LOW-BASAL AREA TREATMENT AND PRESCRIBED FIRE TO RESTORE OAK-PINE SAVANNAS ALTER SMALL MAMMAL COMMUNITIES

By

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Abstract: Following decades of fire suppression, many savanna ecosystems have changed drastically to dense forests. Restoration of these ecosystems is seen as a way to reduce woody encroachment, dangerous fuel loads, and loss of biological diversity. The management practices to achieve these goals, thinning and prescribed fire, have the potential to affect small mammal communities. Because small mammals exercise key ecosystem functions, changes in their community structure and in their habitat use through the direct and indirect effects of land management practices should be monitored carefully. The overall goal of this research was to determine the effects of low-basal area (BA) practices (thinning and prescribed fire) on small mammal communities in southeast Oklahoma. First, I determined how low-BA practices altered small mammal habitat. Low-BA practices significantly changed dominant ground covers and reduced litter and duff depths, BA of live trees, and the distance of vulnerability (DOV), a measure of understory vegetation structure and animal vulnerability to terrestrial predators. Overall, my results showed that low-BA practices increased ground layer productivity. Second, I assessed whether low-BA management practices altered the community structure of small mammal species in southeast Oklahoma. I found significant differences between the small mammal communities of thinned stands that were burned frequently (low-BA stands) and stands that were not thinned recently and not burned as frequently (high-BA stands). Significant differences in the capture rates of *Peromyscus leucopus* were documented and differences in the community assemblage between low- and high-BA stands were recorded. Third, I determined habitat preferences of three common small mammal species in southeast Oklahoma: *P. leucopus*, *P. maniculatus*, and *R. fulvescens*. All species preferentially selected low-BA stands. In low-BA stands, *P. leucopus* selected sites with higher volumes of coarse woody debris and longer DOV, while *P. maniculatus* selected sites with shorter DOV. In high-BA stands, *P. leucopus* selected sites with higher ground cover of down woody debris and longer DOV, while *P. maniculatus* did not appear to respond to those characteristics. *Reithrodontomys fulvescens* selected low-BA stands with shorter DOV. Knowing how low-BA practices affect small mammals can inform land managers on how to manage for small mammal diversity.

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CHAPTER I

INTRODUCTION

The thesis was written in four chapters, including this introduction. The second, third, and fourth chapters will be submitted for publication in appropriate peer-reviewed journals.

Fire was an important process that shaped the historical plant communities in the United States (Abrams 1992, Courtwright 2007). By suppressing fire in Oklahoma, Euro-American settlers altered an anthropogenic disturbance regime introduced by the native people and with which landscapes evolved (Day 1953, Stambaugh et al. 2013). Increased tree densities, denser midstories, changes in species composition, and decreased understory vegetation cover were consequences of fire suppression (Sparks et al. 1998, DeSantis et al. 2011). In southeast Oklahoma, oak-pine savannas turned into closed-canopy oak-pine forests.

Thinning, coupled with reintroduction of prescribed fires, is advocated as a management practice to reverse the effects of fire suppression (Brose and Van Lear 1998, Sparks et al. 1998, Andre et al. 2007). Fire alone can increase understory species richness, forbs, and C3 grass production (Burton et al. 2011). However, large trees are highly tolerant of fire and low intensity annual burns cannot open tree canopy (Burton et al. 2011). For this reason, oak-pine savanna restoration is more efficient when tree thinning, which reduces tree basal area (BA), precedes prescribed burning; prescribed burning can then maintain oak-pine savanna ecosystems in early successional stages (Masters et al. 1993). Other benefits of this restoration include increased forage production for ungulate species and increased habitat diversity (Masters et al. 1993).

However, management practices, such as thinning and prescribed fire, have the potential to affect small mammal communities (Homyack et al. 2005, Alford et al. 2012).

Small mammals exercise key ecosystem functions, and they can have positive and negative effects on other species and on landscapes. Through seed harvesting and caching, they promote seed dispersal and germination (Hollander and Vander Wall 2004). They also disperse mycorrhizal fungal spores through mycophagy and defecation (Ovaska and Herman 1986, Pyare and Longland 2001, Schickmann et al. 2012). By consuming grass litter, they can accelerate the cycling of nutrients (Hole 1981). They are important components of food webs: they prey upon bird eggs, insects, etc. and are preyed upon by many avian, reptilian, and mammalian species (e.g., Korschgen and Stuart 1972, Shepard et al. 2004, Rulison et al. 2012). Moreover, some species are hypothesized to regulate ectoparasite populations (Kaunisto et al. 2012), while other species are hosts to parasites and vectors of diseases (Charles et al. 2012, Pitts et al. 2013). Mole and rodent burrows can contribute to soil aeration and soil erosion (Hole 1981). Finally, small mammals can act as keystone ecological engineers. For instance, the middens of some woodrat species, such as *Neotoma albigula* Hartley (White-Throated Woodrat) and *Neotoma micropus* Baird (Southern Plains Woodrat), form nutrient-rich patches with distinct micro-climates favoring arthropod diversity (Whitford and Steinberger 2010). Small mammals can therefore be considered as bioindicators of ecological services; as such, changes in their community structure and in their habitat use through the direct and indirect effects of land management practices should be monitored carefully (Fuller et al. 2004, Pearce and Venier 2005). Studying the effects of oak-pine savanna restoration on small mammal communities is important because changes in small mammal communities could potentially alter ecosystem functions.

In the Ouachita Mountains of Oklahoma and Arkansas, fire and tree thinning (hereafter: low-BA practices) are increasingly being used to restore habitat to savannas similar to pre-settlement. Although small mammal response to low-BA practices have been studied in this region, most studies took place for a single season per year, possibly misinterpreting results by not looking into seasonal variation (Converse et al. 2006). For example, Masters et al. (1998) and Perry and Thill (2005) only studied the effect of low-BA practices on small mammal communities during winter. Moreover, these studies only used one type of trap, possibly biasing the species of small mammals captured (Dizney et al. 2008, Torre et al. 2010). Therefore, a study over several seasons and using two types of traps could improve our understanding of small mammal communities and their response to oak-pine savanna restoration in the Ouachita Mountains.

The overall goal of this research was to determine the effects of low-BA practices on small mammal species and communities in southeast Oklahoma. The findings from this research will be used to improve land management practices. The next three chapters report the research and its findings. Chapter II concerns effects of low-BA practices on habitat variables important for small mammal species. Chapter III concerns effects of low-BA practices on the community structure of small mammal species. Finally, chapter IV concerns small mammal habitat preferences through site occupancy modeling.

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CHAPTER II

LOW-BASAL AREA TREATMENT AND PRESCRIBED FIRE TO RESTORE OAK-PINE SAVANNAS ALTER SMALL MAMMAL HABITAT

ABSTRACT

Following decades of fire suppression many savanna ecosystems have changed drastically to dense forests. Restoration of these ecosystems is seen as a way to reduce woody encroachment, dangerous fuel loads, and loss of biological diversity. The management practices to achieve these goals, thinning and prescribed fire, have the potential to affect small mammal communities. I undertook a study to determine how thinning, followed by frequent prescribed fires (hereafter: low-basal area (BA) practices), influenced small mammal habitat in oak-pine tallgrass prairies in southeast Oklahoma. I focused on six habitat variables that can influence small mammal abundance and species composition: BA of live trees, BA of snags, volume of coarse woody debris (CWD), percent ground cover by functional group, forest floor depth, and the distance of vulnerability (DOV), a measure of understory vegetation structure and animal vulnerability to predators. Low-BA practices significantly increased the ground cover of graminoids, forbs, bare ground, and down woody debris and reduced the forest floor depth, BA of live trees, and DOV. Overall, my results showed that low-BA practices increased ground layer productivity. Thus, low-BA stands should favor small mammal species whose abundance is positively correlated with graminoid and forb production, and non-treated, high-BA stands should favor species whose presence is positively correlated with forest floor depth or BA of live trees. Therefore, different specialist small mammal species are expected to occupy low- and high-BA stands.

INTRODUCTION

In the South Central United States, landscapes evolved under a fire regime with a strong anthropogenic component (Day 1953, Courtwright 2007, Stambaugh et al. 2013). However, starting in the 1920’s, Euro-American settlers altered this disturbance regime through fire suppression (Guyette et al. 2006, Burton et al. 2011, DeSantis et al. 2011, Stambaugh et al. 2013). Increased tree densities, decreased understory vegetation biomass, denser midstories, and altered species composition followed, leading to changes in plant communities and vegetation structure (Sparks et al. 1998, DeSantis et al. 2011). In Oklahoma, closed-canopy oak-pine forests replaced open oak-pine savannas (Schuler et al. 2006, Burton et al. 2011, DeSantis et al. 2011), with potential consequences on forest productivity, carbon cycling, and many other ecological services.

Land managers have tried to recreate historic fire regimes to restore ecosystems to pre-settlement conditions, with limited success. For example, studies by Franklin et al. (2003) and Burton et al. (2011) determined that burning could not reduce the stem density of large trees (diameter at breast height > 3.8cm [Franklin et al. 2003] or > 5.0cm [Burton et al. 2011]). However, frequent prescribed fires following tree thinning (hereafter: low-basal area [BA] practices) can successfully maintain reduced tree densities and increase understory vegetation productivity (Brose and Van Lear 1998, Sparks et al. 1998, Masters et al. 2009).

The primary objective of this study was to compare habitat characteristics between stands treated for lower BA (hereafter: low-BA stands) and stands treated for higher BA (hereafter: high-BA stands). Because this study was part of a larger project determining the effects of low-BA practices on small mammal communities, I focused on six habitat variables that can influence small mammal abundance and species composition. (1) BA of live trees: Some species, such as *Reithrodontomys fulvescens* Allen (Fulvous Harvest Mouse) and *Sigmodon hispidus* Say and Ord (Cotton Rats) are associated with low-BA stands (Masters et al. 1998, Perry and Thill 2005). This association likely reflects their use of ground layer monocots as forage, which usually increases with low-BA practices (Masters et al. 1998). (2) BA of snags: Snags can provide nesting and cover for small mammal species and thus can be one of the “most important covariates in predicting small mammal occupancy” (Kalies et al. 2012). (3) Coarse woody debris (CWD): Small mammals can use CWD as corridors for movement, nesting habitat, cover, and forage grounds (Pearce and Venier 2005, Fauteux et al. 2012). The abundance of some species of small mammals, such as *Peromyscus gossypinus* (LeConte) (Cotton Mouse), is positively correlated with CWD (Loeb 1999). (4) Ground cover: Jones et al. (2003), Stancampiano and Schnell (2004), and Kalies et al. (2012) observed significant affinities between small mammals and ground cover types; these relationships were species specific and based on macro- and micro-habitat analyses. These findings reflect the relative importance of different ground cover as forage, nesting habitat, refuges, etc. for different small mammal species. (5) Forest floor (litter and duff) depths: Differences in litter depth influence the abundance of shrew prey (Churchfield 1982, Ober and DeGroote 2011) and can provide a moderated micro-climate protecting shrews from extreme temperatures and low humidity (Matlack et al. 2002). As such, the abundance of some shrew species, e.g., *Blarina hylophaga* Elliot (Elliot's Short-Tailed Shrew), can be significantly correlated with litter depth (Matlack et al. 2002). (6) Distance of vulnerability (DOV): The DOV is a measure of understory vegetation structure and animal vulnerability to predators. Although the DOV has not been used to assess small mammal habitat characteristics, studies such as Perry and Thill’s (2005) have determined that understory vegetation structure can influence the abundance of small mammal species.

Because low-BA practices typically convert closed-canopy, oak-pine forests to open oak-pine savannas, I expected low-BA practices to cause major changes in small mammal habitat. For example, low-BA practices should increase the amount of light that reaches the ground layer, which, in turn, should increase the cover of graminoids and forbs. Increased fire frequencies in the low-BA stands should reduce the amount of time available for litter and duff to accumulate. Moreover, lower tree BA should result in lower canopy production of litter. Therefore, the cover of litter and the depth of the forest floor should be significantly lower in low-BA stands. Lower tree BA should also result in less potential sources of CWD and snags. Therefore, the BA of snags and the volume of CWD should be lower in the low-BA stands. Finally, by increasing vegetation productivity at the ground layer, low-BA practices should decrease the DOV. These habitat changes should benefit some small mammal species while hindering the persistence of others.

