AVIAN RESPONSES TO FIRE FREQUENCY

IN THE OKLAHOMA CROSS TIMBERS

By

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Abstract: Disturbance in the form of fire is an important ecological process. The presence or long term absence of fire is an important determinant of forest vegetative cover by mediating regeneration, tree establishment, and canopy cover. In temperate forests of North America, a long history of human ignitions produced a fire tolerant landscape that required continued, typically low intensity, disturbance to persist. Since European settlement, concerted fire suppression has been the norm. Low-intensity, dormant-season fires in the Cross Timbers have been found to have a modest influence on canopy cover, but an outsized impact on understory structure and composition. We examined breeding songbird communities in oak-hickory forest in response to a gradient of prescribed fire treatments under 68-100% canopy closure. Point counts for breeding birds, flying insect sampling, and vegetation sampling were conducted at 158 plots in 2015 and 2016 in Okmulgee County, Oklahoma. We used multivariate techniques to elucidate the effects of fire frequency on community composition and used AIC to determine if those variables were important to explaining the densities of 10 avian species. Fire treatments had the expected effect on understory vegetation, but no discernible effect on abundance and biomass of flying insect orders, and a comparatively small effect on breeding bird community composition. Increased fire frequency resulted in increased densities of Eastern Wood-Pewee (*Contopus virens*), Summer Tanager (*Piranga rubra*), and Indigo Bunting (*Passerina cyanea*), and reductions in the breeding density of Black-and-white Warbler (*Mniotilta varia*). Of the 10 species tested, three responded positively and one negatively to increases in fire frequency. This suggests that most species do not experience negative population effects of low intensity fire frequency. Assuming a lack of ecological traps, our results suggest that managers in the Central Hardwoods and Cross Timbers can apply biennial fire low-intensity burns that will help them achieve their objectives for restoration without widespread negative population effects to small breeding landbirds.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

AVIAN RESPONSES TO FIRE FREQUENCY IN THE OKLAHOMA CROSS TIMBERS

Disturbance in the form of fire is an important ecological process. Fire's frequency, intensity, heterogeneity, scale, and season are all important measures of its role as an agent of change (Archibald et al. 2013). The presence or long term absence of fire is an important determinant of vegetative cover. Fire frequency mediates regeneration, tree establishment, and canopy cover in forests (DeSantis and Hallgren 2011, DeSantis et al. 2010b, Stambaugh et al. 2014). Some systems, such as the bush in Australia, are so productive that they can have both a frequent and high severity fire regime (Sitters et al. 2014). Others, including most savannah systems, are maintained by high frequency low severity burns (Bond and Keeley 2005, DeSantis et al. 2010a, DeSantis et al. 2010b, Stambaugh et al. 2009).

In the temperate forests of North America, a long history of human ignitions produced a fire tolerant landscape that required continued, typically low intensity, disturbance to persist (Bowman et al. 2009, Pausas and Keeley 2009). Since European settlement, fire driven disturbance regimes in eastern forests have shifted with the introduction of logging, introduction of invasive species, the repeated clearing of land for farming, continued intentional fires in some areas, and concerted fire suppression in most areas (DeSantis et al. 2010a, Nowacki and Abrams 2008, Pausas and Keeley 2009). Since implementation of fire suppression in the 1920s, most disturbance regimes have shifted to dramatically longer intervals, including reduced overall fire frequency (Pausas and Keeley 2009). The effect of fire suppression has resulted in increased abundance of fire intolerant plants and densification, or increase tree stem density, sometimes occurring with increases in basal area (Abrams and Nowacki 2015, Hanberry et al. 2012).

In historically oak-hickory communities, this trend towards densification of forests in North America includes the spread of fire intolerant *Juniperus* species (Hanberry et al. 2014). Compositional transitions toward more fire intolerant species, as a result of changes in the disturbance regime, have been well documented in oak-hickory savannas and forests (Allen and Palmer 2011, Burton et al. 2010, Ratajczak et al. 2014, Stambaugh et al. 2009). Low intensity understory fires temporarily remove understory species that cannot tolerate fire, resulting in a more open understory with increased grass and forb cover and less vertical shading (Barrioz et al. 2013, Burton et al. 2011, Hutchinson et al. 2005, Maynard and Brewer 2013). Canopy closure is reduced as fewer seedlings make it to maturity and openings created by wind damage, ice storms, herbicide application, or tree harvest are preserved, resulting in a more open understory with less leaf litter and more herbaceous cover (Burton et al. 2011, Maynard and Brewer 2013, Nowacki and Abrams 2008).

In the grassland-forest ecotones of the US Great Plains, frequent, low intensity fires were an important driver of forest structure, including the primary determinant of tree basal area (DeSantis and Hallgren 2011, DeSantis et al. 2010a, Stambaugh et al. 2009). Research on these oak savanna-woodlands has focused on the response of vegetation to low-severity, dormant-season fires like those typically set annually by native peoples in these landscapes prior to European colonization. Important vegetation responses include resprouting following fire by pyrophilic oak species and the establishment and maintenance of an herbaceous understory in these oak woodlands (DeSantis and Hallgren 2011, Stambaugh et al. 2014). While dormant season fires do not have an immediate impact on canopy composition, they have been found to alter the structure and composition of the forest midstory and understory. These fires reduce litter depth and increase herbaceous cover and biomass while their exclusion promotes the growth of woody species not adapted to fire (Burton et al. 2011, DeSantis et al. 2010b).

Although structural changes in vegetation from fire in oak woodlands are generally predictable, we know comparatively less about the influence of these changes on other native species in these systems. Breeding songbirds and other small landbirds can provide insights into the effects of frequent, dormant-season fire in the oak woodlands of the eastern Great Plains. Structural differences among vegetation types largely determine what bird communities are present (Brawn et al. 2001, Cody 1981, Holoubek and Jensen 2015, Karr and Roth 1971, MacArthur 1958). Sitters et al. (2014) found that vegetation structure was a better predictor of bird species richness than time since fire in forests that varied in speed of structural response to fire. Bird responses to fire severity, frequency, and time since fire vary by species (Brawn et al. 2001). Watson et al. (2012) found that some bird species responded more strongly to time since fire than to vegetation structure in forests with lesser variation in speed of vegetative response to fire. Brawn (2006) found differences in avian community structure between Illinois oak savanna and nearby closed canopy oak forests where prescribed fire and mechanical thinning were used to restore oak savannas.

The Cross Timbers ecotone defines a broad transition from oak-hickory forest to tallgrass prairie in the US Southern Great Plains states of Kansas, Oklahoma, and Texas. There are notable examples of research on vegetation structural changes in response to prescribed fire in this region (Burton et al. 2010, DeSantis and Hallgren 2011, Stambaugh et al. 2009), but thus far only two attempts to examine specific influences of any understory structure treatments (herbicide and prescribed fire) on breeding bird communities, Holoubek and Jensen (2015) and Schulz et al. (1992). One 1992 study found that 17 of 20 bird species occurred at similar rates in areas with structural understory differences similar to those caused by fire (Schulz et al. 1992). Holoubek and Jensen (2015) focused on how bird communities varied among broad categories of canopy cover and structure in the Kansas Cross Timbers. Holoubek and Jensen (2015) found differences in bird species densities between adjacent grassland and woodland patches with some differences in response to potential understory variables like shrub cover under canopy cover.

Arthropod abundance and biomass have been found to vary with vegetation structure and composition, and to correlate with density of some bird species (Greenberg et al. 2010, George et al. 2013). It follows that horizontal cover differences from prescribed fire could affect food availability for insectivorous birds. Indeed Holoubek and Jensen (2015) found that density of the aerial-sallying Eastern Wood-Pewee increased where fire reduced horizontal cover in oak woodlands, but they could not determine if that affect was related to an increase in flying insects, easier foraging through a more open understory, or both.

Low-intensity, dormant-season fires have been found to have only a modest influence on canopy cover in the Cross Timbers, but understory influence can be dramatic (Burton et al. 2011), which can be an important driver of bird community structure. For example, Holoubek and Jensen (2015) found that shrub density was not linked to tree cover or density but that occupancy of Eastern Wood-Pewee (*Contopus virens*), Northern Mockingbird (*Mimus polyglottos*), Lark Sparrow (*Chondestes grammacus*), Indigo Bunting (*Passerina cyanea*), and Brown-headed Cowbird (*Molothrus ater*) were related to shrub density. Many breeding birds rely on understory structure to provide foraging and nesting substrate (Brown et al. 2011, Holmes and Schultz 1988, Schulz et al. 1992), suggesting that prescribed fire in these systems could affect food availability and search tactics of insectivorous birds.

