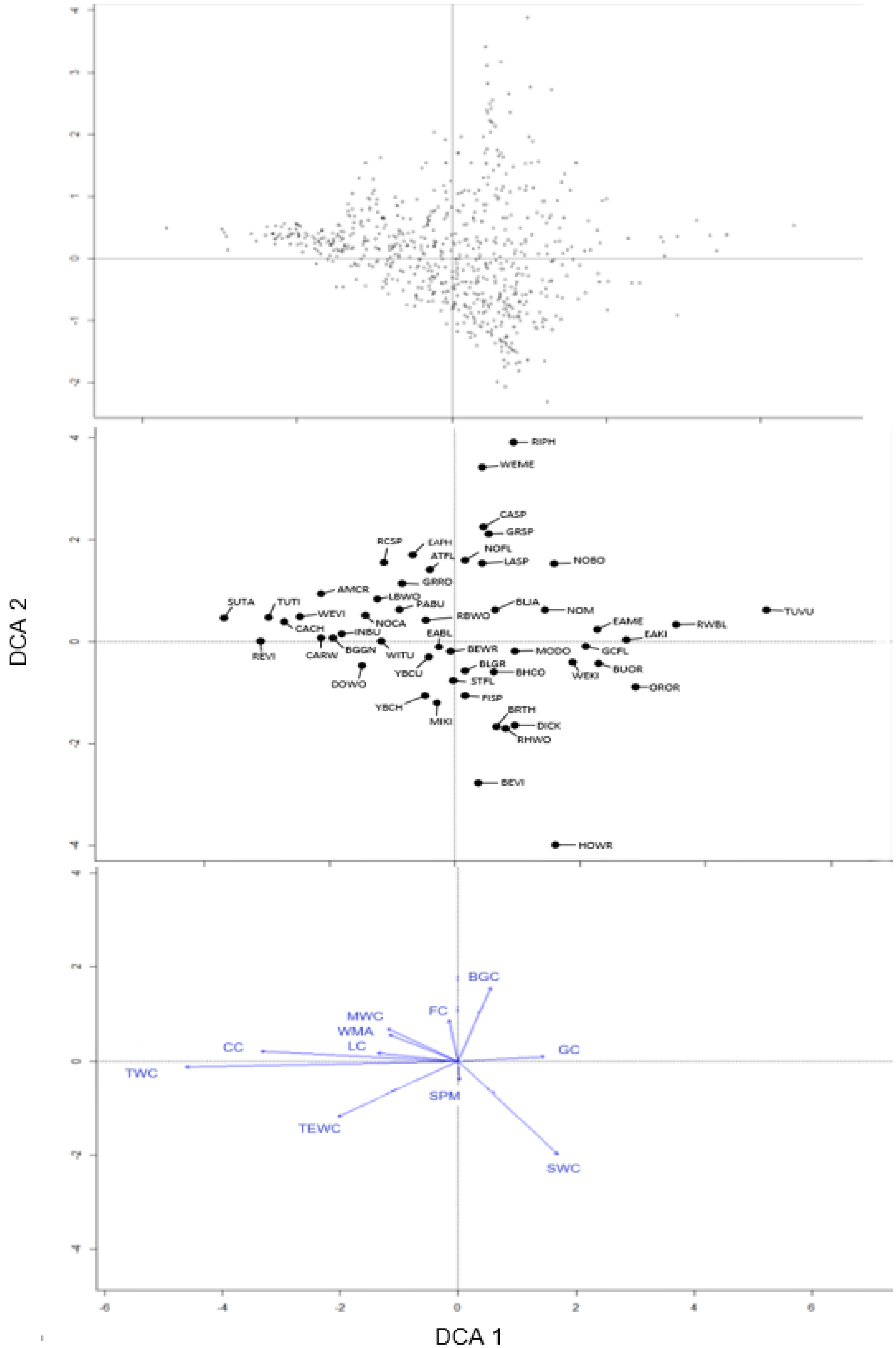


Figure 2: Detrended Correspondence Analysis performed on bird and vegetation samples collected in western Oklahoma May–July, 2018–2020. Top graph shows the spread of sites across the environmental gradient. Middle graph shows the span of bird species across the environmental gradient and the final graph shows the span of vegetation variables across the environmental gradient. The environmental gradient represented by the X-axis, trees (positive) to savannas (negative). The environmental gradient represented by Y-axis is grassland (positive) to shrubland (negative). See Table 3 for bird species codes and Table 2 for vegetation variable abbreviations.



DCA 2
DCA 1
RIPH
WEME
CASP
GRSP
RCSP
EAPH
NOFL
ATFL
LASP
NOBO
GRRO
AMCR
LBWO
PABU
BLJA
NOM
SUTA
TUTI
WEVI
NOCA
RBWO
EAME
RWBL
TUVU
CACH
INBU
EAKI
REVI
CARW
BGGN
WITU
EABL
BEWR
MODO
GCFL
YBCU
BLGR
BHCO
WEKI
BUOR
DOWO
STFL
OROR
YBCH
FISP
MIKI
BRTH
DICK
RHWO
BEVI
HOWR
BGC
MWC
FC
WMA
CC
LC
GC
TWC
SPM
TEWC
SWC

Figure 3: Threshold responses in frequency and abundance of bird species in western Oklahoma to the total cover of woody plants May–July, 2018–2020. TITAN analysis in program R used to identify threshold responses. Red indicates species that showed a negative response and gray indicates species that showed a positive trend following this threshold point. Z-score is a measure of reliability and purity with higher scores indicating a more reliable threshold.