FIELD-SITE DESCRIPTION

Pushmataha Wildlife Management Area (PWMA) is located at the western edge of the Ouachita Highland Province (34°32’N, 95°21’W) near Clayton, Oklahoma. The 15-year daily average air temperature for Clayton ranged from 5.1°C in winter to 28.9 °C in summer while the average yearly rainfall was 113.9 cm (Oklahoma Climatological Survey 2014a, b).

The Oklahoma Department of Wildlife Conservation (ODWC) established PWMA as a deer refuge in 1946 (Masters 1991); it now covers 7,690 ha of rugged terrain. PWMA was divided into management units with different treatments. Management tools included prescribed burning, tree thinning, and brush hogging. Thinning was conducted by hydro-axe feller bunchers, skidders with grapples, de-limbers, loaders, and logging trucks. Hand tools were also occasionally used. No tree thinning occurred in proximity to water courses to maintain riparian corridors and to protect streams (J. Waymire - ODWC, pers. comm. 2013). The main goal of the management practices was to enhance habitat for game species such as *Odocoileus virginianus* [Zimmermann] (White-tailed Deer), *Cervus elaphus* L. (Elk) and *Meleagris gallopavo silvestris*, Vieillot (Eastern Wild Turkey) (Masters and Engle 1994). For example, restoring savannas should improve forage quality and quantity for ungulates.

Habitat variables were measured in four low- and four high-BA stands (Figure 1). The soil in these stands belonged to the Carnasaw-Stapp association characterized by moderately to well-drained slowly permeable soils (Soil Survey Staff **-** NRCS 2013, National Cooperative Soil Survey 2014a, b). Between 2008 and 2009, contractors were instructed to thin trees to 6.9 m^2ha^{-1} in the low-BA stands. These stands were burned 6 or 7 times in the past 17 years and were last burned in March 2013. Low-BA stands were oak-pine savannas, dominated by *Quercus stellata* Wangenh. (Post Oak) and *Pinus echinata* Mill. (Shortleaf Pine). The understory of these stands was strongly dominated by *Schizachyrium scoparium* (Michx.) Nash (Little Bluestem), *Andropogon gerardii* Vitman (Big Bluestem), and *Carex* L. spp (Sedges). In contrast, high-BA stands were closed-canopy oak-pine forests dominated by *Q. stellata* and *P. echinata* with minor canopy components of *Q. marilandica* Münchh. (Blackjack Oak) and *Carya tomentosa* (Lam. ExPoir.) Nutt. (Mockernut Hickory). Litter was the major ground cover in these stands. High-BA stands had not been thinned for at least 20 years and were last burned in 2003 or 2011. They had been burned 3 or 5 times in the past 17 years. Prior to thinning, low-BA stands were structurally similar to high-BA stands.

METHODS

Small Mammal Habitat Measurements

In each stand, habitat variables were measured at 10 m intervals along a 370 m transect, for a total of 37 samples per stand. To reduce edge effects, transects were located in the middle of stands ≥ 2.5 ha not dissected by roads (active or abandoned) or watercourses. Moreover, stands with human infrastructure or water bodies were avoided. I identified potential stands in ArcMap**™** 10.0 (ESRI), then did a final selection through field reconnaissance. Because the same transects were used for small mammal trapping (Chapters III and IV), sample points were the same as Sherman trap locations, except where there were Sherman and pitfall traps at a trapping location. At these locations, sample points were moved to the mid-point between traps. To minimize variation due to temporal change, each habitat variable was measured across all stands in a period of 10 days or less. Measurements were taken between May and August 2013.

The BA of live trees was measured with a Criterion® RD 1000 (Laser Technology Inc.) set at a BA factor of 2.296 m^2ha^{-1}. Trees included in the BA count were recorded by species. To determine if borderline trees should be included in the count, diameter and distance from the observer were recorded. The same procedure was used to determine the BA of snags.

CWD volume was assessed by measuring all logs within a circle of 6 m diameter (area = 28.3 m^2). CWD was defined as any woody debris longer than 91 cm, larger than 7.5 cm in diameter, < 45° from horizontal, and detached from a tree. The length (L), diameter at the small end (d), and diameter at the large end (D) of all logs were recorded. The volume of each log was calculated using the formula of the frustum of a right circular cone:

$$\text{Volume} = 1/3\pi L[(d/2)^2 + D/2*d/2 + (D/2)^2]. \tag{1}$$

The volume of all logs within a circle was then totaled and transformed to m^3ha^{-1}.

The same circle used for CWD measurements was also used to estimate ground cover by functional group, following the Daubenmire method (Daubenmire 1959). The functional groups were: graminoids with basal rosettes (e.g., *Dichantelium* Gould [rosette grass]), other graminoids, forbs, legumes, litter, woody plants, rocks, bare ground, and down woody debris (DWD). The percent ground cover of graminoids was divided into two categories, because graminoids with basal rosettes can provide forage that is higher in nutrients during winter when food is scarce (Short 1971, Masters et al. 1993). DWD included any woody debris with a diameter ≥ 6 mm, < 45° from horizontal, and detached from a tree.

Litter and duff depths were measured in each cardinal direction, 1m from each sample point. Forest floor depth was defined as the sum of litter and duff depths. All measurements for the DOV were also taken in each cardinal direction. I used a modified version of the protocol for the “cone of vulnerability” by Kopp et al. (1998). Instead of calculating a volume within which an animal was vulnerable to predators (cone of vulnerability), I measured the distance at which the animal was vulnerable to predators (distance of vulnerability). To represent a small mammal, I used an oversize tennis ball (diameter: 7.0cm) spray-painted in blue and cut in half. I laid the half-ball directly on the ground and recorded the minimum distance at which the object was 100 percent obstructed from my view, 1m from the ground. For each measurement, I also recorded the main category responsible for the visual obstruction. The potential obstacle categories were: woody plants, forbs and legumes, graminoids, stumps and snags, topography, rocks, and woody debris.

Data Analysis

Means were calculated for each sample point when a variable was measured more than once at a sample point. For each variable, means were then calculated at each stand to produce four means in low-and four means in high-BA stands. Using Levene’s test, the mean of each variable in low- and high-BA stands were tested for homogeneity of variance (Snedecor and Cochran 1980). The effect of low-BA practices compared to high-BA practices was determined by the *t*-test (n = 8). For each variable, Bonferroni adjustments were performed when necessary: three measures of BA were tested, so α was adjusted to 0.017; nine functional groups were tested for ground cover, so α was adjusted to 0.006; and the importance of seven visual obstacles was compared for the DOV, so α was adjusted to 0.007. All statistical analyses were performed in IBM SPSS Statistics for Windows version 21.0 (IBM Corp 2012).

RESULTS

Low-BA treatments reduced the total BA of all live trees (4.4 ± 0.6 m^2ha^{-1} vs 22.6 ± 1.1 m^2ha^{-1}, $P < 0.001$), including hardwoods (3.1 ± 0.3 m^2ha^{-1} vs 9.0 ± 0.5 m^2ha^{-1}, $P < 0.001$) and conifers (1.3 ± 0.4 m^2ha^{-1} vs 13.6 ± 1.2m^2ha^{-1}, $P < 0.001$, Figure 2). The sole conifer species, *P. echinata*, was present in all stands. *Quercus stellata* was found in all low- and high-BA stands, *C. tomentosa*, and *Q. marilandica* were found in all high-BA stands but in none of the low-BA stands, while *Ulmus alata* Michx. (Winged Elm) and *Q. velutina* Lam. (Black Oak) were only found in three of the four high-BA stands. The mean BA of all live trees in low-BA stands was lower than the management goal of 6.9 m^2ha^{-1} ($P = 0.02$). Low-BA practices did not significantly reduce the BA of snags (0.4 ± 0.2 m^2ha^{-1} vs 1.0 ± 0.2 m^2ha^{-1}, $P = 0.053$).

The abundance of CWD was not significantly affected by low-BA practices ($P = 0.465$). Mean values for CWD were 7.3 ± 1.3 m^3ha^{-1} in low-BA stands and 5.4 ± 2.0 m^3ha^{-1} in high-BA stands (Figure 3).

Low-BA practices significantly increased the percent ground cover of graminoids without basal rosettes ($P = 0.001$), forbs ($P = 0.004$), bare ground ($P < 0.001$), and DWD ($P = 0.005$), and significantly decreased the percent ground cover of litter ($P < 0.001$), but had no significant effect on the percent ground cover of graminoids with basal rosettes ($P = 0.422$), legumes ($P = 0.552$), woody plants ($P = 0.131$), or rocks ($P = 0.224$) (Figure 4). The most prevalent ground covers in low-BA stands were graminoids without basal rosettes (68.4 ± 5.7 %), rocks (23.4 ± 11.3 %), and forbs (13.8 ± 1.7 %), compared to litter (76.6 ± 5.1 %), graminoids without basal rosettes (20.4 ± 5.4 %), and woody plants (17.8 ± 3.9 %) in high-BA stands.

The forest floor depth was shallower in low-BA stands compared to high-BA stands. Low-BA treatments reduced litter (0.6 ± 0.1 cm vs 2.7 ± 0.2 cm, $P = 0.001$) and duff depths (0.6 ± 0.1 cm vs 1.2 ± 0.1 cm, $P = 0.002$, Figure 5).

The DOV was significantly lower in low-BA stands (3.6 ± 0.5 m) compared to high-BA stands (8.7 ± 0.3m, $P < 0.001$, Figure 6). The most important visual obstacles in low-BA stands were graminoids (75.2 ± 4.5 %), woody plants (10.1 ± 2.9 %), and forbs and legumes (7.9 ± 2.4 %) compared to woody plants (58.2 ± 4.6 %), graminoids (20.3 ± 5.8 %), and topography (11.1 ± 3.2 %) in high-BA stands. Graminoids were significantly more important visual obstacles in low-BA stands than in high-BA stands ($P < 0.001$), while woody vegetation was a significantly less important visual obstacle in low-BA stands than in high-BA stands ($P < 0.001$). Other obstacles were not significantly different between low- and high-BA stands (Figure 7).

DISCUSSION

At PWMA, low-BA practices caused important changes in small mammal habitat. The percent ground cover by functional group was strongly affected, the forest floor depth was shallower, and the DOV was shortened by more than fifty percent.

Only two species of trees, *P. echinata* and *Q. stellata* were part of the BA counts in all low-BA stands compared to four to six species in the high-BA stands. This could be the result of either selective thinning in low-BA stands or of differences in the original species composition between low and high-BA stands. However, the species only found in high-BA stands, *C. tomentosa*, *Q. marilandica*, *Q. velutina*, and *U. alata*, were infrequently encountered.

As expected, low-BA practices reduced the BA of live trees. My results provided evidence that the management goal to reduce the BA of trees to 6.9 $m^2 ha^{-1}$ was missed due to cutting too severely in the low-BA stands. High-BA stands should therefore favor small mammal species whose niche requirements include denser stands, while low-BA stands should favor species thriving in more open habitats.

Although low-BA treatments should have reduced the source of snags and CWD, results did not show fewer snags and a smaller volume of CWD in low-BA stands. My findings likely reflected the short time interval between the thinning process and the data collection. A study by Polo et al. (2013) in the Cross-Timbers of Oklahoma determined that different fire frequencies did not significantly affect the volume of snags or CWD. At the PWMA, increased prescribe fire and thinning also did not seem to alter the volume of snags or CWD. Management practices at PWMA thus encouraged the short-term retention of snags and CWD. Snags and CWD can benefit small mammal species by providing cover, nesting habitat, forage grounds, and running corridors (Kalies et al. 2012).

As expected, the percent ground cover of graminoids without basal rosettes and forbs was higher in low-BA stands than in high-BA stands. These findings were consistent with Masters et al. (1993) who found that thinning and prescribed burning increased the percent cover of graminoids and forbs. I found that the percent ground cover of legumes was not significantly different between low- and high-BA stands, while Masters et al. (1993) found that thinning and prescribed burning tended to increase the percent ground cover of legumes, but not consistently. Based on my results and those from Masters et al. (1993), small mammal species that feed primarily on understory vegetation, such as *S. hispidus* (Fleharty and Olson 1969, Kincaid and Cameron 1985), should benefit from low-BA practices.