To better resolve the potential influence of prescribed fire on biodiversity in Cross Timbers oak woodland, we studied breeding bird communities in an area where various fire return intervals have been restored over the course of approximately 30 years. Our objectives were to 1) examine how structural and compositional differences in vegetation resulting from prescribed fire influenced breeding bird communities and the breeding densities of several individual forest inhabitant species, and 2) to examine how differences in bird communities could be predicted by availability of flying insects along a gradient of horizontal cover.

METHODS

Study Area

We carried out our study at the Oklahoma Department of Wildlife Conservation's Okmulgee Wildlife Management Area (OWMA) and the nearby Okmulgee Lake and Recreation Area (OLRA) in Okmulgee County, Oklahoma, USA (Figure 1). Both sites are located in the Cross Timbers USEPA Level II ecoregion of the US Southern Plains that marks a broad ecotone separating oak-hickory forests to the east and Great Plains grasslands to the west (United States Environmental Protection Agency 2013). Vegetation cover in the Cross Timbers is primarily driven by disturbance regime (primarily fire), land use, and topography. Native upland Cross Timbers' forests are dominated by post (*Quercus stellata*) and blackjack (*Q. marilandica*) oaks (Hoagland et al. 1999).

OWMA has a well-documented, 29-year history of prescribed fire (Burton et al. 2011) over 4400 ha with 13 individual management units ranging from 0.0–4.3 fires per decade (Table 1). These 13 management units were established to provide variable habitat for hunted populations of White-tailed Deer (*Odocoileus virginianus*) and Wild Turkey (*Meleagris gallopavo*). We included an upland 40 ha patch of the nearby OLRA with similar vegetation cover and at least a 25-year history of fire exclusion to provide additional unburned areas to sample (Joseph Hahn, personal communication, 14 May 2015).

We placed 3 to 17 sampling plots in each of OWMA's management units, depending on the size of the unit, and 7 plots in OLRA (Figure 1). We focused on sampling from forest locations with canopy cover >50% over 0.5 ha. We buffered unit edges, roads, and perennial streams by at least 100 m (upland) and separated all plots by at least 200 m. We sampled 72 plots in 2015 and 86 in 2016 (Figure 1). Measurement plots were restricted to ≥68% canopy cover.

Bird Density Sampling Design

We surveyed breeding passerines and other small land birds using a modified point count (Ralph et al. 1995) with a fixed radius of 100 m centered on the center point of all of the year's plots. We counted all individuals of all species heard or seen during the count. Based on distance sampling, removal modeling is a technique that allowed us to correct recorded observations to account for differences in detectability of each species by each observer (Farnsworth et al. 2002). We divided 6-min counts into 3 2-min time intervals. Surveys for breeding birds were conducted 15 May–30 June in 2015 and 2016. All surveys took place from approximately 0.5–4.0 hours after local sunrise. We surveyed each point twice per year, separating first and second surveys by at least 7 days and rotated points between the observers whenever possible. For each point in a given year, we compiled a species list of occurrence that included each species found on at least one of the counts. Due to temporal spread of sampling (May–late June), the maximum number of a species detected between two visits was used when calculating bird densities for each plot.

Vegetation Structure Sampling Design

We conducted vegetation surveys at each bird sampling plot between May and June of 2015 and 2016. For vegetation sampling, we established a 10 X 10 m plot centered on each point count. Within these plots, we recorded species and diameter at breast height (DBH) of every woody stem, with no minimum diameter. For information at a finer scale, we sampled from four 1 X 1 m subplots placed along the inside edge of each side of the 10 X 10 m plot. Within these subplots, we recorded litter depth using a litter trowel and used a concave spherical densiometer to record canopy cover from each side of the subplots, resulting in a total of 16 measurements per 10 X 10 m plot (Figure 2). Within each subplot, we recorded percent cover class of bare ground, rock, litter, and live vegetation up to 1 m above the ground, which was further split into graminoids, legumes, forbs, and all woody plants as a percent of the total subplot using a Daubenmire percent cover class method (Burton et al. 2011). We also recorded the dominant woody plant species by percent cover of live leaves in the subplot. If a tree was rooted in a subplot, the area covered was not included in the total amount of space in the subplot as the purpose of the subplot was to get samples of the under-understory and area close to the ground. We calculated total basal area for each tree species within the larger plot and averaged the 16 measures of litter depth and percent canopy cover for one value per large plot. We averaged percent cover of the 4 subplots using the midpoint of each cover class.

Food Availability Sampling Design

Sampling for flying insects was conducted during the summer of 2016 using blue vane traps from BioCare by SpringStar (86 plots). Blue vane traps attract flying insects using a visual lure, and trap them using a funnel into a collection jar (Figure 3). Each trap was wired to a wooden stake at 1.5 m in height near the center of each plot. To reduce immediate visual obstruction, traps were placed so that no vegetation was within a 1 m diameter of the vane trap. After 24 hours, collection jars were removed and placed in a freezer overnight. Samples were transferred to zip-top bags and stored in a freezer until they could be sorted to order and counted. Hymenoptera were further sorted to ant, bee, wasp, and sawfly groups to sort out non-target ants that crawled into the trap. Insects were thawed, then dried at 60C for 48 hours and weighed for dry biomass. Dry weight of the flying insects caught at each trap was used as a possible index of food availability for flycatching species at each point in 2016.

Statistical Analysis

We were interested in the influence of fire on the understory of relatively closed-canopy woodlands so we excluded from analysis plots in the bottom decile of average canopy cover where canopy openness resulted in savanna-like structure (Figure 4). Bird species not well suited to detection by point counts (e.g., vultures, swallows, raptors) were excluded from analysis. We used count removal modeling to calculate detection probabilities for each observer and species and thus determine breeding bird densities (Farnsworth et al. 2002). We explored important gradients using multivariate analysis together and separately for each year in CANOCO 5.03.

We performed a constrained redundancy analysis using all vegetation variables and avian species. Bird species with fewer than 10 encounters between years were excluded from this analysis to reduce the likelihood of rare encounters exaggerating the importance of individual plots in the exploratory analysis after a preliminary analysis found down weighting to not be effective with these comparatively "rare" species. Preliminary analysis found that the year of measurement (2015, 2016) was the primary variable, so we analyzed each year of bird community data separately. For each year, we included all variables in analysis but figures presented here include only the variables with the longest gradient length (largest effect) and we re-ran each RDA with only these variables for ease of interpretation. We tested all combinations, except interactions, of the strongest explanatory variables from both years as explanatory variables for bird species densities in Generalized Linear Mixed Models (GLMMs), with management unit and year as random effects. We compared models for each species using Akaike Information

Criterion (Akaike 1987). Indigo Bunting and Summer Tanager (*Piranga rubra*) were detected at different frequencies between years so each year was analyzed separately.

RESULTS

Understory Structure and Food Availability

We collected data in 72 plots in 2015 and 86 in 2016, sampling different plots within each management unit (Figure 1). Woody stems with a DBH ≥8 cm were dominated by post oak, winged elm (*Ulmus alata*), blackjack oak, and black hickory (*Carya texana*) at 67%, 14%, 10%, and 8%, respectively. These four species made up 86% of all woody stems at 1.5 m within measurement plots (Figure 5). Increased fire frequency resulted in increased live vegetative cover in the understory. Graminoid cover responded most strongly to increased fires and woody cover in the understory. Graminoid cover initially increased with any fire frequency above zero and then tapered off after more than 2.5 fires per decade. This is consistent with previous work in the Cross Timbers, including Okmulgee WMA (Barrioz et al. 2013, Burton et al. 2011). Density of small stems (DBH <8cm) was higher in areas that had not burned or had only burned once per decade. All vegetation variables used in analysis were tested against each other for correlation before being used as explanatory variables. Of those, increased fires per decade was subtly correlated with both a decrease in small stem count (DBH <8cm) and a decrease in canopy cover (-0.35 and -0.38, respectively).

Captured insects were primarily members of Coleoptera (over 1,800 individuals) with Hymenoptera, Lepidoptera, and Diptera second, third, and fourth with fewer than 100 individuals each (Figure 6). Coleoptera similarly dominated total biomass making up

10,000 mg of the total with Hymenoptera second (a little over 2,000 mg) and Lepidoptera third (under 1,000 mg, Figure 7). We collected 3–80 individuals in each trap with a dry weight of 10.4–836.5 mg (Figure 8). Neither raw count nor dry weight varied predictably with fire frequency or time since fire. Neither insect variables were correlated ($|r| > 0.7$) with other vegetation measures including small stem count, canopy cover, or graminoid or forb cover in the understory.

Breeding Bird Densities

We conducted 316 avian point counts in two visits to 72 plots in 2015, and at 86 plots in 2016 (Figure 1). We found 18 species regularly enough to be suitable for calculating breeding bird densities using detection probabilities (Table 2). The five most common species were Blue-gray Gnatcatcher (*Polioptila caerulea*), Carolina Chickadee (*Poecile carolinensis*), Tufted Titmouse (*Baeolophus bicolor*), Northern Cardinal (*Cardinalis cardinalis*), and Indigo Bunting.