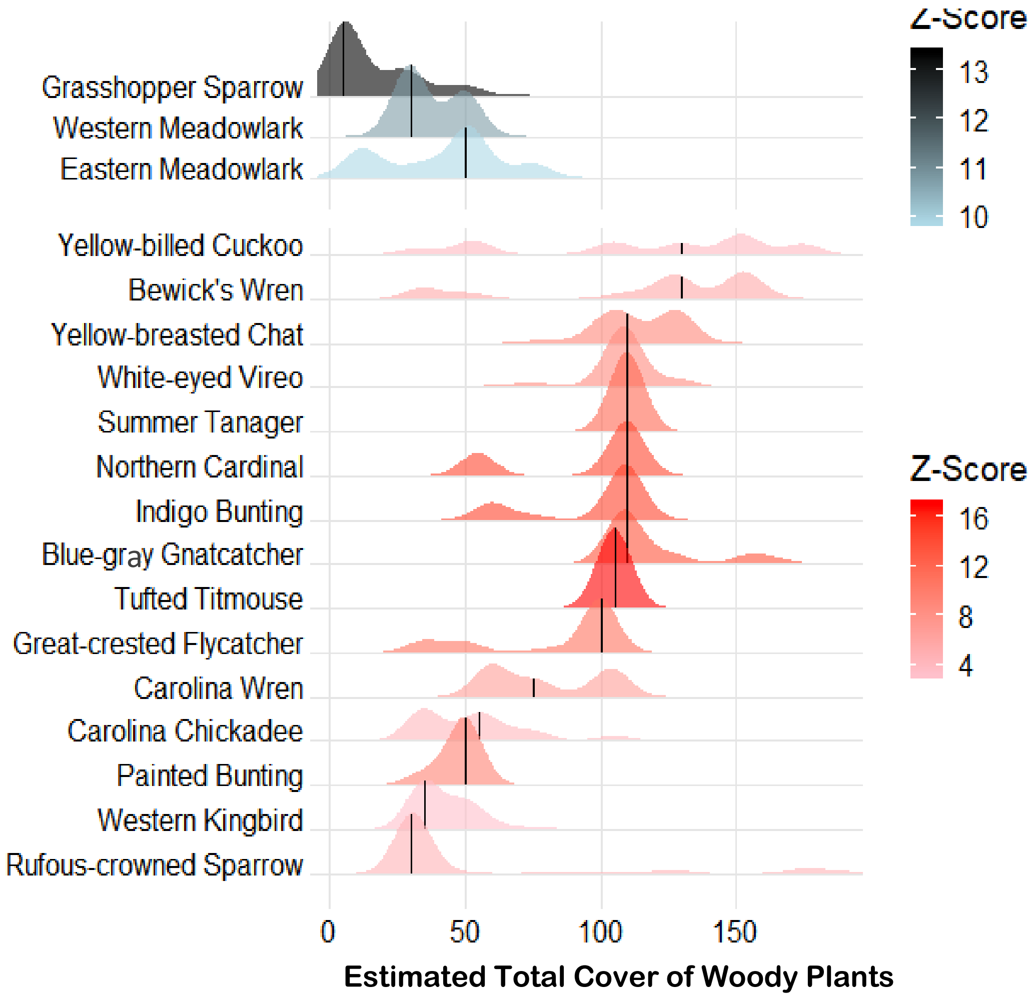


Figure 4: Threshold responses in frequency and abundance of bird species in western Oklahoma to the total cover of woody plants that are shorter than 2 meters tall during breeding season 2018-2020. TITAN analysis in program R used to identify threshold responses. Red indicates species that showed a negative trend and grey indicates species that showed a positive trend following this threshold point. Z-score is a measure of reliability and purity with higher scores indicating a more reliable threshold.