Although I expected the percent ground cover of graminoids with basal rosettes to be significantly higher in low-BA stands than in high-BA stands, my results showed no significant difference. This prediction was based on an earlier study that concluded thinning and prescribed burning caused a higher standing crop of graminoids with basal rosettes (Masters et al. 1993). The contrasting results could either be due to the timing of the ground cover measurements (*Dichantelium* were not fully grown at the time of the survey) or to the low sample size. The results also revealed that the percent ground cover of woody vegetation was not significantly different between low- and high-BA stands. These results were consistent with those from Masters et al. (1993).

Low-BA practices significantly increased the percent cover of bare ground and down woody debris. Although the effect was statistically significant, it is arguable that the 1.8% difference for down woody debris may not be biologically meaningful to small mammal species, which may not perceive this difference.

There are two explanations for the higher percent ground cover of litter and deeper forest floor in the high-BA stands. First, higher BA resulted in greater canopy production of litter. Second, longer time since fire in the high-BA stands resulted in more time to accumulate litter and duff compared to low-BA stands. All low-BA stands were last burned in 2013 while three of the high-BA stands were last burned in 2011 and one in 2003. According to litter accumulation equations from earlier research (Stambaugh et al. 2006, Bale 2009), stands burned in 2011 would have had litter depths 53 to 59% of equilibrium; stands burned in 2003, 98 to 99%; and stands burned in 2013, less than 10%. It appears the greater amount of herbaceous vegetation in the low-BA stands did not make up for the loss of litter production by trees or for the shorter accumulation time between fires. By having a greater forest floor depth that provides protection from extreme temperatures and low humidity (Matlack et al. 2002), high-BA stands should provide suitable habitat for *B. hylophaga* (Matlack et al. 2002).

As expected, low BA-practices significantly lowered the DOV. A more productive ground layer (i.e., increased graminoid and forb production) in the low-BA stands provided more obstacles reducing the DOV. In comparison, high-BA stands were characterized by a scarcity of visual obstacles, which indicated a less complex understory structure. Therefore, in the low-BA stands, a predator would have to be closer to a small mammal to see it (and vice-versa), which may alter small mammal behavior.

CONCLUSION

Low-BA practices altered key characteristics of small mammal habitat in the Ouachita Mountains of southeast Oklahoma. Between low- and high-BA stands, I found significant differences in ground cover, forest floor depth, BA of live trees, and the DOV. Overall, my results showed that low-BA stands had a more productive ground layer than high-BA stands. Low-BA stands should thus favor small mammal species whose abundance is positively correlated with graminoid and forb production. In contrast, high-BA stands should favor species whose presence is positively correlated with litter and duff depths or BA of live trees. Therefore, different specialist small mammal species are expected to occupy low- and high-BA stands.

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FIGURES

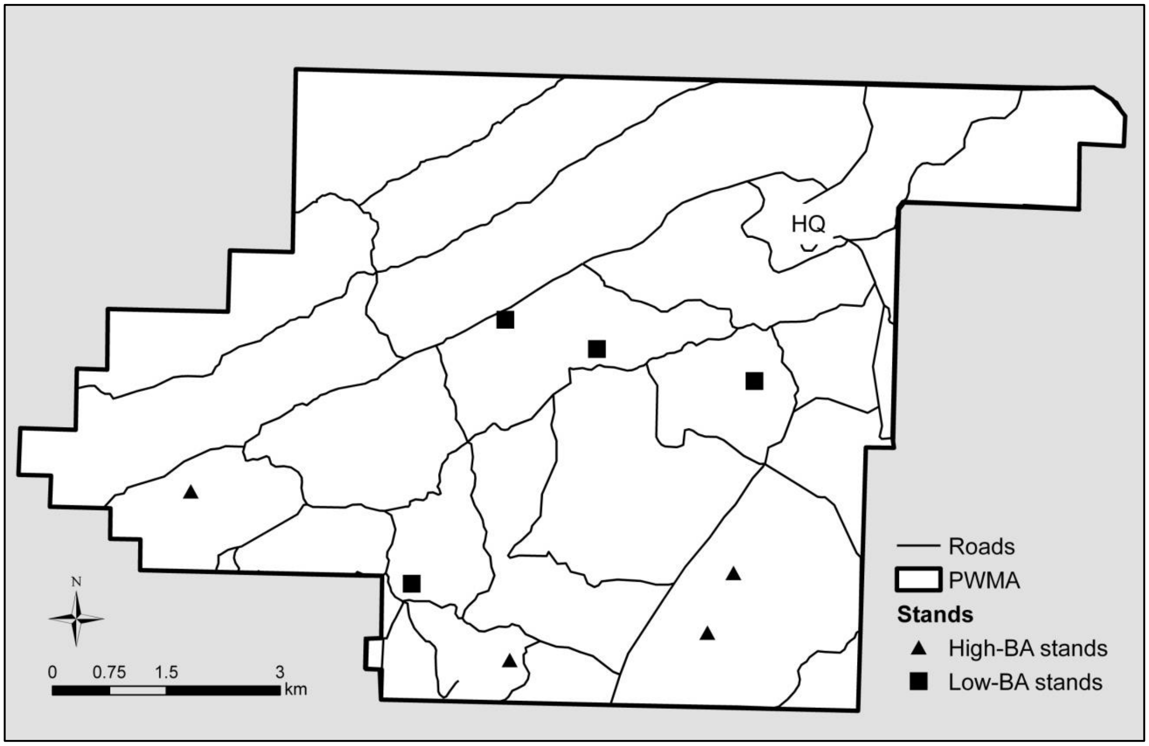

Figure 1: Stand location at PWMA. Roads were used for fire breaks and treatment boundaries.

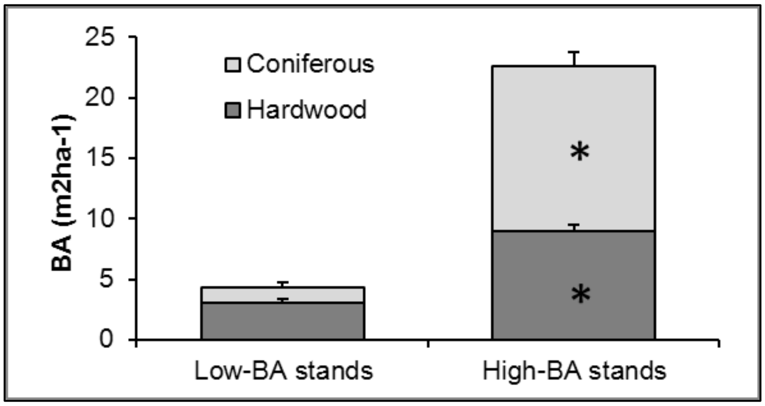

Figure 2: Effects of low-BA practices on the BA of hardwood and coniferous species. Asterisks indicate significant treatment effects (*P*<0.001). Thin bars represent standard errors.

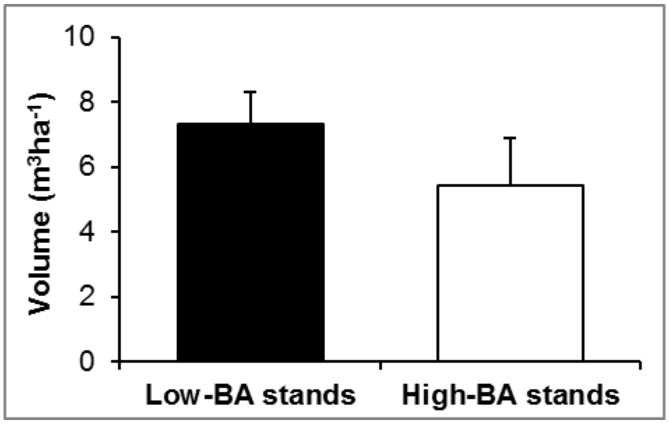

Figure 3: Effects of low-BA practices on CWD volume. Treatment effects were not significant (*P*=0.465). Thin bars represent standard errors.

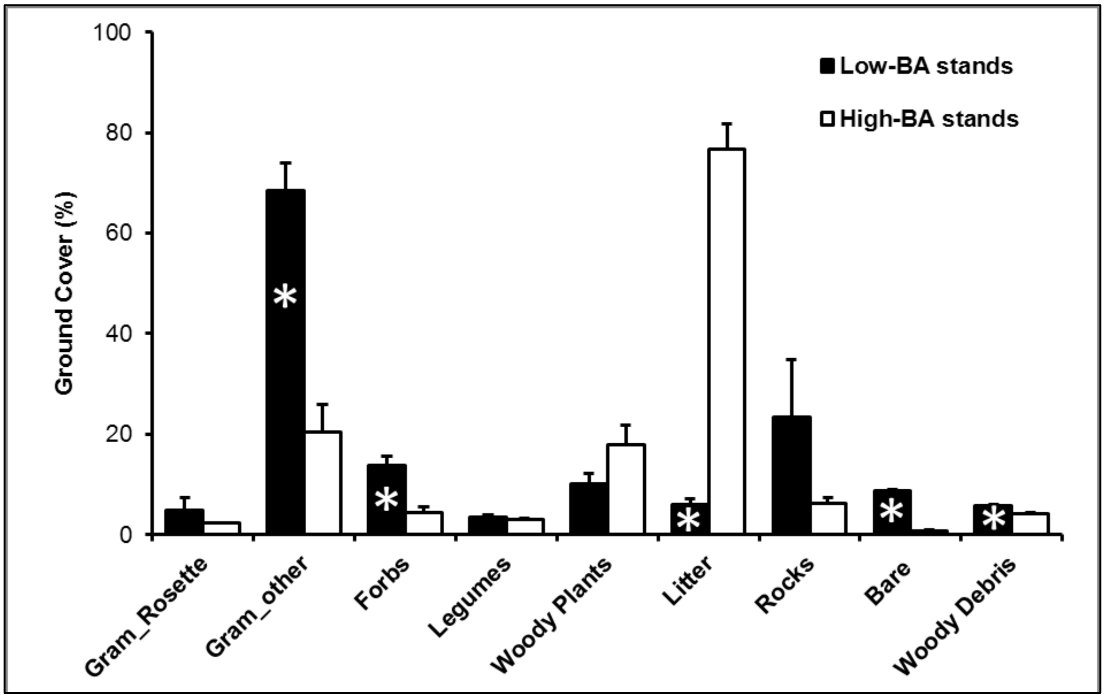

Figure 4: Effects of low-BA practices on percent ground cover. Asterisks indicate significant treatment effects (*P*<0.006). Thin bars represent standard errors. “Gram_Rosette”: graminoids with basal rosettes; “Gram_Other”: graminoids without basal rosettes.

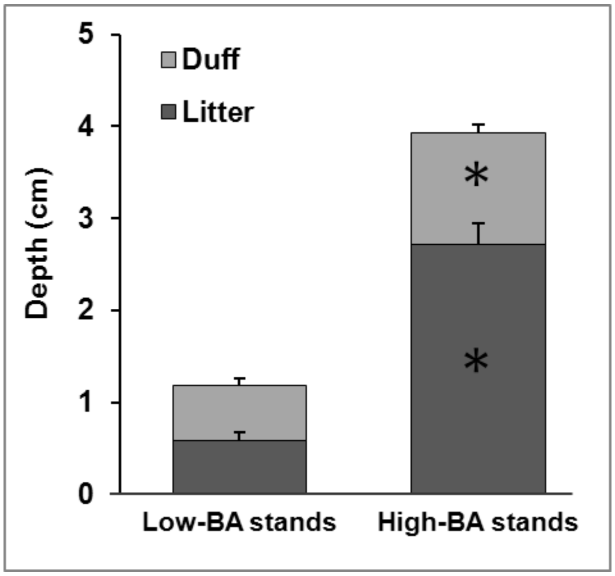

Figure 5: Effects of low-BA practices on forest floor depth. Asterisks indicate significant treatment effects (litter: *P*=0.001; duff: *P*=0.002). Thin bars represent standard errors.