Drivers of Avian Community Composition

The primary driver of the axis one in 2016 was fires per decade joined by percent bare ground, which was the primary driver in 2015 multivariate analysis of the 18 species densities (Figures 9 and 10, Tables 3 and 4). The second axis was driven by canopy cover in 2016 and percent cover of woody vegetation, with some contribution from small stem count in 2015. When we included the total dry weight of insects with the full variable analysis in 2016, dry insect weight was the primary driver of variation along axis 1 (Figure 11). Including insect weight explained an additional 5% of the variation in species composition in 2016 (21% of total variation with insects, bare ground, and canopy cover). Percent bare ground and canopy cover were the drivers of axis 2. Flycatching species Great Crested Flycatcher (*Myiarchus crinitus*), Eastern Wood-Pewee, Eastern Bluebird (*Sialia sialis*), Red-bellied Woodpecker (*Melanerpes carolinus*), Summer Tanager) increased with fires per decade and decreased with more bare ground in 2016. Except for Summer Tanager, these flycatching species increased with dry weight of insects when that variable was added. In both years, Great Crested Flycatcher was associated with decreases in canopy cover while Summer Tanager was associated with increases. Great Crested Flycatcher, Indigo Bunting, Blue-gray Gnatcatcher, and Red-breasted Woodpecker were associated with each other in both 2016 RDAs, decreasing with increased canopy closure, increasing with insect weight, and are weakly associated with increase in fire frequency. Great Crested Flycatcher and Blue-gray Gnatcatcher increased with percent bare ground and decreased counts of small stems in 2015. The adjusted explained variation was 3.3% in 2015 and 1.0% in 2016 (Table 5).

Species Level Responses to Understory Structure

In our GLMMs, we tested fires per decade, percent cover of bare ground, percent openness of canopy, percent cover of live woody species, count of small woody stems (DBH <8cm) and scaled stem count, to see which of these variables was most important at the species level (Tables 6 and 7). Indigo Bunting density was associated with reduced canopy cover in both years while Black-and-white Warbler (*Mniotilta varia*) density increased with canopy cover. Blue-gray Gnatcatcher and Northern Cardinal had lower densities with increased fire frequency. Densities increased with increased fire frequency for Eastern Wood-Pewee, Indigo Bunting in 2015, and Summer Tanager in 2015. Percent cover of bare ground (not rock cover, which was measured separately) was positively correlated with two flycatching species Great Crested Flycatcher in both years and Summer Tanager in 2015). Increased percent cover of woody species in the understory was correlated with higher densities of Carolina Wren (*Thryothorus ludovicianus*). We did not find strong relationships explaining Carolina Chickadee, Brown-headed Cowbird, or 2016 Summer Tanager densities.

DISCUSSION

We did not find much spread along the gradients measured in our RDA in either year, suggesting that understory conditions related to fire frequency were not important drivers of bird community composition at this scale. Among responses of individual bird species, Eastern Wood-Pewee density showed a positive association with increased fire frequency. Percent cover of woody species within 1 m of the ground, which captures shrubby vegetation, was not strongly or independently associated with Eastern Wood-Pewee density. This suggests that the subtle but cumulative effects of fires per decade on understory vegetation are important to this species at this scale and that while other variables not as important along but the cumulative effect of fires per decade is important in some other way not measured. Similarly, Holoubek and Jensen (2015) found Eastern Wood-Pewee densities increased with shrub (not sapling) cover and peaked at intermediate levels of canopy cover at the 50 m scale, but not the 100 m scale (radius of point counts).

Summer Tanager and Indigo Bunting both showed positive correlations with increasing fires per decade, but only in 2015. We found no association with any of the variables tested for Summer Tanager. In both years, canopy cover was an important variable explaining Indigo Bunting densities. This annual difference in the relevance of fire frequency might be explained by the difference in precipitation between the two years: 2015 was one of the wettest years on record in central Oklahoma. The summer of 2016 was a more typical year, but the vegetative response to years of dramatic changes in precipitation can be delayed (Sala et al. 2012, Sherry et al. 2008, Yahdjian and Sala 2006).

Indigo Bunting had a positive relationship with more open canopy, paralleling Schulz et al. (1992) who found that, at the end of the breeding season, Indigo Buntings were only present in areas with substantially reduced canopy cover. Holoubek and Jensen (2015) found Indigo Bunting densities to increase with trees per hectare and shrubs in the understory of the Kansas Cross Timbers while Roberts and King (2017) found that Indigo Bunting had a minimum opening requirement of 0.56 ha within a larger matrix of forest with 90% canopy cover in Massachusetts.

Black-and-white Warbler density was associated with canopy cover, with higher densities observed where canopy cover was greatest. Black-and-white Warblers also exhibited a positive relationship with small woody stems (DBH <8cm). This supports the findings of previous studies on their response to fire, including Greenberg et al. (2013), who found higher densities of Black-and-white Warblers where it had been longer since the last fire, which is correlated with fires per decade.

Some of the differences in responses between 2015 and 2016 may be partially explained by the radically different weather between the two field seasons. Exceptionally high rainfall was recorded in Okmulgee County in 2015 (184.6 cm, PRISM Climate Group 2017). 2016 had more typical rainfall pattern with 86.3 cm of precipitation in the county

(PRISM Climate Group 2017). However, vegetation, including both graminoids and trees, may have delayed response to extremely dry periods (Sala et al. 2012, Sherry et al. 2008, Yahdjian and Sala 2006), making the importance of each relative year difficult to isolate. Although weather variability between annual breeding seasons is typical of the Cross Timbers, rainfall experienced in 2015 falls outside normal weather variability expected in the region (PRISM Climate Group 2017). Anecdotally, the field crew noticed that leaf litter had been pushed by storm events into piles, leaving large swaths of bare mineral soil where there was once leaf litter. This appeared to be widespread and not limited to areas with steep slopes or other easily discernable features typically associated with first order streams. Since there were no burns between the 2015 and 2016 field seasons, this effect may have remained on the landscape between years. This litter clearing action may have been associated with some indirect effect on bird densities that was not explored by this study. Additionally, our study did not compare vital statistics of species between management units. It is possible that the singing rates of some species are not directly correlated with nest success, or the correlation may even be negative (George et al. 2013). We also focused on breeding birds and did not address the importance of, for example, a grassy understory vs a shrub understory on survival of overwintering species. It is possible that food availability in the form of seed production is different between treatments, for which further study would be required for species like Northern Cardinal.

Blue vane traps are specialized to attract to pollinators, particularly bees (Kimoto et al. 2012, Stephen and Rao 2005). Because the traps work as visual lures, we predicted that capture rates would vary according to differences in visual obstruction in our plots.

Horizontal obstruction was greater in units that burned less often (e.g., 1 fire per decade) than in those burned more often (e.g., >2.5 fires per decade), so we presumed that overall biomass of insect captures would be higher in units burned more frequently. This could be due to life history attributes of the species we captured being unaffected by the specific fire prescription applied (i.e., generally ground fires during the non-growing season). Alternatively, the scale at which the blue vane traps attract insects is finer than our 50m avian sampling plots. Insect biomass explained an additional 5% of the variation in species composition in 2016, which is consistent with other studies (Brown et al. 2011, George et al. 2013, Marshall and Cooper 2004). Our results fit into a larger pattern of contradictory results when looking at how, or even if, fire frequency predicts insect abundance and diversity (Brown et al. 2011, Coleman and Rieske 2006, Greenberg et al. 2010, Marshall and Cooper 2004, Reidy et al. 2014). This calls for further investigation to better understand the relationship between flying insect biomass and fire frequency.

CONCLUSIONS

We examined breeding songbird communities in oak-hickory forest in response to a gradient of prescribed fire treatments. Fire treatments had the expected effect on understory vegetation, but no discernible effect on abundance and biomass of flying insect orders, and a comparatively small effect on breeding bird community composition, especially in comparison to the effect of prescribed fire on understory vegetation. The breeding songbird community in oak forest burned at 3.9 fires per decade was not substantially different from the breeding songbird community in immediately adjacent oak forest not burned in nearly 30 years. However, increased fire frequency resulted in increased densities of Eastern Wood-Pewee, Summer Tanager, and Indigo Bunting, and reductions in the breeding density of Black-and-white Warbler. It is helpful to managers to know that large areas of the Cross Timbers, and likely more of the Central Hardwoods, can be treated with heterogeneous application of prescribed fire without an expectation of local extirpation of these species in these ecosystems. We found three species responded positively, one responded negatively, and six responded inconclusively or did not respond to increases in fire frequency at our site. This suggests that most species do not experience negative population effects of low intensity fire frequency. Assuming a lack of ecological traps, our results suggest that managers in the Central Hardwoods and Cross Timbers can apply biennial fire low-intensity burns that will help them achieve their objectives for restoration without widespread negative population effects to small breeding landbirds.

