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I am submitting herewith a thesis written by Christine Ann Henderson entitled "Avian Ecology During Oak Savanna and Woodland Restoration in the Mid-South." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Patrick Keyser, Major Professor

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**Avian Ecology During Oak Savanna and Woodland Restoration in the
Mid-South**

**A Thesis Presented for the
Master of Science
Degree**

The University of Tennessee, Knoxville

Christine Ann Henderson

December 2017

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ABSTRACT

Disturbance-dependent ecosystems in the eastern United States have been declining since European settlement, and, in recent years, early-successional species have followed. My objective for this research was to determine if oak savanna and woodland restoration (i.e., overstory thinning and prescribed fire) was a viable method of recovering declining early-successional species to the landscape of the Mid-South. At 3 sites, Catoosa Wildlife Management Area (CWMA; Tennessee), Green River Game Lands (GRGL; North Carolina), and Land Between the Lakes National Recreation Area (LBL; Tennessee), oak savanna and woodland restoration projects were established and maintained. Closed-canopy stands were thinned and a 2-year burn schedule was implemented. In Chapter One, I present on nest- and stand-level vegetation metrics associated with Prairie Warbler (*Setophaga discolor*) nest survival and nest-site selection at CWMA 7 years after canopy disturbance and consistent burning. In 2015 and 2016, Prairie Warblers had average nest success (0.937 ± 0.007) compared with other studies and selected for increased herbaceous groundcover around the nest compared with available habitat. Nest survival in 2015 was lower than in 2016. A positive trend between groundcover and nest survival was found. In Chapter Two, I describe nest- and stand-level vegetation metrics associated with Red-headed Woodpecker (*Melanerpes erythrocephalus*) nest survival and nest-site selection at CWMA 7 years after canopy disturbance and consistent burning. Red-headed Woodpeckers had very high nest success (84.1%) compared with other studies and selected nest sites with greater herbaceous groundcover, dead basal area, and midstory density (in 2016) compared with available habitat. A negative trend was found between nest survival and live basal area. In Chapter Three, I describe vegetation metrics (herbaceous groundcover, live and dead basal area, and midstory density) influencing 28 bird species'

abundances at CWMA, GRGL, and LBL 2010–2012 and 2014–2016. Moderate to high amounts of disturbance were associated with increased populations of early-successional species while low to moderate amounts of disturbance either did not affect or were positively associated with populations of most mature forest species. Oak savanna and woodland restoration is a viable method to increase populations of early-successional bird species while retaining most mature forest species.

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INTRODUCTION

Open forest communities, barrens, prairies, and scrubland were once common across the eastern United States prior to Europeans arrival (Askins 2002). Natural fires and Native Americans, who used fire to facilitate hunting and to clear land for agriculture, maintained these areas (Van Lear and Waldrop 1989, Askins 2002). Since European settlement, many of these disturbance-dependent ecosystems have been almost eliminated throughout the United States and are considered as critically imperiled ecosystems (Noss et al. 1995). Oak savannas, in particular, have dwindled to about 0.02% of the original extent in the Midwest (Nuzzo 1986). Disturbance, such as fire and thinning, is necessary to maintain such ecosystems to prevent succession to closed canopy conditions (Brawn et al. 2001, Hunter et al. 2001, Artman et al. 2005, Au et al. 2008).

Disturbance-dependent avian declines

Recent research has reinforced our understanding of the connection between disturbance and some avian communities (Davis et al. 2000, Brawn et al. 2001, Greenberg et al. 2013). In the last 50 years, fire and disturbance-dependent bird species have been declining (Askins 1999, Hunter et al. 2001, Sauer et al. 2013). In the United States, 15 grassland species and 22 scrubland species have experienced “significant population decline” since 1966 (Sauer et al. 2013). Specifically, Red-headed Woodpecker (*Melanerpes erythrocephalus*) and Prairie Warbler (*Setophaga discolor*) have declined respectively 2.35% and 1.85% annually, range-wide (Askins 1999, Hunter et al. 2001, Sauer et al. 2013). Red-headed Woodpecker, Prairie Warbler, and many other species of grassland and open-woodland species depend on disturbed areas for breeding, and without these, they are at risk of continued declines (Davis et al. 2000, Hunter et al. 2001, Brawn 2006, Reidy et al. 2014). Red-headed Woodpecker, in particular, is described as

an oak-savanna obligate and needs these areas for breeding and foraging. Several conservation initiatives, including Partners in Flight, have recommended increasing the breeding populations of many of these species (Southwell 2001, Rosenberg et al. 2016). Reintroducing fire and thinning can increase preferred habitat for early successional species, therefore contributing to their conservation (Gram et al. 2003, Artman et al. 2005). Oak savannas and woodlands are known for their park-like openness and are comprised of a thick, herbaceous understory and scattered mature oak trees at about 7–14 m² ha⁻¹ basal area. These communities are known for their benefits to several bird species (Davis et al. 2000, Brawn 2006, Vander Yacht et al. 2016), but little is known about the effect on avian ecology during the restoration process.

Studying nest survival is an informative method to research avian population dynamics. If areas that are in the process of being restored have high nest survival, restoration may help increase populations of declining bird species. Information can also be collected on nest-site selection to determine what ideal conditions should be targeted to attract certain species. In most cases, nest survival studies cannot simultaneously be done on several species due to logistical issues. However, researching abundance using point counts is a way to collect information on an entire bird community at once to determine how bird species are reacting to certain vegetation variables, for instance. Because of the range of niches available along the oak savanna to oak forest continuum, these communities could attract both early-successional and mature forest species.

Nest-site selection

Obtaining information about nest-site selection can facilitate nest searching, making the process more productive, and ultimately steer management towards conditions attractive to these

species. Several studies have reported on Red-headed Woodpecker and Prairie Warbler nest-site selection, but not in the context of an oak savanna restoration framework.

Red-headed Woodpeckers tend to prefer nest sites with greater amounts of dead limb length and snags than random points, a preference likely related to increased foraging opportunities and increased availability of perches for protecting the nest (Rodewald et al. 2005, King et al. 2007). Selection for greater diameter at breast height (DBH) of nest trees, greater shrub density, and greater percentage of high-severity fire within 1-km of the nest site has been reported for nest sites in Black Hills, South Dakota (Vierling and Lentile 2006). In restored savannas in Wisconsin, Red-headed Woodpeckers preferred areas with greater amounts of basal area, and greater cavity density which was hypothesized to improved nest concealment and reduced predator search efficiency, respectively (King et al. 2007). Red-headed Woodpeckers also chose nest patches that produced more hard mast than non-nest patches (Rodewald et al. 2005) and preferred more decayed nest trees (Jackson 1976). Understory selection preferences have not been extensively studied, although one study in Virginia reported woodpeckers avoided nesting or occupying areas with dense understory (Conner 1976). Many of the habitat attributes Red-headed Woodpeckers have selected for can be found in areas being restored to oak savannas and woodlands, suggesting the potential benefit such sites could have to this species and its conservation

Prairie Warbler nest-site selection information is generally lacking in the literature although a few studies have researched this species' preferences. Opportunistic selection of substrate species has been documented for Prairie Warblers in Florida and Indiana (Nolan 1978, Prather and Cruz 1995) so likely, this species does not have a strong preference for any one species. Nolan (1978) documented Prairie Warblers nests over a wide range of heights, 24 cm to

13.7 m high. Prairie Warblers also prefer nest sites with lower canopy cover and select for more woody stems within 2 m of the nest (Slay 2010, Akresh 2012).

Factors affecting nest survival

Research has been conducted on avian nest survival in oak savannas and woodlands for individual species (e.g. Viste-Sparkman 2005, Hudson and Bollinger 2013, Kendrick et al. 2013) as well as avian communities (Brawn 2006, Reidy et al. 2014). However, no studies have taken place in the Mid-South. Both early-successional and mature forest species can benefit from disturbance in a close-canopy system. Brawn (2006) reported 11 of the 13 species he studied in a recently restored oak savanna, had greater nest productivity in a savanna vs. closed-canopy forest, but the remaining 2 had lower productivity. Bakermans et al. (2012) found that nest survival for all mature forest species they studied in unmanaged mature forest increased 10.5% for every 1% increase in canopy openness and decreased 1.4% for every 5% increase in understory vegetation density. In Missouri, Gram et al. (2003) evaluated 3 treatments (even-aged cutting, uneven-aged cutting, and controls with no cutting) and their impact on nest survival and productivity and concluded that nest survival did not change from pre-treatment to post-treatment when all species' nests were combined. In uneven-aged treatments, Wood Thrush (*Hylocichla mustelina*) and Ovenbird (*Seiurus aurocapilla*), mature forest species, declined about 60% in productivity compared with untreated controls. However, Indigo Bunting (*Passerina cyanea*), an early-successional species, productivity increased 75% in even-aged and uneven-aged treatments (Gram et al. 2003). Responses to disturbance are clearly species-specific, but these studies did not identify habitat variables associated with these responses. Information on specific habitat variables that benefit priority species would be valuable to land managers and need to be studied.

Furthermore, nest survival can be related to factors not directly connected to management. Nest survival has been known to differ with height and placement within the landscape for both Prairie Warblers and Red-headed Woodpeckers. One Red-headed Woodpecker study in Illinois found nest survival was positively correlated with nest height and nest age (Hudson and Bollinger 2013), but another study was unable to duplicate these findings (Berl et al. 2014). For early-successional songbirds including Prairie Warbler, nest height did not influence nest survival (Nolan 1963, Best 1978). Additionally, in regards to landscape context, King et al. (2001) found no difference in a shrubland bird's daily nest survival rates between the edge and interior of clearcuts in eastern deciduous forests.

Predation and brood parasitism

Management technique, and subsequent habitat structure, can change the predator community in an area enough to affect nest survival (Thompson 2007). Nest survival for 3 forest songbird species was lower in fragmented vs. contiguous forested habitat, which could have been attributed to predator and parasite population differences (Donovan et al. 2009). Brown-headed Cowbird (*Molothrus ater*) brood parasitism is an additional important consideration in oak savanna and woodland restoration as several studies examining their response to restoration have found their abundance to positively correlate with disturbance (Annand and Thompson 1997, Davis et al. 2000, Reidy et al. 2014). Brown-headed Cowbirds increased with increasing restoration efforts (i.e., increased burn frequency, fewer trees, lower leaf area index, and increased importance of dead trees) in Minnesota (Davis et al. 2000). Cowbirds have also been found to decrease with increasing canopy cover which could be related to having fewer opportunities to perch and observe adult host birds building nests (Barber 2001). Cowbirds were also more abundant in clearcuts and at points with lower canopy cover and intermediate percent

forest cover over the landscape (Annand and Thompson 1997, Reidy et al. 2014). In an experiment in Ohio forests, Brown-headed Cowbird relative abundance increased 70% in all treatment plots including those that had been burned and thinned (Dennis 2002). In contrast, Brawn (2006) found that habitat did not affect brood parasitism rates across a range of conditions that included closed-canopy forest and oak savannas managed with prescribed fire.

Abundance and occupancy in oak savanna

Oak-savanna and woodland restoration is a management method that created habitat that early-successional species prefer while keeping enough structure (i.e., overstory trees) for mature forest species' nesting and foraging. Avian abundance and occupancy have not been extensively studied in oak savanna and woodland restoration, and only two studies have been done in the Mid-South, one on occupancy (Vander Yacht et al. 2016), and the other on relative abundance (Barrioz et al. 2013). In Illinois, 12 out of 31 bird species, including Red-headed Woodpecker, responded positively to oak savanna restoration compared with closed-canopy forests. Only 5 species responded negatively and 14 were unaffected by restoration (Brawn 2006).

In Minnesota, Au et al. (2008) found greater avian species richness in dry oak savannas than in prairies, oak woodlands, or oak woodlands undergoing restoration through fire and removal of woody vegetation. Relative abundance of grassland, savanna, and scrub-shrub species, including Prairie Warbler, and Red-headed Woodpecker, was found to increase with greater number of burns, more snags, greater shrub density, and reduced canopy cover. Responses of mature forest species to the same treatments were largely opposite, with the exception of snags, which they also responded to positively (Rodewald and Smith 1998, Davis et al. 2000, Wood et al. 2004, Au et al. 2008, Reidy et al. 2014).

Artman et al. (2001) found that after 4 years of repeated burning in a mixed-oak forest in Ohio, ground and low-shrub nesting bird density (number of pairs per 40 ha) declined but canopy nesting bird density was unaffected. In a separate study, Red-eyed Vireo (*Vireo olivaceus*), a canopy nester, was more common in closed-canopy forests vs. restored savannas likely due to forage substrate (i.e., canopy) availability (Brawn 2006). Some mature forest species were more frequent at points with increased trees and snags and were positively correlated to canopy biomass, as well as subcanopy tree size (Anderson and Shugart 1974, Crawford et al. 1981).

Annand and Thompson (1997) evaluated avian abundance and richness in response to harvest treatments in a forested landscape in Missouri and found Field Sparrow relative abundance greater in clearcuts than shelterwood, group, and single-tree selection treatments, but red-eyed vireo followed the opposite pattern. Among all species studied, however, species richness was greater in cut than uncut areas. On the other hand, species abundance did not differ between selectively logged stands and uncut stands (Robinson and Robinson 1999, Doyon et al. 2005). Early successional bird density generally increased in response to disturbance consisting of even- and uneven-aged cutting (Gram et al. 2003).

Disturbance through oak savanna restoration would likely lead to an increase in early-successional and disturbance-dependent species but may cause declines for mature forest species. However, the dramatic increases for early-successional species would outweigh the limited declines in mature forest species. Research on avian nest survival and abundance in oak savannas in the process of being restored is not well represented in the literature and needs to be explored further.

Therefore, in 2015 and 2016 at one site in Tennessee, I collected nest-site selection and nest survival data on Prairie Warblers and Red-headed Woodpeckers in an oak savanna and

woodland restoration experiment. Additionally, at three sites across the Mid-South, I continued collection of point count data started in 2010. Each site had been logged to a savanna or woodland residual basal area and burned 1–3 times biennially. Results suggested oak savanna and woodland restoration was possibly a viable method for increasing Prairie Warbler and Red-headed Woodpecker populations. Furthermore, moderate levels of disturbance lead to an increase in abundance of early-successional species while continuing to provide habitat for mature forest species.

Literature Cited

- Akresh, M. E. (2012). Prairie Warbler nest-site selection, nest survival, and demographic response to management in a pitch pine-scrub oak barren. *Thesis*.
- Anderson, S. H., and H. H. Shugart (1974). Habitat selection of breeding birds in an east Tennessee deciduous forest. *Ecology* 55:828–837.
- Annand, E. M., and F. R. Thompson (1997). Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61:159–171.
- Artman, V. L., T. F. Hutchinson, and J. D. Brawn (2005). Fire ecology and bird populations in eastern deciduous forests. *Studies in Avian Biology* 30:127–138.
- Artman, V. L., E. K. Sutherland, and J. F. Downhower (2001). Prescribed burning to restore mixed-oak communities in southern Ohio: Effects on breeding-bird populations. *Conservation Biology* 15:1423–1434.
- Askins, R. A. (1999). History of grassland birds in eastern North America. *Studies in Avian Biology* 19:60–71.
- Askins, R. A. (2002). Restoring North America's birds: Lessons from landscape ecology. In 2nd ed. Yale University Press.
- Au, L., D. E. Andersen, and M. Davis (2008). Patterns in bird community structure related to restoration of Minnesota dry oak savannas and across a prairie to oak woodland ecological gradient. *Natural Areas Journal* 28:330–341.
- Bakermans, M. H., A. D. Rodewald, and A. C. Vitz (2012). Influence of forest structure on density and nest success of mature forest birds in managed landscapes. *Journal of Wildlife Management* 76:1225–1234.
- Barber, D. R., T. E. Martin, M. A. Melchiors, R. E. Thill, and T. B. Wigley (2001). Nesting

- success of birds in different silvicultural treatments in southeastern U.S. pine forests. *Conservation Biology* 15:196–207.
- Barrioz, S., P. Keyser, D. Buckley, D. Buehler, and C. Harper (2013). Vegetation and avian response to oak savanna restoration in the Mid-South USA. *The American Midland Naturalist* 169:194–213.
- Berl, J. L., J. W. Edwards, J. S. Bolsinger, and T. E. Katzner (2014). Survival of Red-headed Woodpeckers' (*Melanerpes erythrocephalus*) nests in northern New York. *The Wilson Journal of Ornithology* 126:700–707.
- Best, L. B. (1978). Field Sparrow reproductive success and nesting ecology. *The Auk* 95:9–22.
- Brawn, J. D. (2006). Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20:460–469.
- Brawn, J. D., S. K. Robinson, and F. R. Thompson (2001). The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32:251–276.
- Conner, R. N. (1976). Nesting habitat for Red-headed Woodpeckers in southwestern Virginia. *Bird-Banding* 47:40–43.
- Crawford, H. S., R. G. Hooper, and R. W. Titterington (1981). Songbird population response to silvicultural practices in central Appalachian hardwoods. *Journal of Wildlife Management* 45:680–692.
- Davis, D. W. Peterson, P. B. Reich, M. Crozier, T. Query, E. Mitchell, J. Huntington, and P. Bazakas (2000). Restoring savanna using fire: Impact on the breeding bird community. *Restoration Ecology* 8:30–40.
- Dennis, T. (2002). Responses of avian communities to shelterwood cuts and prescribed burns in eastern deciduous forests. *Thesis*. [Online.] Available at

http://rave.ohiolink.edu/etdc/view?acc_num=ohiou1037129102.

- Donovan, T. M., F. R. Thompson, J. Faaborg, and J. R. Probst (1995). Reproductive success of migratory birds in habitat sources and sinks. *Society for Conservation Biology* 9:1380–1395.
- Doyon, F., D. Gagnon, and J.-F. Giroux (2005). Effects of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest. *Forest Ecology and Management* 209:101–116.
- Gram, W. K., P. A. Porneluzi, R. L. Clawson, J. Faaborg, and S. C. Richter (2003). Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conservation Biology* 17:1324–1337.
- Greenberg, C. H., T. a. Waldrop, J. Tomcho, R. J. Phillips, and D. Simon (2013). Bird response to fire severity and repeated burning in upland hardwood forest. *Forest Ecology and Management* 304:80–88.
- Hudson, N. C., and E. K. Bollinger (2013). Nest success and nest site selection of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) in East-central Illinois. *The American Midland Naturalist* 170:86–94.
- Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel (2001). Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29:440–455.
- Jackson, J. A. (1976). A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied Woodpeckers in Kansas. *The Condor* 78:67–76.
- Kendrick, S. W., F. R. Thompson, and J. L. Reidy (2013). Eastern Wood-Pewee (*Contopus virens*) breeding demography across a gradient of savanna, woodland, and forest in the

- Missouri Ozarks. *The Auk* 130:355–363.
- King, D. I., R. M. Degraaf, and C. R. Griffin (2001). Productivity of early successional shrubland birds in clearcuts and groupcuts in an eastern deciduous forest. *Journal of Wildlife Management* 65:345–350.
- King, R. S., K. E. Brashear, and M. Reiman (2007). Red-headed Woodpecker nest-habitat thresholds in restored savannas. *Journal of Wildlife Management* 71:30–35.
- Van Lear, D. H., and T. A. Waldrop (1989). History, uses, and effects of fire in the Appalachians. *USDA Forest Service General Technical Report*.
- Nolan, V. (1963). Reproductive success of birds in a deciduous scrub habitat. *Ecology* 44:305–313.
- Nolan, V. (1978). The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). *Ornithological Monographs* 26.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott (1995). Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. National Biological Service, Biological Report 28. U.S. Department of the Interior, Washington, D.C., USA.:83.
- Nuzzo, V. (1986). Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6:6–36.
- Prather, J. W., and A. Cruz (1995). Breeding biology of Florida Prairie Warblers and Cuban Yellow Warblers. *The Wilson Bulletin* 107:475–484.
- Reidy, J. L., F. R. Thompson, and S. W. Kendrick (2014). Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *Forest Ecology and Management* 313:34–46.
- Robinson, W. D., and S. K. Robinson (1999). Effects of selective logging on forest bird

- populations in a fragmented landscape. *Conservation Biology* 13:58–66.
- Rodewald, P. G., M. J. Santiago, and A. D. Rodewald (2005). Habitat use of breeding Red-headed Woodpeckers on golf courses in Ohio. *Wildlife Society Bulletin* 33:448–453.
- Rodewald, P. G., and K. G. Smith (1998). Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. *Journal of Wildlife Management* 62:1411–1417.
- Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Fprd, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, et al. (2016). *Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States*.
- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski (2013). The North American breeding bird survey 1966–2011: summary analysis and species accounts. *North American Fauna* 79:1–32.
- Slay, C. M. (2010). An evaluation of reproductive success, adult survivorship and habitat use of shrubland birds on conservation-managed fields in western Connecticut.
- Southwell, D. K. (2001). Conservation assessment for Prairie Warbler (*Dendroica discolor*). USDA Forest Service.
- Thompson, F. R. (2007). Factors affecting nest predation on forest songbirds in North America. *Ibis* 149:98–109.
- Vierling, K., and L. Lentile (2006). Red-headed Woodpecker nest-site selection and reproduction in mixed ponderosa pine and aspen woodland following fire. *The Condor* 108:957–962.
- Viste-Sparkman, K. (2005). White-breasted Nuthatch density and nesting ecology in oak woodlands of the Willamette Valley, Oregon. Thesis.

Wood, D. R., L. W. Burger Jr., J. L. Bowman, and C. L. Hardy (2004). Avian community response to pine-grassland restoration. *Wildlife Society Bulletin* 32:819–828.

Vander Yacht, A. L., P. D. Keyser, D. A. Buehler, C. A. Harper, D. S. Buckley, and R. D. Applegate (2016). Avian occupancy response to oak woodland and savanna restoration. *Journal of Wildlife Management* 80:1091–1105.

**1. PRAIRIE WARBLER NEST-SITE SELECTION AND NEST SURVIVAL
DURING OAK SAVANNA AND WOODLAND RESTORATION IN THE
MID-SOUTH**

Abstract

Disturbance-dependent bird species, including the Prairie Warbler (*Setophaga discolor*), have experienced substantial population declines since 1966, likely due to loss of open, disturbed habitats such as oak savannas. Therefore, oak savanna and woodland restoration may be a viable method to increase populations of these species. To evaluate this approach, we studied nesting Prairie Warblers on a site (Catoosa Wildlife Management Area near Crossville, Tennessee) where restoration of oak savannas has been ongoing since 2008 with selective logging leaving low, savanna ($7.2 \text{ m}^2 \text{ ha}^{-1}$) or high, woodland ($14.4 \text{ m}^2 \text{ ha}^{-1}$) residual basal areas and spring or fall burns conducted on a two-year interval. We monitored 107 Prairie Warbler nests in summers 2015–2016. We measured vegetation near the nest sites (11.3-m radius) and in the surrounding stand (20 ha). A priori models were created, analyzed in Program MARK, and compared using AICc values. Support was found for a year effect, but among habitat covariates, only herbaceous groundcover at the nest (positive) received any support. Daily survival rate was 0.894 ± 0.018 in 2015, 0.954 ± 0.008 in 2016, and 0.937 ± 0.007 across both years. Variation in annual nest survival may have been influenced by time since burning. With respect to nest sites, birds selected for greater herbaceous groundcover (>45%) compared with available habitat. Nest-site selection and nest survival could be associated with predation or landscape-level variables but these relationships were not conclusive as data was not collected on these factors. Oak savanna and woodland restoration appears to offer some promise as a viable method to Prairie Warbler conservation but additional productivity data is needed to clarify relationships with prescribed fire timing.

Introduction

The Prairie Warbler (*Setophaga discolor*) is a scrub-shrub species common across the eastern and central United States (Nolan et al. 2014). Despite having a wide distribution, this species has experienced a significant range-wide population decline (-1.85% annually) since 1966 (Askins 1999, Hunter et al. 2001, Sauer et al. 2013). Prairie Warblers are listed as a species of conservation concern by Partners in Flight (Rosenberg et al. 2016) and the U.S. Department of Agriculture (USDA) Forest Service recognizes the conservation need for this species (Southwell 2001). Prairie Warblers depend on disturbed areas for breeding, and without these, are at risk of continued declines (Davis et al. 2000, Brawn 2006, Reidy et al. 2014).