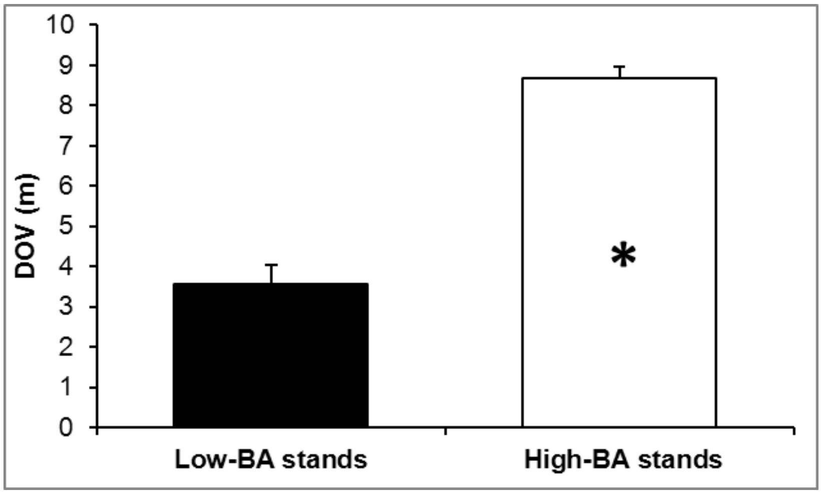

Figure 6: Effects of low-BA practices on DOV. The asterisk indicates significant treatment effects (*P*<0.001). Thin bars represent standard errors.

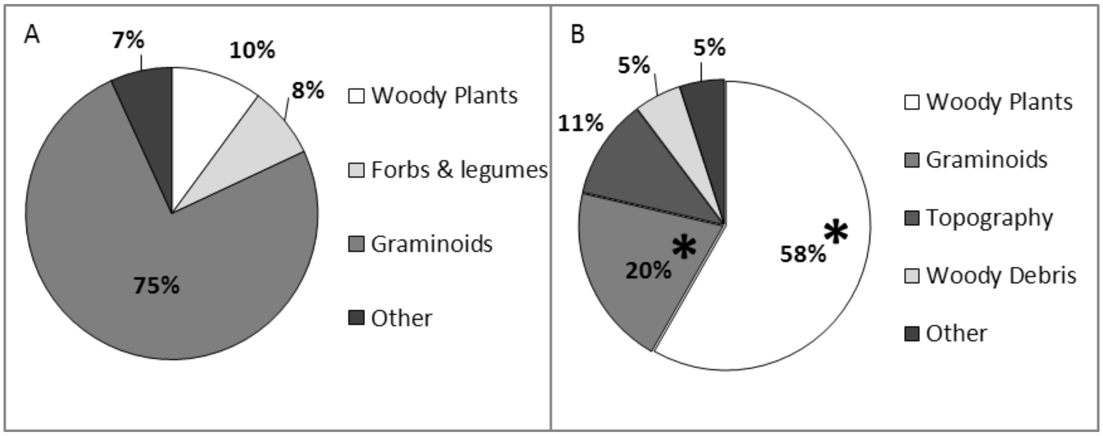

Figure 7: Effects of low-BA practices on relative importance of visual obstructions in low- (A) and high-BA stands (B). Asterisks indicate significant treatment effects (*P*<0.001). "Other" includes obstacles responsible for less than 5% of obstructions (stumps and snags, topography, rocks, and woody debris (A) or stumps and snags, forbs, and legumes, and rocks (B).

CHAPTER III

LOW-BASAL AREA TREATMENT AND PRESCRIBED FIRE TO RESTORE OAK-PINE SAVANNAS ALTER SMALL MAMMAL COMMUNITIES

ABSTRACT

Small mammals provide crucial ecosystem services such as seed and mycorrhizal fungal spore dispersal, nutrient cycling, and soil aeration. It is important to assess the effects of land management practices on their communities, because changes in small mammal communities could potentially alter ecosystem functions. Thinning, followed by prescribed burning (hereafter: low-basal area [BA] practices), is advocated to restore savannas that have changed to dense forests following decades of fire suppression. The primary objective of this study was to assess whether low-BA management practices altered the community structure of small mammal species in southeast Oklahoma. I found significant differences between the small mammal communities of thinned stands that were burned frequently (low-BA stands) and stands that were not thinned recently and not burned as frequently (high-BA stands). Findings included significant differences in the capture rate of *Peromyscus leucopus* and in the community assemblage between low- and high-BA stands. *Cryptotis parva*, *Reithrodontomys fulvescens*, *R. humulis*, and *Sigmodon hispidus* were caught only in low-BA stands, while *Mus musculus*, *R. montanus,* and *P. attwateri* were caught only in high-BA stands. These results suggest land managers should maintain low- and high-BA stands to ensure small mammals species diversity.

INTRODUCTION

Small mammals provide crucial ecosystem services such as seed and mycorrhizal fungal spore dispersal (Pyare and Longland 2001, Hollander and Vander Wall 2004, Schickmann et al 2012), nutrient cycling (Hole 1981), and soil aeration (Hole 1981). They are also important components of food webs (Korschgen and Stuart 1972, Shepard et al. 2004, Rulison et al. 2012). It is important to assess the response of small mammal communities to management practices, such as thinning and prescribed burning, because changes in small mammal communities could potentially alter ecosystem services.

Fire suppression by Euro-American settlers starting in the 1920's led to perceptible habitat changes including increased basal area (BA), denser midstories, changes in species composition, and decreased understory vegetation (Sparks et al. 1998, DeSantis et al. 2011). In Oklahoma, open oak-pine savannas turned into closed-canopy oak-pine forests (Schuler et al. 2006, Burton et al. 2011, DeSantis et al. 2011). Thinning, followed by prescribed burning (hereafter: low-BA practices), is an advocated management practice to restore oak-pine savannas (Brose and Van Lear 1998, Sparks et al. 1998, Andre et al. 2007, Masters et al. 2009).Thinning can be used to reduce tree BA, and then frequent fires can maintain the habitat at an early successional stage (Masters et al. 1993). However, animal communities that have developed in high-BA stands for the past 50-100 years may change following low-BA practices. Moreover, management practices occurring at the edge of a species range may cause changes in its distribution by altering the habitat (Gaston 2009).

Small mammals often respond to savanna restoration on a species-specific basis. For example, species whose abundance is positively correlated with litter depth should respond negatively to low-BA practices, because fire consumes litter and lower BA results in lower canopy production of litter (chapter II). One such species, *Blarina hylophaga* Elliot (Elliot's

Short-Tailed Shrew), seeks out deeper litter because deeper litter moderates extreme temperatures and humidity, and litter depth also influences prey abundance (Churchfield 1982, Matlack et al. 2002, Ober and DeGroote 2011). In contrast, species whose abundance is negatively correlated with BA should benefit from low-BA practices. For example, *Reithrodontomys fulvescens* Allen (Fulvous Harvest Mice) and *Sigmodon hispidus* Say and Ord (Hispid Cotton Rats) use grasses as forage (Masters et al. 1998, Perry and Thill 2005). By increasing graminoid production, low-BA practices should indirectly increase the abundance of *R. fulvescens* and *S. hispidus.* Moreover, the response of a species to fire and thinning can vary temporally and spatially (Converse et al. 2006). Therefore, it is important to study the response of small mammal communities at the location of interest and over multiple seasons.

Scientists have investigated the response of small mammal communities to savanna restoration in southeast Oklahoma and across the Ouachita Mountains. However, they often reached conclusions using data gathered over only one season of the year and only using one type of trap. For example Masters et al. (1998) and Perry and Thill (2005) only trapped small mammals during winter, with Sherman live traps. By not taking into account seasonal variability in small mammal communities, they might have over-simplified community structures. Moreover, using more than one type of trap could have maximized the number of individuals and species caught (Dizney et al. 2008, Torre et al. 2010). Therefore, a study over several seasons and using multiple trapping methods could greatly improve our understanding of small mammal communities and their response to oak-pine savanna restoration in southeast Oklahoma.

The primary objective of my study was to assess whether low-BA practices altered the community structure of small mammal species. To do so, I compared small mammal communities in stands where frequent prescribed fires followed thinning (hereafter: low-BA stands) with those in stands that have not been thinned within the past 20 years and were not burned as frequently (hereafter: high-BA stands). I hypothesized that low-BA practices would induce significant changes in small mammal communities. The study was conducted throughout the year to learn whether the results were seasonally variable. Both Sherman live traps and pitfall live traps were used to more thoroughly sample the small mammal community.

FIELD-SITE DESCRIPTION

The research took place at Pushmataha Wildlife Management Area (PWMA) in Pushmataha County, southeast Oklahoma (34°32’N, 95°21’W). PWMA is located near Clayton at the western edge of the Ouachita Mountains and is comprised of steep slopes and rocky terrain. The average temperature for the past 15 years ranged from 4.9 °C (winter) to 28.9 °C (summer), with an average yearly rainfall of 113.8 cm (Oklahoma Climatological Survey 2014a, b).

PWMA covers 7,690 ha and was established as a deer refuge in 1946 (with expansions occurring in 1949 and 1950) by the Oklahoma Department of Wildlife Conservation (ODWC) (Masters 1991). The ODWC managed PWMA for game species, such as *Odocoileus virginianus* (Zimmermann) (White-tailed Deer), *Cervus elaphus* L. (Elk), and *Meleagris gallopavo silvestris* Vieillot (Eastern Wild Turkey) (Masters and Engle 1994). Management practices varied by location, but included: prescribed fires (no fires to yearly fires), tree thinning to 7 or 14 m^2ha^{-1}, and brush hogging at predetermined locations (J. Waymire - ODWC, pers. comm. 2013).

Small mammal communities were compared between four low- and four high-BA stands (Figure 1). In the low-BA stands, trees had been thinned between 2008 and 2009. In contrast, trees had not been thinned within the past 20 years in the high-BA stands. Low-BA stands had been burned 5 or 6 times between 1997 and 2012 and were burned in March 2013 prior to the start of this study. Moreover, two of the four low-BA stands were burned during the course of the study (February 2014). In comparison, high-BA stands had been burned 3 to 5 times between

1997 and 2012 and none were burned in 2013. Only one high-BA stand was burned during the course of the study (March 2014). Low-BA stands were oak-pine savannas, while high-BA stands were oak-pine forests. Prior to thinning, low-BA stands were also oak-pine forests. The dominant tree species in low- and high-BA stands were *Quercus stellata* Wangenh. (Post Oak) and *Pinus echinata* Mill. (Shortleaf Pine). The understory of low-BA stands was dominated by *Schizachyrium scoparium* (Michx.) Nash (Little Bluestem), *Andropogon gerardii* Vitman (Big Bluestem), and *Carex* L. spp (Sedges), while the ground surface in high-BA stands was mostly covered in litter.

METHODS

Small Mammal Sampling

Small mammal communities were sampled on 370 m long transects (one per stand). To reduce edge effects, transects were located in the middle of stands at least 420 m by 60 m without roads (active or abandoned), human infrastructure, water bodies, or watercourses. To reduce variability in habitat caused by soil types, all stands were located in the Carnasaw-Stapp association, based on a USDA soil map (Soil Survey Staff **-** NRCS 2013). Potential stands fitting these descriptions were identified using orthoimagery and vector layers in ArcMap™ 10.0 (ESRI). Field reconnaissance was conducted to confirm suitability of stand locations.

Small mammal trapping and handling was compliant with protocols from the Institutional Animal Care and Use Committee (ACUP AG-12-16). In each low- and high-BA stand, I set up one permanent trapping transect made of 37 trapping stations spaced 10 m apart. Transects were chosen over grid trapping because transects are more efficient than grids for studying small mammal community composition (Pearson and Ruggiero 2003). A combination of Sherman live traps (7.6 x 8.9 x 22.9 cm) and pitfall live traps was used to maximize the number of individuals and species captured (Dizney et al. 2008, Torre et al. 2010). One Sherman trap was placed within 1 m of every trapping station and one pitfall trap was installed within 2 m of every third trapping station, for a total of 37 Sherman (10 m apart) and 12 pitfall traps (30 m apart) per transect. The pitfall traps were made of PVC pipes (with aluminum screen mesh at the bottom) buried flush to the ground (16.25 cm [diameter] x 20.3 cm [depth]). Woody debris or rocks found within 1 m (Sherman trap) or 2 m (pitfall traps) of a trapping station were used to act as drift fences directing small mammals into the traps. Between trapping sessions, all Sherman traps were removed and pitfall traps were closed.