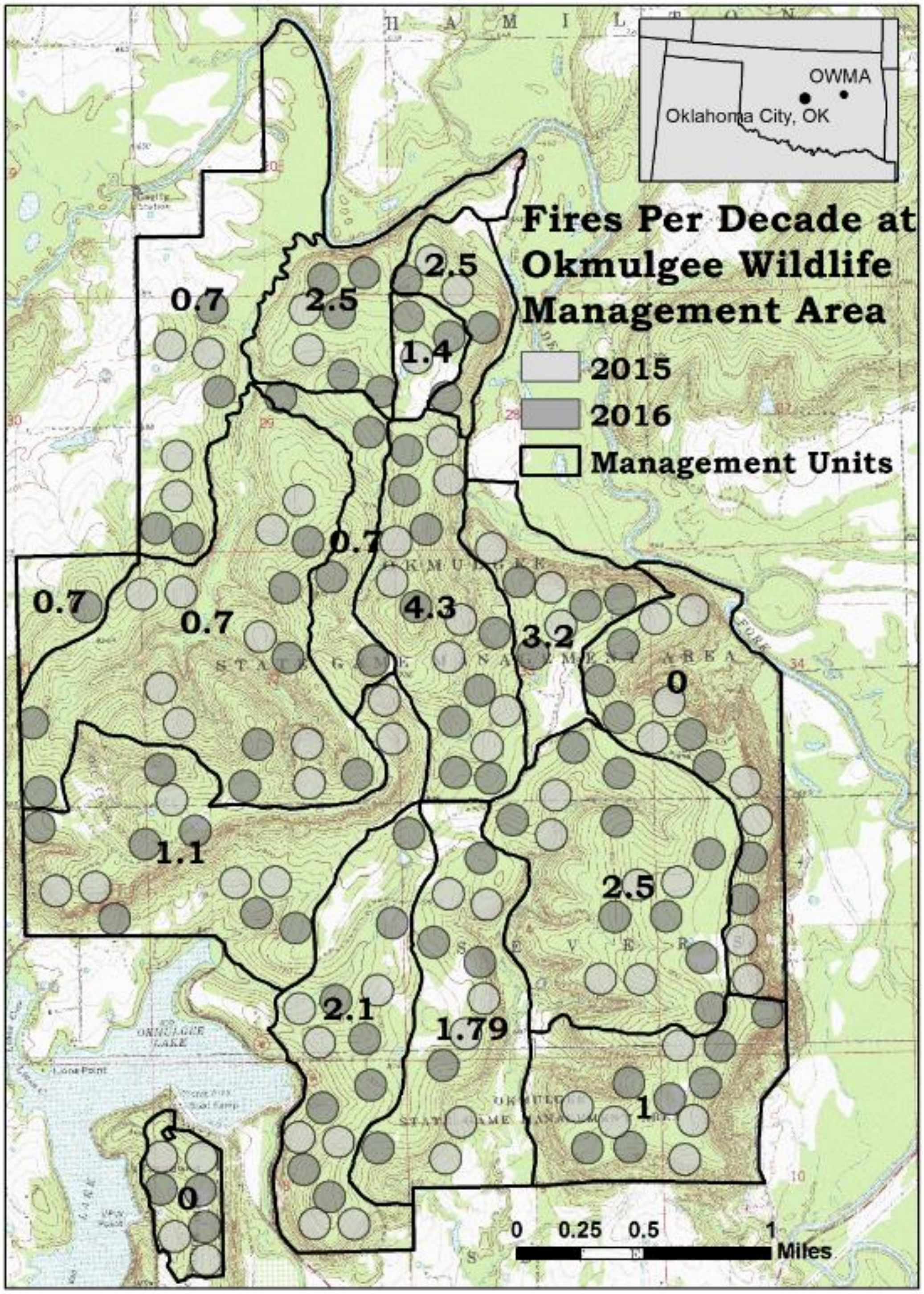

Figure 1. Study sites. Okmulgee Wildlife Management Area and Okmulgee Lake and Recreation Area, Oklahoma, USA. Management unit are labeled with 29-year average of

fires per decade and a to-scale representation of the 100 m area sampled for birds via fixed radius point counts.

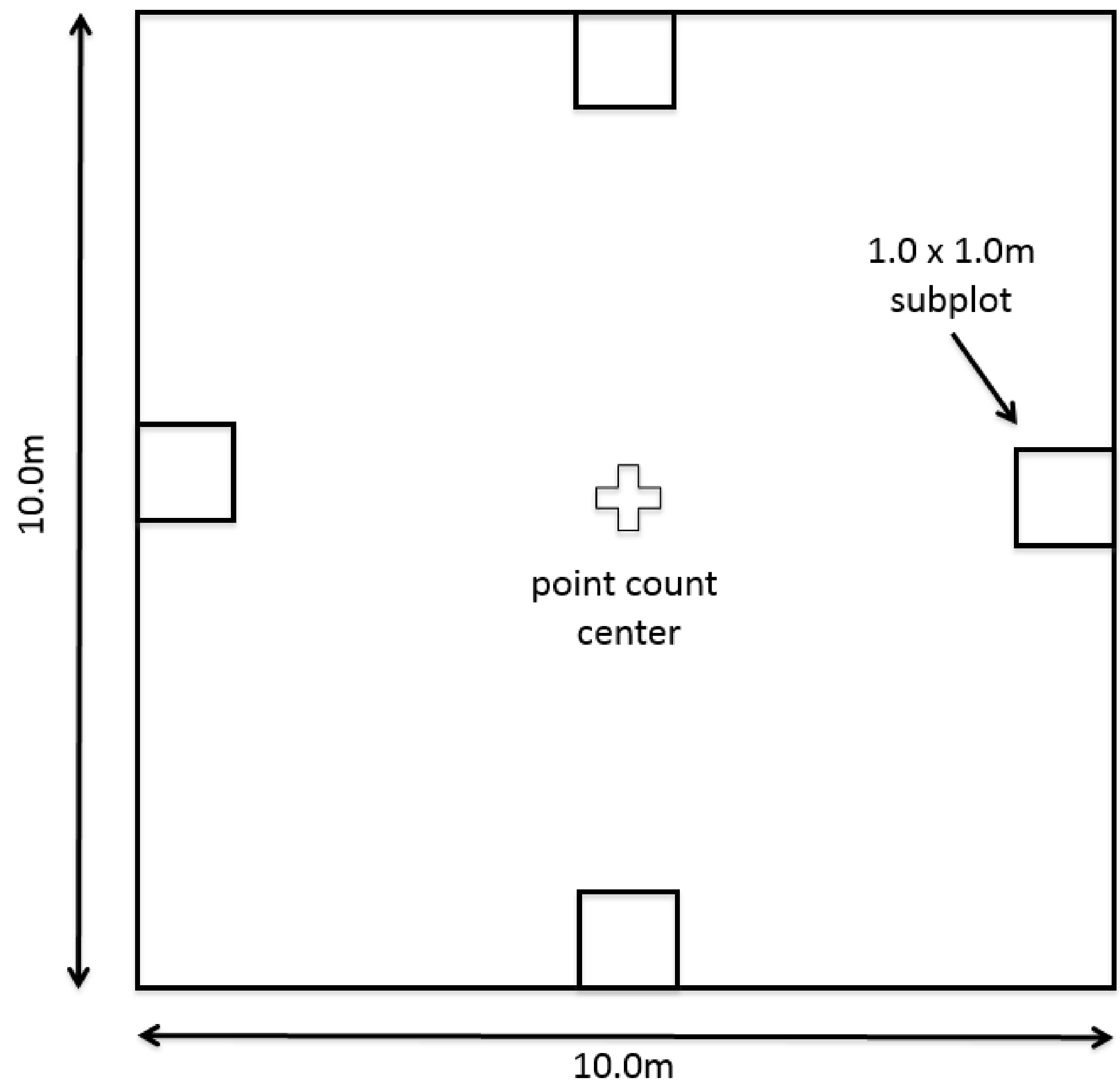

Figure 2. Plot design for vegetation sampling. From the center of each point count location, we established a vegetation sampling plot of 10 X 10 m with four 1 X 1 m subplots 5 m from the center.

Figure 3. Blue vane trap in the field. The blue vane and yellow jar attract pollinators that fly in, slip down the funnel, and are trapped in the jar. Traps were set up near the center of each plot so that no vegetation was within a 1 m of the vane trap itself.