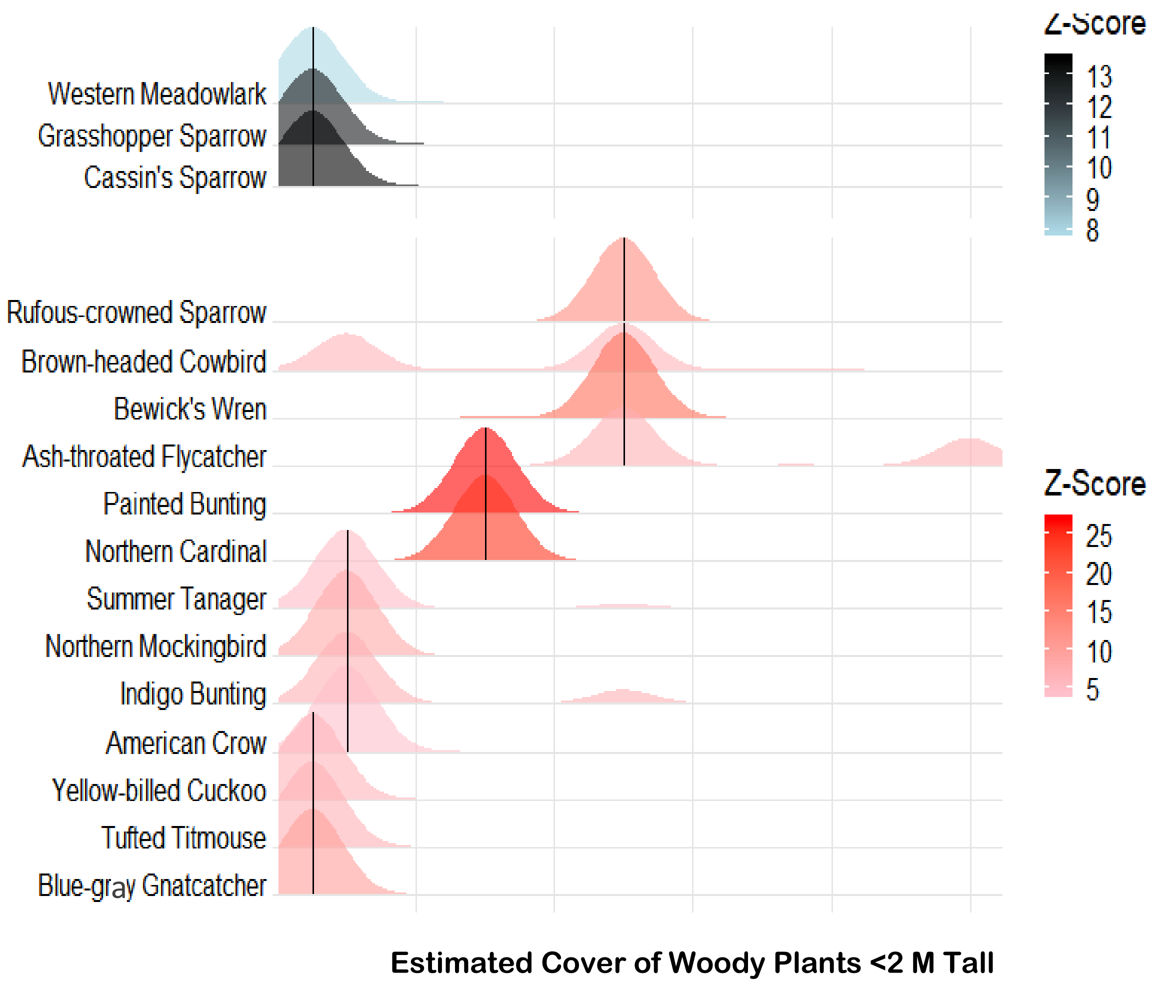


Figure 5: Threshold responses in frequency and abundance of bird species in western Oklahoma to the total cover of woody plants that are 2 to 4 meters tall during breeding season 2018–2020. TITAN analysis in program R used to identify threshold responses. Red indicates species that showed a negative trend and grey indicates species that showed a positive trend following this threshold point. Z-score is a measure of reliability and purity with higher scores indicating a more reliable threshold.