Sampling occurred in April, June, and September 2013 (spring, summer, and fall 2013), and in January and March 2014 (winter 2013 and spring 2014). During each sampling periods, traps were opened for three nights. I checked traps in the mornings and closed them during the day to reduce risk of heat-induced mortality. I also added polyester bedding in the traps to reduce risk of hypothermia-induced mortality during colder months (Matlack et al. 2008). Sherman traps were baited with a mixture of peanut butter and rolled oats (Stancampiano and Schnell 2004, Johnston and Anthony 2008, Matlack et al. 2008). Because shrews are mostly caught in pitfall traps and have a high metabolic rate that puts them at risk of death by dehydration, I added approximately 30 g of wet dog food to the pitfall traps. However, *Solenopsis invicta* Buren (Red Imported Fire Ant; hereafter, fire ants) were attracted to the trapping stations, especially to dog food. Therefore I did not use dog food during the second and third day of trapping in June. A modification to the ACUP protocol was approved, allowing for the use of 5% Carbaryl insecticide (GardenTech® Sevin-5 Ready to Use 5 % Dust) around all traps in subsequent sampling periods.

All animals captured were marked under the chin with a felt-tip permanent marker, identified to species, and released at the site of capture. The marking technique was chosen because it was non-invasive, required little training, and should have lasted for the duration of each sampling period. However, identifying recaptured animals was not always possible.

Small Mammal Habitat Measurements

During summer 2013, I measured six habitat variables: coarse woody debris (CWD), percent ground cover, forest floor depths (i.e., litter and duff depths), BA of live trees, BA of snags, and the distance of vulnerability (DOV), a measure of ground vegetation structure and animal vulnerability to predation. Measurements were taken around each trapping station, and then averaged by stand. For a complete descriptions of habitat measurement protocols, please refer to chapter II.

Data Analysis

Each stand had a single transect and was considered a sampling unit. Low capture rates made it necessary to combine data for separate seasons before analysis: (1) spring 2013 and 2014, (2) summer, fall, and winter 2013, and (3) all sampling periods combined. Because identifying recaptured animals was not possible for all sampling periods, analyses were performed using new captures and recaptures combined. Bonferroni adjustments were implemented ($\alpha = 0.017$), because the analyses were performed three times.

To compare capture rates and species composition, I used the frequency of captured small mammal species (number of traps containing a species divided by the number of adjusted trap-nights) as a measure of abundance. I adjusted the number of trap-nights to account for unavailable traps (empty sprung traps and closed traps with a captured animal) as per Beauvais and Buskirk (1999):

Number of adjusted trap-nights = (number of traps * number of nights opened)

$$- (\text{number of unavailable traps} * 0.5). \qquad (1)$$

Using Levene's test, the mean capture rates between low- and high-BA stands were tested for homogeneity of variance (Snedecor and Cochran 1980). I then performed *t*-tests in IBM SPSS Statistics for Windows version 21.0 (IBM Corp 2012) to determine whether the capture rates were significantly different (Heisler et al. 2013). This analysis was performed for abundant species (≥ 20 captures) and for all species combined.

For each sampling unit, I estimated species richness by rarefaction in EstimateS version 9 (Colwell 2013), with the Chao2 estimator (Brose 2002). To determine whether species richness was different between low-BA and high-BA stands, I then performed a *t*-test in IBM SPSS Statistics for Windows version 21.0 (IBM Corp 2012).

A Canonical Correspondence Analysis (CCA) was executed to determine if small mammal communities were different between low- and high-BA stands (ter Braak 1986). This analysis was performed in Canoco 5.03 (ter Braak and Šmilauer 2013) using BA as the sole explanatory variable tested. For the analysis, frequencies were log-transformed and rare species were down weighted.

In an exploratory analysis, I determined what environmental variables were correlated with differences in small mammal species composition between low- and high-BA stands. To do so, I performed a Detrended Correspondence Analysis (DCA, Hill and Gauch Jr. 1980) in Canoco 5.03 (ter Braak and Šmilauer 2013). For the analysis, frequencies were log-transformed, rare species were down weighted, and habitat variables were used as supplementary variables.

RESULTS

5396.5 adjusted trap-nights resulted in 274 captures from 10 small mammal species (Tables 1, 2). Only one species, *Cryptotis parva* (Say) (Least Shrew), was captured in pitfall traps; all other species were caught in Sherman traps. Capture rates were low, ranging from 1.9 % in winter 2013 to 12.5 % in spring 2014, with an average trapping success of 5.1 % per sampling period.

The pooled capture rate for all species from all sampling periods combined was not significantly different between low- and high-BA stands (n = 274, *P* = 0.031). Only three species were caught ≥ 20 times: *Peromyscus leucopus* (Rafinesque) (White-Footed Mouse, n = 176), *P. maniculatus* (Wagner) (Deer Mouse, n = 32), and *R. fulvescens* (n = 33). Low-BA practices significantly increased the capture rate of *P. leucopus* (*P* = 0.002), but not *P. maniculatus* (Figure 2). *Reithrodontomys fulvescens* was only caught in low-BA stands.

The pooled spring capture rate (2013 & 2014) for all species combined was not significantly different between low- and high-BA stands (n = 188, *P* = 0.074). Three species were caught ≥ 20 times: *P. leucopus* (n = 115), *P. maniculatus* (n = 22), and *R. fulvescens* (n = 29). Low-BA practices did not significantly alter the capture rates of *P. leucopus* or *P. maniculatus* (Figure 3). However, *R. fulvescens* was only caught in low-BA stands.

The pooled capture rates for summer, fall, and winter 2013 for all species combined was not significantly different between low- and high-BA stands (n = 86, *P* = 0.049). *Peromyscus leucopus* was the only species caught ≥ 20 times during these sampling periods (n = 61); low-BA practices significantly increased its capture rate (*P* = 0.016, Figure 4).

Low-BA practices did not significantly alter species richness for all sampling periods combined, for spring captures (2013 and 2014) only, or for captures from summer, fall, and winter 2013 only (Table 3).

The CCA for all sampling periods combined revealed different small mammal community compositions between low- and high-BA stands (*P* = 0.002, Figure 5). The CCA primary axis (BA) had a fairly high eigenvalue of 0.3070 while the eigenvalue of the 1st residual axis (0.1953) was lower. This implies that low-BA practices had a relatively strong influence on small mammal communities. *Cryptotis parva*, *R. fulvescens*, *R. humulis* [Audubon and Bachman] [Eastern Harvest Mouse], and *S. hispidus* were only caught in low-BA stands; *Mus musculus* L. (House Mouse), *P. attwateri* Allen [Texas Mouse], and *R. montanus* (Baird) (Plains Harvest Mouse) were only captured in high-BA stands; *P. gossypinus* (LeConte) (Cotton Mouse), *P. leucopus*, and *P. maniculatus* were caught in both low- and high-BA stands.

The CCA for captures from spring 2013 and 2014 combined showed the same pattern (*P* = 0.002, Figure 6). *Cryptotis parva*, *R. humulis*, *R. fulvescens*, and *S. hispidus* were only caught in low-BA stands; *M. musculus*, and *P. attwateri* were only captured in high-BA stands; *P. gossypinus*, *P. leucopus*, and *P. maniculatus* were caught in both low- and high-BA stands.

The CCA for captures from summer, fall, and winter 2013 also showed that low- and high-BA stands had different small mammal community compositions (*P* = 0.002, Figure 7). *Reithrodontomys fulvescens* and *S. hispidus* were only caught in low-BA stands; *R. montanus* and *P. gossypinus* were only captured in high-BA stands; and *P. leucopus* and *P. maniculatus* were caught in both low- and high-BA stands.

Low- and high-BA stands also formed two distinct groups along the DCA primary axis for all captures combined, and for pooled spring (2013 and 2014) captures only (Figure 8a, 9).

The primary axis thus likely represented BA for these time periods. There was an overlap between low- and high-BA stands when analyzing captures from summer, fall, and winter 2013 only (Figure 10). The primary axis for these pooled sampling periods is thus unknown.

Figure 8b displays habitat variables as supplementary variables for the DCA for all sampling periods combined (similar results were obtained for other time periods). The following habitat variables were strongly positively correlated at PWMA: snags BA, litter depth, woody plant ground cover, litter ground cover, tree BA, DOV, and duff depth. However, these variables were strongly negatively correlated with rocky ground cover, graminoids without basal rosettes ground cover, forbs ground cover, bare ground cover, woody debris ground cover, and CWD volume. Because of the strong positive and negative correlations between the habitat variables, I was not able to determine which variables caused small mammal communities to respond to low-BA practices.

DISCUSSION

Low-BA practices altered small mammal communities in southeast Oklahoma. The most noticeable effect of low-BA practices was the difference in the assemblage of small mammal communities between low- and high-BA stands. Differences in the capture rate of *P. leucopus* were also documented. Moreover, the second most frequently captured species, *R. fulvescens*, was only caught in low-BA stands.

Low capture rates prevented a separate analysis for each season. Severe and moderate drought conditions that persisted until April of 2013 (NOAA 2014a, b) likely partly explained these low capture rates in 2013 (NOAA 2014a, b). The big increase in capture rates in spring 2014 may have resulted from more normal moisture conditions for the rest of 2013 and early 2014 allowing small mammal populations to recover from the drought. However, the only other small mammal study at PWMA also experienced relatively low trapping success over a range of conditions from normal moisture to severe drought (M. Howery - ODWC, pers. comm. 2014).

Thinning, followed by frequent prescribed fires, did not significantly alter the overall small mammal capture rate. However, low-BA practices strongly increased the capture rate of *P. leucopus* for all sampling periods combined and for summer, fall, and spring 2013 sampling periods. These results contradicted those from previous studies that found *P. leucopus* in greater densities in high-BA stands (Baker 1968, Linzey et al. 2012). This may reflect differences in detection probabilities and/or geographic differences for the preferred habitat of *P. leucopus*. Unfortunately, problems with the marking technique prevented an analysis with detection probabilities.

The second species most frequently caught, *R. fulvescens*, was only captured in low-BA stands. These results were consistent with previous research according to which *R. fulvescens* typically is a grassland species (Kincaid et al. 1983, Spencer and Cameron 1988, Turner and Grant 1987).

The effects of low-BA practices on species richness tend to vary geographically and with time since disturbance (Fisher and Wilkinson 2005). For example, Sullivan et al. (2008) did not find significant differences in species richness of sites with different BA in mixed Douglas Fir - Lodgepole Pine forests of British Columbia. However, Alford et al. (2012) found that small mammal species richness was higher following tree removal in tallgrass prairies of Oklahoma. At PWMA, small mammal species richness was not significantly influenced by low-BA practices.

Although I found significant differences in small mammal communities between low- and high-BA stands, other factors could have contributed to this difference. For example, a greater abundance of fire ants were observed in low-BA stands compared to high-BA stands (personal observation, but also reported in other studies, e.g., Todd et al. 2008). The greater abundance of fire ants in low-BA stands could explain some of the variation reported (Pedersen et al. 2003). Therefore, results should be interpreted cautiously.

Interpreting what habitat variables most likely explained variation in small mammal communities was complicated by the high correlation among habitat variables, as shown in the DCA plot. Much of this correlation was directly or indirectly caused by the management practices. For example, thinning reduced stand BA; this allowed more light to reach the ground layer. In turn, more forbs and graminoids were produced, and this increase in forbs and graminoids then led to a shorter DOV. To speculate on what habitat variables likely contributed to differences in community structure between low- and high-BA stands, I will draw parallels between the results of this study and results obtained from other studies.