Ecosystems that rely on fire disturbance events, such as prairies, scrublands, and open-canopy forests, were common in North America until the arrival of Europeans (Nuzzo 1986, Askins 2002). Since the arrival of Europeans, these fire-dependent communities have almost been completely eliminated, and are now considered critically imperiled (Noss et al. 1995). Exemplifying this dilemma are oak savannas and woodlands, with only an estimated 0.02% of the original 11–13 million ha of the Midwest range remaining (Nuzzo 1986). Disturbance, specifically fire and thinning, is important in maintaining these ecosystems and keeping them from becoming closed-canopy forests (Brawn et al. 2001, Hunter et al. 2001, Artman et al. 2005).

Many avian communities require disturbance, as much recent research has documented (Davis et al. 2000, Brawn et al. 2001, Greenberg et al. 2013). In particular, reintroducing fire and thinning can increase habitat for Prairie Warblers, therefore contributing to the conservation of this disturbance-dependent species (Gram et al. 2003, Artman et al. 2005). Burning tends to increase abundance of Prairie Warbler and many other early-successional passerines with

impacts evident for 1-3 years post-burning (Tucker et al. 2006, Grant et al. 2011, Greenberg et al. 2013). Oak savanna and woodland restoration involves thinning and regular use of prescribed fire, and in addition to achieving community conservation goals, may provide beneficial transitional habitat during the restoration process. However, avian response to oak savanna and woodland restoration has only received limited attention in the literature, and only then in the Midwest (Davis et al. 2000, Artman et al. 2001, Brawn 2006). These Midwestern studies have only examined fire effects on the relative abundance of birds, and only Brawn (2006) examined nesting success; however, he did not study Prairie Warblers. More recently, Barrioz et al. (2013) and Vander Yacht et al. (2016) have reported on relative abundance and occupancy, respectively, of breeding bird communities in the context of restoration in the Mid-South. At Catoosa Wildlife Management Area (CWMA) specifically, these workers reported an increase in early-successional species' relative abundance (Barrioz et al. 2013) and occupancy (Vander Yacht et al. 2016) with minimal effects on late-successional species with increasing disturbance.

Many studies have estimated abundance and occupancy of disturbance-dependent species, but these parameters by themselves can be misleading indicators of habitat quality (Van Horne 1983, Vickery et al. 1992). Nest survival and productivity, alternatively, can be an effective means of evaluating influences of habitat on populations (Martin and Geupel 1993). For Prairie Warblers, nest studies have been conducted in Arkansas (Barber et al. 2001), Connecticut (Slay 2010, Askins et al. 2012), Florida (Prather and Cruz 1995), Indiana (Nolan 1963, 1978), Missouri (Annand and Thompson 1997, Woodward et al. 2001, Fink et al. 2006), and Massachusetts (Schlossberg et al. 2011, Akresh 2012), but none of these have been done in the context of oak savanna restoration. Several of these studies have examined the effects of silvicultural treatments (Annand and Thompson 1997, Barber et al. 2001) and mowing (Slay

2010, Schlossberg et al. 2011, Askins et al. 2012) on nesting Prairie Warblers, but few studies have involved fire (Woodward et al. 2001, Fink et al. 2006, Akresh 2012), and in those cases, fire was incidental and not part of the study design. Furthermore, vegetation features around the nest and in the surrounding stand can affect nest survival by influencing predation risk (Martin 1993), and few studies have included covariates to evaluate these effects (Slay 2010, Akresh 2012); moreover, these two studies were located on the northern extent of the Prairie Warbler's range. Some landscape-level work has been done (Schlossberg et al. 2011), but no studies have examined the influence of stand-level habitat metrics on nest survival of Prairie Warblers. If oak savanna restoration develops vegetation structure that increases nest survival of Prairie Warblers, it may become an important management strategy beneficial to this species' conservation.

Further study of the effects of oak woodland and savanna restoration on nesting songbirds is needed to determine the contribution of this management approach to population conservation of Prairie Warblers and associated disturbance-dependent bird species. Determining which factors specifically influence nest survival of a declining species is imperative to guide management and address population decline. Therefore, we examined nest survival of Prairie Warblers in the context of an oak savanna and woodland restoration experiment in Tennessee that began from closed-canopy conditions and included canopy reductions to savanna and woodland residual basal area targets, followed by repeated spring and fall burns to create a variety of vegetation conditions along the forest-to-savannah continuum. We hypothesized that Prairie Warblers would choose nest sites with less live basal area (LBA), and greater herbaceous groundcover and midstory density compared with the surrounding stand. We also hypothesized nest survival would be greatest in preferred nest sites. Through this study, we sought to

determine the impact of community restoration on Prairie Warbler daily nest survival and productivity.

Study Area

We conducted this study at the 32,374 ha CWMA in Cumberland County, Tennessee where site elevation ranged from 437–521 m with 1–39% slopes. Temperatures during May–August ranged from 13.6–27.4 °C (2015) and 12.4–29.8 °C (2016). Historical accounts and the growth of prairie and savanna flora support a history of oak savanna and woodlands on this site (Barrioz et al. 2013). Before experimental treatments began in 2008, dominant overstory species were white (*Quercus alba*), southern red (*Q. falcata*), black (*Q. velutina*), and scarlet (*Q. coccinea*) oaks, red maple (*Acer rubrum*), sourwood (*Oxydendrum arboreum*), and hickory (*Carya* spp.). Before a pine bark beetle (*Dendroctonus frontalis*) outbreak during 1999–2000, shortleaf pine (*Pinus echinata*) had been a common overstory component. Midstories were dominated by blackgum (*Nyssa sylvatica*), downy serviceberry (*Amelanchier arborea*), red maple, sourwood, and sassafras (*Sassafras albidum*). The ground-layer contained limited herbaceous vegetation and was composed primarily of blueberry (*Vaccinium* spp.), litter, and some woody plant regeneration. Average vegetation measurements in 2008, before restoration began, were 85% canopy cover, 17.8 m² ha⁻¹ LBA, 1,936 midstory stems ha⁻¹ (woody stems >1.37m tall, <12.7 cm diameter at breast height [DBH]), and 4.4% herbaceous groundcover (Vander Yacht et al. 2017). Late successional bird species (Ehrlich et al. 1988) were prevalent in the area prior to treatment, including Red-eyed Vireo (*Vireo olivaceus*), Ovenbird (*Seiurus aurocapilla*), Hooded Warbler (*Setophaga citrina*), Scarlet Tanager (*Piranga olivacea*), and Black-and-white Warbler (*Mniotilta varia*) (Barrioz et al. 2013). Only 6 Prairie Warbler detections were made in 2008 (Barrioz et al. 2013).

Beginning in 2008, an oak savanna and woodland experiment was initiated with 20-ha experimental units (stands) established in a completely randomized design. One of 5 treatments was assigned to each stand with two replicates of each treatment: control, fall burn with low residual basal area (savanna, 7.2 m² ha⁻¹; FaS), fall burn with high residual basal area (woodland, 14.4 m² ha⁻¹; FaW), spring burn with savanna residual basal area (SpS), and spring burn with woodland residual basal area (SpW). Logging was completed in summer 2008; burns occurred in October 2010, 2012, 2014 (fall) and March 2011, 2013, 2015 (spring).

Methods

Nest searching and monitoring

Nest searching and monitoring techniques were based on Martin and Geupel (1993). We searched for and monitored active nests of Prairie Warblers from 6 May to 15 July, 2015–2016. We monitored nests every 3–4 days until fledging or the nest was abandoned or destroyed. If nest height precluded direct observation, we used an extendable pole with a mirror to see nest contents. For each nest, we recorded the number of host eggs and young, Brown-headed Cowbird (*Molothrus ater*) eggs and young, date and time checked, and fate (failed or fledged). A nest was considered successful if ≥ 1 host nestling fledged. If the nest was found empty at the time of fledging and the nest was intact, we assumed the nest had fledged.

Vegetation sampling

We recorded Universal Transverse Mercator coordinates at nest locations using a handheld global positioning system (Garmin, eTrex 10, Olathe, Kansas). Vegetation at the nest was sampled using the same protocol as a restoration study conducted on the same study site (Vander Yacht et al. 2017), and a continuation of this study provided stand-level means.

Vegetation sampling at nests was conducted during early- to mid-July in both years, after the nesting attempt had been completed. Nest height and substrate species were recorded for each nest. Midstory density (number of saplings >1.37-m in height and <12.7-cm DBH) was recorded in five, 3-m radius plots surrounding the nest. One plot was centered on the nest, while the other four were located 12.5-m from the nest (plot center) and aligned based on topography (uphill, downhill, and parallel to the contour of the slope in opposite directions). We measured herbaceous vegetation composition and cover using two, 25-m point-intercept transects (Elzinga et al. 1998); the first running parallel and the second perpendicular to the prevailing slope, both centered on the nest site. Vegetation type <1-m tall was recorded at 1-m intervals along each transect. At plot center, we recorded live basal area using a 2.5 m² ha⁻¹ prism.

Analytical methods

We used program R 3.2.2 (R Development Core Team 2008) to complete a resource selection analysis ($\alpha = 0.05$) using Manly selection ratios (Manly et al. 2002) to compare used nest sites to available sites to determine which habitat variables were important in nest-site selection. Habitat variables examined in this analysis were midstory density (stems ha⁻¹), LBA (m² ha⁻¹), and herbaceous groundcover (%) based on the inclusion of these variables in a previous oak savanna restoration study that examined avian occupancy (Vander Yacht et al. 2016) and on their previously reported biological importance to Prairie Warblers (Nolan 1978, Slay 2010, Akresh 2012, Askins et al. 2012). Furthermore, these variable reflected key structural attributes associated with woodland and savanna restoration as it progressed from closed-canopy conditions.

We used the Mayfield nest survival model (Mayfield 1961) within Program MARK (White and Burnham 1999) to analyze nest survival. We developed candidate models that

included biological and habitat covariates and compared these models using estimates of effect size (β) and Akaike information criterion corrected for small sample size (AICc) to determine which model best ($\Delta\text{AICc} < 2$) explained variation in nest survival (Burnham and Anderson 2002). Treatments served as the foundation for creating a range of conditions on the oak savanna-oak forest continuum but were not included in the analysis because we were more interested in nest-vegetation connections. Additionally, due to variability in burn severity, vegetation within treatments was highly variable. Identifying optimum nesting condition within the restoration framework would yield more reliable recommendations for managers.

All covariates were tested for correlation using Person's correlation analysis prior to being used in the analysis, and if covariates were strongly correlated ($r > 0.6$), the variable that made the most biological sense was retained. All variables except for year were used in linear and quadratic form to detect possible thresholds that may have influenced nest survival. Initially, we evaluated temporal models with year and linear and quadratic day of season (day 1–70; 6 May–14 July) as covariates, both individually and interactively. Based on the top model ($\Delta\text{AICc} = 0$) from this step, we added nest- and stand-level habitat covariates (per year, corresponding to each nest) in linear and quadratic forms: midstory density, LBA, and herbaceous groundcover. We also added individual nest covariates in linear and quadratic forms: nest height (m) and nest age (days since start of laying). We further explored relationships among covariates by examining combinations of key variables with the top model from the previous step and retained covariates that improved model fit. Period survival was calculated based on 4 laying, 12 incubation, and 8 nestling days for a total of 24 nest exposure days (Nolan et al. 2014). Values presented in the Results section are means \pm SE.

Results

Stand-wide LBA across all treatments (not including controls) was $4.9 \pm 0.3 \text{ m}^2 \text{ ha}^{-1}$ in 2015 and $6.9 \pm 0.4 \text{ m}^2 \text{ ha}^{-1}$ in 2016. Herbaceous groundcover was $30.7 \pm 2.3\%$ in 2015 and $38.3 \pm 2.6\%$ in 2016. Midstory density was $6,002 \pm 650 \text{ stems ha}^{-1}$ in 2015 and $5,360 \pm 272 \text{ stems ha}^{-1}$ in 2016. Control stands, which were unoccupied by Prairie Warblers across both years, had LBA of $15.2 \pm 2.0 \text{ m}^2 \text{ ha}^{-1}$, herbaceous groundcover of $1.6 \pm 0.2\%$, and midstory density of $4,452 \pm 575 \text{ stems ha}^{-1}$.

Across two breeding seasons, we found a total of 107 nests (39 in 2015, 68 in 2016), which included monitoring of 1,180 exposure days. The difference in nests found between years can likely be attributed to yearly differences in abundance (0.8 ± 0.1 per ha in 2015; 1.7 ± 0.3 per ha in 2016) (Henderson 2017). Nesting season duration was 70 days, the earliest nest was found on 6 May, and the latest active nest day was 14 July. No nests were found in the closed-canopy control stands. Cowbird parasitism was detected at 5.6% of nests, and therefore, this factor was not included explicitly in the analysis. Only two (1.9%) nests were abandoned for unknown reasons and were not included in analysis, leaving 105 nests used in nest survival modeling. Prairie Warbler nest height was $1.5 \pm 1.2 \text{ m}$ ranging from 0-8.5 m. The average size for clutches that we could determine were completed was 3.6 ± 0.1 eggs. The average number of fledglings was 3.3 ± 0.1 . Productivity was 1.13 fledglings per nesting attempt.

Based on 107 nests, most (63.6%) were placed in red maple followed by blackberry (10.3%; *Rubus* spp.), perhaps a reflection of the prevalence of red maple (55.3% study-wide) within lower (groundlayer and midstory) strata. Birds built nests at sites with a range of LBA values ($0\text{--}25 \text{ m}^2 \text{ ha}^{-1}$) and did not demonstrate selectivity within this range in either year, although some selection for more open sites ($0\text{--}2.4 \text{ m}^2 \text{ ha}^{-1}$) was suggested in 2015 (Figure 1.1).

Birds selected against nest sites with limited (<15%) herbaceous groundcover in 2015 more than in 2016, and selected for sites with >45% groundcover in both years, but more strongly in 2015 than in 2016 (Figure 1.2). When comparing this information to abundance data from our concurrent study, Prairie Warblers were also most abundant at >45% herbaceous groundcover (Henderson 2017). Birds selected against nest sites with >8,500 stems ha⁻¹ in 2015 and 4,000–8,500 stems ha⁻¹ in 2016; selection for more midstory (>8,500 stems ha⁻¹) was suggested in 2016 (Figure 1.3). This selection against greater midstory density contrasts with our abundance study where Prairie Warblers were most abundant between 7,500 stems ha⁻¹ (Henderson 2017).

The model with year received the most support in explaining temporal variation in daily nest survival (Table 1.1). We found limited support for daily variation and, therefore, only retained yearly variation in subsequent models that incorporated habitat variables. The constant survival model was $\Delta\text{AICc} > 8$ from the top model (Table 1.2), so some variation in daily survival rate (DSR) was explained by our variables. The top nest survival model included herbaceous groundcover at the nest and year (Table 1.2, Figure 1.4). Despite being included within the top model, the 95% confidence interval for herbaceous groundcover marginally overlapped zero (Table 1.3). Nest survival tended to increase with groundcover each year (Figure 1.4). Yearly nest survival varied between years (Table 1.3). In the final set, 13 models had a $\Delta\text{AICc} < 2$ indicating these were comparable to the top model (Burnham and Anderson 2002). Variables in these models included herbaceous groundcover at the nest and stand, year the nest was found, nest age, LBA at the nest and stand, and nest height. However, when these variables were added to the top model, ΔAIC increased and the model received less support (Table 1.2). Herbaceous groundcover either at the nest or the stand was present in 11 of the top 13 models (Table 1.2). Daily nest survival based on the null model with constant survival was 0.937 ± 0.007

with a calculated period survival of 20.7%. Daily nest survival based on the top model for 2015 was 0.894 ± 0.018 with a calculated period survival of 6.8% and for 2016 was 0.954 ± 0.008 with a calculated period survival of 32.5%. Post hoc analysis was done to determine if the recent burn caused the lower nest survival in 2015. Modeling daily nest survival as varying by burn in 2015 but not in 2016 had a $\Delta AICc = 1.37$ when included in the model set. This shows some evidence that season of burn had an effect on nest survival in 2015 although confidence intervals overlapped. Likely, the late growing season burn in October 2014 had a similar effect on herbaceous vegetation as the March 2015 fire and groundcover was unable to recover from either, leading to lower Prairie Warbler nest survival. In 2015, spring burns had a daily survival rate of 0.873 ± 0.035 and fall burn survival rate was 0.904 ± 0.021 .

Discussion

Our study is the first to examine the relationships between oak savanna and woodland restoration on nest-site selection and nest survival of Prairie Warblers. Oak savanna and woodland restoration lead to an increase in the number of Prairie Warblers nesting at CWMA when compared with closed-canopy controls; no Prairie Warblers or nests were found in controls. Nest survival in this study was low in 2015, but across both years, was comparable to other studies performed in recently-disturbed areas (Annand and Thompson 1997: 21%, Barber et al. 2001: 16.5–20.5%, Akresh 2012: 36%). We believe that the reduced nest survival in 2015 was influenced by the impact of recent burns (October 2014 and March 2015) on the amount of cover on our study stands in spring 2015. Regardless, low nest survival in some years could be compensated for with high survival in other years (Askins et al. 2012). Also, Prairie Warblers have been known to double brood (Nolan 1978). Assuming a 100% renesting rate whether the first attempt was successful or not, a nest survival rate of 20.7% (this study's average), and 1.8

female young per nest, the average fecundity of 100 females would be 0.75 female young per year; the first and second attempt would yield a total of 41.4 nests, each yielding 1.8 female young based on our average clutch size of 3.6. Across two breeding seasons, replacement of adults would be exceeded. However, despite this estimate, nest survival was still highly variable between years. Oak savanna and woodland restoration habitat may be ideal habitat for increasing Prairie Warbler populations, but more extensive research is required to determine this conclusively. Furthermore, this study is about half-way through the restoration process when considering other ongoing restoration projects at CWMA.

Nest-site selection

Prairie Warblers did select for specific nest-sites in our study; sites with greater levels of herbaceous groundcover were preferred, especially in 2015, the year immediately following burning. Reduced woody cover during spring of 2015 may have increased the value of and, therefore, increased nest placement in areas with greater herbaceous cover. Selection of red-maple saplings for nesting substrate could be a perceived preference, however, and may reflect the availability of red maple saplings in the study areas; other Prairie Warbler nesting studies have also reported opportunistic selection of substrate species (Nolan 1978, Prather and Cruz 1995). The selection for herbaceous cover that we observed could be driven by the need to conceal nests from below. More likely, however, optimizing nestling and fledgling survival and fitness could be driving females to choose these locations as females have been found to make trips as short as 5–10 m during the late nestling stage (Nolan 1978). Furthermore, groundcover could play a role in visually obscuring fledglings from predators in their first few days out of the nest.

Across both years, Prairie Warblers were not consistently selective in relation to LBA and midstory density, perhaps because the range of conditions for these variables on our study area contained the levels preferred by this species (Nolan 1978). Prairie Warblers built nests at a variety of LBA and midstory densities across the study site, but were absent in the untreated controls that had the most LBA and thus, more canopy cover. In Massachusetts, contrary to our findings, preference was shown for nest sites with lesser canopy cover than random sites, and overall, those study sites had less average canopy cover than CWMA (Akresh 2012).

We had predicted selection for more stems and saplings closer to the nest than in the stand as whole because of the increased visual obscurity. However, during both years, birds showed some selection against greater sapling density. It is possible that Prairie Warblers could be selecting at a finer scale (i.e., <11.3-m radius plot) than we evaluated. For example, in shrubland with similar structure to our study site, Prairie Warblers demonstrated selection for more woody stems and structure within 2 m of the nest (Slay 2010, Akresh 2012). Additionally, the selection in regards to > 8500 stems ha⁻¹ flipped from selection against in 2015 to selection for this category in 2016. Possibly, the doubling of the Prairie Warbler abundance led individuals in 2016 to be pushed into less than ideal nesting habitat.

Nest survival

Daily survival rate was significantly less in 2015 than in 2016, a result that may have been influenced by burns completed prior to the breeding season in October 2014 and March 2015. Herbaceous groundcover was much more prevalent in 2016 than in 2015 due to the longer time to grow following the burn. This two-year pattern in groundcover recovery would likely continue after each subsequent burn. Additional years of information would help to determine if the year effect we observed was a result of that burn or other factors. Nest survival for 2015 was

less than reported from almost any other for this species and the lower abundance of Prairie Warblers in 2015 could be another reflection of the less ideal nesting habitat. Abundance estimates for Prairie Warbler on our study site between 2010 and 2016 seem to reinforce the pattern of reduced habitat quality during the growing season immediately following burning (2011 and 2015; we did not collect data in 2013) with greater abundance one year post-burning (2012, 2014, and 2016); mean abundance in each case were 0.56 ± 0.09 and 1.59 ± 0.32 birds ha⁻¹ (Henderson 2017). A similar pattern of Prairie Warbler exploitation of early successional habitat from one year to the next following site disturbance was observed by Keyser et al. (2001); they reported relative abundances that more than doubled from year 1 to year 2 following site harvest.

Despite Prairie Warblers selecting for nonrandom nest sites, nest survival was not strongly related to any of the habitat or nest covariates that we measured. Parameter estimates included zero for the only habitat variable (herbaceous groundcover) present in the top model. However, the beta estimate was positive and only marginally included zero; at $\alpha = 0.07$, the confidence bound would not have included zero. Furthermore, herbaceous groundcover at the nest and stand were in almost all models with $\Delta AICc < 2$. Greater herbaceous cover was the result of increased disturbance levels, such as thinning and burning, as in our study (Vander Yacht et al. 2017), and was associated with an increase in nest survival. In contrast, a Missouri study, with similar levels of LBA and herbaceous groundcover to CWMA, found nest survival was lowest in shrubland edge habitat where herbaceous groundcover and LBA were higher when compared with glades (Fink et al. 2006). However, this lowered nest success could have been due to being an edge where higher predation is more likely (Wilcove et al. 1986, Yahner 1988, Askins 1994). Slay (2010) found that increased woody stem cover from 75–100 cm in height increased nest

survival, likely due to concealment of the nest, and is similar to what taller herbaceous groundcover could provide.

Management techniques such as those we examined, and subsequent changes in habitat structure, can change predator communities enough to influence nest survival (Thompson 2007). Predation was the leading cause of nest failure in our study, but we were not able to determine which predator species were responsible. The predator community in oak savannas and woodlands should be further studied as this could be a driving factor in both nest-site selection and survival and could be complex.

Height of the nest was in our top set of models, but only when included with both herbaceous groundcover at the nest and year. Including height increased total AIC for the top model ($\Delta AICc = 1.26$) and contrary to what we predicted, was not found to influence nest survival. Many studies have found effects of height on nest survival of passerines (e.g., Akresh 2012, Kendrick et al. 2013) but as with our study, others have not found such a connection (e.g., Howlett and Stutchbury 1996, Schlossberg et al. 2011, Roach 2016). Furthermore, the age of the nest and day of season did not influence nest survival, contrary to other studies (Nolan 1978, Slay 2010, Akresh 2012).

Although nest- and stand-level LBA were within 2 ΔAIC of the top model, they did not have a strong influence on nest survival, contrary to what other researchers have found (Barber et al. 2001, Fink et al. 2006). In shrubland habitat, Prairie Warbler density and nest survival were lowest in edge habitat where LBA was higher ($\sim 5 \text{ m}^2 \text{ ha}^{-1}$) when compared with glades and regenerating forests ($\sim 2.5 \text{ m}^2 \text{ ha}^{-1}$; $\sim 0.5 \text{ m}^2 \text{ ha}^{-1}$) (Fink et al. 2006). In an evaluation of silvicultural treatments in pine stands across the southeastern U.S., Prairie Warbler nest survival was greater (20.5%) in thinned stands ($8.5 \text{ m}^2 \text{ ha}^{-1}$ LBA) than stands that were regenerating after

clearcutting (15.8% survival and $\sim 2.0 \text{ m}^2 \text{ ha}^{-1}$ LBA) (Barber et al. 2001). Barber et al. (2001) attributed this difference to the greater prey density and structural diversity present in the clearcut stands which supported greater numbers of predators.

Contrary to our results with midstory density, others have found a positive association between survival and more structure around the nest. Prairie Warblers selected for greater vegetative structure within 1.5 m of the nest, which resulted in improved nest survival in a study in Connecticut (Akresh 2012). In that same study, increased visibility resulted in decreased nest survival. In another study in New England, Prairie Warblers selected for more woody stems within 2–4 m of the nest, which resulted in higher nest survival, possibly as a result of increased fatigue of nest predators while searching (Slay 2010).