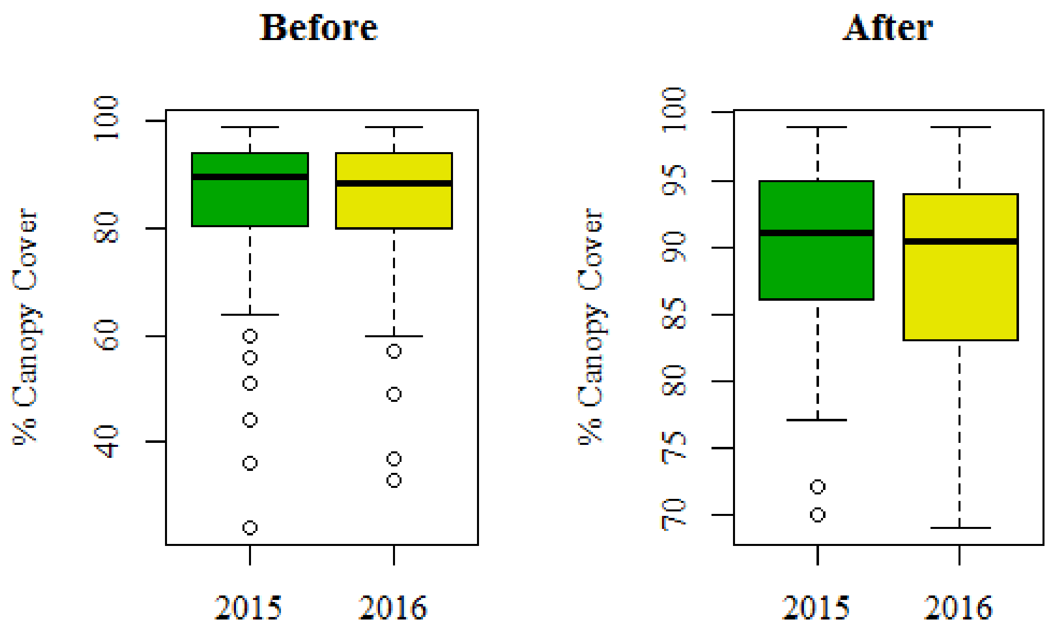

Figure 4. Range of canopy cover. Percent canopy cover before and after removal of 17 plots in the lower decile (≤ 68% canopy cover) in pre-processing. Nine plots were removed from 2015 analysis and eight plots were removed from 2016 analysis.

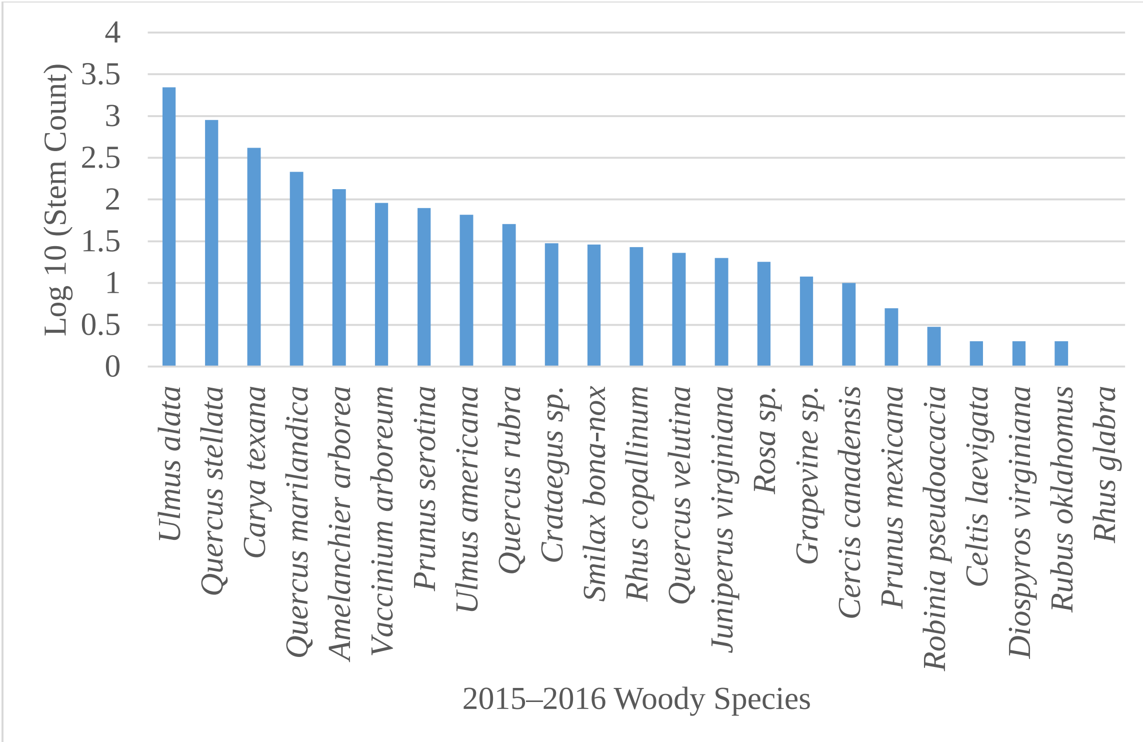

Figure 5. Log_{10} of total stem count of woody vegetation at breast height by species.

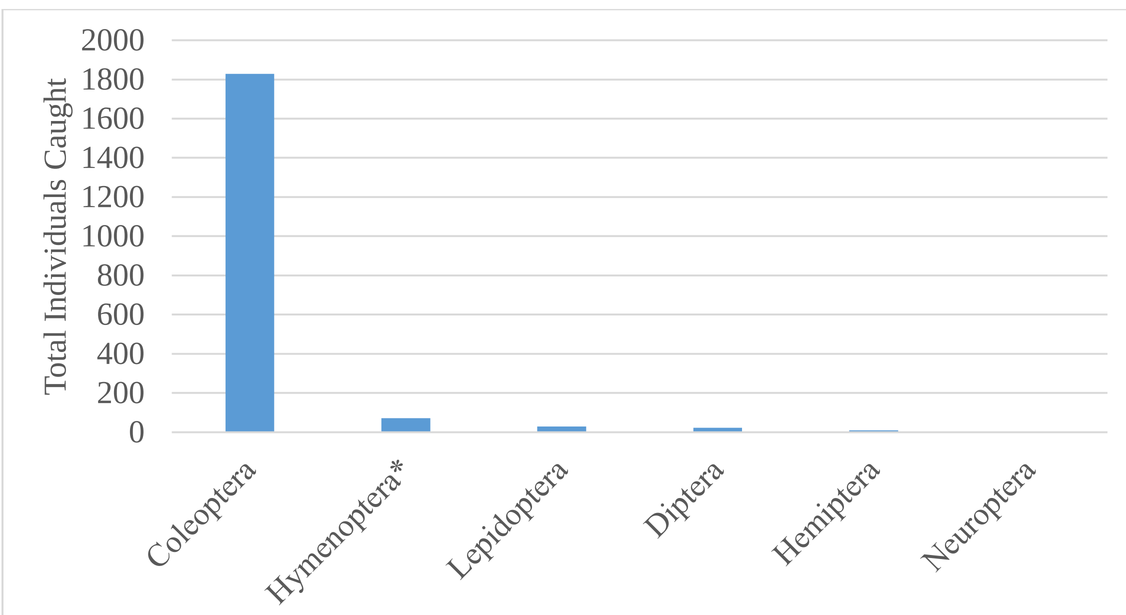

Figure 6. Number of flying insects by taxonomic order. *Ants were excluded from Hymenoptera.

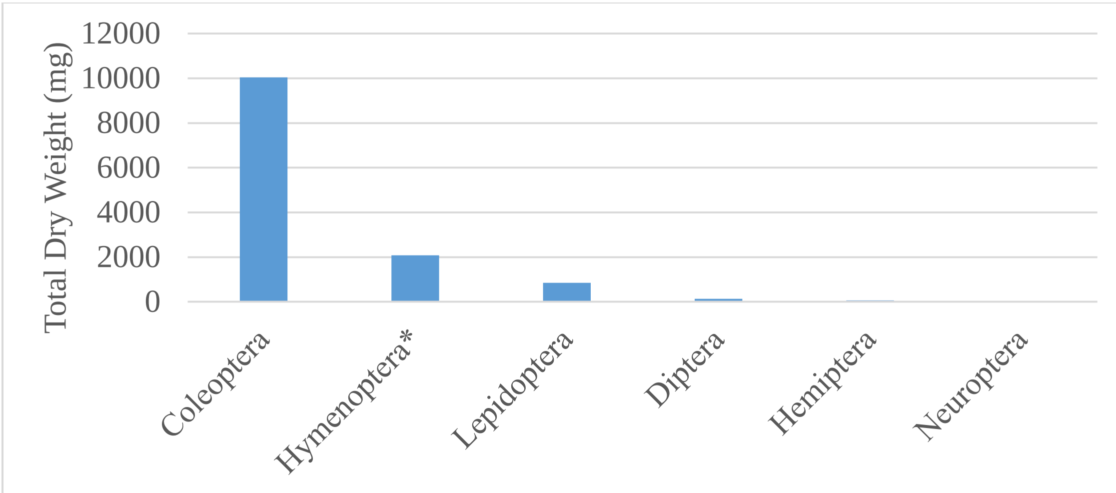

Figure 7. Dry weight of flying insects by taxonomic order. *Ants were excluded from Hymenoptera.