My results showed that *P. leucopus* was more closely associated with low-BA stands. Previous research showed that habitat selection by *P. leucopus* can be influenced by multiple factors such as burning regime, tree density, complexity of the understory layer, volume of woody debris, and density of shrubs, graminoids, and forbs (Kaufman et al. 1983, McMurry et al. 1996, Greenberg 2002, Masters et al. 2002, Anderson and Meikle 2006). For example, Masters et al. (2002) found the abundance of *P. leucopus* was positively correlated with dead woody debris and woody biomass in the understory. However, at PWMA, the CWD volume and percent ground cover of woody vegetation were not significantly different between low- and high-BA stands (chapter II). Because *P. leucopus* is a generalist species, the positive response to low-BA practices may have been due to the increased ground layer productivity and understory complexity.

At PWMA, *P. maniculatus* was captured in low- and high-BA stands. *P. maniculatus* is a generalist species that usually inhabits grassland, but can persist in forests or in shrublands (Mert

1981, Mayfield et al. 2000). The species is omnivorous, and primarily feeds on insects, miscellaneous vegetation, and sometimes ripe-seeds (Kritzman 1974, Pitts and Barbour 1979, Whitaker, Jr. 1966). This broad diet likely allowed it to inhabit both low- and high-BA stands at PWMA.

Sigmodon hispidus was only caught in low-BA stands at PWMA. Masters et al. (1998) also found *S. hispidus* to be associated with harvested stands in the Ouachita Mountains of Oklahoma and Arkansas. My results were also similar to Perry and Thill's (2005) who found this species "associated with grassy understories and relatively low-BA". Because *S. hispidus* uses ground layer monocots as forage (Masters et al. 1998), it is not surprising that it would be associated with low-BA stands at PWMA.

Because of the likelihood of misinterpreting habitat preferences for species caught infrequently, I will not speculate on the habitat preferences of the following species: *C. parva* (n = 2), *Mus musculus* (n = 4), *P. attwateri* (n = 1), *P. gossypinus* (n = 6), *R. humulis* (n = 3), and *R. montanus* (n = 3). However, it is important to point out that *M. musculus* was the only non-native species caught at PWMA. Most studies have shown that *M. musculus* is most commonly associated with human infrastructure such as houses and barns (Caire et al.1989). Even though no infrastructure was located within 30 m of any transects, remnants of old fences, roads, and building foundations were scattered throughout PWMA. Captures from this species likely reflected the ranching history of PWMA.

CONCLUSION

Oak-pine savanna restoration induced changes in small mammal communities in southeast Oklahoma. I found significant differences in the capture rates of *P. leucopus* and in the small mammal community assemblage between thinned stands that were burned frequently (open oak-pine savannas) and stands that were not thinned recently and not burned as frequently (closed-canopy oak-pine forests). Because small mammals exercise key ecosystem functions, low-BA practices could have indirect effects on nutrient cycling, food webs, seed germination, etc. However, the low sample size and capture rates may have affected the results and conclusion should be interpreted with this in mind.

The results of this study suggested land managers should maintain low- and high-BA stands to assure small mammals species diversity. Low-BA practices create habitat for savanna obligates, while high-BA stands provide habitat for species inhabiting forest patches.

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TABLES

	Spring 2013	Summer 2013	Fall 2013	Winter 2013	Spring 2014	Total
Soricomorph	1	0	0	0	1	1
Rodent	7	4	3	5	6	9

Table 1: Number of species captured by season and order.

	Spring 2013	Summer 2013	Fall 2013	Winter 2013	Spring 2014	Total
Soricomorph	1	0	0	0	1	2
Rodent	52	28	35	22	134	271
Capture Rates (%)	5.9	2.5	3.1	1.9	12.5	5.1

Table 2: Number of captures by season and order.

Sampling Periods	**Species Richness**		
	Low-BA Stands	**High-BA Stands**	***P* value**
Spring, summer, fall, and winter 2013 and spring 2014	6.22 ± 0.731	5.48 ± 0.494	0.437
Spring 2013 and 2014	6.42 ± 0.935	4.43 ± 0.564	0.119
Summer, fall, and winter 2013	3.52 ± 0.322	4.02 ± 0.429	0.385

Table 3: Effects of low-BA practices on species richness. Treatment effects were not significant.

FIGURES

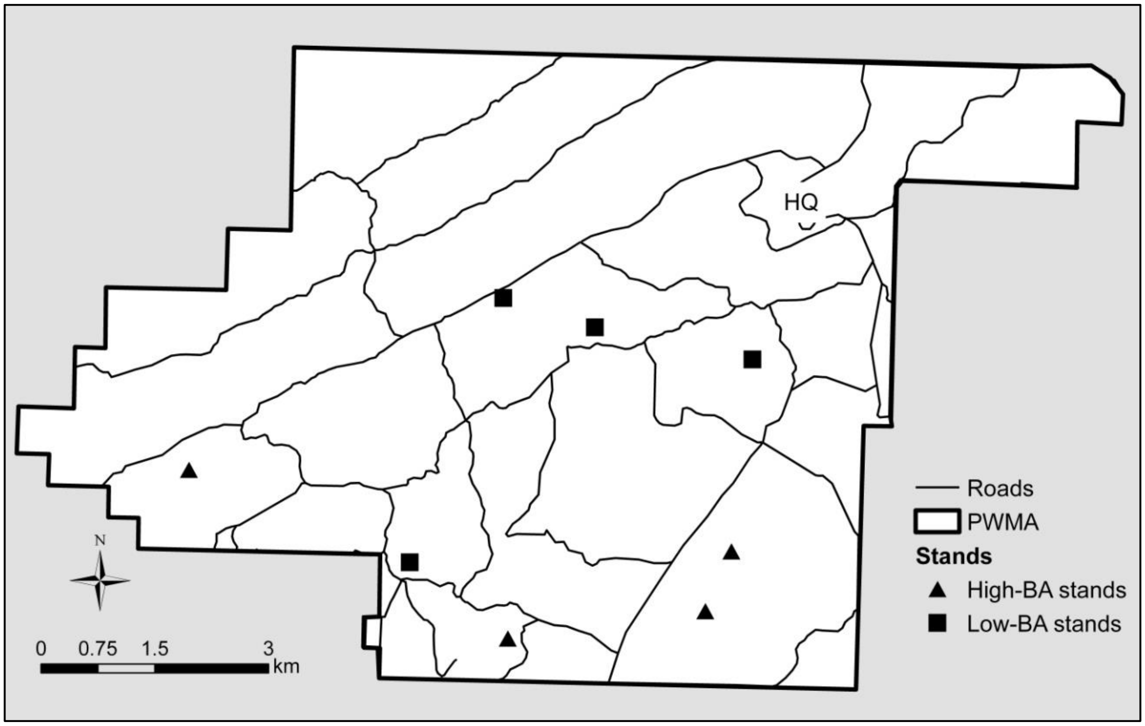

Figure 1: Stand location at PWMA. Roads were used as fire breaks and treatment boundaries.

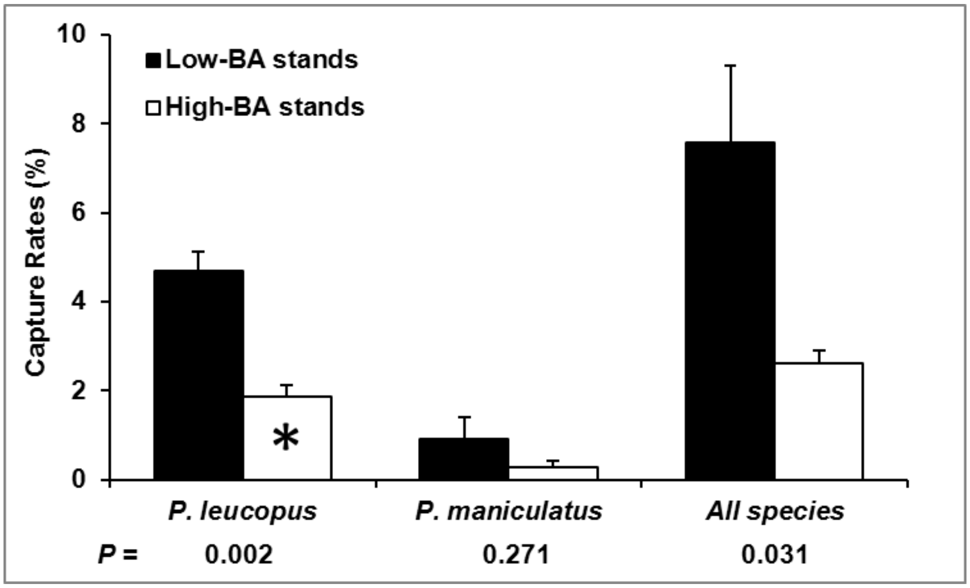

Figure 2: Effects of low-BA practices on capture rates for all sampling periods combined. The asterisk indicates significant treatment effects. Thin bars represent standard errors.

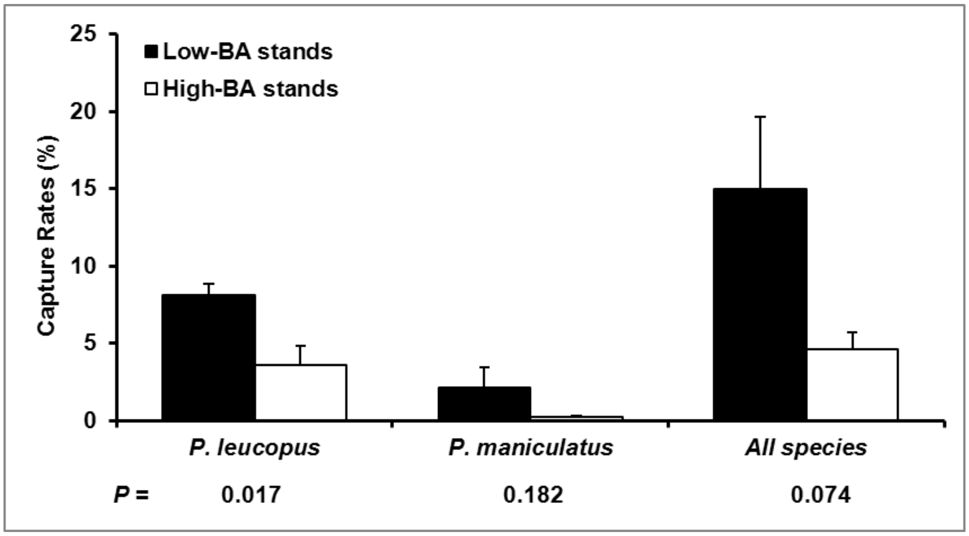

Figure 3: Effects of low-BA practices on capture rates for spring 2013 and 2014 combined. Treatment effects were not significant. Thin bars represent standard errors.

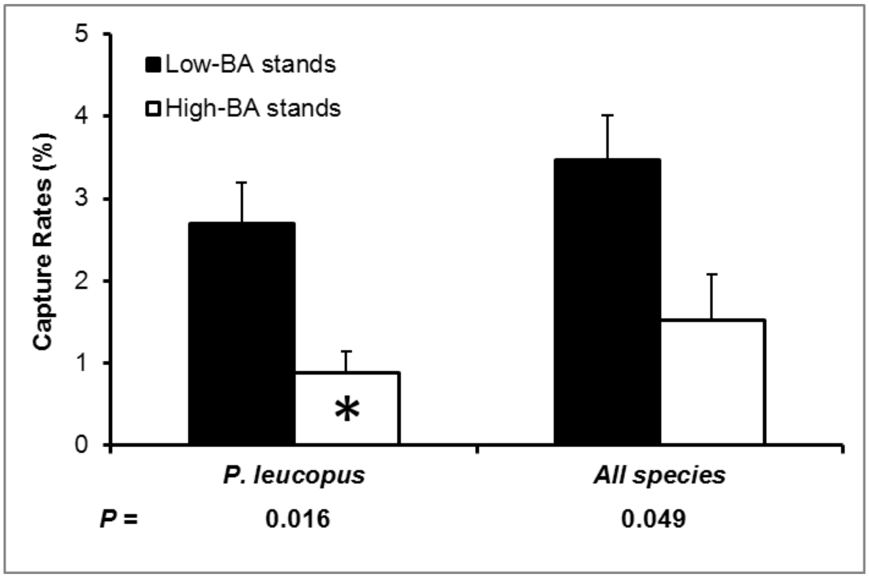

Figure 4: Effects of low-BA practices on capture rates for summer, fall, and winter 2013 combined. The asterisk indicates significant treatment effects. Thin bars represent standard errors.