Nest survival was only minimally influenced by the stand and nest-level variables we measured suggesting that, to some extent, the predator community was complex, or there were other determining factors that we did not evaluate. Nest survival may be better explained by landscape-level factors or abundance of nest predators than by nest-site or stand-level habitat characteristics (Rodewald and Yahner 2001, Thompson 2007). In areas with a diverse predator community and therefore, diverse prey searching techniques, nest-site habitat structure may be less critical (Filliater et al. 1994). We observed snakes, American Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), Eastern chipmunks (*Tamias striatus*), and southern flying squirrels (*Glaucomys volans*) in our study area, all of which could have contributed to nest depredation. American Crow and Blue Jay, both common nest predators on our study area, did not show a preference between disturbed and undisturbed sites in midwestern studies (Annand and Thompson 1997, Brawn 2006), but in our system, where LBA was low, Blue Jays were less abundant and American Crows more abundant (C. Henderson, unpublished

data). Several studies of shrub and grassland species have failed to find a relationship between nest survival and nest-site selection (Filliater et al. 1994, Davis 2005, Bulluck and Buehler 2008) leading to the hypothesis that instead of nest survival, nesting birds could be selecting for sites that improve fledgling survival (Streby et al. 2014). It may be that the cost of renesting for Prairie Warblers is lower when the nest fails than if fledgling mortality is high (Farnsworth and Simons 2001).

Fully restored oak savannas and woodlands are not as ideal for scrub-shrub nesting species such as the Prairie Warbler due to reduced woody stem density. However, the transitional state common during the process of restoration can provide preferred habitat for nesting and foraging, despite being temporary. On the other hand, early-successional species are adapted to exploiting ephemeral patches within a landscape, a fact reinforced by the biennial burning-abundance pattern observed on our study area (Henderson 2017). Ideally, burning could be done in a patchwork pattern to offset the less productive breeding years. Another alternative to mitigate impacts to productivity associated with biennial burns is to slightly extend time between burns. Given the need to suppress woody encroachment during restoration, this may not be a viable option, but could be considered on a case-by-case basis. In this particular study site, nest survival was comparable to other Prairie Warbler studies (on average, across years) and was not strongly influenced by nest- or stand-level habitat variables. Further research is needed to determine influences of landscape and predator communities on survival of Prairie Warblers. Further studies will need to be conducted across the range of historical oak savannas to explore shrubland species nest and fledgling survival in these early successional habitats as predator community, landscape-level factors, and vegetation characteristic can be vastly different.

Literature Cited

- Akresh, M. E. (2012). Prairie Warbler nest-site selection, nest survival, and demographic response to management in a pitch pine-scrub oak barren. Thesis.
- Annand, E. M., and F. R. Thompson (1997). Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61:159–171.
- Artman, V. L., T. F. Hutchinson, and J. D. Brawn (2005). Fire ecology and bird populations in eastern deciduous forests. *Studies in Avian Biology* 30:127–138.
- Artman, V. L., E. K. Sutherland, and J. F. Downhower (2001). Prescribed burning to restore mixed-oak communities in southern Ohio: Effects on breeding-bird populations. *Conservation Biology* 15:1423–1434.
- Askins, R. A. (1994). Open corridors in a heavily forested landscape: Impact on shrubland and forest-interior birds. *Wildlife Society Bulletin* 22:339–347.
- Askins, R. A. (1999). History of grassland birds in eastern North America. *Studies in Avian Biology* 19:60–71.
- Askins, R. A. (2002). Restoring North America's birds: Lessons from landscape ecology. In 2nd ed. Yale University Press.
- Askins, R. A., C. M. Folsom-O'Keefe, and M. C. Hardy (2012). Effects of vegetation, corridor width and regional land use on early successional birds on powerline corridors. *PLoS ONE* 7.
- Barber, D. R., T. E. Martin, M. A. Melchior, R. E. Thill, and T. B. Wigley (2001). Nesting success of birds in different silvicultural treatments in southeastern U.S. pine forests. *Conservation Biology* 15:196–207.
- Barrioz, S., P. Keyser, D. Buckley, D. Buehler, and C. Harper (2013). Vegetation and avian

- response to oak savanna restoration in the Mid-South USA. *The American Midland Naturalist* 169:194–213.
- Brawn, J. D. (2006). Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20:460–469.
- Brawn, J. D., S. K. Robinson, and F. R. Thompson (2001). The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32:251–276.
- Bulluck, L. P., and D. A. Buehler (2008). Factors influencing Golden-winged Warbler (*Vermivora Chrysoptera*) nest-site selection and nest survival in the Cumberland mountains of Tennessee. *The Auk* 125:551–559.
- Burnham, K. P., and D. R. Anderson (2002). Model selection and multimodal inference. In 2nd edition. Springer, Verlag, New York.
- Davis, S. K. (2005). Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *American Ornithological Society* 107:605–616.
- Davis, D. W. Peterson, P. B. Reich, M. Crozier, T. Query, E. Mitchell, J. Huntington, and P. Bazakas (2000). Restoring savanna using fire: Impact on the breeding bird community. *Restoration Ecology* 8:30–40.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye (1988). The birder's handbook: a field guide to the natural history of North American birds. In. Simon & Schuster, New York, New York, USA.
- Elzinga, C. L., D. W. Salzer, and J. W. Willoughby (1998). Measuring and monitoring plant populations. Bureau of Land Management Technical Reference.
- Farnsworth, G. L., and T. R. Simons (2001). How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. *The Auk* 118:9.

- Filliater, T. S., R. Breitwisch, and P. M. Nealen (1994). Predation on Northern Cardinal nests: Does choice of nest-site matter. *Condor* 96:761–768.
- Fink, A. D., F. R. Thompson, and A. A. Tudor (2006). Songbird use of regenerating forest, glade, and edge habitat types. *Journal of Wildlife Management* 70:180–188.
- Gram, W. K., P. A. Porneluzi, R. L. Clawson, J. Faaborg, and S. C. Richter (2003). Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conservation Biology* 17:1324–1337.
- Grant, T. A., T. L. Shaffer, E. M. Madden, and G. B. Berkey (2011). Ducks and passerines nesting in northern mixed-grass prairie treated with fire. *Wildlife Society Bulletin* 35:368–376.
- Greenberg, C. H., T. a. Waldrop, J. Tomcho, R. J. Phillips, and D. Simon (2013). Bird response to fire severity and repeated burning in upland hardwood forest. *Forest Ecology and Management* 304:80–88.
- Henderson, C. (2017). Avian ecology in an oak savanna and woodland restoration framework in the Mid-South. Thesis.
- Howlett, J. S., and B. J. Stutchbury (1996). Nest concealment and predation in Hooded Warblers: Experimental removal of nest cover. *The Auk* 113:1–9.
- Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel (2001). Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29:440–455.
- Kendrick, S. W., F. R. Thompson, and J. L. Reidy (2013). Eastern Wood-Pewee (*Contopus virens*) breeding demography across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *The Auk* 130:355–363.

- Keyser, P.D., J.D. Lanham, and V.L. Ford. 2011. Songbird breeding season use of pine plantations treated chemically for herbaceous vegetation control. *Journal of Fish and Wildlife Management* 2:99–105.
- Manly, B. F., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson (2002). Resource selection by animals: statistical analysis and design for field studies. In. Kluwer, Nordrecht, The Netherlands.
- Martin, T. E. (1993). Nest predation among vegetation layers and habitat types: Revising the dogmas. *American Naturalist* 141:897–913.
- Martin, T. E., and G. R. Geupel (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- Mayfield, H. F. (1961). Nesting success calculated from exposure. *The Wilson Bulletin* 73:255–261.
- Nolan, V. (1963). Reproductive success of birds in a deciduous scrub habitat. *Ecology* 44:305–313.
- Nolan, V. (1978). The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). *Ornithological Monographs* 26.
- Nolan, V., E. D. Ketterson, and C. A. Buerkle (2014). Prairie Warbler (*Setophaga discolor*). In *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott (1995). Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. National Biological Service, Biological Report 28. U.S. Department of the Interior, Washington, D.C., USA.:83.
- Nuzzo, V. (1986). Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6:6–36.

- Prather, J. W., and A. Cruz (1995). Breeding biology of Florida Prairie Warblers and Cuban Yellow Warblers. *The Wilson Bulletin* 107:475–484.
- R Development Core Team (2008). A language and environment for statistical computing. [Online.] Available at <http://www.r-project.org/>.
- Reidy, J. L., F. R. Thompson, and S. W. Kendrick (2014). Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *Forest Ecology and Management* 313:34–46.
- Roach, M. C. (2016). Breeding bird response to pine-savanna and woodland restoration in the Ozark-Ouachita interior highlands.
- Rodewald, A., and R. Yahner (2001). Avian nesting success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *The Auk* 118:1018–1028.
- Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Fprd, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, et al. (2016). *Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States*.
- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski (2013). The North American breeding bird survey 1966–2011: summary analysis and species accounts. *North American Fauna* 79:1–32.
- Schlossberg, S., D. I. King, and R. B. Chandler (2011). Effects of low-density housing development on shrubland birds in western Massachusetts. *Landscape and Urban Planning* 103:64–73.
- Slay, C. M. (2010). An evaluation of reproductive success, adult survivorship and habitat use of

- shrubland birds on conservation-managed fields in western Connecticut.
- Southwell, D. K. (2001). Conservation assessment for Prairie Warbler (*Dendroica discolor*).
USDA Forest Service.
- Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Andersen (2014). Retirement investment theory explains patterns in songbird nest-site choice. *Proceedings. Biological sciences / The Royal Society* 281:20131834.
- Thompson, F. R. (2007). Factors affecting nest predation on forest songbirds in North America. *Ibis* 149:98–109.
- Tucker, J. W., W. D. Robinson, and J. B. Grand (2006). Breeding productivity of Bachman's Sparrows in fire-managed longleaf pine forests. *The Wilson Journal of Ornithology* 118:131–137.
- Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- Vickery, P. D., M. L. Hunter Jr., and J. V. Wells (1992). Is density an indicator of breeding success? *The Auk* 109:706–710.
- White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*.
- Wilcove, D. S., C. H. McLellan, and A. P. Dobson (1986). Habitat fragmentation in the temperate zone. *Conservation Biology: The Science of Scarcity and Diversity*.
- Woodward, A. A., A. D. Fink, and F. R. Thompson (2001). Edge effects and ecological traps: Effects on shrubland birds in Missouri. *Journal of Wildlife Management* 65:668–675.
- Vander Yacht, A. L., S. A. Barrioz, P. D. Keyser, C. A. Harper, D. S. Buckley, D. A. Buehler, and R. D. Applegate (2017). Vegetation response to canopy disturbance and season of burn

during oak woodland and savanna restoration in Tennessee. *Forest Ecology and Management* 390:187–202.

Vander Yacht, A. L., P. D. Keyser, D. A. Buehler, C. A. Harper, D. S. Buckley, and R. D. Applegate (2016). Avian occupancy response to oak woodland and savanna restoration. *Journal of Wildlife Management* 80:1091–1105.

Yahner, R. H. (1988). Changes in wildlife communities near edges. *Conservation Biology* 2:333–339.

Appendix A

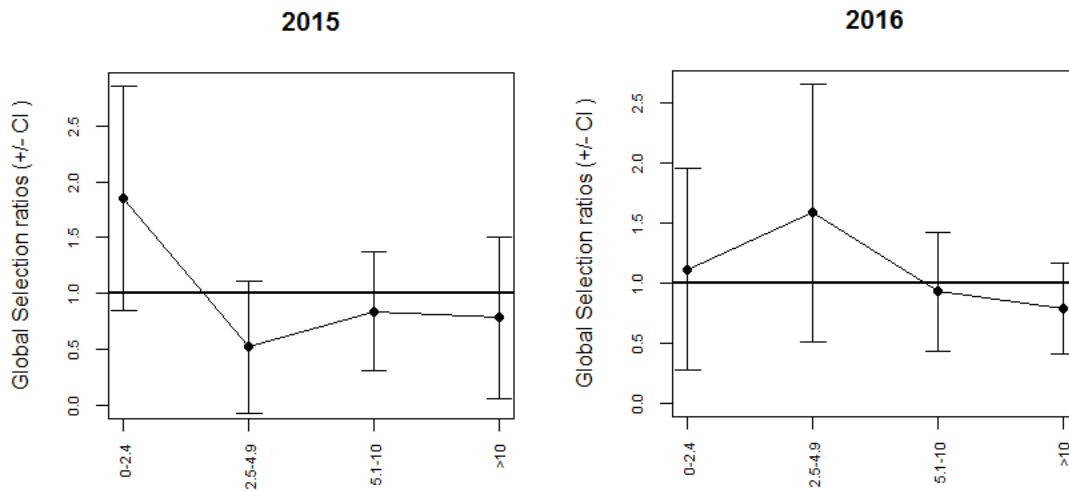


Figure 1.1 Manly selection ratios for live basal area (m² ha⁻¹) comparing used and available habitat for nest sites during a Prairie Warbler nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

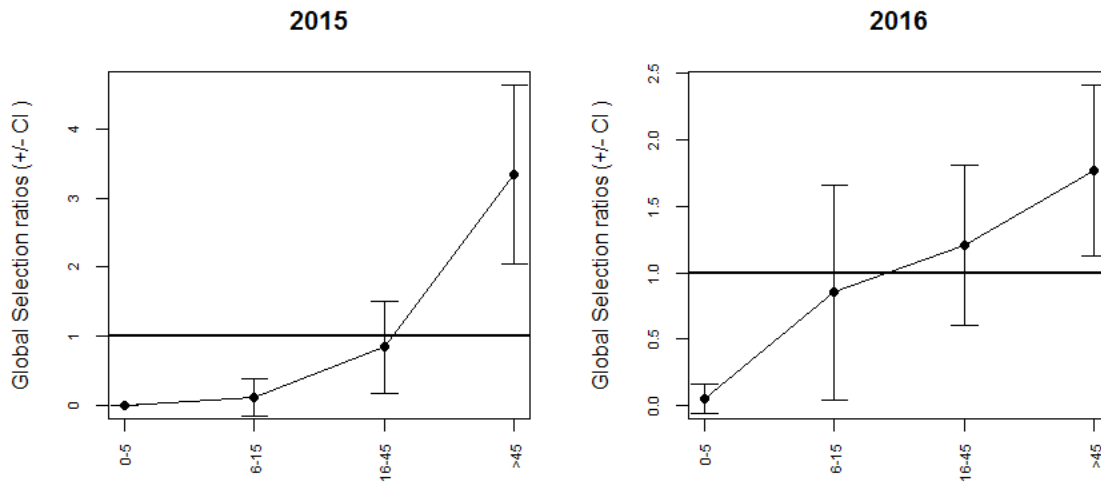


Figure 1.2 Manly selection ratios for herbaceous groundcover (%) comparing used and available habitat for nest sites during a Prairie Warbler nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

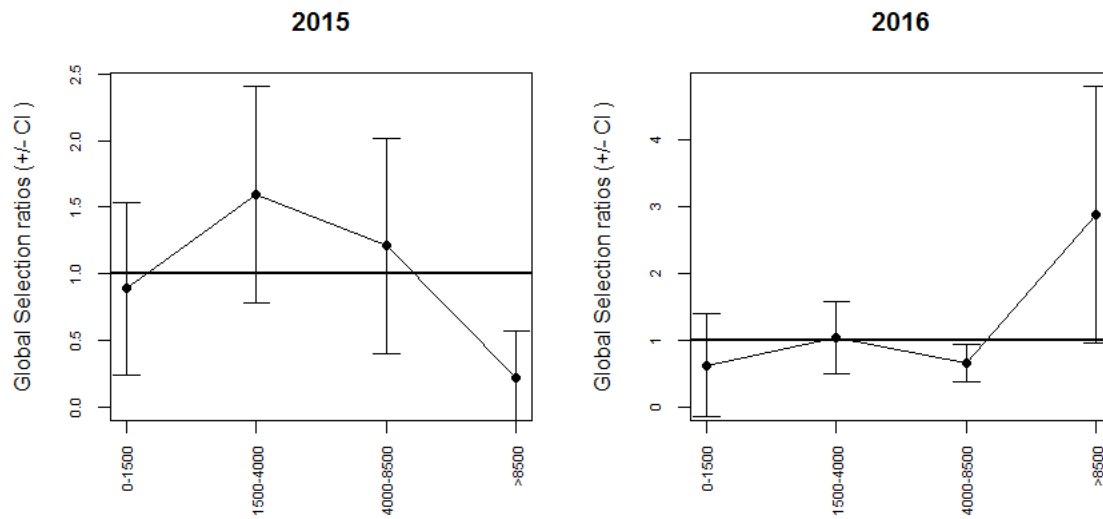


Figure 1.3 Manly selection ratios for midstory density (stems ha⁻¹) comparing used and available habitat for nest sites during a Prairie Warbler nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

Table 1.1 Ranking of temporal models used in Prairie Warbler nest survival analysis at Catoosa Wildlife Management Area, Tennessee, 2015–2016. Covariates included, Year (2015 or 2016) and Day (Julian day of the season).

Model	K ^a	AICc	ΔAICc	wi ^b
S(Year)	2	339.45	0	0.39
S(Year+Day+Day ²)	4	339.65	0.20	0.35
S(Year+Day)	3	341.39	1.94	0.15
S(Year*Day)	4	342.91	3.46	0.07
S(Day+Day ²)	3	345.93	6.48	0.02
S(.)	1	346.00	6.55	0.01
S(Day)	2	346.78	7.32	0.01

^a Number of parameters

^b Model weight

Table 1.2 Top model ($\Delta AICc < 2$) results and null model from final model set for Prairie Warbler nest survival at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

Model	K ^a	AICc	$\Delta AICc$	wi ^b
S(Herb ^a +Year ^b)	3	337.91	0	0.10
S(Herb+Age ^c +Year)	4	338.21	0.30	0.08
S(Herb * Year)	4	338.73	0.82	0.06
S(LBA_ST ^d +LBA_ST ² +Year)	4	338.85	0.94	0.06
S(Herb+Herb ² +Year)	4	338.86	0.96	0.06
S(Herb+Herb_ST ^e +Herb_ST ² +Year)	5	338.93	1.02	0.06
S(Herb_ST+Herb_ST ² +Year)	4	339.11	1.20	0.05
S(Herb+Height ^f +Year)	4	339.17	1.26	0.05
S(Year)	2	339.45	1.55	0.05
S(Herb+Herb_ST+Year)	4	339.48	1.57	0.04
S(Year+Day+Day ²)	4	339.65	1.74	0.04
S(Herb_ST+Year)	3	339.75	1.85	0.04
S(Herb+LBA ^g +Year)	4	339.83	1.93	0.04
S(.)	1	346	8.094	0

^a Number of parameters

^b Model weight

^c Herbaceous groundcover at the nest (%)

^d Year during which nest was found

^e Nest age (days)

^f Live basal area from stand in which nest was located (m² ha⁻¹)

^g Herbaceous groundcover from stand in which nest was located (%)

^h Height from ground to nest cup rim (cm)

ⁱ Live basal area within 11.3 m of nest (m² ha⁻¹)

Table 1.3 Beta estimates from the top model from a Prairie Warbler nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

Parameter	β	SE	Lower CI (95%)	Upper CI (95%)
Intercept	1.6310	0.35888	0.92870	2.33550
Year	0.90404	0.26843	0.37791	1.45017
Herbaceous Groundcover (%)	0.96144	0.51151	-0.04113	1.96400

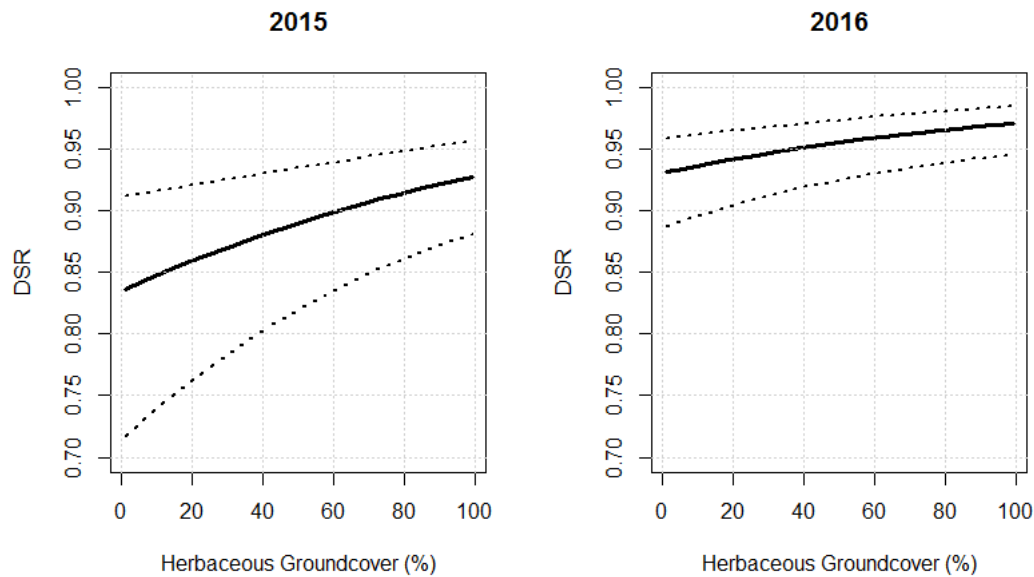


Figure 1.4 Daily survival rate (DSR) and herbaceous groundcover (%) relationship from the top model from a Prairie Warbler nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

**2. RED-HEADED WOODPECKER NEST-SITE SELECTION AND NEST
SURVIVAL DURING OAK SAVANNA AND WOODLAND
RESTORATION IN THE MID-SOUTH**

Abstract

Disturbance-dependent bird species, such as the Red-headed Woodpecker (*Melanerpes erythrocephalus*), have declined more than any other bird guild since 1966, likely due to a reduction in open, disturbed habitats such as oak savannas. At Catoosa Wildlife Management Area located near Crossville, Tennessee, restoration of oak savannas has been ongoing since 2008 with selective logging leaving low, savanna (7.2 m² ha⁻¹) or high, woodland (14.4 m² ha⁻¹) residual basal areas, and biennial burning implemented in either spring or fall. We monitored 47 Red-headed Woodpecker nests during 2015 and 2016. Vegetation data was collected around the nest (11.3-m radius) after success or failure and in the surrounding stands in a concurrent study. When compared with available habitat, Red-headed Woodpeckers selected nest sites that had greater herbaceous groundcover (>45% herbaceous groundcover in 2015 with a similar trend suggested in 2016), and dead basal area (>2.5 m² ha⁻¹ DBA in 2015 and 2016). Woodpeckers tended to select sites with < 8,500 stems ha⁻¹ in 2015 and > 8,500 stems ha⁻¹. Daily nest survival did not vary by year and was very high (0.996 ± 0.003) compared with other studies. Our top model included live basal area around the nest (negative), and quadratic DBH of the nesting tree (positive), but beta coefficients overlapped zero. In the case of live basal area around the nest, beta coefficient confidence bounds would not have included zero at $\alpha = 0.08$. Lower levels of live basal area lead to less clutter around the nest, possibly allowing for greater maneuverability and less visual obscurity to protect the nest from predators. No other habitat covariates were supported in our nest survival models. Red-headed Woodpecker nest survival was high enough that habitat covariates may have been unable to conclusively explain the limited variation in daily nest survival. Increased efforts to restore oak savannas and woodlands in the Mid-South

could create additional foraging and nesting habitat for this species and contribute to population recovery goals.

Introduction

The Red-headed Woodpecker (*Melanerpes erythrocephalus*) is considered an oak-savanna obligate and is prevalent across the eastern and central United States (Frei et al. 2017). Despite having such a large range, Red-headed Woodpeckers have been declining 2.35% annually, range-wide since 1966, and are the fastest declining cavity nester surveyed by the North American Breeding Bird Survey (Askins 1999, Hunter et al. 2001, Sauer et al. 2013). Furthermore, Partners in Flight lists Red-headed Woodpecker as a species of continental concern (Rosenberg et al. 2016). Red-headed Woodpeckers depend on disturbed areas, such as oak-savannas and woodlands, for foraging and breeding, and without disturbance, Red-headed Woodpeckers are at risk of continued declines (Davis et al. 2000, Hunter et al. 2001, Brawn 2006, Reidy et al. 2014).

Before European settlement, disturbance-dependent ecosystems, including savannas and open forest communities, were prevalent across the eastern United States (Nuzzo 1986, Askins 2002). Since European settlement, savannas and woodlands have almost been completely eliminated throughout the US and are considered critically imperiled ecosystems (Noss et al. 1995). For instance, it has been estimated that only about 0.02% of oak savannas now remain of the original 11–13 million ha that had occurred within the Midwestern USA (Nuzzo 1986). Disturbance, including fire and thinning, is essential for keeping these open areas from succeeding to closed-canopy forest (Davis et al. 2000, Brawn et al. 2001, Hunter et al. 2001, Artman et al. 2005). Reintroduction of fire and canopy thinning have been used to restore these open-canopy communities (Barrioz et al. 2013, Vander Yacht et al. 2017) and can increase

preferred habitat for Red-headed Woodpeckers, therefore contributing to the conservation of this species and mitigation of their population decline (Gram et al. 2003, Artman et al. 2005).