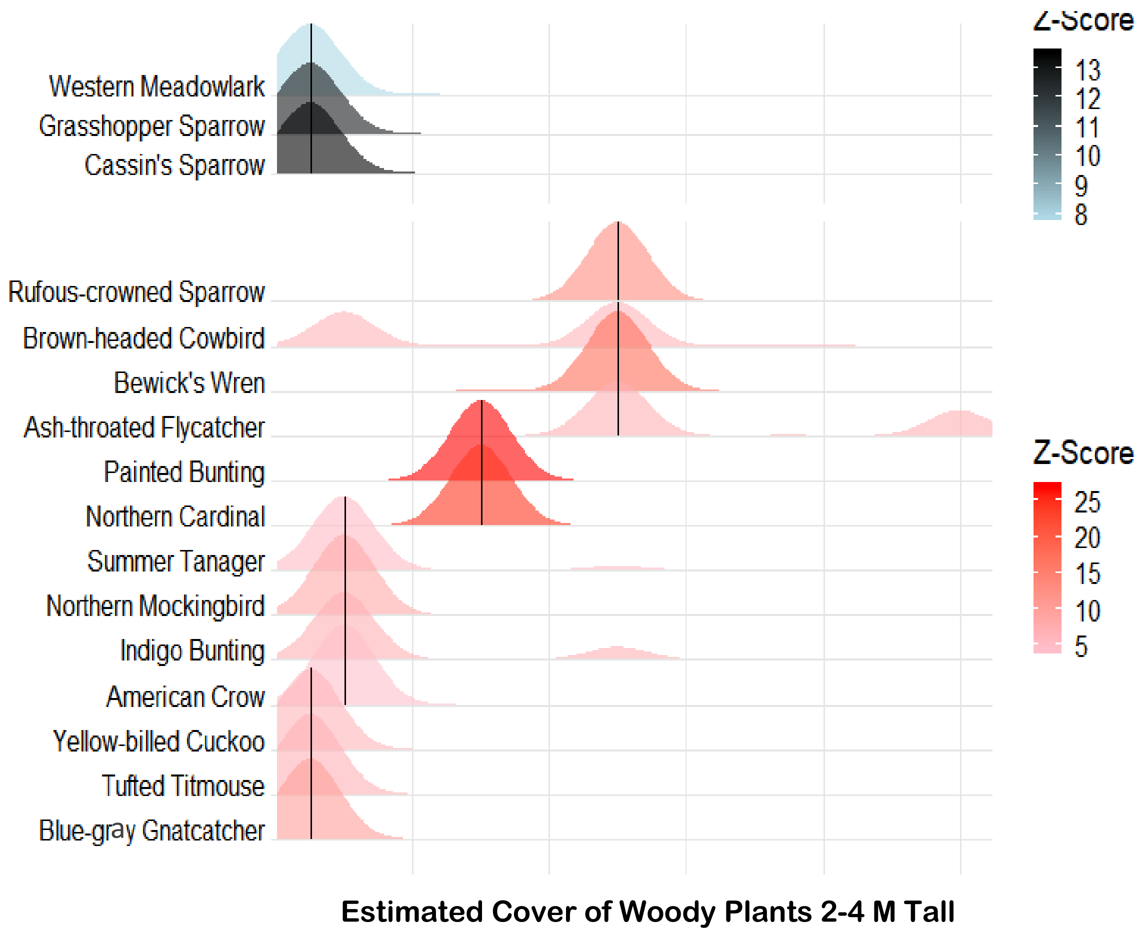
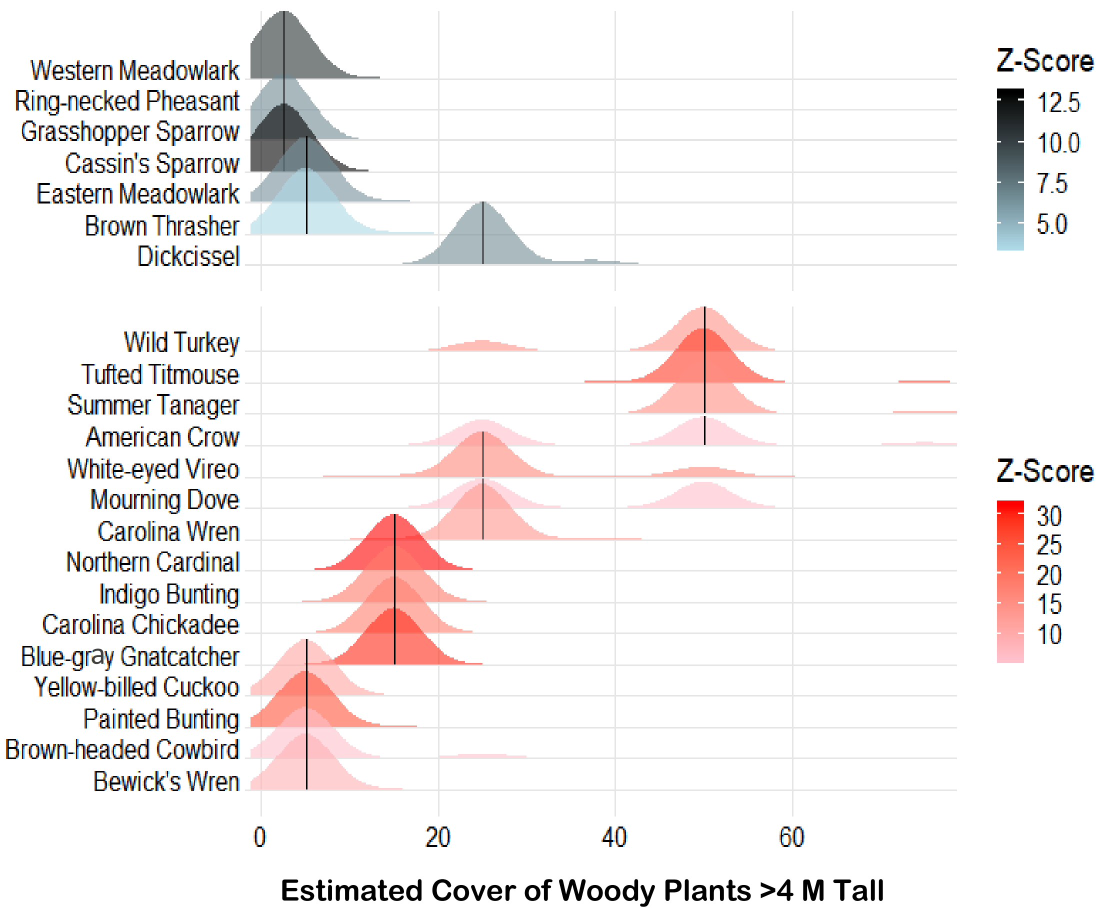


Figure 6: Threshold responses in frequency and abundance of bird species in western Oklahoma to the total cover of woody plants > 4 m during breeding season 2018–2020. TITAN analysis in program R used to identify threshold responses. Red indicates species that showed a negative trend and gray indicates species that showed a positive trend following this threshold point. Z-score is a measure of reliability and purity with higher scores indicating a more reliable threshold.



TABLES

Table 1: Wildlife Management Area (WMA) size, cover type, ecoregion, elevation, and management techniques conducted at each WMA Information gathered from vegetation sampling and additional data extracted from Oklahoma Department of Wildlife Conservation and EPA Ecoregion Classifications.