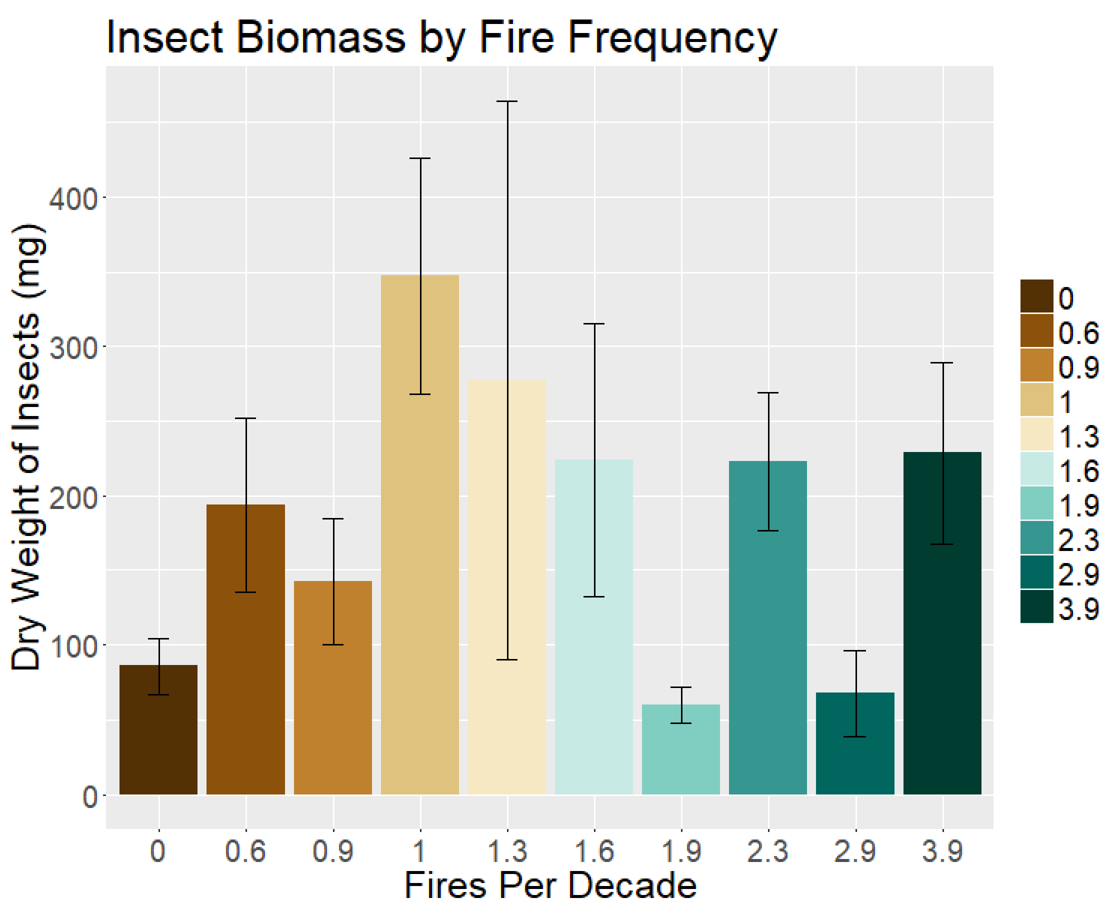

Figure 8. Median dry weight of flying insects by fire frequency.

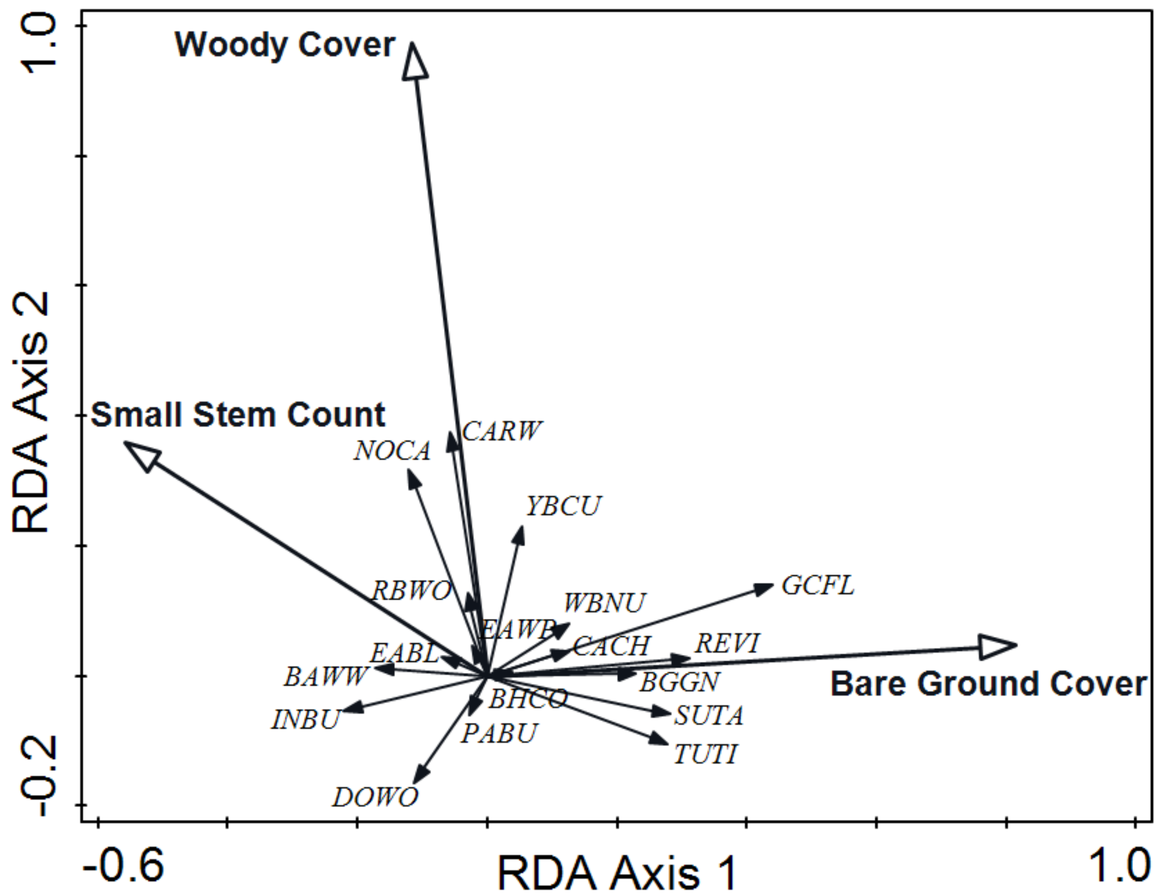

Figure 9. Redundancy analysis biplot of 2015 avian abundance and three most explanatory variables. Table 3 provides the key to variable labels and Table 2 provides the key to species codes.