However, oak savanna and woodland restoration needs to be evaluated to determine the extent of the response by Red-headed Woodpeckers to this potential breeding habitat.

Abundance and occupancy are important considerations when evaluating species-habitat relationships, but can be misleading indicators of habitat quality (Van Horne 1983, Vickery et al. 1992). Therefore, we examined Red-headed Woodpecker nest survival and productivity, which provide an effective means of evaluating influences of habitat on populations (Martin and Geupel, 1993). Factors influencing Red-headed Woodpecker nest survival have not been well documented and many past studies have been conducted on the northern periphery of their range, where population declines are most pronounced (Frei et al. 2013, 2015; Hudson and Bollinger 2013, Berl et al. 2014). Furthermore, Red-headed Woodpecker studies that have addressed nesting have been conducted primarily in the Midwest (Jackson 1976, Rodewald et al. 2005, Vierling and Lentile 2006, King et al. 2007) or other areas with very different landscape contexts than the Mid-South (Conner 1976; Frei et al. 2013, 2015, Berl et al. 2014, 2015). Studies conducted within savannas and/or woodlands (Vierling and Lentile 2006, King et al. 2007, Berl et al. 2014, 2015) have been limited to areas that had already been restored or were intact and had open canopies and well-developed herbaceous groundlayers.

To address these issues, we examined nest survival and productivity of Red-headed Woodpeckers in the context of an oak savanna and woodland restoration experiment in Tennessee that had begun with a closed-canopy system. The study area was manipulated with logging to reduce residual basal area to savanna and woodland targets and biennial burning, either in spring or fall. We hypothesized that Red-headed Woodpeckers would choose nest sites

with lower amounts of live basal area (LBA), and greater amounts of dead basal area (DBA), herbaceous groundcover, and midstory density compared with the conditions available in the surrounding stand. We also hypothesized woodpecker nest survival would be greatest in habitat that was selected most often for nest-sites. Through this study, we hoped to identify ranges of habitat conditions associated with oak savanna and woodland restoration that could contribute to enhanced Red-headed Woodpecker daily nest survival and productivity. This information could inform targets for land managers seeking to contribute to Red-Headed Woodpecker conservation.

Study Area

We conducted this study at the 32,374 ha Catoosa Wildlife Management Area (CWMA) in Cumberland County, Tennessee where site elevation ranged from 437–521 m with 1–39% slopes. Temperature range for May–August of 2015 and 2016 were 13.6–27.4 °C and 12.4–29.8 °C, respectively. Historical accounts and the growth of prairie and savanna flora soon after implementation of salvage cutting and fire support a history of oak savanna and woodlands for this site (Barrioz et al. 2013). Before experimental treatments began in 2008, dominant overstory species were white (*Quercus alba*), southern red (*Q. falcata*), black (*Q. velutina*), and scarlet (*Q. coccinea*) oaks, red maple (*Acer rubrum*), sourwood (*Oxydendrum arboreum*), and hickory (*Carya* spp.). Before a pine bark beetle (*Dendroctonus frontalis*) outbreak during 1999–2000, shortleaf pine (*Pinus echinata*) was a typical feature of the forest. Midstories were dominated by blackgum (*Nyssa sylvatica*), downy serviceberry (*Amelanchier arborea*), red maple, sourwood, and sassafras (*Sassafras albidum*). The ground-layer contained low amounts of herbaceous vegetation, but primarily was comprised of blueberry (*Vaccinium* spp.), litter, and some woody plant regeneration. Average vegetation measurements in 2008 before restoration began were 85% canopy cover, 17.8 m² ha⁻¹ LBA, 3.9 m² ha⁻¹ DBA, 1,936 midstory stems ha⁻¹ (woody stems

>1.37m tall, <12.7 cm diameter at breast height [DBH]), and 4.4% herbaceous groundcover (Vander Yacht et al. 2017). Mature forest-associated bird species (Ehrlich et al. 1988) were prevalent in the area prior to treatment, including Red-eyed Vireo (*Vireo olivaceus*), Ovenbird (*Seiurus aurocapilla*), Hooded Warbler (*Setophaga citrina*), Scarlet Tanager (*Piranga olivacea*), and Black-and-white Warbler (*Mniotilta varia*) (Barrioz et al. 2013). However, only three Red-headed Woodpeckers detections were detected in 2008 (Barrioz et al. 2013).

Beginning in 2008, an oak savanna and woodland experiment was initiated, with 20-ha experimental units (stands) established in a completely randomized design with two replicates each. One of 5 treatments was assigned to each stand: control, fall burn with a low, savanna (7.2 m² ha⁻¹) residual basal area, fall burn with a high, woodland (14.4 m² ha⁻¹) residual basal area, spring burn with savanna residual basal area, and spring burn with woodland residual basal area. Logging was completed in summer 2008; burns occurred in October 2010, 2012, 2014 (fall) and March 2011, 2013, 2015 (spring).

Methods

Nest searching and monitoring

We searched for and located active nests of Red-headed Woodpecker from 5 May to 17 July, 2015–2016 using parental behavior cues following Martin and Geupel (1993). Adult woodpeckers would be observed and followed to determine if they had an active nest in the area. Once located, we monitored nests every 3–5 days until fledging or failure by predation. We attached a wireless, conical, color camera (229 RCW Backpack System, Environmental Management Systems, Canton, Georgia) to the top of a modified E-50 Hastings pole (Hastings, MI) and placed the camera in the nesting hole to monitor the stage, clutch size, and number of

nestlings of nests for which height did not exceed the reach of our pole (15.2 m). After hatching, we monitored the nests using the camera system and/or visual cues, such as parents entering the nesting hole or carrying food. Fledging was assumed when there was no activity at the nest, fledglings were seen nearby, and/or the nest was empty at the time of fledging. If a nest was thought to be predated, we placed the camera in the nesting hole to confirm, if possible. For each nest, we recorded the number of eggs and young, date and time checked, as well as any comments about adult behavior and if there were anything notable about the state of the nest if it had failed or fledged.

Vegetation sampling

We recorded Universal Transverse Mercator coordinates at nest locations using a handheld global positioning system (Garmin, eTrex 10, Olathe, Kansas). Vegetation at the nest site was sampled using the same protocol as a restoration study conducted on the same study site (Vander Yacht et al. 2017), and a continuation of this study provided stand-level means. Vegetation sampling at nest sites was conducted after the nesting attempt had been completed. Midstory density (number of saplings >1.37 m tall and <12.7-cm DBH) was recorded in five, 3-m radius plots surrounding the nest. One plot was centered on the nest, while the other four were located 12.5 m from the nest (plot center) and aligned based on topography (uphill, downhill, and parallel to the slope contour in opposite directions). We measured herbaceous vegetation composition and cover using two, 25-m point-intercept transects (Elzinga et al. 1998); the first running parallel and the second perpendicular to the prevailing slope, both centered on the nest site. Vegetation <1 m tall was recorded at 1-m intervals along each transect. At plot center, we recorded LBA and DBA using a 2.5 m² ha⁻¹ prism. We recorded height of the nest cavity using an E-50 Hastings pole (Hastings, MI), as well as species and DBH of the nest tree.

Analytical methods

We used program R 3.2.2 (R Development Core Team 2008) to conduct a resource selection analysis ($\alpha = 0.05$) using Manly selection ratios (Manly et al. 2002) to compare used nest sites to available sites to determine which factors were important in nest-site selection. Habitat variables examined in this analysis were midstory density (stems ha^{-1}), LBA($\text{m}^2 \text{ha}^{-1}$), DBA($\text{m}^2 \text{ha}^{-1}$), and herbaceous groundcover (%) based off of the use of these variables in a previous oak savanna restoration study (Vander Yacht et al. 2016) and on their importance to Red-headed Woodpeckers (Frei et al. 2013, Hudson and Bollinger 2013, Berl et al. 2014).

We used the Mayfield nest survival model (Mayfield 1961) within Program MARK (White and Burnham 1999) to analyze nest survival. We compared candidate models using estimates of effect size (β) and Akaike information criterion corrected for small sample size (AICc) to determine which best ($\Delta\text{AICc} < 2$) for explained variation in nest survival (Burnham and Anderson 2002). Treatments served as the foundation for creating a range of conditions on the oak savanna-oak forest continuum but were not included in the analysis because we were more interested in nest-vegetation connections. Additionally, due to variability in burn severity, vegetation within treatments was highly variable. Identifying optimum nesting condition within the restoration framework would yield more reliable recommendations for managers.

All covariates were tested for correlation prior to being used in the analysis, and if covariates were strongly correlated ($r > 0.6$), the variable that made the most biological sense was used. All variables except for year were used in linear and quadratic form to detect possible thresholds that may have influenced nest survival. The initial step included evaluating temporal models using year and linear and quadratic day of season (day 1–111; 8 May–26 August), as well as year and day interaction. Based on the top model ($\Delta\text{AICc} = 0$) from this step, we added

nest- and stand-level habitat covariates in linear and quadratic forms: midstory density, LBA, DBA, and herbaceous groundcover. We also added nest-specific variables: nest tree DBH (cm), nest cavity height (m), and nest age (days since start of laying). We further explored relationships among covariates by examining combinations of key variables with the top model from the previous step and kept covariates in that improved the model fit. Period survival was calculated based on 5 laying, 12 incubation, and 27 nestling days for a total of 44 days (Frei et al. 2017). Values presented in the Results section are means \pm SE.

Results

Stand-wide LBA across all treatments (not including controls) was $4.9 \pm 0.3 \text{ m}^2 \text{ ha}^{-1}$ in 2015 and $6.9 \pm 0.4 \text{ m}^2 \text{ ha}^{-1}$ in 2016. Herbaceous groundcover was $30.7 \pm 2.3\%$ in 2015 and $38.3 \pm 2.6\%$ in 2016. Midstory density was $6,002 \pm 650 \text{ stems ha}^{-1}$ in 2015 and $5,360 \pm 272 \text{ stems ha}^{-1}$ in 2016. DBA was $2.6 \pm 0.2 \text{ m}^2 \text{ ha}^{-1}$ in 2015 and $2.5 \pm 0.2 \text{ m}^2 \text{ ha}^{-1}$ in 2016. Controls stands, which were unoccupied by Red-headed Woodpeckers across both years, had LBA of $15.2 \pm 2.0 \text{ m}^2 \text{ ha}^{-1}$, DBA of $1.9 \pm 0.2 \text{ m}^2 \text{ ha}^{-1}$, herbaceous groundcover of $1.59 \pm 0.20\%$, and midstory density of $4,452 \pm 575 \text{ stems ha}^{-1}$.

Across two breeding seasons, 47 nests were located and used in the analysis (21 in 2015, 26 in 2016), yielding 1,308 exposure days. Abundance of Red-headed Woodpeckers was not proportionate to the number of nests found (0.4 ± 0.1 per ha in 2015 and 1.9 ± 1.6 per ha birds in 2016; Henderson 2017) but the SE for 2016 overlapped the estimate for 2015 and therefore, estimates could be similar across years. The earliest nest initiation date was 1 May. Red-headed Woodpeckers are known to double brood (Ingold 1987), and all but one nest was found before 15 July, a date documented by previous research by which 100% of Red-headed Woodpeckers will have completed initial broods and double brooding becomes possible (Ingold 1989). The late

nest was started 17 July and was not from a pair we had previously found a nest for that summer, as renests had been located for surrounding territories. Thirty-six nests (76.6%) were successful in fledging ≥ 1 young. Predation accounted for 100% of nest failures. Average cavity height was 11.0 ± 0.5 m, ranging from 5.8–18.3 m. Average DBH of nest trees was 28.1 ± 0.9 cm, ranging from 15.0–48.0 cm. We were only able to inspect 40 nests (20 in 2015, 20 in 2016) with the wireless camera to count eggs and/or nestlings. The average size for clutches that we could determine were completed was 4.3 ± 0.3 eggs ($n = 17$). The average number of fledglings was 2.7 ± 0.1 ($n = 35$). Productivity was 2.0 fledglings per nesting attempt.

Including both years, 48 nests were used in nest-site selection analysis; one nest was unable to be used in nest survival analysis as the snag fell before nesting data could be collected. Every nest was built in a completely dead snag, most of which were *Pinus* spp. (76.6%). Only 16.0% of all snags in the study area were *Pinus* spp., suggesting woodpeckers were selecting for this tree type. Red-headed Woodpeckers demonstrated no selectivity for LBA compared with what was available (Figure 2.1). In 2015 Red-headed Woodpeckers tended to select against nest sites with $> 8,500$ stems ha^{-1} and selected somewhat for 1,500–4,000 stems ha^{-1} . In 2016, however, birds tended to select for sites with $> 8,500$ stems ha^{-1} (Figure 2.2). In 2015 birds demonstrated an affinity for nest sites with greater herbaceous groundcover having selected against sites with limited ($<15\%$) and for those with substantial ($>45\%$) herbaceous groundcover; in 2016 the pattern was similar but weaker (Figure 2.3). In both 2015 and 2016, Red-headed Woodpeckers selected against <2.5 m^2 ha^{-1} and selected for ≥ 2.5 m^2 ha^{-1} DBA (Figure 2.4) which follows our abundance work where Red-headed Woodpeckers were most abundant at 4 m^2 ha^{-1} DBA (Henderson 2017).

The constant survival model was the most supported temporal model for nest survival (Table 2.1). However, the models with varying survival between years and linearly by day were within $\Delta 2$ AICc of the constant survival model, suggesting some variation between years and across the season. However, because confidence intervals for beta coefficients of year and day included zero, we concluded daily nest survival (DSR) was not substantially influenced by either day or year and retained constant temporal survival through subsequent analysis of habitat covariates. After adding nest- and stand-level habitat variables, the best supported models included LBA at the nest (negative relationship with DSR) and DBH of the nest tree (negative quadratic with positive relationship with DSR) (Table 2.2). The top model included LBA around the nest, and quadratic DBH of the nest tree (Table 2.2). For all variables in the top model, 95% confidence intervals included zero (Table 2.3). Stand-level variables were absent from the most supported models despite woodpeckers selecting for nest-site habitat that differed from the stand. DSR for the null model with constant survival was 0.991 ± 0.003 . DSR for the top model was 0.996 ± 0.003 with a calculated period survival of 84.1%.

Discussion

Our study is the first to examine the effects of oak savanna and woodland restoration on nest-site selection and nest survival of Red-headed Woodpeckers. On sites subjected to oak savanna and woodland restoration treatments, nest survival rates were high (76.6% of nests produced ≥ 1 fledgling) relative to other studies (Vierling and Lentile 2006: 47%; Frei et al. 2013: 76.7%; Berl et al. 2014: 42%). Productivity per nesting attempt was great enough to replace each adult with one successful nesting attempt, even without double brooding. With these nest success and productivity levels, oak savanna and woodland restoration could make a substantial contribution to the conservation of this declining species.

Nest-site selection

Red-headed Woodpeckers demonstrated selectivity with respect to nest-site vegetation. All nests were placed in dead trees, a pattern which has been well documented in other studies (Jackson 1976, Vierling and Lentile 2006, King et al. 2007). Specifically, woodpeckers were choosing *Pinus* spp. for their nest cavities likely because, as weak excavators, they were selecting for the softer wood and hence easier nest-cavity excavation (Ingold 1994, Hudson and Bollinger 2013). Contrary to our study, others have found that Red-headed Woodpeckers opportunistically select snag species (King et al. 2007, Berl et al. 2015). Due to pine mortality having occurred 8 years prior to restoration events, we hypothesized that other, non-pine snags in the study area created more recently by restoration were likely less decayed and therefore, less useable for woodpeckers.

Contrary to what we expected, Red-headed Woodpeckers selected for greater and against lesser amounts of herbaceous groundcover around the nest, which contrasts with past studies whereby preference was shown for nest-sites with little ground vegetation (Ingold 1989, Berl et al. 2015). In our study, considering pine snags were selected for in most nest sites, canopy would have been opened 8 years prior to restoration, allowing for increased understory vegetation growth. Thus, rather than a preference for the habitat features, these may have been artifacts of preferred nest tree locations. Red-headed Woodpeckers nest-site selection for midstory density followed two different patterns in 2015 compared with 2016. Possibly, the increase of the population led individuals in 2016 to be pushed into less than ideal nesting habitat.

At the nest-site, DBA of $\geq 2.5 \text{ m}^2 \text{ ha}^{-1}$ was preferred when compared with available habitat, a pattern typical of past studies conducted on golf courses (Rodewald et al. 2005) and restored savannas (King et al. 2007); stand-level snag density in these two studies ranged from

0.5–19.5 snags ha⁻¹, a range comparable to that in our study (1.9–24.0 per ha). Red-headed Woodpecker preference for dead limbs has been well documented (King et al. 2007, Frei et al. 2013, Berl et al. 2015), and increasing DBA should lead to an increase in dead limbs. If predation was a “random event” in space and time (Holway 1991, Wilson and Cooper 1998, Bulluck and Buehler 2008), having more DBA around nests could potentially increase the effort required by a predator to search for cavity-nesting prey, therefore, decreasing the likelihood of predation. More snags and limbs may also increase forage availability and allow for improved parental attentiveness by increasing the number of perches from which they could defend the nest (Sedgwick and Knopf 1990, Rodewald et al. 2005, Hollenbeck et al. 2011).

Red-headed Woodpeckers were not selective for LBA, as values associated with nests ranged from 0–25 m² ha⁻¹ and did not differ from what was available. This contrasts with data in our concurrent study showing that Red-headed Woodpecker abundance decreased with increasing LBA (Henderson 2017). In Wisconsin, selection was shown for increased canopy cover and increased basal area in the nest site, but this study had very low LBA (0.6–1.0 m² ha⁻¹) across the study sites (King et al. 2007). In our study, stands woodpeckers were nesting in had an LBA of ≤ 13.1 m² ha⁻¹, so likely woodpeckers were primarily selecting for a stand-level LBA and did not have a preference beyond that. Neither nests nor Red-headed Woodpeckers were found in controls, likely because of the high level of LBA (15.2 ± 2.0 m² ha⁻¹) and lack of open foraging space. Although some nests were found at levels of basal area present in the controls, DBA, herbaceous groundcover, midstory density, and access to foraging habitat were much lower in controls than treatments therefore limiting ideal nesting habitat.

Nest survival

Our results did not conclusively link DSR with the variables we measured. Neither of the two variables included in the top model, LBA at the nest and the quadratic form of nest snag DBH, had parameter estimates that differed from zero. However, some patterns are suggested by the results for LBA as beta was negative, and only marginally included zero; at $\alpha = 0.08$, the confidence bound would not have included zero, and LBA was present in 8 of 9 models with $\Delta AICc < 4.0$. Similarly, both Frei et al. (2013) and Berl et al. (2014) reported that DSR decreased as canopy cover surrounding the nest tree increased, an outcome they attributed to more access by arboreal nest predators and decreased vigilance and maneuverability of adult birds in defense of the nest in more cluttered environments. At CWMA stand-level, LBA in treatments was already low compared with controls and may have led to changes in the predator community that benefited the woodpeckers and contributed to the high DSR we observed.

Quadratic DBH was in the top model, suggesting that it may have some effect on nest survival. Daily survival rate decreased with increasing DBH until 24 cm and then DSR increased with increasing DBH. Selection for nest trees with greater DBH has been documented (Vierling and Lentile 2006, Roach 2016), but few studies have explored the effects of nest tree DBH on nest survival of Red-headed Woodpeckers. Frei et al. (2013) found nest tree DBH tended to increase nest survival by acting as a thermal buffer, but this study was done in Canada where early-season cold weather can be detrimental to nest survival. However, Berl et al. (2014), working at a similar latitude in northern New York, did not find a connection between DBH and nest survival. Nest tree DBH was smaller in our study at 28.1 ± 0.9 cm compared with that reported in other studies (Rodewald et al. 2005: 58.8 ± 10.0 cm, King et al. 2007: 44.2 ± 1.2 cm, Berl et al. 2014: 44.3 ± 2.6 cm).

Several studies, including ours, have not found a connection between DSR and nest height or nest age of Red-headed Woodpeckers (Berl et al. 2014). However, one study in Illinois (Hudson and Bollinger 2013) found increased cavity height resulted in greater DSR, suggesting height may have been an impediment to predators accessing the nest. Greater nest age has been hypothesized to increase parental defense of the nest and, in turn, increased survival (Hudson and Bollinger 2013).

Despite selection for more herbaceous groundcover at the nest site, this habitat metric was not found to influence DSR in our study. Likewise, midstory density around the nest tree did not influence nest survival, a finding supported in other Red-headed Woodpecker studies (Berl et al. 2014, Frei et al. 2015). If arboreal nest predators are the main predator community in our system, as suggested by the influence of LBA, it seems reasonable that understory structure would not affect these predators' access to nests. Similarly, greater DBA around the nest did not influence nest survival despite woodpeckers selecting for it. Several other studies have documented a lack of effect of DBA on nest survival (Hudson and Bollinger 2013, Berl et al. 2014). Woodpeckers could be selecting for more perches to remain vigilant around the nest, but a higher density did not necessarily equate to greater survival.

No stand-level habitat covariates appeared in the top models suggesting that nest-site habitat more directly influenced nest survival than stand-level habitat. Considering the habitat differences between nest-site selection and survival, Red-headed Woodpeckers may be selecting nesting habitat that maximizes defense of the nest against avian predators while still being impacted by arboreal predators. Despite having significant selection differences in nest-site habitat vs. stand averages, habitat and nest variables did not significantly influence Red-headed Woodpecker nest survival. Given the consistently high nest survival on our study area, the range

of habitat conditions among those that we measured may have represented near optimal conditions and therefore, did not exert measurable influence on DSR. Alternatively, habitat values may have varied enough within stands so that stand-level effects were not apparent.

Although predation was assumed to be the main cause of nest failure, we did not use constantly-recording cavity cameras, and predator communities remain unstudied at CWMA. Other factors could be playing a role in nest failure such as nestling starvation; food unpredictability can lead to brood reduction (Ehrlich et al. 1988) and may have been a factor on our sites. Even in successful nests on our study site, brood reduction occurred with mean brood size of 4 but only 2 fledglings per nest. Brood reduction in Red-headed Woodpeckers has been recorded in other studies (Dallas 2015), and food availability in our system may be an issue but will require further research to validate this hypothesis.

Cavity nesters and woodpeckers generally have high nest survival which suggests that nest survival may not be a proximate cause of declines in Red-headed Woodpeckers (Hudson and Bollinger 2013). Rather, the loss of Red-headed Woodpecker nesting habitat resulting from the influence of succession (i.e., lack of appropriate disturbance), or factors unrelated to nesting, such as Cooper's Hawk (*Accipiter cooperii*) and Sharp-shinned Hawk (*Accipiter striatus*) predation on adult woodpeckers (Kilgo and Vukovich 2012, Koenig et al. 2017), or competition with European Starlings (*Sturnus vulgaris*) for cavities during the breeding season (Frei et al. 2015) could be more influential. Furthermore, post-fledging survival, which has yet to be studied in Red-headed Woodpeckers, could be impacting populations.

Red-headed Woodpeckers chose specific vegetation characteristics in the oak savanna and woodland matrix to place their nests, but despite this selection, nest survival was consistently high suggesting oak savanna and woodland restoration provided habitat that approached optimal

conditions for this species. Although Red-headed Woodpeckers are considered oak-savanna obligates, they demonstrated flexibility with respect to woody midstory densities that remained at levels above restoration targets. These birds clearly benefitted from the open, early-successional habitat mosaic of the transitional stage of restoration on our study site that provided foraging and nesting options. In contrast to lower nest survival reported in the northern edge of the Red-headed Woodpeckers range, nest survival on our Mid-South study area was high. Focusing attention on restoring oak savannas and woodlands in the Mid-South can provide quality nesting habitat for Red-headed Woodpeckers and should be pursued by managers seeking to help mitigate the decline of this species.