	Cross Timbers	**Sandy Sanders**	**Packsaddle**	**Beaver River**
Size (Ha)	4,200	12,000	8,100	7,100
Rainfall Mean (CM)	96	69	64	56
Vegetation Cover	Dense hardwoods, Oak Savanna, and Mixed Grass Prairie	Short Grass Prairie, Mesquite-grasslands, Juniper Woodlands, and Sandsage Grasslands	Mixed Grass Prairies and Shinnery Oak	Sandsage Grasslands and Short Grass Prairies
Ecoregion (Level III)	Cross Timbers	Central Great Plains and Southwestern Tablelands	Central Great Plains	Southwestern Tablelands and High Plains
Elevation (M)	258	629	746	730
Management Techniques	Prescribed Fire, Disking, Brush Hogging, and Grazing	Food Plots, Grazing, Disking, Mechanical Shrub Removal and Prescribed Fire	Grazing, Food Plots, and Prescribed Fire	Grazing, Prescribed Fire, and Agricultural Leases

Tables 2: Mean, standard deviation, and range of cover for woody vegetation and functional group and density of shrubs across the 4 study sites in western Oklahoma, 2018-2020.

Vegetation Measure	Abbr.	Collection Method	Mean	Range	Standard Deviation
Cover of Woody Plants 0-2 Meters	SWC	Ocular Estimation	38%	0–100%	+/- 36
Cover of Woody Plants 2-4 Meters	MWC	Ocular Estimation	18%	0–100%	+/- 26
Cover of Woody Plants >4 Meters	TWC	Ocular Estimation	15%	0–100%	+/- 26
Total Covers of Woody Plants	TEWC	Ocular Estimation	72%	0–100%	+/- 43
Cover of Grass	GC	Daubenmire Frame	35%	0–98%	+/- 27
Cover of Forbs	FC	Daubenmire Frame	16%	0–98%	+/- 18
Cover of Bare Ground	BGC	Daubenmire Frame	14%	0–98%	+/- 18
Cover of Litter	LC	Daubenmire Frame	14%	0–98%	+/- 24
Canopy Cover	CC	Spherical Densitometer	11%	0.16–100%	+/- 27
Shrubs per 100 m^2	SPM	Point-centered-quarter	277	0–1,600	+/- 400

Table 3: List of bird species used in the analysis of this study. Included are the common name, four-letter alpha code, the scientific name, number of detections, frequency of occurrence, habitat guild as pulled from Partners in Flight Database (PIF), PIF species score, continental importance, and half-life. PIF scores are a combination of multiple factors (population size, population trends, habitat availability, threats to habitat availability and others) that are scored on a scale of 1–5 and combined to create the total PIF score. Species with PIF scores of greater that 13 are considered species of concern. Continental Importance indicates the status of the species. "CBSD" means Common Bird in Steep Decline and "Watch List" species are those currently on a watch list. The "Yellow D" rating is one of 3 watch list and includes species that are experiencing rapid population declines and have moderate threats to their habitat. The "Half-Life" is the number of years before the population size is half of the current size.

Species	**Abbr.**	**Scientific Name**	**Detect.**	**Freq.**	**Habitat Guild**	**PIF**		
						Score	**Cont. Importance**	**Half-Life**
American Crow	AMCR	*Corvus brachyrhynchos*	13	1%	Open Country Mosaic	6	NA	NA
Ash-throated Flycatcher	ATFL	*Myiarchus cinerascens*	21	2%	Shrubland	8	NA	NA
Bell's Vireo	BEVI	*Vireo bellii*	30	3%	Shrubland	10	NA	NA
Bewick's Wren	BEWR	*Thryomanes bewickii*	102	9%	Shrubland	11	NA	47
Blue Grosbeak	BLGR	*Passerina caerulea*	56	5%	Forest	8	NA	NA
Blue Jay	BLJA	*Cyanocitta cristata*	6	0.5%	Forest	9	NA	105
Blue-gray Gnatcatcher	BGGN	*Polioptila caerulea*	149	13%	Forest	7	NA	NA
Brown Thrasher	BRTH	*Toxostoma rufum*	26	2%	Forest	10	NA	95
Brown-headed Cowbird	BHCO	*Molothrus ater*	138	12%	Open Country Mosaic	7	NA	NA
Bullock's Oriole	BUOR	*Icterus bullockii*	14	1%	Forest	11	NA	NA