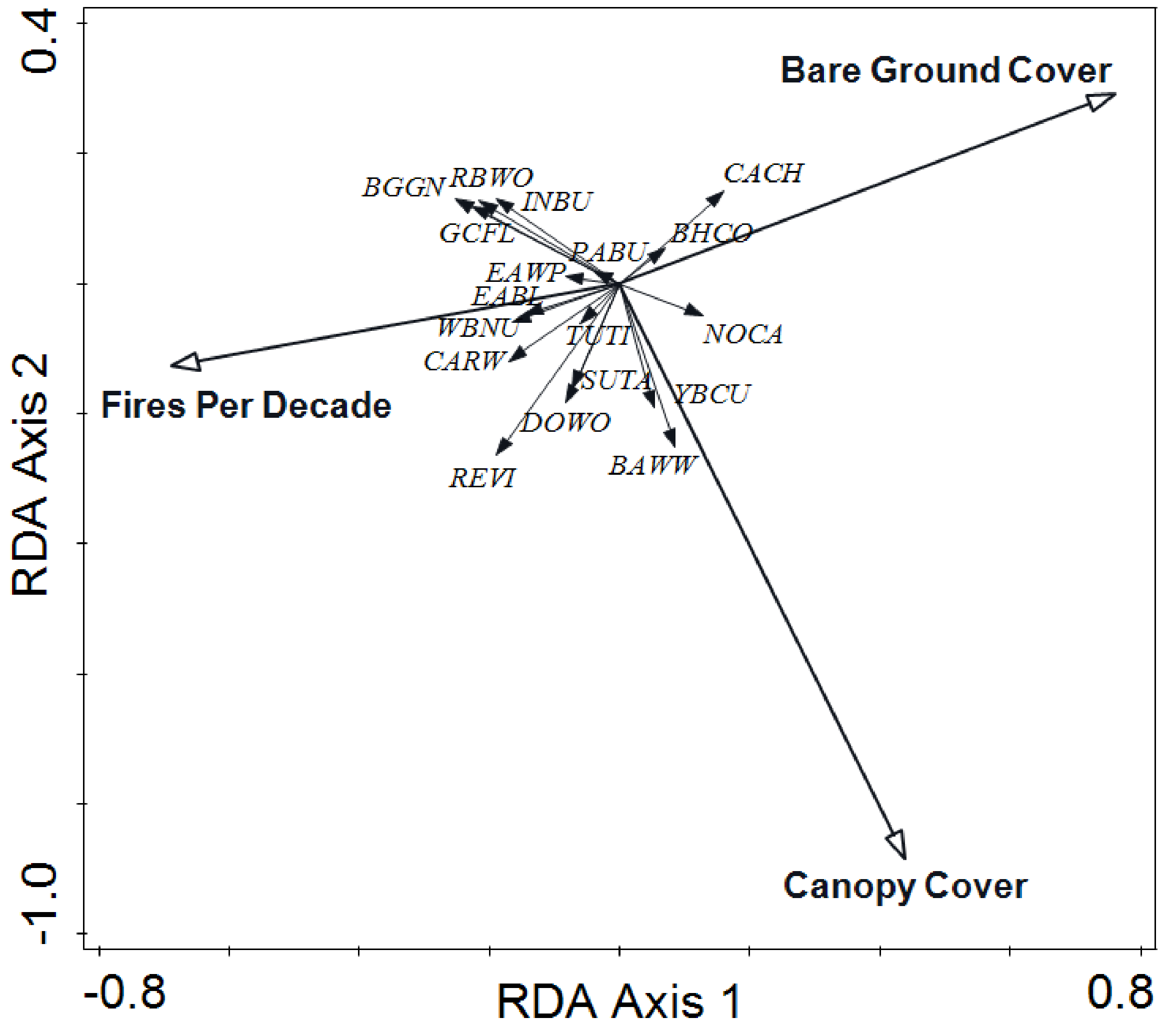

Figure 10. Redundancy analysis biplot of 2016 avian abundance and three most explanatory variables. Table 3 provides the key to variable labels and Table 2 provides the key to species codes.

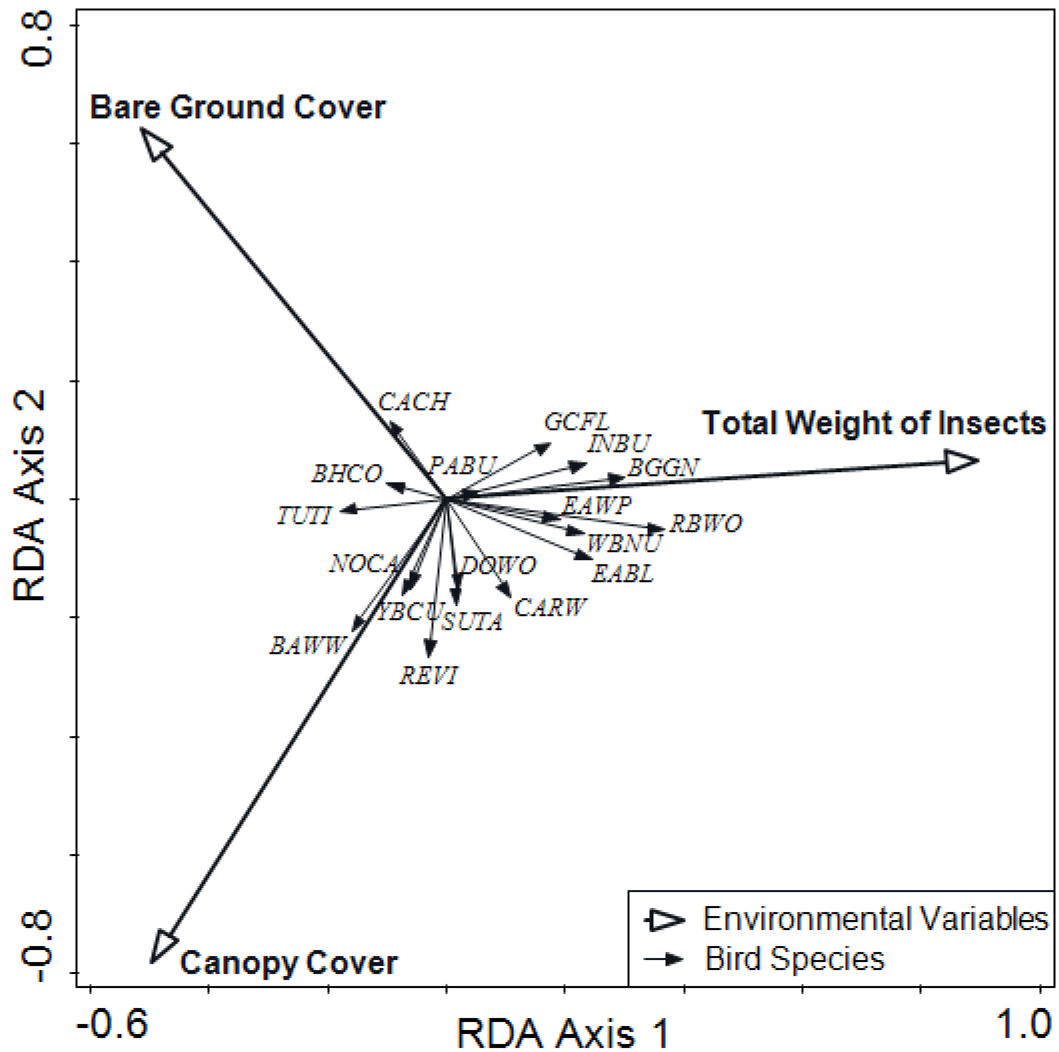

Figure 11. Redundancy analysis biplot of 2016 avian abundance and three most explanatory variables with inclusion of flying insect biomass. Table 3 provides the key to variable labels and Table 2 provides the key to species codes.

Table 1. Burn history of Okmulgee Wildlife Management Area, 1988–2016. All fires occurred between January and March of the year listed, except for one summer burn in 2011. The spatial extent of such fires can be patchy within a management unit, but effort was made to burn the majority of the unit each time. Time since fire (TSF) is measured in years, and fires per decade (FPD) is averaged 1988–2016. Table updated from (Burton et al. 2011).

	Management Unit													
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	TSF
2016														0
2015		1	1									1		1
2014	1							1	1	1				2
2013				1										3
2012														4
2011	1		1			su								5
2010		1												6
2009														7
2008				1		1								8
2007	1	1												9
2006														10
2005			1	1	1		1	1	1	1	1	1		11
2004		1		1				1	1					12
2003	1									1				13
2002				1		1								14
2001	1			1						1				15
2000	1	1	1											16
1999	1													17
1998	1													18
1997	1		1			1			1					19
1996					1		1		1	1	1	1		20
1995	1													21
1994		1		1					1	1				22
1993	1					1		1	1					23
1992		1		1						1				24
1991			1	1										25
1990														26
1989	1													27
1988														28
Total	12	7	6	9	2	5	2	4	7	7	2	3	0	
FPD	4.3	2.5	2.1	3.2	0.7	1.8	0.7	1.4	2.5	2.5	0.7	1.1	0.0	
TSF	2	1	1	3	11	5	11	11	11	11	11	11	28+	

Table 2. Avian detection corrections by observer in 2015 and 2016. P^ is the detection probability of species by observer. N^ is the detection-corrected estimate of abundance by observer (50 m radius). Density (D) is the detection-corrected number of individuals detected per hectare by observer, modeled after Farnsworth et al. (2002) methodology.