Literature Cited

- Artman, V. L., T. F. Hutchinson, and J. D. Brawn (2005). Fire ecology and bird populations in eastern deciduous forests. *Studies in Avian Biology* 30:127–138.
- Askins, R. A. (1999). History of grassland birds in eastern North America. *Studies in Avian Biology* 19:60–71.
- Askins, R. A. (2002). Restoring North America's birds: Lessons from landscape ecology. In. 2nd ed. Yale University Press.
- Barrioz, S., P. Keyser, D. Buckley, D. Buehler, and C. Harper (2013). Vegetation and avian response to oak savanna restoration in the Mid-South USA. *The American Midland Naturalist* 169:194–213.
- Berl, J. L., J. W. Edwards, and J. S. Bolsinger (2015). Scale-dependent and multi-metric nest habitat thresholds for Red-headed Woodpeckers at the northern periphery of their range. *The Condor* 117:203–216.
- Berl, J. L., J. W. Edwards, J. S. Bolsinger, and T. E. Katzner (2014). Survival of Red-headed Woodpeckers' (*Melanerpes erythrocephalus*) nests in northern New York. *The Wilson Journal of Ornithology* 126:700–707.
- Brawn, J. D. (2006). Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20:460–469.
- Brawn, J. D., S. K. Robinson, and F. R. Thompson (2001). The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32:251–276.
- Bulluck, L. P., and D. A. Buehler (2008). Factors influencing Golden-winged Warbler (*Vermivora Chrysoptera*) nest-site selection and nest survival in the Cumberland mountains of Tennessee. *The Auk* 125:551–559.

- Burnham, K. P., and D. R. Anderson (2002). Model selection and multimodal inference. In. 2nd edition. Springer, Verlag, New York.
- Dallas, T. R. (2015). Habitat use and demography of Red-headed Woodpeckers in west-central Illinois.
- Davis, D. W. Peterson, P. B. Reich, M. Crozier, T. Query, E. Mitchell, J. Huntington, and P. Bazakas (2000). Restoring savanna using fire: Impact on the breeding bird community. *Restoration Ecology* 8:30–40.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye (1988). The birder's handbook: a field guide to the natural history of North American birds. In. Simon & Schuster, New York, New York, USA.
- Elzinga, C. L., D. W. Salzer, and J. W. Willoughby (1998). Measuring and monitoring plant populations. Bureau of Land Management Technical Reference.
- Frei, B., J. W. Fyles, and J. J. Nocera (2013). Maladaptive habitat use of a North American woodpecker in population decline. *Ethology* 119:377–388.
- Frei, B., J. J. Nocera, and J. W. Fyles (2015). Interspecific competition and nest survival of the threatened Red-headed Woodpecker. *Journal of Ornithology* 156:743–753.
- Frei, B., K. G. Smith, J. H. Withgott, P. G. Rodewald, P. Pyle, and M. A. Patten (2017). Red-headed woodpecker (*Melanerpes erythrocephalus*). *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/rehwoo>.
- Gram, W. K., P. A. Porneluzi, R. L. Clawson, J. Faaborg, and S. C. Richter (2003). Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conservation Biology* 17:1324–1337.

- Henderson, C. (2017). Avian ecology in an oak savanna and woodland restoration framework in the Mid-South. Thesis.
- Hollenbeck, J. P., V. A. Saab, and R. W. Frenzel (2011). Habitat suitability and nest survival of White-headed Woodpeckers in unburned forests of Oregon. *Journal of Wildlife Management* 75:1061–1071.
- Holway, D. A. (1991). Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. *The Condor* 93:575–581.
- Hudson, N. C., and E. K. Bollinger (2013). Nest success and nest site selection of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) in East-central Illinois. *The American Midland Naturalist* 170:86–94.
- Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel (2001). Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29:440–455.
- Ingold, D. J. (1987). Documented double-broodedness in red-headed woodpeckers. *Journal of Field Ornithology*:234–235.
- Ingold, D. J. (1989). Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpeckers and European Starlings. *American Ornithological Society* 106:209–217.
- Ingold, D. J. (1994). Nest-site characteristics of Red-bellied and Red-headed Woodpeckers and Northern Flickers in east-central Ohio. *Ohio Journal of Science* 94:2–7.
- Jackson, J. A. (1976). A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied Woodpeckers in Kansas. *The Condor* 78:67–76.
- Kilgo, J. C., and M. Vukovich (2012). Factors affecting breeding season survival of Red-headed

- Woodpeckers in South Carolina. *Journal of Wildlife Management* 76:328–335.
- King, R. S., K. E. Brashear, and M. Reiman (2007). Red-headed Woodpecker nest-habitat thresholds in restored savannas. *Journal of Wildlife Management* 71:30–35.
- Koenig, W. D., E. L. Walters, and P. G. Rodewald (2017). Testing alternative hypotheses for the cause of population declines: The case of the Red-headed Woodpecker. *The Condor* 119:143–154.
- Manly, B. F., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson (2002). Resource selection by animals: statistical analysis and design for field studies. In. Kluwer, Nordrecht, The Netherlands.
- Martin, T. E., and G. R. Geupel (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- Mayfield, H. F. (1961). Nesting success calculated from exposure. *The Wilson Bulletin* 73:255–261.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott (1995). Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. National Biological Service, Biological Report 28. U.S. Department of the Interior, Washington, D.C., USA.:83.
- Nuzzo, V. (1986). Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6:6–36.
- R Development Core Team (2008). A language and environment for statistical computing. [Online.] Available at <http://www.r-project.org/>.
- Reidy, J. L., F. R. Thompson, and S. W. Kendrick (2014). Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *Forest Ecology and Management* 313:34–46.

- Roach, M. C. (2016). Breeding bird response to pine-savanna and woodland restoration in the Ozark-Ouachita interior highlands.
- Rodewald, P. G., M. J. Santiago, and A. D. Rodewald (2005). Habitat use of breeding Red-headed Woodpeckers on golf courses in Ohio. *Wildlife Society Bulletin* 33:448–453.
- Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Fprd, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, et al. (2016). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States.
- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski (2013). The North American breeding bird survey 1966–2011: summary analysis and species accounts. *North American Fauna* 79:1–32.
- Sedgwick, J. A., and F. L. Knopf (1990). Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. *Journal of Wildlife Management*.
- Vickery, P. D., M. L. Hunter Jr., and J. V. Wells (1992). Is density an indicator of breeding success? *The Auk* 109:706–710.
- Vierling, K., and L. Lentile (2006). Red-headed Woodpecker nest-site selection and reproduction in mixed ponderosa pine and aspen woodland following fire. *The Condor* 108:957–962.
- White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*.
- Wilson, R. R., and R. J. Cooper (1998). Acadian Flycatcher nest placement: Does placement influence reproductive success? *Condor* 100:673–679.
- Vander Yacht, A. L., S. A. Barrioz, P. D. Keyser, C. A. Harper, D. S. Buckley, D. A. Buehler, and R. D. Applegate (2017). Vegetation response to canopy disturbance and season of burn

during oak woodland and savanna restoration in Tennessee. *Forest Ecology and Management* 390:187–202.

Vander Yacht, A. L., P. D. Keyser, D. A. Buehler, C. A. Harper, D. S. Buckley, and R. D. Applegate (2016). Avian occupancy response to oak woodland and savanna restoration. *Journal of Wildlife Management* 80:1091–1105.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.

Appendix B

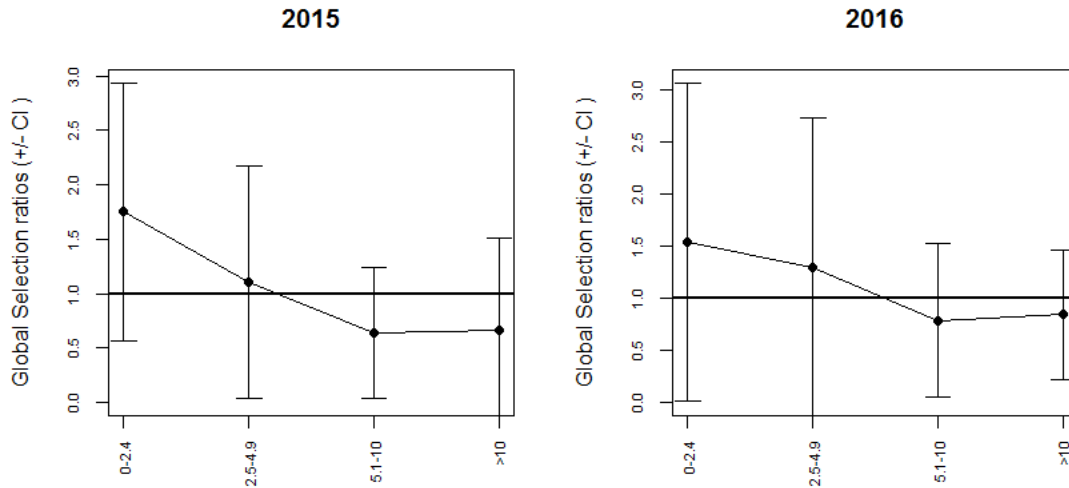


Figure 2.1 Manly selection ratios for live basal area ($\text{m}^2 \text{ha}^{-1}$) comparing used and available habitat for nest sites during a Red-headed Woodpecker nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

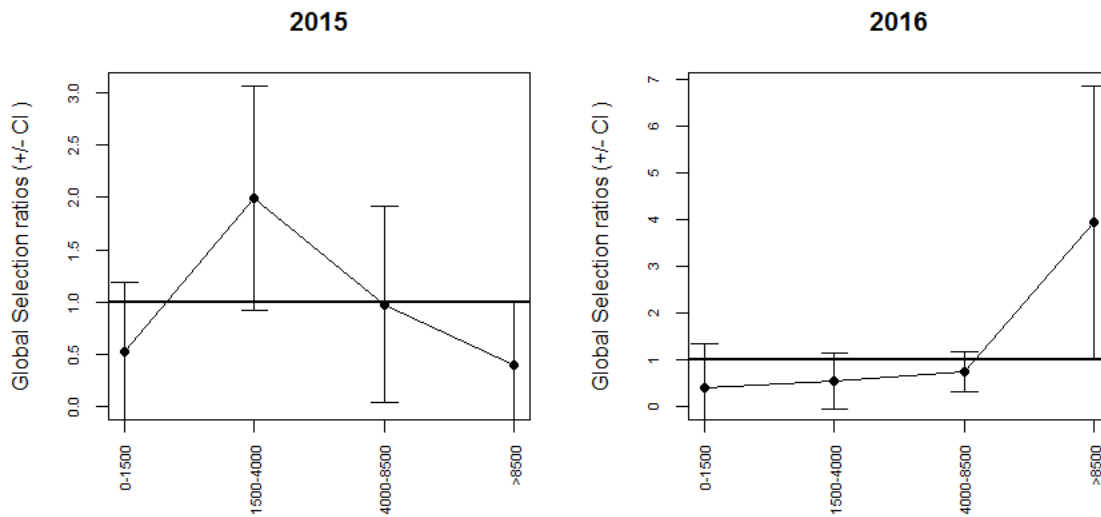


Figure 2.2 Manly selection ratios for midstory density (stems ha^{-1}) comparing used and available habitat for nest sites during a Red-headed Woodpecker nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

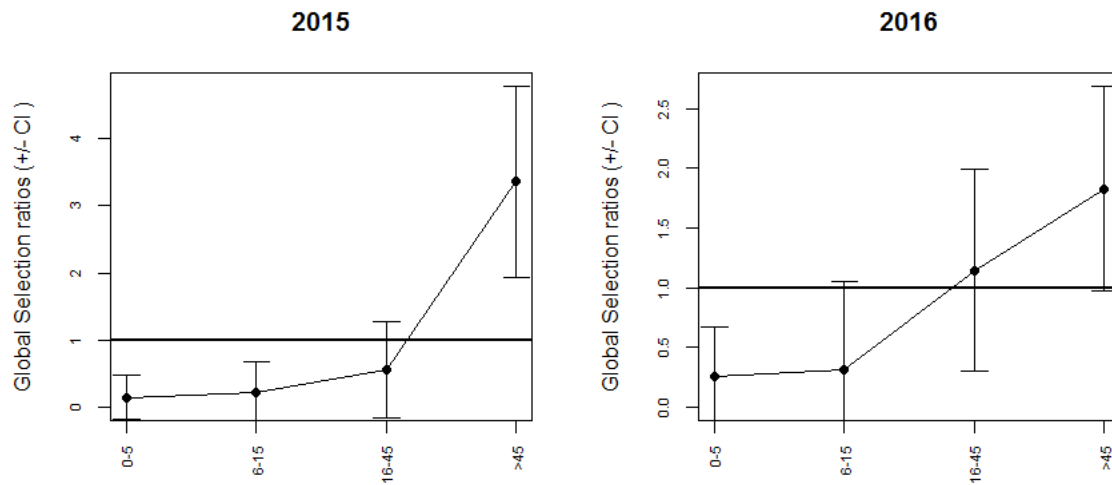


Figure 2.3 Manly selection ratios for herbaceous groundcover (%) comparing used and available habitat for nest sites during a Red-headed Woodpecker nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

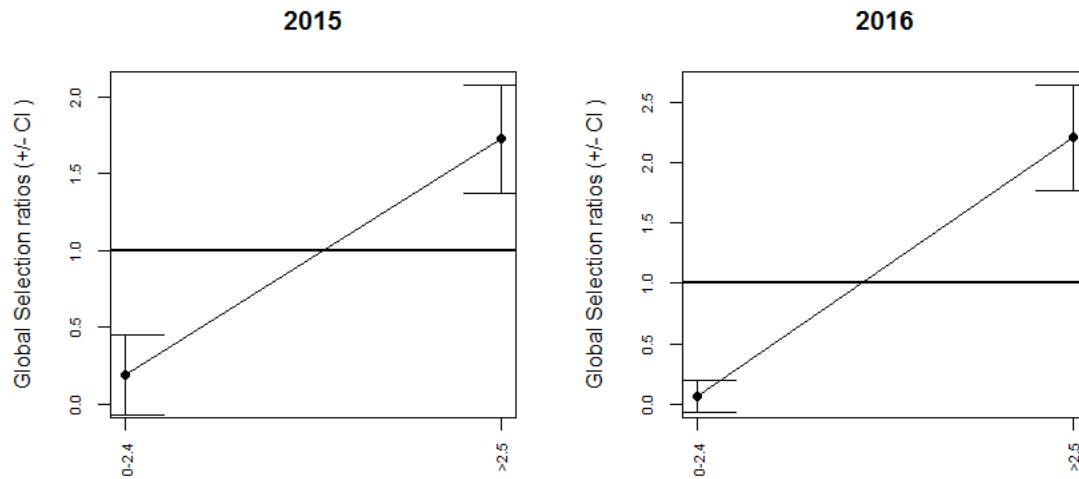


Figure 2.4 Manly selection ratios for dead basal area (m² ha⁻¹) comparing used and available habitat for nest sites during a Red-headed Woodpecker nest survival study at Catoosa Wildlife Management Area, Tennessee, 2015–2016.

Table 2.1 Ranking of temporal models used in Red-headed Woodpecker nest survival analysis at Catoosa Wildlife Management Area, Tennessee, 2015–2016. Covariates included, Year (2015 or 2016) and Day (Julian day of the season).

Model	K ^a	AICc	ΔAICc	wi ^b
S(.)	1	95.64	0	0.38
S(Year)	2	96.73	1.09	0.22
S(Day)	2	97.61	1.97	0.14
S(Year+Day)	3	98.60	2.96	0.09
S(Day+Day ²)	3	98.66	3.02	0.08
S(Year+Day+Day ²)	4	99.59	3.96	0.05
S(Year*Day)	4	100.61	4.97	0.03

^a Number of parameters

^b Model weight

Table 2.2 Ranking of final models for nest survival of Red-headed Woodpeckers at Catoosa Wildlife Management Area, Tennessee, 2015–2016. Models between S(Year) and S(Day) have been excluded from this table for brevity.

Model	K ^a	AICc	ΔAICc	wi ^b
S(LBA ^c +DBH ^d +DBH ²)	4	92.46	0.00	0.21
S(LBA+DBH)	3	94.08	1.62	0.09
S(LBA)	2	94.56	2.10	0.07
S(.)	1	95.64	3.17	0.04
S(LBA+MDens ^e)	3	95.87	3.41	0.04
S(MDens)	2	95.88	3.41	0.04
S(LBA+Age ^f)	3	96.03	3.56	0.04
S(LBA+Height ^g)	3	96.10	3.64	0.03
S(LBA+LBA_ST ^h)	3	96.33	3.87	0.03
S(LBA+DBA ⁱ)	3	96.52	4.06	0.03
S(LBA+LBA ²)	3	96.57	4.10	0.03
S(Year)	2	96.73	4.26	0.02
S(Day)	2	97.61	5.14	0.02

^a Number of parameters

^b Model weight

^c Live basal area within 11.3 m of nest (m² ha⁻¹)

^d Diameter at breast height of nest tree (cm)

^e Midstory density within 12.5 m of nest (stems ha⁻¹)

^f Nest age (days)

^g Height of nest cavity (cm)

^h Live basal area from the stand in which the nest was located (m² ha⁻¹)

ⁱ Dead basal area from the stand in which the nest was located (m² ha⁻¹)

Table 2.3 Beta estimates from the top model from for Red-headed Woodpecker nest survival in Catoosa Wildlife Management Area, Tennessee, 2015–2016.

Parameter	β	SE	Lower CI (95%)	Upper CI (95%)
Intercept	20.7872	15.5143	-9.6208	51.1951
Diameter at breast height (cm)	-1.3122	1.1756	-3.6164	0.9920
(Diameter at breast height ²) (cm)	0.0268	0.0221	-0.0165	0.0700
Live Basal Area (m ² ha ⁻¹)	-0.0684	0.0384	-0.1436	0.0068

3. OAK SAVANNA AND WOODLAND RESTORATION IN THE MID-SOUTH AND THE RELATIONSHIP WITH AVIAN ABUNDANCE

Abstract

Disturbance-dependent bird species have experienced population declines since 1966, due in part to the reduction in open, disturbed habitats, such as oak savannas. In three sites across the Mid-south, Catoosa Wildlife Management Area, Tennessee; Green River Game Lands, North Carolina; and Land Between the Lakes National Recreation Area, Tennessee, restoration of oak savannas has been ongoing since 2008, with selective logging leaving savanna ($7.2 \text{ m}^2 \text{ ha}^{-1}$) or woodland ($14.4 \text{ m}^2 \text{ ha}^{-1}$) residual basal areas. Continued management included either spring or fall burns conducted on a 2-year interval. Point counts were conducted 2–3 times per summer, 2010–2012 and 2014–2016, and abundance for the most frequently detected early-successional bird species ($n = 9$) and mature forest bird species ($n = 10$), as well as 3 nest parasites/predators, and 4 woodpeckers were analyzed using N-mixture models (Program “unmarked”) that accounted for detection. Early-successional species increased in abundance with decreasing live basal area and increasing herbaceous groundcover, while mature forest species benefited from moderate disturbance, reaching a threshold of abundance between $10\text{--}15 \text{ m}^2 \text{ ha}^{-1}$ live basal area and $7,500 \text{ stems ha}^{-1}$ midstory density. Three common, mature forest species declined on sites with greater disturbance. Conditions to benefit all species could be achieved with live basal area between $7\text{--}14 \text{ m}^2 \text{ ha}^{-1}$, herbaceous groundcover near 30%, moderate midstory density ($5\text{--}10,000 \text{ stems ha}^{-1}$), and for cavity-nesting species, $\geq 3 \text{ m}^2 \text{ ha}^{-1}$ dead basal area. Levels of disturbance (i.e., decreasing live basal area and increasing herbaceous groundcover) beyond these ideal conditions could increase early-successional species abundance, but at the cost of eliminating many mature forest species. Oak savanna and woodland restoration will likely lead to increased abundance of disturbance-dependent bird species while continuing to provide habitat for mature forest avian species.

Introduction

Scrubland, barrens, prairies, and open forest communities were once common across the eastern United States prior to Europeans arrival (Nuzzo 1986, Askins 2002), but have been almost completely eliminated and are now considered critically endangered ecosystems (Noss et al. 1995). For example, only about 0.02% of the original 11–13 million ha of oak savannas in the Midwestern US now remain (Nuzzo 1986). Disturbance, most notably fire, has been important in maintaining these ecosystems and keeping them from becoming closed-canopy forests (Davis et al. 2000, Brawn et al. 2001, Hunter et al. 2001, Artman et al. 2005). Recent research has reinforced our understanding of the connection between disturbance and its necessity for sustaining some avian communities (Davis et al. 2000, Brawn et al. 2001, Hunter et al. 2001, Greenberg et al. 2013). In the United States, 50% of grassland and scrubland breeding birds, all of which are considered disturbance-dependent, have experienced significant population decline since 1966 (Askins 1999, Hunter et al. 2001, Sauer et al. 2013).

Several species of declining grassland (e.g., Eastern Meadowlark [*Sturnella magna*], Field Sparrow [*Spizella pusilla*], and Northern Bobwhite [*Colinus virginianus*]) and open-woodland (e.g., Red-headed Woodpecker [*Melanerpes erythrocephalus*], Indigo Bunting [*Passerina cyanea*], Prairie Warbler [*Setophaga discolor*]) species depend on disturbed areas for breeding, and without these, are at risk of continued declines (Davis et al. 2000, Hunter et al. 2001, Brawn 2006, Reidy et al. 2014). Restoration of woodland and savanna communities via reintroduction of fire and canopy thinning can increase preferred habitat for disturbance-dependent birds, therefore contributing to the conservation of these declining species (Gram et al. 2003, Artman et al. 2005). Relative abundance of grassland, savanna, and scrub-shrub bird species has been shown to increase with greater number of burns, snag density, shrub density,

and lower canopy cover (Rodewald and Smith 1998, Davis et al. 2000, Wood et al. 2004, Au et al. 2008, Reidy et al. 2014), all of which result from oak savanna restoration. Restoring open-forest community structure provides early-successional habitat beneficial to declining disturbance-dependent species while keeping overstory structure essential to mature forest species. Furthermore, disturbance within closed-canopy forests can be beneficial to many late-successional species (Marshall et al. 2003, Boves et al. 2013).

Avian community response to oak savanna and woodland restoration has been studied in the western periphery of the historical oak savanna and woodland range in the United States including Missouri (Blake 2005, Reidy et al. 2014), Minnesota (Davis et al. 2000, Au et al. 2008), Illinois (Hartung and Brawn 2005, Brawn 2006), Iowa (Mabry et al. 2010), and Kansas (Holoubek and Jensen 2015). Many of these studies have researched relative abundance (Davis et al. 2000, Blake 2005, Brawn 2006, Au et al. 2008, Mabry et al. 2010), but only two have evaluated occupancy (Hartung and Brawn 2005, Holoubek and Jensen 2015), and only Reidy et al. (2014) examined abundance of avian species. In the eastern portion of the historical oak savanna range, where landscape context is quite different, work on relative abundance (Barrioz et al. 2013) and occupancy (Vander Yacht et al. 2016) is limited, and is entirely lacking for abundance. Furthermore, Vander Yacht et al. (2016) collected information at only one site and did not examine multiple habitat variables in their models for each species.

Although a positive relationship is usually assumed between occupancy and abundance, negative relationships have been documented in bird species (Blackburn et al. 1998). Compared with occupancy, abundance analysis can better represent habitat quality as the density of individual species can be calculated (Freckleton et al. 2006). Calculating the abundance of a species can provide information beyond the point of definite occupancy as densities of

individuals may continue to increase. Furthermore, abundance analysis are better able to detect dramatic changes in densities across time (Gaston et al. 2000) which can be possible in the context of restoration and disturbance events.

To address these issues, we examined abundance of 28 avian species in the context of an oak savanna and woodland restoration experiment at two study sites located in Tennessee and one in North Carolina. Treatments included canopy reductions to savanna and woodland residual basal area targets and spring and fall burns that created a wide range in vegetation structure. All three study areas began from a closed-canopy condition, with no recent history of logging and burning prior to implementation of the experiment. Our objective was to explore the relationship between avian abundance and variation in live basal area (LBA; $\text{m}^2 \text{ha}^{-1}$), dead basal area (DBA; $\text{m}^2 \text{ha}^{-1}$), midstory density (stems ha^{-1}), and herbaceous groundcover (%) along a gradient of oak savanna to oak forest condition. We examined these relationships for early-successional and mature forest species to determine the trade-offs in avian conservation, particularly for declining disturbance-dependent populations, associated with community restoration activities. Using this information, management recommendations could be developed based on these vegetation variables that could contribute to conservation of these declining populations.