Carolina Chickadee	CACH	*Poecile carolinensis*	46	4%	Forest	10	NA	103
Carolina Wren	CARW	*Thryothorus ludovicainus*	35	3%	Forest	7	NA	71
Cassin's Sparrow	CASP	*Peucaea cassinii*	85	8%	Grassland	11	NA	70
Dickcissel	DICK	*Spiza americana*	577	51%	Grassland	11	NA	NA
Downy Woodpecker	DOWO	*Picoides pubescens*	10	0.8%	Forest	7	NA	NA
Eastern Bluebird	EABL	*Sialia sialis*	12	1%	Forest	7	NA	NA
Eastern Kingbird	EAKI	*Tyrannus tyrannus*	12	1%	Open Country Mosaic	11	NA	51
Eastern Meadowlark	EAME	*Sturnella magna*	86	8%	Grassland	11	CBSD	23
Eastern Phoebe	EAPH	*Sayornis Phoebe*	15	1%	Open Country Mosaic	8	NA	NA
Grasshopper Sparrow	GRSP	*Ammodramus savannarum*	40	4%	Grassland	12	CBSD	51
Great Crested Flycatcher	GCFL	*Myiarchus crinitus*	288	26%	Forest	8	NA	NA
Greater Roadrunner	GRRO	*Geococcyx californianus*	6	.5%	Shrubland	8	NA	60
Indigo Bunting	INBU	*Passerina cyanea*	83	7%	Forest	9	NA	78
Ladder-backed woodpecker	LBWO	*Dryobates scalaris*	6	0.5%	Shrubland	9	NA	NA
Lark Sparrow	LASP	*Chondestes grammacus*	127	11%	Open Country Mosaic	10	NA	NA
Mississippi Kite	MIKI	*Ictinia mississippiensis*	8	0.7%	Forest	9	NA	NA
Mourning Dove	MODO	*Zenaida macroura*	109	10%	Open Country Mosaic	6	NA	86
Northern Bobwhite	NOBO	*Colinus virginianus*	118	10%	Open Country Mosaic	12	CBSD	10
Northern Cardinal	NOCA	*Cardinalis cardinalis*	325	29%	Open Country Mosaic	5	NA	NA
Northern Mockingbird	NOMO	*Mimus polyglottus*	112	10%	Open Country Mosaic	8	NA	61

Orchard Oriole	OROR	*Ictreus spurius*	8	0.7%	Forest	10	NA	NA
Painted Bunting	PABU	*Passerina ciris*	366	32%	Forest	10	NA	NA
Red-bellied Woodpecker	RBWO	*Melanerpes carolinus*	22	2%	Forest	7	NA	NA
Red-eyed Vireo	REVI	*Vireo olivaceus*	5	0.5%	Forest	6	NA	NA
Red-headed Woodpecker	RHWO	*Melanerpes erythrocephalus*	58	1%	Forest	13	Watch List: Yellow D	56
Red-winged Blackbird	RWBL	*Agelaius phoeniceus*	11	5%	Open Country Mosaic	8	NA	97
Ring-necked Pheasant	RNPH	*Phasianus colchicus*	7	0.6%	Grassland	7	NA	NA
Rufous-crowned Sparrow	RCSP	*Aimophila ruficeps*	54	5%	Shrubland	11	NA	55
Scissor-tailed Flycatcher	STFL	*Tyrannus forficatus*	56	5%	Grassland	11	NA	37
Summer Tanager	SUTA	*Piranga rubra*	29	3%	Forest	9	NA	NA
Tufted Titmouse	TUTI	*Baeolophus bicolor*	51	5%	Forest	7	NA	NA
Turkey Vulture	TUVU	*Cathartes aura*	15	1%	Open Country Mosaic	5	NA	NA
Western Kingbird	WEKI	*Tyrannus verticalis*	29	3%	Grassland	9	NA	NA
Western Meadowlark	WEME	*Sturnella neglecta*	44	4%	Grassland	10	NA	50
White-eyed Vireo	WEVI	*Vireo griseus*	43	4%	Forest	8	NA	NA
Wild Turkey	WITU	*Meleagris gallopavo*	7	0.6%	Forest	7	NA	NA
Yellow-billed Cuckoo	YBCU	*Coccyzus americanus*	78	7%	Forest	12	CBSD	29
Yellow-breasted Chat	YBCH	*Icteria virens*	14	1%	Forest	11	NA	86

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APPENDICES

Figure 1: Frequency and abundance of Tufted Titmouse across a gradient of woody vegetation cover May–July 2018–2020.