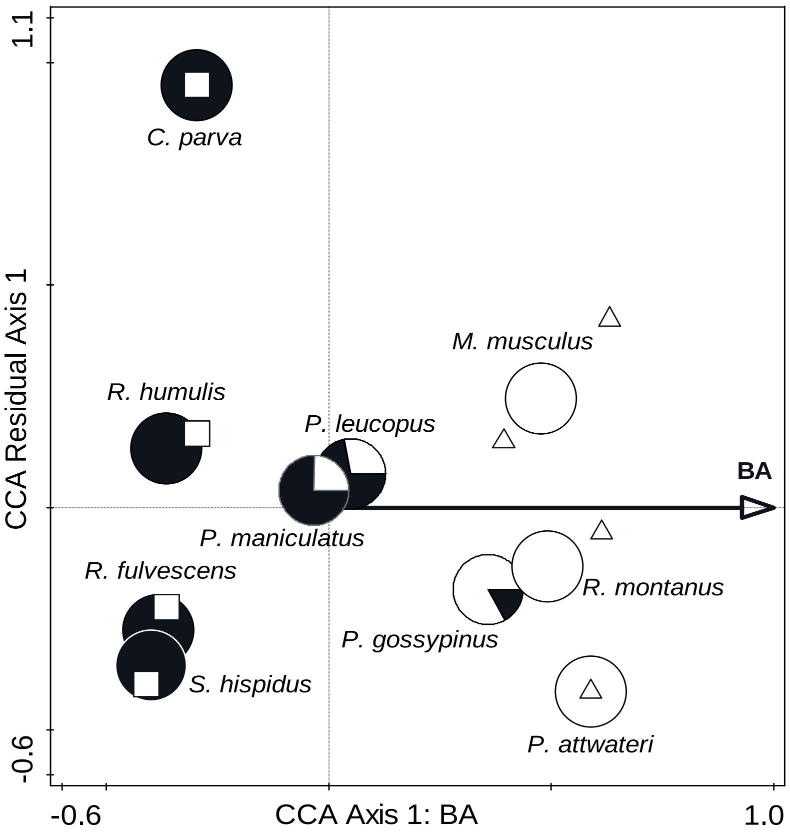

Figure 5: CCA results for all sampling periods combined: effects of low-BA practices on small mammal community composition. Treatment effects were significant (*P* = 0.002). For each species, a pie chart shows the proportion of captures in low- (black) and high-BA stands (white). Species towards the left of the graph were more closely associated with low-BA stands, and species towards the right, with high-BA stands. Squares represent low-BA stands and, triangles, high-BA stands.

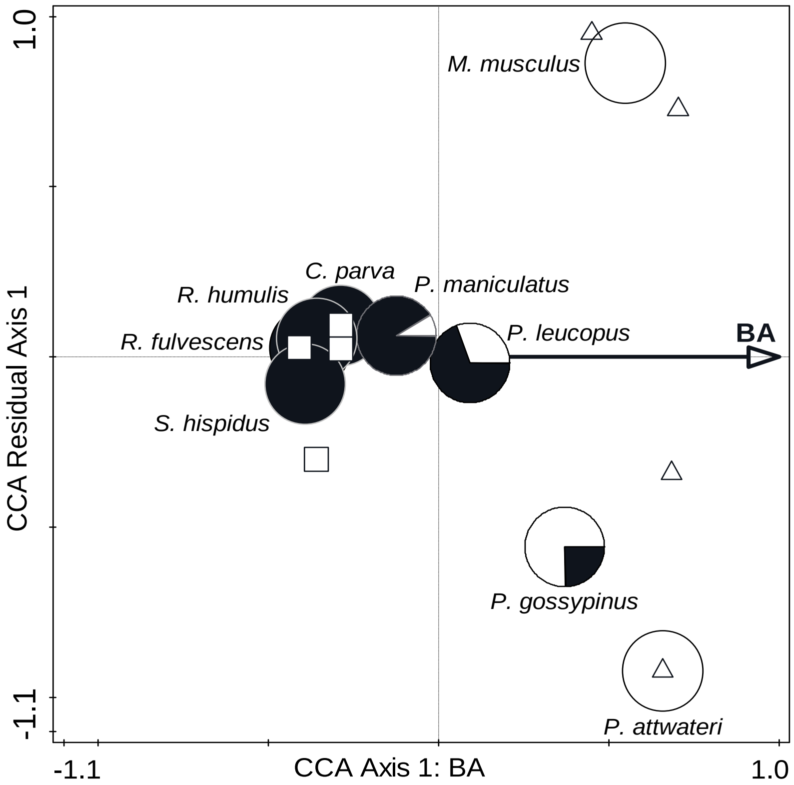

Figure 6: CCA results for captures from spring 2013 & 2014: effects of low-BA practices on small mammal community composition. Treatment effects were significant (*P* = 0.002). For each species, a pie chart shows the proportion of captures in low- (black) and high-BA stands (white). Species towards the left of the graph were more closely associated with low-BA stands, and species towards the right, with high-BA stands. Squares represent low-BA stands and, triangles, high-BA stands.

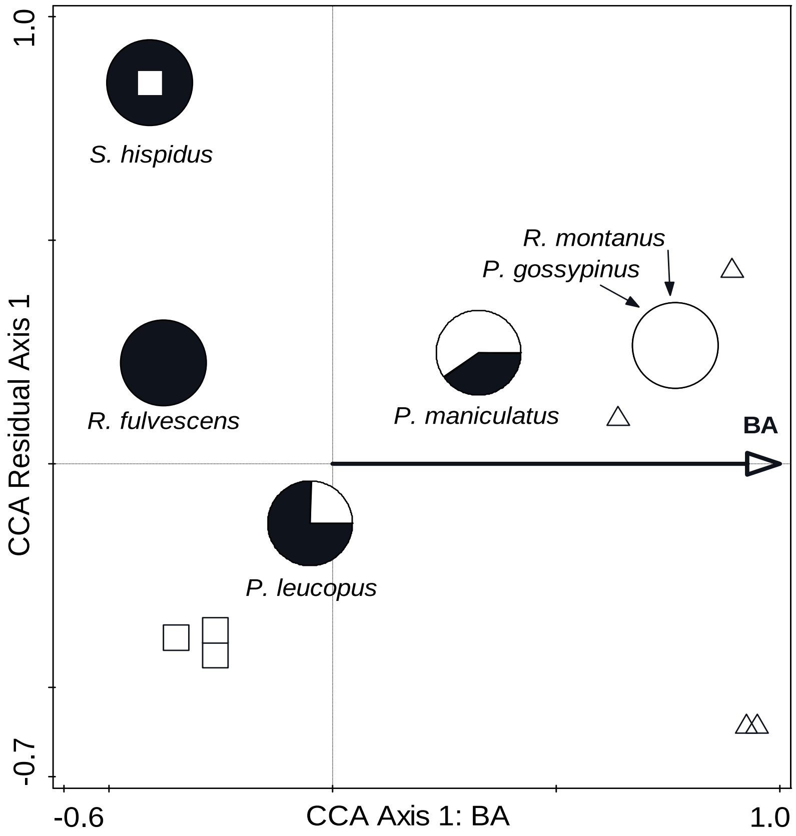

Figure 7: CCA results for captures from summer, fall, and winter 2013: effects of low-BA practices on small mammal community composition. Treatment effects were significant (*P* = 0.002). For each species, a pie chart shows the proportion of captures in low- (black) and high-BA stands (white). Species towards the left of the graph were more closely associated with low-BA stands, and species towards the right, with high-BA stands. Squares represent low-BA stands and, triangles, high-BA stands.

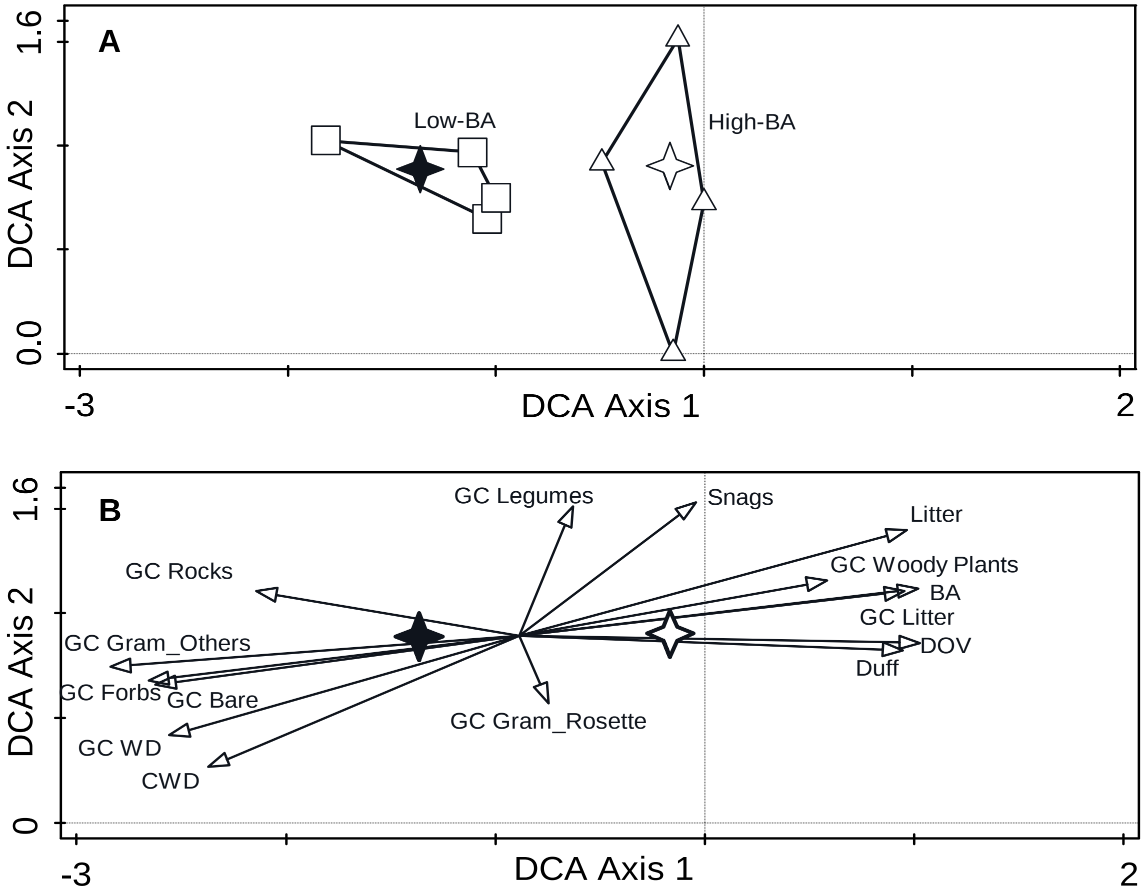

Figure 8: Positions of stand scores along DCA axis 1 and 2 (A), and relationships among 15 habitat variables on the same DCA axes (B), analyzed for all sampling periods combined. The treatments (low- vs high-BA practices) were set as supplementary variables (represented by stars). Squares represent low-BA stands and, triangles, high-BA stands. The shape of the envelopes (A) describes how similar stands were along the primary and secondary axis.