Study Areas

We conducted the study at the 32,374-ha Catoosa Wildlife Management Area (CWMA) in Cumberland County, Tennessee, the 7,543-ha Green River Game Lands (GRGL) in Henderson and Polk counties, North Carolina, and the 68,797-ha Land Between the Lakes (LBL) National Recreation Area in Stewart County, Tennessee. At CWMA, soils were mesic and typical hapludults (Soil Survey Staff, Natural Resources Conservation Service 2017) and elevation ranged from 451–518 m with 1–38% slopes. Historical accounts and the growth of prairie and

savanna flora soon after the salvage cutting and fire were implemented support a history of oak savanna and woodlands for this site (Barrioz et al. 2013). Before experimental restoration treatments began, dominant overstory species were red maple (*Acer rubrum*), white (*Quercus alba*), scarlet (*Q. coccinea*), southern red (*Q. falcata*), and black (*Q. velutina*) oaks, sourwood (*Oxydendrum arboreum*), and hickory (*Carya* spp.). Dominant midstory species were blackgum (*Nyssa sylvatica*), downy serviceberry (*Amelanchier arborea*), red maple, sourwood, and sassafras (*Sassafras albidum*). Shortleaf pine and Virginia pine (*Pinus virginiana*) became a minimal component of the stands resulting from pine mortality from a southern pine bark beetle (*Dendroctonus frontalis*) outbreak in 1999–2000. Study sites at GRGL had mesic and typic hapludult soils with elevation ranges of 573–829 m and 3–75% slopes. Forests were dominated by chestnut (*Q. montana*), scarlet, white, and black oaks, yellow poplar (*Liriodendron tulipifera*), sourwood, red maple, and hickory. Dominant midstory species were mountain laurel (*Kalmia latifolia*), red maple, rosebay rhododendron (*Rhododendron maximum*), blackgum, and sourwood. At LBL, soils were dominated by typic hapludults and paleudults. Study site elevation ranged from 122–192 m with 0–37% slopes. Forests in LBL were dominated by chestnut, white, black, and post (*Quercus stellata*) oaks, and hickory. Dominant midstory species were blackgum, winged elm (*Ulmus alata*), eastern hophornbeam (*Ostrya virginiana*), hickory, and sugar maple (*Acer saccharum*).

The ground layer for all three sites was dominated by blueberry (*Vaccinium* spp.), leaf litter, some woody plant regeneration, and low amounts of herbaceous vegetation. Mature forest bird species (Ehrlich et al. 1988) were prevalent in the area prior to treatment and included Red-eyed Vireo (*Vireo olivaceus*), Ovenbird (*Seiurus aurocapilla*), Hooded Warbler (*Setophaga citrina*), and Scarlet Tanager (*Piranga olivacea*).

Methods

Experimental design and data collection

Beginning in 2008, we initiated an oak savanna and woodland experiment with 20-ha experimental units (stands, $n = 28$) established in a completely randomized design with two replicates each at CWMA ($n = 10$) and LBL ($n = 12$) and one at GRGL ($n = 6$). We randomly assigned a control and one of five treatments to each stand: closed-canopy control, fall burn with no thinning (except at CWMA), fall burn with savanna ($7.2 \text{ m}^2 \text{ ha}^{-1}$) residual basal area (FaS), fall burn with woodland ($14.4 \text{ m}^2 \text{ ha}^{-1}$) residual basal area (FaW), spring burn with savanna residual basal area (SpS), and spring burn with woodland residual basal area (SpW). At CWMA, logging was completed in winter 2008–2009, burns occurred in October 2010, 2012, 2014, 2016 (fall) and March 2011, 2013, 2015 (spring). At GRGL, logging was completed in winter 2012–2013, burns occurred in October 2014, and March 2015. At LBL, FaS and FaW stands were logged in fall and winter 2010, SpS logging was completed in September 2011, and SpW logging was completed in 2012. Burns occurred in March and April 2015 and 2016; due to logistical constraints, fall burns could not be implemented during the study period.

Following Ralph et al. (1995), we installed 4 permanent point count stations in each stand at CWMA, GRGL, and LBL. Point count locations were as close as 149 m in some cases because of proximity of stands to one another and as such, could have increased the risk of double-counting for louder birds such as American Crow (*Corvus brachyrhynchos*); however, only observations <100 m were used in our analyses. We surveyed each point 2–3 times between mid-May and mid-June; each round of surveys was completed at all sites before initiating the subsequent round. We used 10-minute counts separated into 4 time intervals: 0–2.5, 2.5–5.0, 5.0–7.5, and 7.5–10.0 min, with 4 distance intervals: 0–25, 26–50, 51–100, >100 -m, and

flyovers (birds flying overhead but not coming from or going to the survey radius) counted separately. An individual bird was only counted in the time interval during which it was first encountered. Surveys were started just before sunrise and finished no more than 5 hours after sunrise.

At the beginning of each field season, we trained technicians in identification of bird species in sight and sound at each field site. Counts were not conducted during periods of excessive wind, rain, thunder, or lightning. When at all possible, we surveyed all points within each stand on the same morning on each visit and survey times were varied across visits to reduce daily temporal bias. Observers were varied across visits and points in each year to reduce observer bias. From 2010–2016, we collected point count data each breeding season except 2013 (funding unavailable; n=6 years).

Vegetation was sampled as part of a concurrent restoration study (A. Vander Yacht, University of Tennessee, unpublished data) that provided stand-level means. Growing-season vegetation measurements were taken annually at 15 plots per stand, located on a 70 x 70-m grid with a random start point (Avery and Burkhart 2002). We selected the vegetation variables based on their importance to species of interest, ease of measurement, and being able to characterize the entire oak savanna to forest gradient. We measured diameter at breast height (DBH) of all live and dead overstory (>12.7 cm DBH, >3.05 m tall) trees within 11.3 m of each plot to calculate LBA and DBA ($\text{m}^2 \text{ha}^{-1}$). We calculated midstory density (stems ha^{-1}) using woody stem (>1.37 m tall, < 12.7 cm DBH) counts from 7 3-m radius sub-plots. To calculate percent herbaceous groundcover, we used the point intercept method (Bonham 1989) to categorize groundcover <1.37 m at 1-m intervals along a 50-m transect and recorded the percentage of

points containing forbs and grasses. Transects ran perpendicular to the slope and through each plot center (Vander Yacht et al. 2016).

Analytical methods

We analyzed abundance for 10 early-successional and 10 mature forest species previously examined in an occupancy analysis from one of our study sites (CWMA) from 2010–2012 (Vander Yacht et al. 2016) (Table 3.1). Additionally, 2 nest predators, one nest parasite, and 5 woodpecker species were added (Ehrlich et al. 1988) because of their potential impact on the avian community and importance in open-forest communities (i.e., woodpeckers). Collectively, these 28 species provided the opportunity to gain a comprehensive perspective on the impacts of restoration on avian communities. We restricted the analysis to singing males to prevent overestimation of the population that could be caused by detections of non-territorial individuals (including females). We also excluded individuals detected >100 m away and flyovers so that an accurate abundance could be calculated.

Initial modeling showed weak and/or biologically unimportant interactions for species among sites, therefore we combined all three in subsequent analyses. Furthermore, we wanted the broadest possible inference frame to be able to inform management across the entire region; abundance-habitat relationships that remained apparent regardless of site-specific variability could be especially important to managers. Additionally, any effort to understand the complex interactions among sites and their respective landscape contexts would have been non-trivial and well beyond the scope of the current analyses. Incorporating a variable that captured the years since initiation of restoration activities proved problematic in that it was correlated ($r = 0.6$, $P < 0.001$) with herbaceous groundcover, which therefore served as a useful surrogate of

management progress encompassing the temporal differences in restoration start times between the sites.

We used program R 3.2.2 (R Development Core Team 2008) for data analysis. We estimated detection and abundance using the N-mixture model in the R package “unmarked” (Royle et al. 2004, Fiske and Chandler 2011). Modeling provided estimates of 2 parameters: the probability of detection per individual (p) and the mean abundance of birds per hectare (λ). We used covariates for day of season and year to account for variability in detection. Additional likely sources of variability in detection such as observer bias, meteorological conditions, and daily temporal effects were accounted for in our study design. We developed candidate models and compared them using AIC estimates (Akaike 1973) to determine which had the best support for explaining variation in detection and abundance (Burnham and Anderson 2002). A series of 6 initial detection models (Table 3.2) were created and the top detection model was then carried through the abundance modeling process.

For abundance, we examined each of our 28 study species individually. Since our objective was to make estimates on the abundance of birds in relation to habitat features, we modeled abundance as a function of stand-level vegetation covariates. We evaluated several covariates including year, and stand-level vegetation measurements of LBA and DBA, midstory density (stems ha^{-1}), and herbaceous groundcover (%). We tested covariates for correlation using Pearson’s correlation analysis and then built models using only uncorrelated ($r < 0.5$) covariates. We only included DBA in subsequent models for all cavity nesters ($n = 9$ species). Snags can be used as perches for several species, but it has not been shown to be an important factor in avian occupancy for species than are not dependent on them for nesting (Vander Yacht et al. 2016).

After running initial abundance models (Table 3.2), either the linear or quadratic form of each habitat variable (whichever had the most support) was combined with the most supported forms of the other habitat variables in each possible combination and run again. Models that had $>2 \Delta AIC$ were run again as a negative binomial version in order to confirm we had used the most appropriate distribution to model our data.

Results

Over 6 field seasons, we encountered 95 species and 20,206 individuals across our 3 sites. The 5 most frequently detected species were Red-eyed Vireo, Prairie Warbler (*Setophaga discolor*), Indigo Bunting, Tufted Titmouse (*Baeolophus bicolor*), and Hooded Warbler (Table 3.1). Nineteen observers participated in surveys and only 2 participated for more than one year.

Vegetation

At CWMA, LBA was the lowest among all 3 sites while DBA, herbaceous groundcover, and midstory density were higher at CWMA compared with the other 2 sites (Table 3.3). LBA was reduced at all sites compared with pre-treatment conditions with the least reduction occurring at LBL. At CWMA, DBA, midstory density, and herbaceous groundcover may have been greater as a result of the greater number of fires that had been implemented. Herbaceous groundcover and LBA were correlated across all sites ($r = -0.77$; $P < 0.001$). No other variables were correlated.

Detection modeling

Hairy Woodpecker (*Leuconotopicus villosus*) was the only species to have constant detection across years and the day-of-season (confidence intervals for detection variables included 0). For most species, the best detection model was one with yearly variation in

detection, but some species also varied by the day-of-season (Table 3.4). For some species, some detection variable's beta confidence intervals included zero despite having these covariates in their top models. We found varying detection by year for every species except Prairie Warbler and Hairy Woodpecker (Table 3.4). We found varying detection (confidence bounds did not include zero) by day-of-season for Common Yellowthroat (*Geothlypis trichas*), Field Sparrow, Prairie Warbler, Eastern Wood-pewee (*Contopus virens*), Hooded Warbler, Ovenbird, Scarlet Tanager, Tufted Titmouse, White-breasted Nuthatch (*Sitta carolinensis*), Northern Flicker (*Colaptes auratus*), Pileated Woodpecker (*Hylatomus pileatus*), and Brown-headed Cowbird (*Molothrus ater*).

Abundance modeling

Three species' top models for abundance did not have a covariate for which confidence intervals did not include zero (Black-and-white Warbler [*Mniotilta varia*], Hairy Woodpecker, and Pileated Woodpecker) indicating their abundance was constant across the range of habitat conditions on our study areas.

Across our study sites, LBA was associated with changes in abundance estimates (beta confidence intervals did not include zero) for 5 early-successional species, 6 mature forest species, 2 woodpeckers, and 3 nest predators/parasites. All 5 early-successional species (Carolina Wren [*Thryothorus ludovicianus*], Chipping Sparrow [*Spizella passerina*], Eastern Towhee [*Pipilo erythrophthalmus*], Indigo Bunting, and Mourning Dove [*Zenaida macroura*]) had a negative relationship with LBA where abundances were maximized at or below 10 m² ha⁻¹ (Fig. 3.1A). Of the 6 mature forest species associated with LBA differences, 5 included this term in its quadratic form in the top model (Table 3.4) with maximum abundance observed between 10.0 and 17.0 m² ha⁻¹ (Fig. 3.1B). White-breasted Nuthatch, despite being a mature forest species, had

a negative linear relationship with LBA (Table 3.4). Our estimate of White-breasted Nuthatch abundance was more than 2 times greater than those for the other 5 mature forest species (Fig. 3.1B), likely because of the low detection for this species. Two woodpeckers (Red-bellied Woodpecker [*Melanerpes carolinus*] and Red-headed Woodpecker) had differing abundance trends in relation to LBA (Fig. 3.1C). Red-bellied Woodpecker had a quadratic trend with maximum abundance near $15 \text{ m}^2 \text{ ha}^{-1}$ (Table 3.4; Fig. 3.1C). On the other hand, Red-headed Woodpecker abundance decreased linearly with LBA (Fig. 3.1C; Table 3.4). Abundance for all 3 nest predators/parasites was associated with changes in LBA but had differing trends. American Crow had a negative linear relationship with LBA (Table 3.4; Fig. 3.1D). Brown-headed cowbird abundance, however, was best modeled as an interactive relationship between LBA and midstory density (Table 3.4). Below $1,393 \text{ stems ha}^{-1}$, brown-headed cowbird abundance had a positive relationship with LBA, was constant despite increasing LBA at $1,393 \text{ stems ha}^{-1}$, and was negatively related to LBA at $>1,393 \text{ stems ha}^{-1}$. Blue Jay (*Cyanocitta cristata*) demonstrated a negative quadratic relationship between abundance and LBA, reaching a maximum at $>25 \text{ m}^2 \text{ ha}^{-1}$ and a minimum near $10 \text{ m}^2 \text{ ha}^{-1}$ (Table 3.4; Fig. 3.1D).

Herbaceous groundcover was associated with abundance differences for 4 early-successional species, 3 mature forest species, one woodpecker, and no nest predators/parasites. All early-successional species (Common Yellowthroat, Field Sparrow, Prairie Warbler, and Yellow-breasted Chat) had a positive relationship with herbaceous groundcover and were almost absent where groundcover was $<10\%$. Abundances of early-successional species were maximized at or above 50% groundcover (Fig. 3.2A). All 3 mature forest species (Hooded Warbler, Ovenbird, and Scarlet Tanager) had a negative relationship with herbaceous groundcover. Scarlet Tanager was the only mature forest species with estimates of $>1 \text{ bird ha}^{-1}$ at

>40% groundcover (Fig. 3.2B). Northern Flicker abundance increased linearly with increasing herbaceous groundcover (Fig. 3.2C).

Midstory density was associated with varying abundance for half of our study species: 6 early-successional species, 4 mature forest species, 3 woodpeckers, and one nest parasite. Early-successional species had varying relationships to midstory density. Common Yellowthroat and Field Sparrow had positive linear relationships, and Prairie Warbler had a positive quadratic relationship between abundance and midstory density (Fig. 3.3A). Abundance was maximized near 9,000 stems ha^{-1} for Prairie Warbler (Fig. 3.3A). Eastern Towhee had an interactive relationship between LBA and midstory density (Table 3.4). Between 1.5–4.9 $\text{m}^2 \text{ha}^{-1}$ LBA, Eastern Towhee abundance had a negative relationship with midstory density, was constant despite increasing midstory density at 4.9 $\text{m}^2 \text{ha}^{-1}$, and was positively related to midstory density at $>4.9 \text{m}^2 \text{ha}^{-1}$. Carolina Wren had a negative quadratic relationship between abundance and midstory density with the lowest abundance near 7,500 stems ha^{-1} (Table 3.4; Fig. 3.3A). Chipping Sparrow abundance followed a decreasing linear trend (Table 3.4; Fig. 3.3A). Mature forest species (Hooded Warbler, Red-eyed Vireo, Tufted Titmouse, and White-breasted Nuthatch) also followed differing trends. Hooded Warbler and Red-eyed Vireo had a similar, but weak increasing quadratic trends with Hooded Warbler reaching maximum abundance near 6,000 stems ha^{-1} and Red-eyed Vireo near 12,500 stems ha^{-1} (Table 3.4; Fig. 3.3B). Tufted titmouse abundance decreased with a weak linear relationship with increasing midstory density but was still present even at the greatest midstory stem densities observed on our study areas (Table 3.4; Fig. 3.3B). For woodpeckers, Northern Flicker and Red-headed Woodpecker both had positive quadratic responses to midstory stem density, reaching maximum abundance above 12,000 stems ha^{-1} (Table 3.4; Fig. 3.3C). Red-bellied Woodpecker had a negative linear response

to midstory density (Table 3.4; Fig. 3.3C). Only one nest predator/parasite was associated with varying midstory density and had an interactive effect of LBA and midstory density: brown-headed cowbird (Table 3.4). Between 1.5–3.9 m² ha⁻¹LBA brown-headed cowbird abundance had a positive relationship with midstory density, was constant despite increasing midstory density at 3.9 m² ha⁻¹, and was negatively related to midstory density at >3.9 m² ha⁻¹LBA.

One mature forest and 4 woodpecker species were associated with changes in DBA. Downy Woodpecker (*Picoides pubescens*) and White-breasted Nuthatch decreased linearly with increasing DBA, while Northern Flicker and Red-headed Woodpecker increased (Table 3.4; Fig. 3.4). Red-bellied Woodpecker was equally abundant at low and high DBA (Fig. 3.4).

Discussion

Based on the 4 vegetation metrics we examined, abundance for most of our species was associated with disturbance imposed during oak savanna and woodland restoration. Our results are similar to other studies of oak savanna restoration, with early-successional species having responded positively to disturbance, while other species had moderate declines (Brawn 2006, Vander Yacht et al. 2016). In our case, only 5 species had consistently negative relationships associated with restoration activities: Blue Jay (LBA), Hooded Warbler (herbaceous cover and midstory density), Ovenbird and Scarlet Tanager (herbaceous cover), and Downy Woodpecker (DBA). Conversely, of the 15 models for early-successional species with significant betas, only one was negative, Chipping Sparrow for midstory density.

All 4 vegetation variables were useful for explaining abundance, but over half of the species analyzed were associated with changes in LBA. Every species with a significant relationship (n = 16) with LBA, except for Blue Jay, increased abundance at levels requiring some disturbance through thinning. All early-successional species increased in abundance with

either decreasing LBA or increasing herbaceous groundcover, thus supporting our hypothesis that increasing disturbance will lead to increased abundance of early-successional species, as has been reported elsewhere (Gram et al. 2003, Brawn 2006, Grundel and Pavlovic 2007). All mature forest species sensitive to LBA maximized abundance below $20 \text{ m}^2 \text{ ha}^{-1}$, supporting the notion that these species respond positively to some level of moderate canopy disturbance. Red-bellied Woodpeckers followed a trend similar to the mature forest species demonstrating greatest abundance with intermediate levels of LBA. On the other hand, Red-headed Woodpeckers followed a pattern similar to early-successional species with greater abundance being observed at lower LBA. In the case of woodpeckers, areas with very high LBA, which were the least disturbed areas in the study, may have had less DBA for nesting and foraging. At an LBA of $>20 \text{ m}^2 \text{ ha}^{-1}$, DBA did not increase above $2 \text{ m}^2 \text{ ha}^{-1}$. White-breasted Nuthatch, also a cavity-nester, reacted similarly to Red-headed Woodpecker. The most consistent predictor of abundance of nest predators and parasites was LBA. Combined abundances of these species were minimized between $15\text{--}20 \text{ m}^2 \text{ ha}^{-1}$. In contrast, Annand and Thompson (1997) found that abundances of Blue Jay and American Crow did not differ among silvicultural treatments. Brown-headed cowbird's negative relationship with LBA could be related to the higher number of host birds in low basal area sites (Annand and Thompson 1997).

As expected, 4 early-successional species increased with increasing herbaceous groundcover, but only Field Sparrow and Common Yellowthroat nest on the ground and in this groundcover type. The 2 shrubland associates (Prairie Warbler and Yellow-breasted Chat) may have been attracted to patches of herbaceous groundcover within a well-developed woody midstory (Ehrlich et al. 1988, Vander Yacht et al. 2016). It is also worth noting that the 2 shrubland species demonstrated a similar threshold for herbaceous cover (near 45%), above

which they began to decline in abundance. By comparison, Field Sparrow and Common Yellowthroat had not reached a peak within the range of herbaceous cover we observed on our sites, although a threshold was implied (near 65%) for Common Yellowthroat. Only 3 of 10 mature forest species declined with increasing herbaceous groundcover (i.e., disturbance). Among our 28 species, Ovenbird demonstrated the strongest negative response to disturbance. Northern Flicker was the only woodpecker species with a relationship to herbaceous groundcover. The strong positive response could likely have been influenced by this species being a ground forager whose diet consists mainly of ants (Ehrlich et al. 1988). Certain species of ants have been shown to be more abundant in areas of higher herbaceous groundcover (Lubertazzi and Tschinkel 2003).

In contrast to the patterns observed for LBA and herbaceous cover, early-successional species had mixed responses to midstory density suggesting that responses may have been species- or nesting guild-specific. All early-successional species that increased in abundance with increasing midstory density were ground- and shrub-nesting species and may have been responding to the increase in nesting and foraging substrate (Ehrlich et al. 1988, Davis et al. 2000). Being a shrub-nester, Hooded Warbler was almost completely absent at midstory densities $<2,500$ stems ha^{-1} . All other mature forest species associated with changes in midstory density were still present at all stem densities. Northern Flicker and Red-headed Woodpecker were both more abundant at densities $>10,000$ stems ha^{-1} and therefore, where disturbance tended to be greatest. In our study area, when midstory density increased to $>7,500$ stems ha^{-1} , LBA was never >10 m^2 ha^{-1} , which is likely the cause for the significant upswing for these species at high densities of midstory density. Possibly, as these 2 species are flycatchers, these areas could produce greater numbers of arthropods (Vierling and Lentile 2006). Red-bellied Woodpecker,

however, had a negative relationship with midstory density, likely due to the species' preference for forested and less disturbed habitat for breeding (Ingold 1994). Carolina Wren, White-breasted Nuthatch, Northern Flicker, and Red-headed Woodpecker all had similar reactions to midstory density and initially declined as midstory density increased, reaching a low abundance near 5,000 stems ha⁻¹ and then increasing above approximately 7,500 stems ha⁻¹. All 4 of these species are cavity nesters and higher midstory density may help conceal the nest from ground-dwelling predators. Stands with both low LBA and midstory density harbor the most brown-headed cowbirds (Barber et al. 2001, Chalfoun et al. 2002), and these open savanna-like stands had the greatest number of species that are susceptible to nest parasitism.

Increasing DBA did not ensure increasing abundance of species typically associated with snags, a result that we did not expect. Downy Woodpecker and White-breasted Nuthatch declined, dramatically in the case of the woodpecker, with increasing DBA, while Northern Flicker and Red-headed Woodpecker increased at a very modest rate. All species were present at all levels of DBA, but the early-successional woodpecker species benefited most from increasing DBA. Other than Downy Woodpecker, 4 of the species associated with changes in DBA included 2 other variables in their top models, suggesting that these species need more specific requirements to maximize abundance along with DBA. Some level of restoration-induced disturbance was associated with maximized abundance of all woodpecker species (i.e., low-mid level LBA, high herbaceous groundcover, midstory density, and DBA). Northern Flicker, Red-headed Woodpecker, and Red-bellied Woodpecker all had 3 significant variables in the top model, suggesting that these species were responding to several aspects of restoration and their requirements may be more specific and difficult to achieve.

As we approached savanna conditions, all 9 early-successional species increased markedly and 3 mature forest species declined by a similar magnitude. Most mature forest and woodpecker species responded positively to moderate-high levels of restoration-induced disturbance. As restoration progresses, we anticipate that midstory density will decline and be replaced with increasing amounts of herbaceous groundcover. Thus, scrub-shrub species will likely decline but remain present. Keeping some areas in transitional phases will create habitat to maintain, if not increase, populations of these species.

Working with stands that were 20 ha ensured that species' home ranges were exceeded but completing restoration on a larger scale would be preferable. Although we examined habitat factors within the stands, we did not extend our analysis to landscape-level factors. Percent forest cover, grassland cover, number of roads, etc. could all possibly influence avian abundances and would help identify additional factors to consider in identifying areas on which to implement restoration. Creating oak savannas and woodlands at the scale we studied is a viable technique to increase abundance of early-successional species.

Management Implications

We analyzed abundance for 28 bird species represented along the gradient from oak forests to oak savannas. Several of these species, especially those associated with early-successional habitat conditions, are of high conservation concern and increasing their populations should be a priority. Oak savannas are a useful tool to increase disturbance-dependent bird populations while minimizing declines of mature forest species. Focusing on keeping LBA between 7–14 m² ha⁻¹, herbaceous groundcover near 30%, maintaining a moderate midstory density (5–10,000 stems ha⁻¹) and keeping snags standing would benefit early-successional birds, and likely help some mature forest birds, and minimize declines in the few

species that are affected by these aspects of oak savanna restoration. As restoration progresses with continued low-intensity prescribed fires in thinned areas, litter-covered ground will further progress to herbaceous groundcover leading to more benefits to these early-successional species while keeping LBA levels stable. Managers should implement oak savanna restoration on a scale of 20 ha or larger to realize the full potential of this management technique.