Species	Observer Initials	P-hat	N-hat	Density (per ha)	SE-P^	SE-N^	SE-D
Black-and-white Warbler							
	CML	0.98	64.29	0.59	0.02	1.31	0.02
	RAC	1.00	17.01	0.25	0.00	0.02	0.00
	ZC	0.96	7.28	0.17	0.09	0.67	0.02
Blue-gray Gnatcatcher							
	CML	1.00	326.15	2.99	0.00	0.14	0.00
	RAC	0.86	289.35	4.23	NA	NA	NA
	ZC	1.00	97.39	2.34	0.01	0.58	0.02
Brown-headed Cowbird							
	CML	0.95	75.6	0.69	0.04	3.24	0.03
	RAC	0.96	36.34	0.53	0.05	1.78	0.03
	ZC	0.99	19.23	0.46	0.02	0.45	0.02
Carolina Chickadee							
	CML	0.99	196.51	1.80	0.01	1.06	0.01
	RAC	1.00	51.03	0.75	0.00	0.06	0.00
	ZC	1.00	40.04	0.96	0.00	0.07	0.00
Carolina Wren							
	CML	0.85	51.93	0.48	0.23	13.91	0.13
	RAC	0.89	46.09	0.67	0.18	9.35	0.14
	ZC	1.00	8.00	0.19	3.82	30.57	0.73
Downy Woodpecker							
	CML	0.95	32.62	0.30	0.06	2.03	0.02
	RAC	0.93	23.62	0.35	0.08	2.02	0.04
	ZC	0.93	9.65	0.23	0.17	1.76	0.05
Eastern Bluebird							
	CML	0.40	2.53	0.01	889.96	5690.4	13.03
	RAC	0.93	24.62	0.09	0.11	2.79	0.01
Eastern Wood-Pewee							
	CML	0.99	25.31	0.06	0.02	0.52	0.00
	RAC	0.96	15.65	0.06	0.11	1.77	0.01
	ZC	1.00	9.00	0.05	0.00	0.00	0.00
Great Crested Flycatcher							

	CML	1.00	45.15	0.41	0.00	0.22	0.00
	RAC	0.99	16.16	0.24	0.02	0.37	0.01
	ZC	1.00	9.00	0.22	0.00	0.00	0.00
Indigo Bunting							
	CML	0.99	80.56	0.74	0.01	0.76	0.01
	RAC	0.99	109.08	1.6	0.01	1.15	0.02
	ZC	1.00	34.01	0.82	0.00	0.02	0.00
Northern Cardinal							
	CML	0.98	97.15	0.89	0.02	2.29	0.03
	RAC	0.99	33.31	0.49	0.02	0.52	0.01
	ZC	1.00	13	0.31	0.00	0.00	0.00
Painted Bunting							
	CML	0.99	11.16	0.10	0.03	0.37	0.00
	RAC	1.00	8.03	0.12	0.01	0.11	0.00
	ZC	0.41	2.41	0.06	814.42	4736.71	113.79
Red-bellied Woodpecker							
	CML	1.00	11.01	0.10	0.00	0.04	0.00
	RAC	1.00	22.04	0.32	0.00	0.09	0.00
	ZC	1.00	3.00	0.07	0.00	0.00	0.00
Red-eyed Vireo							
	CML	1.00	9.00	0.08	NA	NA	NA
	RAC	0.98	13.32	0.2	0.09	1.25	0.02
	ZC	1.00	2.00	0.05	10.55	21.10	0.51
Summer Tanager							
	CML	0.99	73.89	0.68	0.01	0.99	0.01
	RAC	0.96	85.3	1.25	0.03	3.07	0.05
	ZC	1.00	15.03	0.36	0.01	0.11	0.01
Tufted Titmouse							
	CML	0.99	163.16	1.49	0.01	1.50	0.02
	RAC	1.00	135.1	1.98	0.00	0.12	0.00
	ZC	0.98	34.53	0.83	0.03	1.08	0.03
White-breasted Nuthatch							
	CML	1.00	77.33	0.18	0.01	0.41	0.00
	RAC	0.96	52.2	0.31	0.05	2.5	0.02
	ZC	1.00	21.00	0.13	0.00	0.00	0.00
Yellow-billed Cuckoo							
	CML	0.99	57.3	0.52	0.01	0.36	0.01
	RAC	0.94	55.25	0.81	0.07	3.95	0.06
	ZC	0.98	11.28	0.27	0.06	0.67	0.02

Table 3. Avian species included in multivariate community models. The minimum number of a species detected at any one point was zero.
* indicates species also modeled individually.

Code	Official Common Name	Scientific Name	Percent of Plots Species Present	Maximum Number of Individuals at a Point	Standard Deviation
BGGN*	Blue-gray Gnatcatcher	*Polioptila caerulea*	84.2	7	1.6
TUTI	Tufted Titmouse	*Baeolophus bicolor*	69.6	7.1	1.4
INBU *	Indigo Bunting	*Passerina cyanea*	60.1	5.1	0.9
CACH*	Carolina Chickadee	*Poecile carolinensis*	59.5	9.1	1.4
SUTA *	Summer Tanager	*Piranga rubra*	50	6.1	0.9
WBNU	White-breasted Nuthatch	*Sitta carolinensis*	47.5	6	0.9
BHCO*	Brown-headed Cowbird	*Molothrus ater*	44.3	3.2	0.6
YBCU	Yellow-billed Cuckoo	*Coccyzus americanus*	43	3.2	0.5
NOCA*	Northern Cardinal	*Cardinalis cardinalis*	41.8	4.1	0.7
BAWW*	Black-and-white Warbler	*Mniotilta varia*	34.8	3.1	0.5
CARW*	Carolina Wren	*Thryothorus ludovicianus*	29.7	5.9	1
DOWO	Downy Woodpecker	*Picoides pubescens*	25.3	3.2	0.6
GCFL*	Great Crested Flycatcher	*Myiarchus crinitus*	22.8	6	1.2
EAWP*	Eastern Wood-Pewee	*Contopus virens*	20.9	2.1	0.3
RBWO	Red-bellied Woodpecker	*Melanerpes carolinus*	15.8	2	0.3
REVI	Red-eyed Vireo	*Vireo olivaceus*	8.9	2	0.3
PABU	Painted Bunting	*Passerina ciris*	8.2	2.4	0.5
EABL	Eastern Bluebird	*Sialia sialis*	7	4.3	0.7

Table 4. Variable codes and descriptions for multivariate community models.		
Variable Names	Variable Description	Range
Canopy Cover	Percent canopy cover	68–99
Fires Per Decade	Fire frequency for the management unit of the plot	0.0–4.3
Small Stem Count	Number of all woody stems < 8 cm at breast height in plot	0–160
Bare Ground Cover	Percent cover of bare ground measured from a height of 1 m	0–39
Woody Cover	Percent cover of woody plant species under 1 m in height	0–69
Total Weight of Insects	Total weight in mg of insects	10.4–836.5

Table 5. Variability explained within each multivariate community model.

Year	Explanatory Variables	Cumulative Variability Explained	Adjusted Explained Variation	pseudo-F	P	Figure
2015	Woody Cover, Small Stem Count, and Bare Ground Cover	7.9	3.3	1.7	0.005	8
2016	Bare Ground Cover, Fires Per Decade, and Canopy Cover	4.8	1.0	1.3	0.113	9
2016	Bare Ground Cover, Canopy Cover, and Total Weight of Insects	5.5	1.6	1.4	0.033	10

Table 6. Explanatory variables used in individual species models.

Abbreviation	Variable	Min	Max	Mean	SD
AWood	Average percent cover live woody vegetation	0.0	69.3	24.6	13.9
ABare	Average percent cover bare ground	0.0	38.6	3.1	5.1
FPD	Fires per decade	0.0	4.3	1.5	1.2
Openness	Average percent open canopy	1.0	31.0	11.3	7.3
StemSmCt*	Count of woody stems under 8 cm at breast height	0.0	160.0	20.7	31.5
StemSmCtScaled**	Scaled StemSmCt	-0.7	4.4	0.0	1.0

*Not used in any models.
**Used in models instead of StemSmCt.

Table 7. Top and competing individual species models. ΔAIC under 2.

				Direction of effect and significance level, where α is 0 <0.001 ***, ≤0.001 = **, ≤0.01 = *, ≤0.05 = .									
AIC	Δ AIC	df	weight	AWood	*	ABare	*	FPD	*	Open-ness	*	StemSm CtScaled	*
Black-and-white Warbler													
266.3	0	5	0.18							-	**	+	
266.5	0.2	4	0.16							-	**		
Blue-gray Gnatcatcher													
547.2	0	4	0.12					-	*				
Brown-headed Cowbird													
300.9	0	3	0.17	(null)									
Eastern Wood-Pewee													
183.1	0	4	0.12					+	.				
184.5	1.5	3	0.06	(null)									
Northern Cardinal													
316.9	0	4	0.15					-	**				
Carolina Chickadee													
501.2	0	3	0.10	(null)									
501.2	0	4	0.09							+			
Carolina Wren													
279.7	0	4	0.23	+	*								
Great Crested Flycatcher													
238.1	0	4	0.19			+	**						
Indigo Bunting in 2015													
114.3	0	4	0.15			-	.			+	**		
114.7	0.5	4	0.12			-		+	*				
116.1	1.9	3	0.06					+	**				
Indigo Bunting in 2016													
230.8	0	3	0.19							+	*		
Summer Tanager in 2015													
122.6	0	4	0.25			+	***	+	*				
Summer Tanager in 2016													
208.9	0	2	0.13	(null)									

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