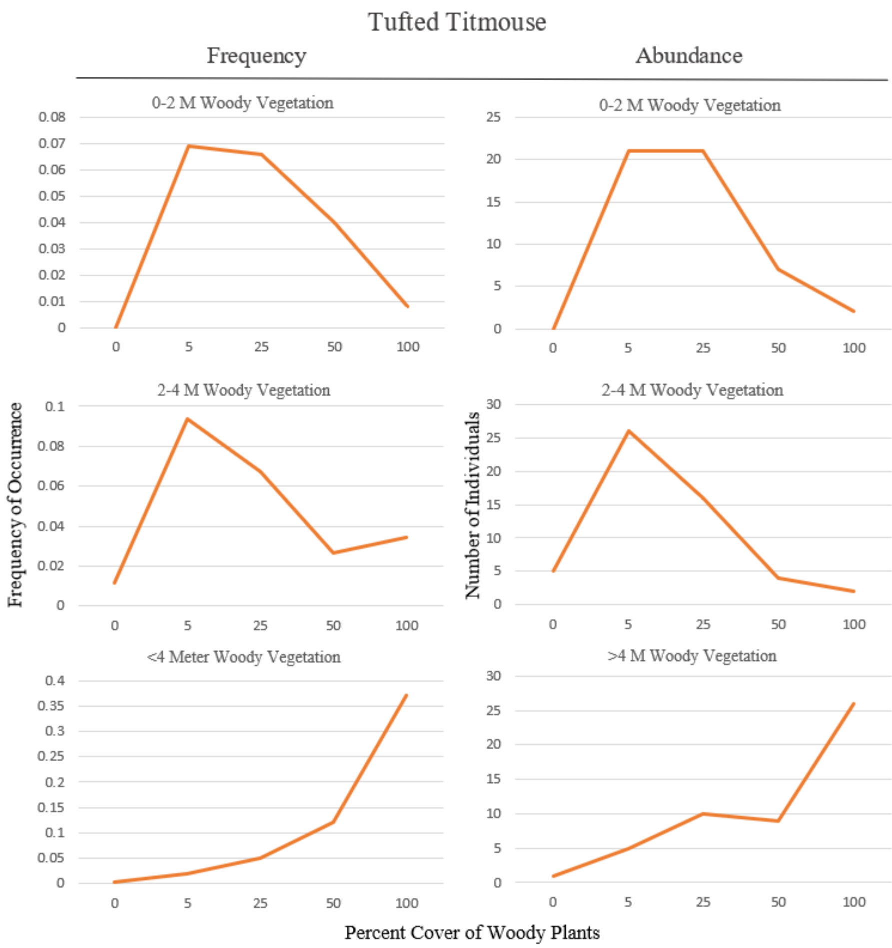

Figure 2: Frequency and abundance of Western Meadowlark across a gradient of woody vegetation cover, May–July 2018–2020.

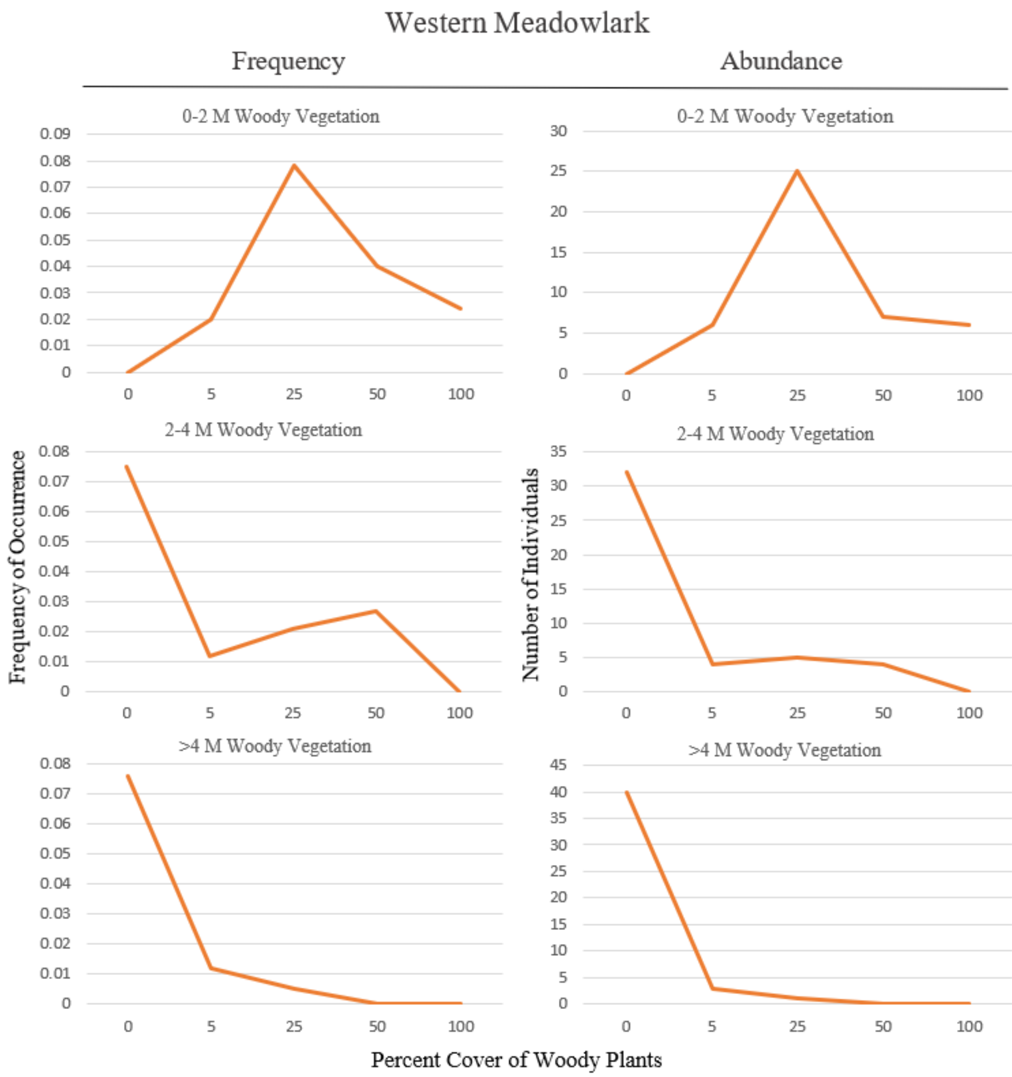

Table 1: Bird species detected on May–July point counts at four Wildlife Management Areas in western Oklahoma, 2018–2020. Included are the common names, number of detections, and frequency of occurrence by WMA sampled.