Literature Cited

- Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In International Symposium on Information Theory. pp. 267–281.
- Annand, E. M., and F. R. Thompson (1997). Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61:159–171.
- Artman, V. L., T. F. Hutchinson, and J. D. Brawn (2005). Fire ecology and bird populations in eastern deciduous forests. *Studies in Avian Biology* 30:127–138.
- Askins, R. A. (1999). History of grassland birds in eastern North America. *Studies in Avian Biology* 19:60–71.
- Askins, R. A. (2002). Restoring North America's birds: Lessons from landscape ecology. In 2nd ed. Yale University Press.
- Au, L., D. E. Andersen, and M. Davis (2008). Patterns in bird community structure related to restoration of Minnesota dry oak savannas and across a prairie to oak woodland ecological gradient. *Natural Areas Journal* 28:330–341.
- Avery, T. E., and H. E. Burkhart (2002). Forest measurements. In. Fifth edit. McGraw-Hill, New York, New York, USA.
- Barber, D. R., T. E. Martin, M. A. Melchior, R. E. Thill, and T. B. Wigley (2001). Nesting success of birds in different silvicultural treatments in southeastern U.S. pine forests. *Conservation Biology* 15:196–207.
- Barrioz, S., P. Keyser, D. Buckley, D. Buehler, and C. Harper (2013). Vegetation and avian response to oak savanna restoration in the Mid-South USA. *The American Midland Naturalist* 169:194–213.
- Blackburn, T. M., K.J. Gaston, J.J.D. Greenwood, and R.D. Gregory (1998). The anatomy of the

- interspecific abundance-range size relationship for the Birtich avi-fauna. II. Temporal dynamics. *Ecology Letters* 1:47–55.
- Blake, J. G. (2005). Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. *Biological Conservation* 121:519–531.
- Bonham, C. D. (1989). Measurements for terrestrial vegetation. In. John Wiley and Sons, New York, New York, USA.
- Boves, T. J., D. A. Buehler, J. Sheehan, P. B. Wood, A. D. Rodewald, J. L. Larkin, P. D. Keyser, F. L. Newell, G. A. George, M. H. Bakermans, A. Evans, et al. (2013). Emulating natural disturbances for declining late-successional species: A case study of the consequences for Cerulean Warblers (*Setophaga cerulea*). *PLoS ONE* 8.
- Brawn, J. D. (2006). Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20:460–469.
- Brawn, J. D., S. K. Robinson, and F. R. Thompson (2001). The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32:251–276.
- Burnham, K. P., and D. R. Anderson (2002). Model selection and multimodal inference. In. 2nd edition. Springer, Verlag, New York.
- Chalfoun, A. D., M. J. Ratnaswamy, and F. R. Thompson (2002). Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. *Ecological Applications* 12:858–867.
- Davis, D. W. Peterson, P. B. Reich, M. Crozier, T. Query, E. Mitchell, J. Huntington, and P. Bazakas (2000). Restoring savanna using fire: Impact on the breeding bird community. *Restoration Ecology* 8:30–40.

- Ehrlich, P. R., D. S. Dobkin, and D. Wheye (1988). *The birder's handbook: a field guide to the natural history of North American birds*. In. Simon & Schuster, New York, New York, USA.
- Fiske, I., and R. Chandler (2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1–23.
- Freckleton, R. P., D. Noble, and T. J. Webb (2006). Distributions of habitat suitability and the abundance-occupancy relationship. *The American Naturalist* 167:260–275.
- Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton (2000). Abundance-occupancy relationships. *Journal of Applied Ecology* 37:39–59.
- Gram, W. K., P. A. Porneluzi, R. L. Clawson, J. Faaborg, and S. C. Richter (2003). Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conservation Biology* 17:1324–1337.
- Greenberg, C. H., T. a. Waldrop, J. Tomcho, R. J. Phillips, and D. Simon (2013). Bird response to fire severity and repeated burning in upland hardwood forest. *Forest Ecology and Management* 304:80–88.
- Grundel, R., and N. B. Pavlovic (2007). Response of bird species densities to habitat structure and fire history along a midwestern open-forest gradient. *The Condor* 109:734–749.
- Hartung, S. C., and J. D. Brawn (2005). Effects of savanna restoration on the foraging ecology of insectivorous songbirds. *The Condor* 107:879–888.
- Holoubek, N. S., and W. E. Jensen (2015). Avian occupancy varies with habitat structure in oak savanna of the south-central United States. *Journal of Wildlife Management* 79:458–468.
- Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel (2001). Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society*

Bulletin 29:440–455.

- Ingold, D. J. (1994). Nest-site characteristics of Red-bellied and Red-headed Woodpeckers and Northern Flickers in east-central Ohio. *Ohio Journal of Science* 94:2–7.
- Lubertazzi, D., and W. R. Tschinkel (2003). Ant community change across a ground vegetation gradient in north Florida's longleaf pine flatwoods. *Journal of Insect Science* 3:21.
- Mabry, C. M., L. A. Brudvig, and R. C. Atwell (2010). The confluence of landscape context and site-level management in determining Midwestern savanna and woodland breeding bird communities. *Forest Ecology and Management* 260:42–51.
- Marshall, M. R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper (2003). Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. *Forest Ecology and Management* 183:127–135.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott (1995). Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. National Biological Service, Biological Report 28. U.S. Department of the Interior, Washington, D.C., USA.:83.
- Nuzzo, V. (1986). Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6:6–36.
- R Development Core Team (2008). A language and environment for statistical computing. [Online.] Available at <http://www.r-project.org/>.
- Ralph, C. J., S. Droege, and J. R. Sauer (1995). Managing and monitoring birds using point counts: Standards and applications. USDA Forest Service General Technical Report:161–168.
- Reidy, J. L., F. R. Thompson, and S. W. Kendrick (2014). Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks.

- Forest Ecology and Management 313:34–46.
- Rodewald, P. G., and K. G. Smith (1998). Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. *Journal of Wildlife Management* 62:1411–1417.
- Royle, J. A., D. K. Dawson, and S. Bates (2004). Modeling abundance effects in distance sampling. *Ecology* 85:1591–1597.
- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski (2013). The North American breeding bird survey 1966–2011: summary analysis and species accounts. *North American Fauna* 79:1–32.
- Service, S. S. S. N. R. C. (2017). Soil Survey Staff Natural Resources Conservation Service. United States Department of Agriculture, Web Soil Survey. <<http://websoilsurvey.nrcs.usda.gov/>>.
- Vierling, K., and L. Lentile (2006). Red-headed Woodpecker nest-site selection and reproduction in mixed ponderosa pine and aspen woodland following fire. *The Condor* 108:957–962.
- Wood, D. R., L. W. Burger Jr., J. L. Bowman, and C. L. Hardy (2004). Avian community response to pine-grassland restoration. *Wildlife Society Bulletin* 32:819–828.
- Vander Yacht, A. L., P. D. Keyser, D. A. Buehler, C. A. Harper, D. S. Buckley, and R. D. Applegate (2016). Avian occupancy response to oak woodland and savanna restoration. *Journal of Wildlife Management* 80:1091–1105.

Appendix C

Table 3.1 Species used, total detections, and measured detectability from an oak savanna and woodland restoration experiment conducted at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes National Recreation Area, TN, 2010–2016.

Species	Species Code	Detections	Detectability ^a
Early-successional			
Carolina Wren (<i>Thryothorus ludovicianus</i>)	CAWR	558	26.1 ± 2.9
Chipping Sparrow (<i>Spizella passerina</i>)	CHSP	211	16.7 ± 3.3
Common Yellowthroat (<i>Geothlypis trichas</i>)	COYE	172	22.9 ± 3.9
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	EATO	786	36.5 ± 2.5
Field Sparrow (<i>Spizella pusilla</i>)	FISP	276	36.8 ± 3.4
Indigo Bunting (<i>Passerina cyanea</i>)	INBU	1,217	43.0 ± 2.2
Mourning Dove (<i>Zenaida macroura</i>)	MODO	242	15.5 ± 3.2
Prairie Warbler (<i>Setophaga discolor</i>)	PRAW	1,275	50.6 ± 1.9
Yellow-breasted Chat (<i>Icteria virens</i>)	YBCH	933	46.1 ± 2.2
Mature Forest			
Black-and-white Warbler (<i>Mniotilta varia</i>)	BAWW	583	13.1 ± 3.0
Blue-gray Gnatcatcher (<i>Poliptila caerulea</i>)	BGGN	997	23.8 ± 2.7
Eastern Wood-Pewee (<i>Contopus virens</i>)	EAWP	872	29.4 ± 2.8
Hooded Warbler (<i>Setophaga citrina</i>)	HOWA	1,011	34.2 ± 2.5
Ovenbird (<i>Seiurus aurocapilla</i>)	OVEN	849	33.9 ± 2.3
Red-eyed Vireo (<i>Vireo olivaceus</i>)	REVI	1,902	30.4 ± 2.5
Scarlet Tanager (<i>Piranga olivacea</i>)	SCTA	501	17.2 ± 2.9
Tufted Titmouse (<i>Baeolophus bicolor</i>)	TUTI	1,182	27.0 ± 2.6
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	WBNU	425	0.8 ± 2.6
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	YTVI	237	17.5 ± 3.5
Woodpeckers			
Downy Woodpecker (<i>Picoides pubescens</i>)	DOWO	155	4.2 ± 3.4
Hairy Woodpecker (<i>Leuconotopicus villosus</i>)	HAWO	84	8.2 ± 3.8
Northern Flicker (<i>Colaptes auratus</i>)	NOFL	183	10.4 ± 3.2
Pileated Woodpecker (<i>Hylatomus pileatus</i>)	PIWO	136	4.4 ± 2.8
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	RBWO	449	11.3 ± 3.0
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	RHWO	369	19.9 ± 2.7
Nest Predators/Parasites			
American Crow (<i>Corvus corax</i>)	AMCR	260	2.5 ± 2.3
Brown-headed Cowbird (<i>Molothrus ater</i>)	BHCO	302	19.2 ± 3.3
Blue Jay (<i>Cyanocitta cristata</i>)	BLJA	194	6.4 ± 2.7

^a Detectability estimates were calculated from the most supported detection model for each species including all three sites and all six years

Table 3.2 Detection and abundance models used in analysis of point count data from an oak savanna restoration study, 2010–2016 at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes, TN.

Detection Models	Abundance Models
NULL ^a	NULL
DAY ^b	YEAR
DAY+DAY ²	LBA ^d
YEAR ^c	DBA ^e
YEAR+DAY	HCOV ^f
YEAR+DAY+DAY ²	MDENS ^g
	LBA+LBA ²
	DBA+DBA ²
	HCOV+HCOV ²
	MDENS+MDENS ²
	LBA × MDENS
	HCOV × MDENS

^a Constant

^b Day of season

^c Year of point count

^d Live basal area in the stand (m² ha⁻¹)

^e Dead basal area in the stand (m² ha⁻¹)

^f Herbaceous groundcover in the stand (%)

^g Midstory density in the stand (stems ha⁻¹)

Table 3.3 Six-year means and ranges for vegetation metrics in an oak savanna and woodland restoration experiment conducted at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes National Recreation Area, TN, 2010–2012, 2014–2016.

Site	Live Basal Area (m ² ha ⁻¹)		Dead Basal Area (m ² ha ⁻¹)		Herbaceous Groundcover (%)		Midstory Density (stems ha ⁻¹) ^a	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Catoosa Wildlife Management Area	10.9	1.5–23.3	2.8	0.8–6.2	25.2	0.5–69.9	5,167	51–16,550
Green River Game Lands	15.9	3.7–28.7	1.0	0–2.3	14.8	2.0–50.8	4,241	776–12,374
Land Between the Lakes National Recreation Area	15.6	9.8–22.1	1.1	0–2.5	15.1	1.6–34.8	2,316	217–6,952

^a woody stems >1.37 m tall and <12.7 cm

Table 3.4 Top ($\Delta AIC < 2.0$) and null abundance (λ) and detection (p) models from avian abundance analysis for an oak savanna and woodland restoration experiment conducted at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes, TN, 2010-2012 and 2014–2016.

Species	Model	K	AIC	ΔAIC	wi
Early-successional					
Carolina Wren (<i>Thryothorus ludovicianus</i>)	$\lambda(lba+lba^2+mdens+mdens^2) p(year)$	11	2137.93	0	0.56
	$\lambda(lba+lba^2+mdens+mdens^2) p(year)NB$	12	2138.7	0.76	0.39
	$\lambda(.) p(.)$	2	2300.46	162.53	0.00
Chipping Sparrow (<i>Spizella passerina</i>)	$\lambda(lba+mdens+mdens^2) p(year+day)NB$	12	1161.54	0	0.52
	$\lambda(lba*mdens) p(year+day)NB$	12	1161.67	0.13	0.48
	$\lambda(.) p(.)$	2	1287.11	125.57	0.00
Common Yellowthroat (<i>Geothlypis trichas</i>)	$\lambda(hcov+hcov^2+mdens) p(year+day+day^2)$	12	928.48	0	0.23
	$\lambda(lba+mdens) p(year+day+day^2)$	11	928.53	0.048	0.23
	$\lambda(lba+mdens) p(year+day+day^2)NB$	12	929.09	0.608	0.17
	$\lambda(hcov+hcov^2+mdens) p(year+day+day^2)NB$	13	930.02	1.534	0.11
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	$\lambda(.) p(.)$	2	1069.76	141.28	0.00
	$\lambda(lba*mdens) p(year+day)NB$	12	2534.45	0	1.00
	$\lambda(.) p(.)$	2	2781.22	246.77	0.00
Field Sparrow (<i>Spizella pusilla</i>)	$\lambda(hcov+hcov^2+mdens+mdens^2) p(year+day)$	12	1051.99	0	0.59
	$\lambda(hcov+hcov^2+mdens+mdens^2) p(year+day)NB$	13	1053.03	1.04	0.35
	$\lambda(.) p(.)$	2	1457.49	405.5	0.00
Indigo Bunting (<i>Passerina cyanea</i>)	$\lambda(lba+lba^2) p(year+day+day^2)$	11	3008.34	0	0.55
	$\lambda(lba+lba^2) p(year+day+day^2)NB$	12	3009.09	0.75	0.38
	$\lambda(.) p(.)$	2	3427.08	418.74	0.00
Mourning Dove (<i>Zenaida macroura</i>)	$\lambda(lba) p(year+day)NB$	10	1280.02	0	0.52
	$\lambda(lba+mdens) p(year+day)NB$	11	1281.3	1.29	0.27
	$\lambda(lba^2) p(year+day)NB$	11	1282.3	1.98	0.19
	$\lambda(.) p(.)$	2	1393.16	116.39	0.00
Prairie Warbler (<i>Setophaga discolor</i>)	$\lambda(hcov+hcov^2+mdens+mdens^2) p(year+day)NB$	13	2951	0	0.92
	$\lambda(.) p(.)$	2	3503.75	552.74	0.00
Yellow-breasted Chat (<i>Icteria virens</i>)	$\lambda(hcov+hcov^2) p(year+day)NB$	11	2621.75	0	1.00
	$\lambda(.) p(.)$	2	2974.56	352.8	0.00

Table 3.4 continued

Species	Model	K	AIC	Δ AIC	wi
Mature Forest					
Black-and-white Warbler (<i>Mniotilta varia</i>)	$\lambda(\text{year}) p(\text{year})$	12	2326.91	0.00	0.11
	$\lambda(.) p(\text{year})$	7	2327.09	0.18	0.10
	$\lambda(\text{lba}+\text{lba}^2) p(\text{year})$	9	2327.12	0.21	0.10
	$\lambda(.) p(\text{year}+\text{day})$	8	2327.74	0.82	0.07
	$\lambda(\text{dba}) p(\text{year})$	8	2327.8	0.89	0.07
	$\lambda(\text{mdens}) p(\text{year})$	8	2328.44	1.52	0.05
	$\lambda(\text{hcov}) p(\text{year})$	8	2328.72	1.81	0.05
	$\lambda(\text{lba}) p(\text{year})$	8	2328.86	1.95	0.04
	$\lambda(\text{year}) p(\text{year})\text{NB}$	13	2328.91	2.00	0.04
Blue-gray Gnatcatcher (<i>Poliopitila caerulea</i>)	$\lambda(\text{lba}+\text{lba}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	12	3083.92	0	0.51
	$\lambda(\text{lba}+\text{lba}^2+\text{mdens}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	13	3084.04	0.12	0.48
	$\lambda(.) p(.)$	2	3211.36	127.45	0.00
Eastern Wood-Pewee (<i>Contopus virens</i>)	$\lambda(\text{lba}+\text{lba}^2+\text{mdens}) p(\text{year}+\text{day})$	11	2750.44	0	0.40
	$\lambda(\text{lba}+\text{lba}^2) p(\text{year}+\text{day})$	10	2751.2	0.75	0.28
	$\lambda(.) p(.)$	2	2872.47	122.03	0.00
Hooded Warbler (<i>Setophaga citrina</i>)	$\lambda(\text{hcov}+\text{hcov}^2+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	14	3013.08	0	0.93
	$\lambda(.) p(.)$	2	3154.63	141.55	0.00
Ovenbird (<i>Seiurus aurocapilla</i>)	$\lambda(\text{hcov}+\text{hcov}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	12	2580.52	0	0.75
	$\lambda(.) p(.)$	2	2945.82	365.3	0.00
Red-eyed Vireo (<i>Vireo olivaceus</i>)	$\lambda(\text{lba}+\text{lba}^2+\text{mdens}+\text{mdens}^2) p(\text{year})$	11	4087.78	0	0.59
	$\lambda(\text{lba}+\text{lba}^2+\text{mdens}+\text{mdens}^2) p(\text{year})\text{NB}$	12	4089.45	1.67	0.25
	$\lambda(.) p(.)$	2	4204.82	117.04	0.00
Scarlet Tanager (<i>Piranga olivacea</i>)	$\lambda(\text{hcov}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	11	2125.38	0	0.31
	$\lambda(\text{hcov}+\text{hcov}^2+\text{mdens}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	13	2125.66	0.29	0.27
	$\lambda(\text{hcov}+\text{hcov}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	12	2125.77	0.39	0.25
	$\lambda(.) p(.)$	2	2204.59	79.21	0.00
Tufted Titmouse (<i>Baeolophus bicolor</i>)	$\lambda(\text{lba}+\text{lba}^2+\text{mdens}) p(\text{year}+\text{day})$	11	3283.69	0	0.27
	$\lambda(\text{dba}+\text{lba}+\text{lba}^2+\text{mdens}) p(\text{year}+\text{day})$	12	3284.52	0.83	0.18
	$\lambda(\text{lba}+\text{lba}^2+\text{mdens}) p(\text{year}+\text{day})\text{NB}$	12	3284.94	1.25	0.15
	$\lambda(\text{dba}+\text{lba}+\text{lba}^2) p(\text{year}+\text{day})$	11	3285.68	1.99	0.10
	$\lambda(.) p(.)$	2	3462.54	178.85	0.00
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	$\lambda(\text{dba}+\text{lba}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day}+\text{day}^2)$	13	1990.42	0	0.37
	$\lambda(\text{dba}+\text{lba}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	14	1991.66	1.24	0.20
	$\lambda(.) p(.)$	2	2037.75	47.33	0.00
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	$\lambda(\text{lba}+\text{lba}^2) p(\text{year})\text{NB}$	10	1300.02	0	0.54
	$\lambda(\text{lba}+\text{lba}^2+\text{mdens}) p(\text{year})\text{NB}$	11	1300.93	0.9	0.34
	$\lambda(.) p(.)$	2	1348.6	48.58	0.00

Table 3.4 continued

Species	Model	K	AIC	Δ AIC	wi
Woodpeckers					
Downy Woodpecker (<i>Picoides pubescens</i>)	$\lambda(\text{dba}) p(\text{year})$	8	968.24	0	0.18
	$\lambda(\text{dba}) p(\text{year})\text{NB}$	9	968.98	0.73	0.12
	$\lambda(\text{dba}+\text{lba}) p(\text{year})$	9	969.69	1.45	0.09
	$\lambda(\text{dba}+\text{dba}^2) p(\text{year})$	9	969.99	1.75	0.07
	$\lambda(\text{dba}+\text{hcov}) p(\text{year})$	9	970.18	1.94	0.07
	$\lambda(\text{dba}+\text{mdens}) p(\text{year})$	9	970.23	1.99	0.07
	$\lambda(.) p(.)$	2	1030.4	62.15	0.00
Hairy Woodpecker (<i>Leuconotopicus villosus</i>)	$\lambda(\text{dba}) p(\text{year}+\text{day})\text{NB}$	10	636.12	0	0.15
	$\lambda(\text{dba}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day})\text{NB}$	12	636.21	0.10	0.14
	$\lambda(.) p(\text{year}+\text{day})\text{NB}$	9	636.42	0.30	0.12
	$\lambda(\text{lba}*\text{mdens}) p(\text{year}+\text{day})\text{NB}$	12	636.75	0.63	0.11
	$\lambda(\text{lba}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day})\text{NB}$	12	637.33	1.21	0.08
	$\lambda(\text{dba}+\text{lba}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day})\text{NB}$	13	637.37	1.25	0.08
	$\lambda(\text{dba}+\text{hcov}) p(\text{year}+\text{day})\text{NB}$	11	637.57	1.45	0.07
	$\lambda(\text{dba}+\text{hcov}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day})\text{NB}$	13	638.08	1.97	0.05
Northern Flicker (<i>Colaptes auratus</i>)	$\lambda(.) p(.)$	2	655.5	19.38	0.00
	$\lambda(\text{dba}+\text{dba}^2+\text{hcov}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day}+\text{day}^2)$	14	1051.24	0	0.26
	$\lambda(\text{dba}+\text{dba}^2+\text{lba}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day}+\text{day}^2)$	14	1051.43	0.19	0.23
	$\lambda(\text{dba}+\text{dba}^2+\text{lba}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	15	1052.44	1.2	0.14
	$\lambda(\text{dba}+\text{dba}^2+\text{hcov}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	15	1052.71	1.47	0.12
Pileated Woodpecker (<i>Hylatomus pileatus</i>)	$\lambda(.) p(.)$	2	1147.72	96.48	0.00
	$\lambda(.) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	10	913.04	0	0.17
	$\lambda(\text{dba}+\text{dba}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	12	913.38	0.33	0.14
	$\lambda(\text{hcov}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	11	913.63	0.59	0.12
	$\lambda(\text{lba}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	11	914.33	1.29	0.09
	$\lambda(\text{dba}+\text{dba}^2+\text{hcov}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	13	914.35	1.31	0.09
	$\lambda(\text{dba}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	11	914.37	1.33	0.09
	$\lambda(\text{mdens}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	11	914.48	1.44	0.08
	$\lambda(\text{dba}+\text{dba}^2+\text{lba}) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	13	914.65	1.61	0.07
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	$\lambda(.) p(.)$	2	943.12	30.08	0.00
	$\lambda(\text{dba}+\text{dba}^2+\text{lba}+\text{lba}^2+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day})\text{NB}$	15	1976.93	0	0.31
	$\lambda(\text{dba}+\text{dba}^2+\text{lba}+\text{lba}^2+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day})$	14	1977.28	0.35	0.26
	$\lambda(\text{dba}+\text{dba}^2+\text{lba}+\text{lba}^2) p(\text{year}+\text{day})\text{NB}$	13	1977.82	0.9	0.20
	$\lambda(\text{dba}+\text{dba}^2+\text{lba}+\text{lba}^2) p(\text{year}+\text{day})$	12	1978.41	1.49	0.15
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	$\lambda(.) p(.)$	2	2063.5	86.57	0.00
	$\lambda(\text{dba}+\text{dba}^2+\text{lba}+\text{mdens}+\text{mdens}^2) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	15	1569.79	0	0.88
	$\lambda(.) p(.)$	2	1857.74	287.95	0.00

Table 3.4 continued

Species	Model	K	AIC	ΔAIC	wi
Nest Predators/Parasites					
American Crow (<i>Corvus brachyrhynchos</i>)	$\lambda(lba+lba^2) p(\text{year}+\text{day})\text{NB}$	11	1464.65	0	0.89
	$\lambda(.) p(.)$	2	1551.46	86.81	0.00
Brown-headed Cowbird (<i>Molothrus ater</i>)	$\lambda(lba*mdens) p(\text{year}+\text{day}+\text{day}^2)\text{NB}$	13	1492.64	0	1.00
	$\lambda(.) p(.)$	2	1620.77	128.13	0.00
Blue Jay (<i>Cyanocitta cristata</i>)	$\lambda(lba+lba^2) p(\text{year}+\text{day})\text{NB}$	11	1169	0	0.67
	$\lambda(lba+lba^2+mdens) p(\text{year}+\text{day})\text{NB}$	12	1170.42	1.43	0.33
	$\lambda(.) p(.)$	2	1231.11	62.11	0.00

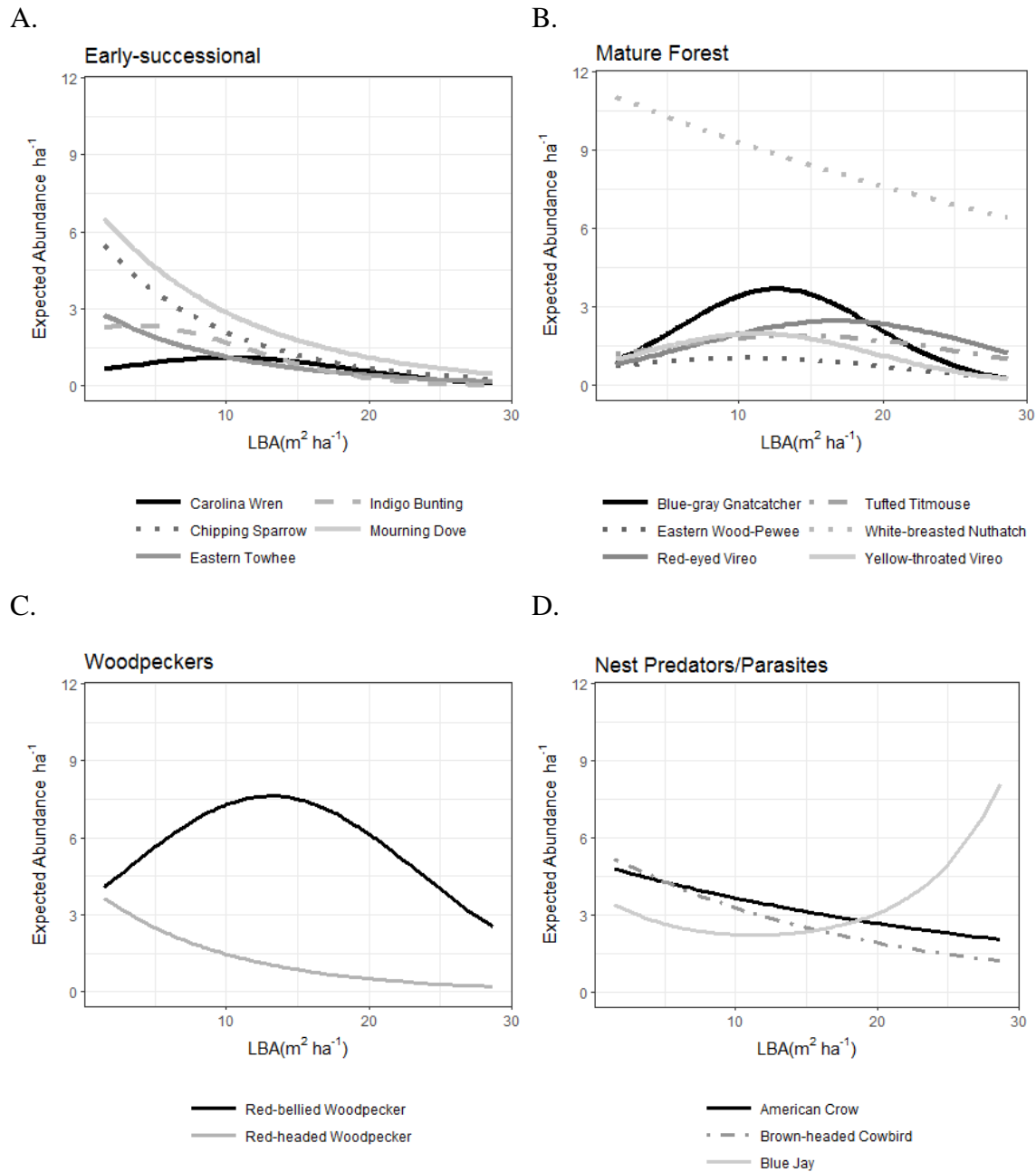
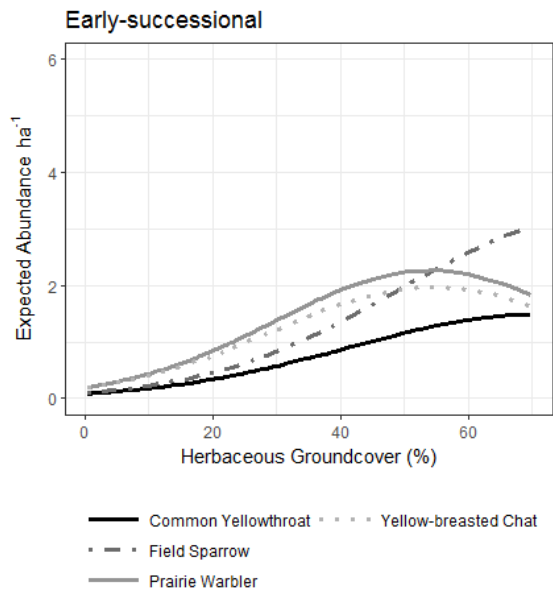
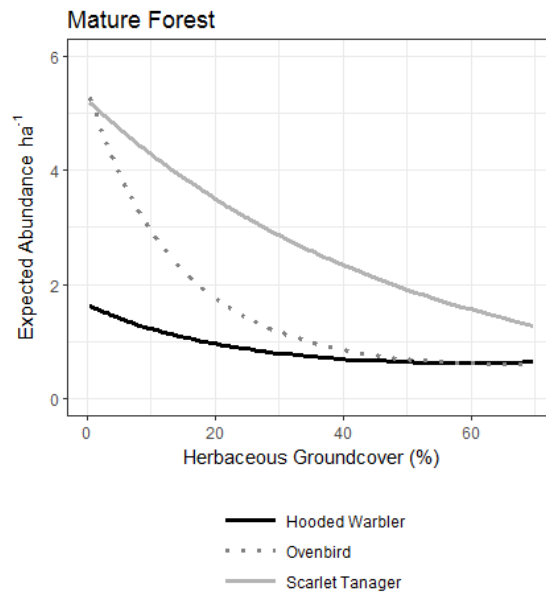


Figure 3.1 Species with live basal area in the top model and beta estimate 95% confidence intervals that did not include zero in an avian abundance analysis for an oak savanna and woodland restoration experiment conducted at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes, TN, 2010–2016. If additional covariates were present in the top model, presented variables are displayed at mean values of the other variable(s). Relationships are presented by 4 groups: early-successional passerines (including mourning dove), mature forest passerines, woodpeckers, and nest predators/parasites.

A.



B.



C.

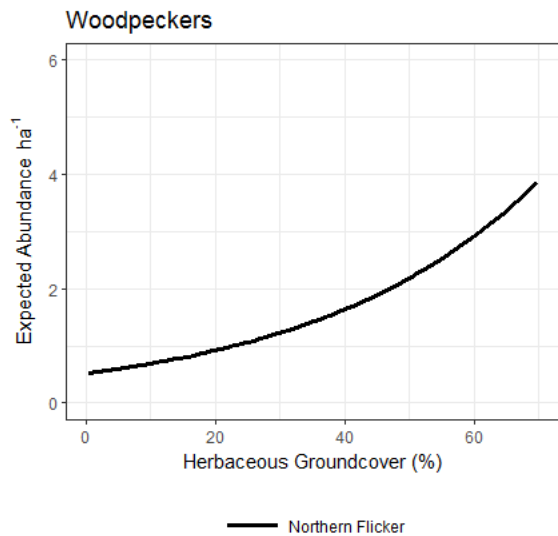


Figure 3.2 Species with herbaceous groundcover in the top model and beta estimate 95% confidence intervals that did not include zero in an avian abundance analysis for an oak savanna and woodland restoration experiment conducted at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes, TN, 2010–2016. If additional covariates were present in the top model, presented variables are displayed at mean values of the other variable(s). Relationships are presented by 3 groups: early-successional passerines, mature forest passerines, and woodpeckers.

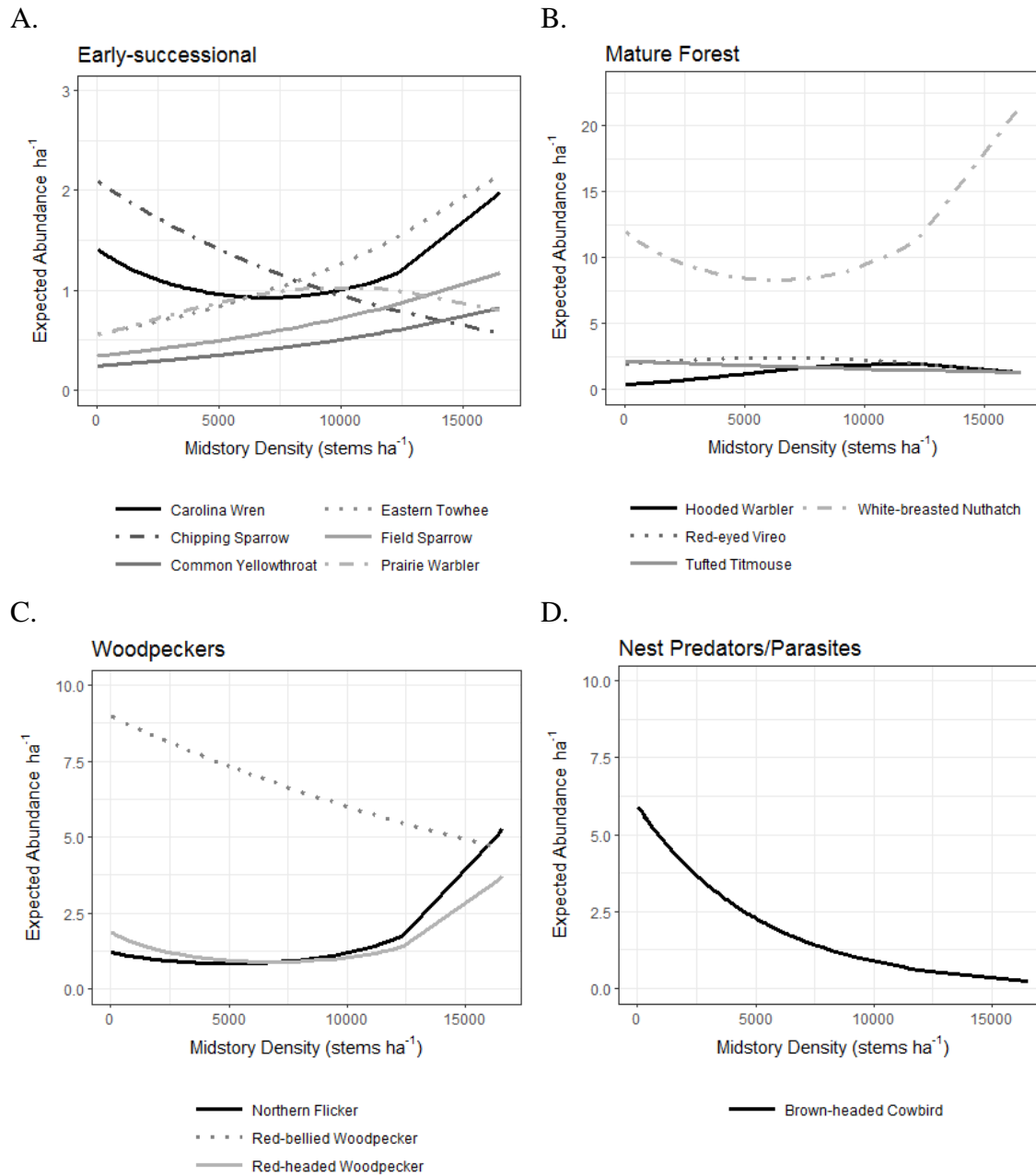


Figure 3.3 Species with midstory density in the top model and beta estimate 95% confidence intervals that did not include zero in an avian abundance analysis for an oak savanna and woodland restoration experiment conducted at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes, TN, 2010–2016. If additional covariates were present in the top model, presented variables are displayed at mean values of the other variable(s). Relationships are presented by 3 groups: early-successional passerines, mature forest passerines, and woodpeckers.

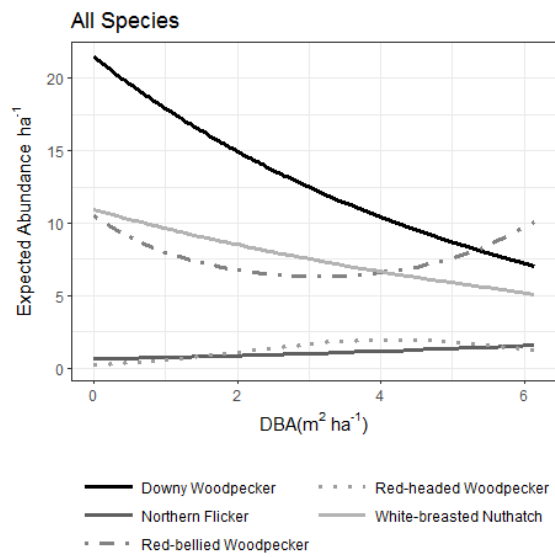


Figure 3.4 Species with dead basal area in the top model and beta estimate 95% confidence intervals that did not include zero in an avian abundance analysis for an oak savanna and woodland restoration experiment conducted at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes, TN, 2010–2016. If additional covariates were present in the top model, presented variables are displayed at mean values of the other variable(s).

Table 3.5 Beta estimates from each species' top abundance model from an avian abundance analysis for an oak savanna and woodland restoration experiment conducted at Catoosa Wildlife Management Area, TN, Green River Game Lands, NC, and Land Between the Lakes, TN, 2010-2016.

Species	Covariate	β	SE	LCL	UCL
Early-successional					
Carolina Wren (<i>Thryothorus ludovicianus</i>)	Intercept	1.1449	0.2068	0.7396	1.5502
	lba	-0.2923	0.0650	-0.4197	-0.1649
	lba ²	-0.2757	0.0608	-0.3949	-0.1565
	mdens	-0.1507	0.0754	-0.2985	-0.0029
	mdens ²	0.0752	0.0236	0.0289	0.1215
Chipping Sparrow (<i>Spizella passerina</i>)	Intercept	1.4909	0.3869	0.7326	2.2492
	lba	-0.7093	0.1144	-0.9335	-0.4851
	mdens	-0.3316	0.1506	-0.6268	-0.0364
	mdens ²	0.0508	0.0528	-0.0527	0.1543
Common Yellowthroat (<i>Geothlypis trichas</i>)	Intercept	0.0323	0.4401	-0.8303	0.8949
	hcov	1.0058	0.1597	0.6928	1.3188
	hcov ²	-0.1677	0.0677	-0.3004	-0.0350
	mdens	0.2190	0.0942	0.0344	0.4036
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	Intercept	0.8980	0.2080	0.4903	1.3057
	lba	-0.6590	0.0618	-0.7801	-0.5379
	mdens	0.2420	0.0854	0.0746	0.4094
	lba:mdens	0.1780	0.0578	0.0647	0.2913
Field Sparrow (<i>Spizella pusilla</i>)	Intercept	0.3351	0.4497	-0.5463	1.2165
	hcov	1.1187	0.1518	0.8212	1.4162
	hcov ²	-0.1579	0.0555	-0.2667	-0.0491
	mdens	0.4104	0.1612	0.0944	0.7264
	mdens ²	-0.0492	0.0371	-0.1219	0.0235
Indigo Bunting (<i>Passerina cyanea</i>)	Intercept	1.2260	0.1239	0.9832	1.4688
	lba	-0.9700	0.0628	-1.0931	-0.8469
	lba ²	-0.3070	0.0481	-0.4013	-0.2127
Mourning Dove (<i>Zenaida macroura</i>)	Intercept	1.8620	0.6206	0.6456	3.0784
	lba	-0.6050	0.0886	-0.7787	-0.4313

Table 3.5 continued

Species	Covariate	β	SE	LCL	UCL
Earl-successional (cont.)					
Prairie Warbler (<i>Setophaga discolor</i>)	Intercept	0.9495	0.1115	0.7310	1.1680
	hcov	1.0070	0.0709	0.8680	1.1460
	hcov ²	-0.2502	0.0352	-0.3192	-0.1812
	mdens	0.2210	0.0726	0.0787	0.3633
	mdens ²	-0.0544	0.0219	-0.0973	-0.0115
Yellow-breasted Chat (<i>Icteria virens</i>)	Intercept	0.8520	0.1509	0.5562	1.1478
	hcov	0.9460	0.0801	0.7890	1.1030
	hcov ²	-0.2310	0.0423	-0.3139	-0.1481
Mature Forest					
Black-and-white Warbler (<i>Mniotilta varia</i>)	Intercept	1.3660	0.8080	-0.2177	2.9497
	year2011	2.8410	1.0750	0.7340	4.9480
	year2012	0.3640	1.4880	-2.5525	3.2805
	year2014	0.7800	1.6560	-2.4658	4.0258
	year2015	-1.2260	0.8570	-2.9057	0.4537
	year2016	0.6390	1.2230	-1.7581	3.0361
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	Intercept	2.4400	0.5395	1.3826	3.4974
	lba	-0.1100	0.0513	-0.2105	-0.0095
	lba ²	-0.4260	0.0517	-0.5273	-0.3247
Eastern Wood-Pewee (<i>Contopus virens</i>)	Intercept	1.1377	0.1491	0.8455	1.4299
	lba	-0.1473	0.0529	-0.2510	-0.0436
	lba ²	-0.1666	0.0487	-0.2621	-0.0711
	mdens	-0.0886	0.0541	-0.1946	0.0174
Hooded Warbler (<i>Setophaga citrina</i>)	Intercept	1.1158	0.1573	0.8075	1.4241
	hcov	-0.3723	0.0601	-0.4901	-0.2545
	hcov ²	0.0794	0.0397	0.0016	0.1572
	mdens	0.5888	0.0705	0.4506	0.7270
	mdens ²	-0.1269	0.0283	-0.1824	-0.0714
Ovenbird (<i>Seiurus aurocapilla</i>)	Intercept	1.7300	0.5115	0.7275	2.7325
	hcov	-0.7990	0.0701	-0.9364	-0.6616
	hcov ²	0.1470	0.0549	0.0394	0.2546

Table 3.5 continued

Species	Covariate	β	SE	LCL	UCL
Mature Forest (cont.)					
Red-eyed Vireo (<i>Vireo olivaceus</i>)	Intercept	1.9876	0.1322	1.7285	2.2467
	lba	0.2002	0.0341	0.1334	0.2670
	lba ²	-0.1906	0.0304	-0.2502	-0.1310
	mdens	0.0779	0.0438	-0.0079	0.1637
	mdens ²	-0.0543	0.0232	-0.0998	-0.0088
Scarlet Tanager (<i>Piranga olivacea</i>)	Intercept	2.4050	1.6044	-0.7396	5.5496
	hcov	-0.3450	0.0645	-0.4714	-0.2186
Tufted Titmouse (<i>Baeolophus bicolor</i>)	Intercept	1.7703	0.2095	1.3597	2.1809
	lba	0.0241	0.0419	-0.0580	0.1062
	lba ²	-0.1171	0.0368	-0.1892	-0.0450
	mdens	-0.0964	0.0470	-0.1885	-0.0043
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	Intercept	3.3065	0.4009	2.5207	4.0923
	dba	-0.1509	0.0628	-0.2740	-0.0278
	lba	-0.1255	0.0607	-0.2445	-0.0065
	mdens	-0.1240	0.0855	-0.2916	0.0436
	mdens ²	0.0822	0.0278	0.0277	0.1367
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	Intercept	1.7790	1.5262	-1.2124	4.7704
	lba	-0.2020	0.0946	-0.3874	-0.0166
	lba ²	-0.2840	0.0923	-0.4649	-0.1031
Woodpeckers					
Downy Woodpecker (<i>Picoides pubescens</i>)	Intercept	3.8800	1.0862	1.7510	6.0090
	dba	-0.2200	0.0969	-0.4099	-0.0301
Hairy Woodpecker (<i>Leuconotopicus villosus</i>)	Intercept	1.9880	0.9810	0.0652	3.9108
	dba	-0.2340	0.1590	-0.5456	0.0776
Northern Flicker (<i>Colaptes auratus</i>)	Intercept	1.0497	0.6233	-0.1720	2.2714
	dba	0.3146	0.1344	0.0512	0.5780
	dba ²	-0.0671	0.0527	-0.1704	0.0362
	hcov	0.4933	0.0798	0.3369	0.6497
	mdens	-0.1131	0.1441	-0.3955	0.1693
	mdens ²	0.1331	0.0451	0.0447	0.2215
Pileated Woodpecker (<i>Hylatomus pileatus</i>)	Intercept	2.5800	0.5870	1.4295	3.7305

Table 3.5 continued

Species	Covariate	β	SE	LCL	UCL
Woodpeckers (cont.)					
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	Intercept	3.0759	0.5701	1.9585	4.1933
	dba	-0.1605	0.0707	-0.2991	-0.0219
	dba ²	0.0763	0.0366	0.0046	0.1481
	lba	-0.0093	0.0680	-0.1426	0.1239
	lba ²	-0.1900	0.0607	-0.3090	-0.0710
	mdens	-0.1826	0.0854	-0.3499	-0.0152
	mdens ²	0.0520	0.0329	-0.0125	0.1165
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	Intercept	1.1510	0.3399	0.4848	1.8172
	dba	0.7010	0.1209	0.4640	0.9380
	dba ²	-0.1830	0.0482	-0.2775	-0.0885
	lba	-0.6730	0.0907	-0.8508	-0.4952
	mdens	-0.2620	0.1231	-0.5033	-0.0207
	mdens ²	0.1370	0.0387	0.0611	0.2129
Nest Predators/Parasites					
American Crow (<i>Corvus brachyrhynchos</i>)	Intercept	2.4750	0.2733	1.9393	3.0107
	lba	-0.2320	0.0994	-0.4268	-0.0372
	lba ²	-0.1610	0.0908	-0.3390	0.0170
Brown-headed Cowbird (<i>Molothrus ater</i>)	Intercept	2.1480	0.4388	1.2880	3.0080
	lba	-0.3370	0.0971	-0.5273	-0.1467
	mdens	-0.5700	0.1383	-0.8411	-0.2989
	lba:mdens	-0.3730	0.0869	-0.5433	-0.2027
Blue Jay (<i>Cyanocitta cristata</i>)	Intercept	1.9620	0.4279	1.1233	2.8007
	lba	0.1140	0.0882	-0.0589	0.2869
	lba ²	0.1730	0.0710	0.0338	0.3122

CONCLUSION

In the eastern United States, ecosystems that rely on thinning and fire-related disturbance have been declining since European settlement. Additionally, disturbance-dependent birds have been disappearing from the landscape in recent years which can possibly be attributed to the decline in disturbed ecosystems such as oak savannas and woodlands. The objective of our research was to determine if oak savanna and woodland restoration was a useful method to recover early-successional species and increase their numbers in the Mid-South. We studied nest-site selection, nest survival, and avian abundance at three sites across the Mid-South. Closed-canopy stands were thinned and a 2-year burn schedule was implemented. At Catoosa Wildlife Management Area, in 2015 and 2016, Prairie Warblers (*Setophaga discolor*) had average nest success (0.937 ± 0.007) compared with other studies and selected for increased herbaceous groundcover around the nest compared with the available habitat. Nest survival in 2015 was considerably lower than in 2016, however. A positive linear trend between groundcover and nest survival was found. Red-headed Woodpeckers (*Melanerpes erythrocephalus*) had very high nest success (84.1%) compared with other studies and selected nest sites with greater herbaceous groundcover, dead basal area, and midstory density (in 2016) compared with the available habitat. A negative linear trend between live basal area and nest survival was found. After studying avian abundance at all three sites from 2010–2016 we found that moderate to high amounts of disturbance increased populations of early-successional species while low to moderate amounts of disturbance were found to either not affect or increase populations of most mature forest species. Oak savanna and woodland restoration is a viable method to increase populations of early-successional bird species, both in abundance and through nesting, while retaining most mature forest species.

VITA

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