	Beaver River		**Cross Timbers**		**Packsaddle**		**Sandy Sanders**	
Species	**Detect.**	**Freq. (%)**	**Detect.**	**Freq. (%)**	**Detect.**	**Freq. (%)**	**Detect.**	**Freq. (%)**
American Crow	0	0.00	0	0.00	1	0.36	2	0.68
Ash-throated Flycatcher	0	0.00	0	0.00	1	0.36	20	6.76
Bell's Vireo	7	2.45	7	2.45	10	3.58	0	0.00
Bewick's Wren	14	4.90	14	4.90	16	5.73	52	17.57
Blue-gray Gnatcatcher	2	0.70	2	0.70	23	8.24	0	0.00
Brown-headed Cowbird	30	10.49	30	10.49	44	15.77	36	12.16
Blue Grosbeak	15	5.24	15	5.24	25	8.96	9	3.04
Blue Jay	1	0.35	1	0.35	0	0.00	2	0.68
Brown Thrasher	10	3.50	10	3.50	11	3.94	5	1.69
Bullock's Oriole	13	4.55	13	4.55	0	0.00	1	0.34
Carolina Chickadee	0	0.00	0	0.00	3	1.08	0	0.00
Cassin's Sparrow	58	20.28	58	20.28	11	3.94	16	5.41
Carolina Wren	0	0.00	0	0.00	1	0.36	0	0.00
Dickcissel	99	34.62	99	34.62	285	102.15	42	14.19
Downy Woodpecker	0	0.00	0	0.00	2	0.72	0	0.00
Eastern Bluebird	0	0.00	0	0.00	8	2.87	0	0.00
Eastern Kingbird	9	3.15	9	3.15	3	1.08	0	0.00
Eastern Meadowlark	26	9.09	26	9.09	43	15.41	4	1.35
Eastern Pheobe	0	0.00	0	0.00	7	2.51	3	1.01
Great Crested Flycatcher	39	13.64	39	13.64	158	56.63	5	1.69
Greater Roadrunner	0	0.00	0	0.00	1	0.36	5	1.69
Grasshopper Sparrow	21	7.34	21	7.34	13	4.66	0	0.00
House Wren	6	2.10	6	2.10	0	0.00	0	0.00
Indigo Bunting	8	2.80	8	2.80	2	0.72	0	0.00
Lark Sparrow	17	5.94	17	5.94	30	10.75	67	22.64

Ladder-backed Woodpecker	0	0.00	0	0.00	0	0.00	6	2.03
Mississippi Kite	0	0.00	0	0.00	3	1.08	2	0.68
Mourning Dove	28	9.79	28	9.79	29	10.39	35	11.82
Northern Bobwhite	44	15.38	44	15.38	19	6.81	40	13.51
Northern Cardinal	4	1.40	4	1.40	31	11.11	132	44.59
Northern Flicker	0	0.00	0	0.00	0	0.00	5	1.69
Northern Mockingbird	25	8.74	25	8.74	2	0.72	58	19.59
Orchard Oriole	6	2.10	6	2.10	0	0.00	2	0.68
Painted Bunting	5	1.75	5	1.75	24	8.60	198	66.89
Red-bellied Woodpecker	0	0.00	0	0.00	5	1.79	6	2.03
Rufous-crowned Sparrow	1	0.35	1	0.35	7	2.51	50	16.89
Red-eyed Vireo	0	0.00	0	0.00	1	0.36	0	0.00
Red-headed Woodpecker	6	2.10	6	2.10	4	1.43	1	0.34
Ring-necked Pheasant	7	2.45	7	2.45	0	0.00	0	0.00
Red-winged Blackbird	44	15.38	44	15.38	9	3.23	1	0.34
Scissor-tailed Flycatcher	2	0.70	2	0.70	22	7.89	10	3.38
Summer Tanager	0	0.00	0	0.00	0	0.00	0	0.00
Tufted Titmouse	0	0.00	0	0.00	1	0.36	0	0.00
Turkey Vulture	15	5.24	15	5.24	0	0.00	0	0.00
Western Kingbird	21	7.34	21	7.34	0	0.00	7	2.36
Western Meadowlark	35	12.24	35	12.24	1	0.36	8	2.70
White-eyed Vireo	0	0.00	0	0.00	2	0.72	0	0.00
Wild Turkey	1	0.35	1	0.35	0	0.00	2	0.68
Yellow-breasted Chat	4	1.40	4	1.40	0	0.00	0	0.00
Yellow-billed Cuckoo	7	2.45	7	2.45	13	4.66	17	5.74

Table 2: Woody vegetation cover summarized from 1,129 samples across four Wildlife Management Areas in western Oklahoma 2018–2020.

Vegetation Measures	**Beaver River**			**Cross Timbers**			**Packsaddle**			**Sandy Sanders**		
	Avg	Range	Stdev	Avg	Range	Stdev	Avg	Range	Stdev	Avg	Range	Stdev
0–2m	56	0–100	40	28	0–100	29	53	0–100	37	16	0–100	18
≥2m–<4m	7	0–100	18	16	0-100	19	8	0–100	14	41	0–100	30
≥4m	3	0–100	11	35	0-100	36	8	0–100	18	16	0–100	22
Total	66	0–155	40	79	0-200	48	69	0–175	43	73	0–205	40

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