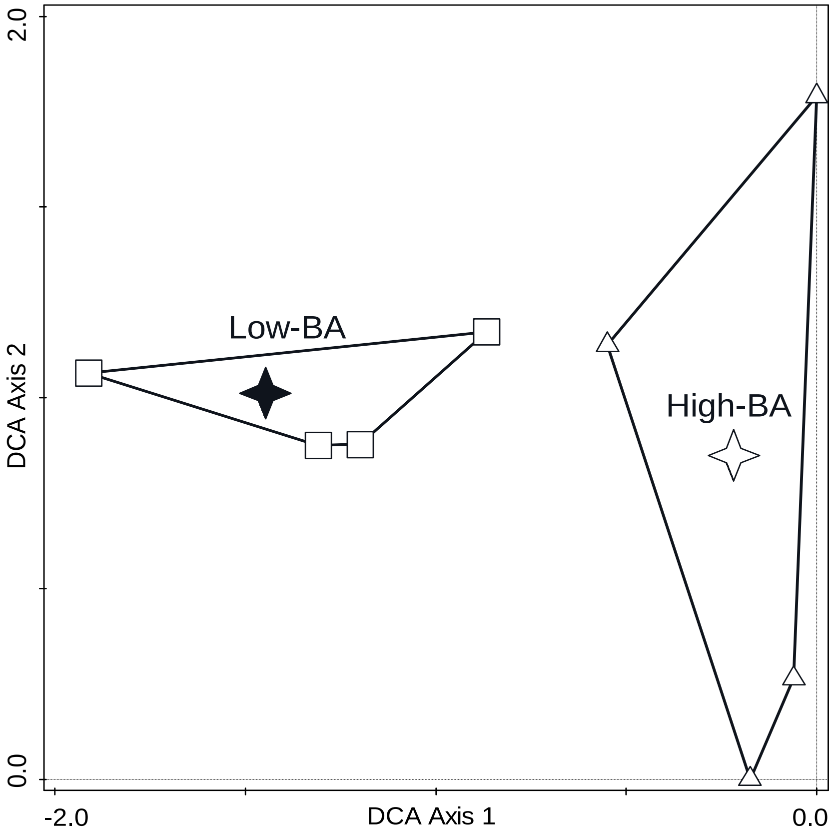

Figure 9: Positions of stand scores along DCA axis 1 and 2, analyzed for captures from spring 2013 and 2014. The treatments (low- vs high-BA practices) were set as supplementary variables (represented by stars). Squares represent low-BA stands and, triangles, high-BA stands. The shape of the envelopes describes how similar stands were along the primary and secondary axes.

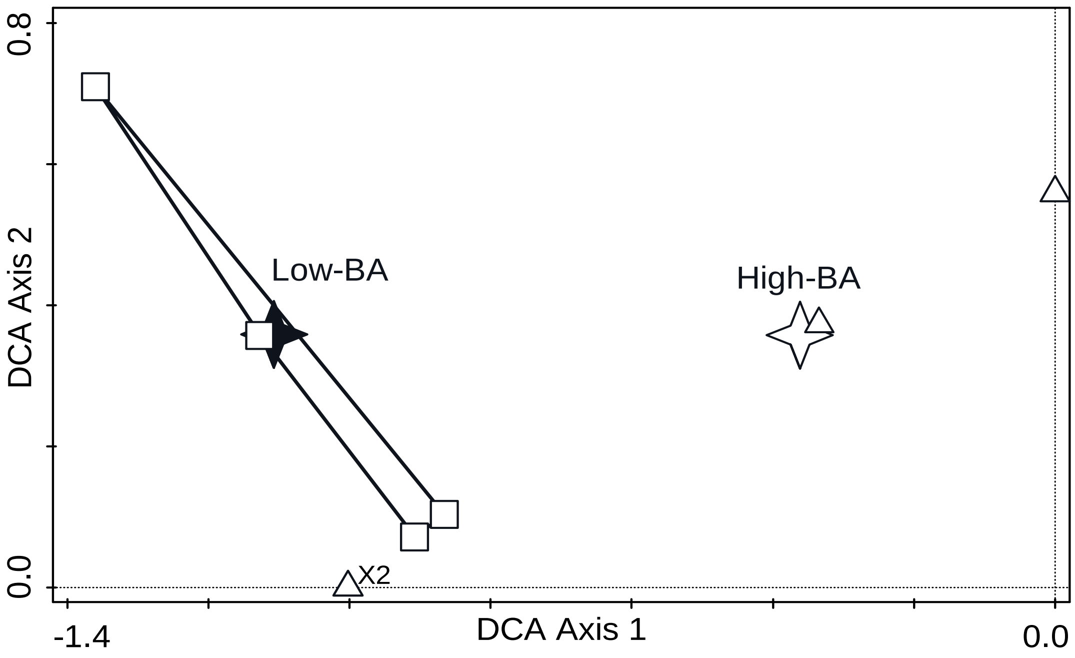

Figure 10: Positions of stand scores along DCA axis 1 and 2, analyzed for captures from summer, fall, and winter 2013. The treatments (low- vs high-BA practices) were set as supplementary variables (represented by stars). Squares represent low-BA stands and, triangles, high-BA stands. The shape of the envelope for low-BA stands describes how similar stands were along the primary and secondary axes. An envelope could not be drawn for high-BA stands.

CHAPTER IV

HABITAT PREFERENCES OF *PEROMYSCUS LEUCOPUS*, *P. MANICULATUS,* AND *REITHRODONTOMYS FULVESCENS* IN OAK-PINE FORESTS AND OAK-PINE SAVANNAS OF SOUTHEAST OKLAHOMA

ABSTRACT

There is widespread interest in restoring oak-pine savannas following decades of woody encroachment resulting from fire suppression. Thinning, followed by prescribed burning (hereafter: low-basal area (BA) practices) is advocated for such restoration. However, low-BA practices can alter small mammal communities (chapter III). To explain habitat preferences of common species in stands treated with low-BA practices (low-BA stands) and untreated stands (high-BA stands), I developed site occupancy models for *Peromyscus leucopus* and *P. maniculatus*. I used capture data from five sampling periods at all seasons of the year in southeast Oklahoma. I included the distance of vulnerability (DOV), an index of vulnerability to predation and understory complexity, in the candidate models tested. Significant differences in occupancy were modeled between low- and high-BA stands. In low-BA stands, *P. leucopus* preferentially selected trap sites with higher volume of coarse woody debris and longer DOV, while *P. maniculatus* preferentially selected shorter DOV. In high-BA stands, *P. leucopus* preferentially selected sites with higher ground cover of down woody debris and longer DOV, while *P. maniculatus* did not appear to select for or against those characteristics. Although a site

occupancy model was not fitted for *Reithrodontomys fulvescens*, I did find this species significantly more often in the low-BA stand with the shortest DOV. Knowing the habitat preferences of these species in southeast Oklahoma can help inform land managers on how to manage for small mammal diversity by altering habitat structure.

INTRODUCTION

Small mammals provide ecosystem services through their feeding, caching, and burrowing habits and through interactions with other species. For example, they are important prey to many avian, mammalian, and reptilian species (Korschgen and Stuart 1972, Shepard et al. 2004, Rulison et al. 2012). They also influence the population demographics of other species through their feeding habits and by carrying diseases and pathogens (Charles et al. 2012, Pitts et al. 2013). Species that dig burrows and cache seeds increase soil aeration, aid in mycorrhizal fungal spore and seed dispersion, and help seed germination (Hole 1981, Pyare and Longland 2001, Hollander and Vander Wall 2004, Schickmann et al 2012). Some species are also considered keystone ecosystem engineers that can enhance habitat for other species (Whitford and Steinberger 2010). Therefore, land management practices that alter small mammal communities could have cascading effects at various trophic levels and could indirectly alter ecosystem services.

In Oklahoma, oak-pine savannas are being restored to reverse woody encroachment resulting from decades of fire suppression. Thinning, followed by prescribed burning (hereafter: low-basal area (BA) practices) is advocated for such restoration (Brose and Van Lear 1998, Sparks et al. 1998, Andre et al. 2007). In chapter III, I provided evidence that low-BA practices altered small mammal communities at Pushmataha Wildlife Management Area (PWMA) in southeast Oklahoma. Low-BA practices were used to restore oak-pine savannas that had turned into closed-canopy oak-pine forests. Different capture rates and community assemblages were documented between thinned stands burned frequently (low-BA stands) and stands that were not thinned recently and not burned as frequently (high-BA stands). However, identifying the main factors responsible for these changes proved challenging, because changes in habitat characteristics following low-BA practices were strongly correlated. Site occupancy models could offer an alternative way to identify factors responsible for changes in the occupancy of common species.

Site occupancy is defined as the probability of a site being occupied by a species. Using occupancy as an alternative to abundance can reduce data collection cost and effort, while still providing valuable information (Royle and Nichols 2003, Eaton et al. 2011). The primary goal of this study was to develop site occupancy models for *Peromyscus leucopus* (Rafinesque) (White-footed Mouse) and *P. maniculatus* (Wagner) (Deer Mouse). Hierarchical models were built, first with experiment-level characteristics, then with structural habitat characteristics. Because low- and high-BA stands were drastically different (low-BA stands were oak-pine savannas while high-BA stands were closed-canopy oak-pine forests), I expected these species to preferentially select different habitat characteristics in low- and high-BA stands.

The secondary goal of this study was to describe the preferred habitat of *Reithrodontomys fulvescens* Allen (Fulvous Harvest Mouse) at PWMA. Because of the limited number of stands in which *R. fulvescens* was caught, a valid site occupancy model could not be built. Instead, a description of its preferred habitat was provided based on the unique characteristics of the stands in which it was most frequently captured.

The tertiary goal of this study was to determine whether the distance of vulnerability (DOV) can be used to characterize small mammal habitat. The DOV is an index of vulnerability to predation and understory complexity. Although it has never been used to describe small mammal habitat, similar indexes have been used to describe Northern Bobwhite (*Colinus virginiana* L.) habitat (Kopp et al. 1998, Cram et al. 2002). I included the DOV as a potential habitat characteristic influencing small mammal occupancy.

The overall objective of this research was to understand why low-BA practices favored some species, while reducing the probability of occupancy of others. I suspected different species responded to different structural habitat characteristics. If we know how preferences vary among species, management practices can be used to alter habitat to manage for small mammal diversity.

FIELD-SITE DESCRIPTION

The field site was located at Pushmataha Wildlife Management Area (PWMA) in southeast Oklahoma (34°32’N, 95°21’W). PWMA lies at the western edge of the Ouachita mountain range, approximately 6 km southeast of Clayton in Pushmataha County. The 15 year average temperature ranged from 4.9 °C (January) to 28.9 °C (August), with an average yearly rainfall of 113.8 cm (Oklahoma Climatological Survey 2014a, b).

Established as a deer refuge in 1946 by the Oklahoma Department of Wildlife Conservation (ODWC), the WMA covers 7,690 ha managed for game species (Masters and Engle 1994). Management tools include: prescribed fires (no fires to yearly fires), tree thinning (no thinning, thinning to 7 or to 14 m^2ha^{-1}), and brush hogging in small patches (J. Waymire - ODWC, pers. comm. 2013).

Habitat variables and small mammals were sampled on four low- and four high-BA stands (Figure 1). Low-BA stands were oak-pine savannas (4.4 m^2ha^{-1}) while high-BA stands were oak-pine forests (22.6 m^2ha^{-1}) (Chapter II). However, before low-BA practices were implemented, all stands were structurally similar to high-BA stands. Two species dominated the canopy in all stands: *Quercus stellata* Wangenh. (Post Oak) and *Pinus echinata* Mill. (Shortleaf Pine). Graminoids were the main ground cover in low-BA stands, with *Schizachyrium scoparium* (Michx.) Nash (Little Bluestem), *Andropogon gerardii* Vitman (Big Bluestem), and *Carex* L. spp (Sedges) as the dominant species. In contrast, the dominant ground cover in high-BA stands was litter. Low-BA stands were thinned between 2008 and 2009. They were burned 5 or 6 times between 1997 and 2012 and burned again in March 2013 prior to the start of this study. Two of the four stands were also burned in February 2014 before the last small mammal sampling. In contrast, high-BA stands were not thinned within the past 20 years. They were burned 3 or 5 times between 1997 and 2012, not burned in 2013, and only one stand was burned before the last small mammal sampling (March 2014).

METHODS

Small Mammal Sampling

To determine site occupancy, we conducted small mammal trapping on live-trapping transects. Each stand had one transect, with 37 trapping stations spaced 10 m apart. Each trapping station had one Sherman trap while every third trapping station was supplemented by one pitfall live trap (12 per stand). Small mammal sampling took place in April, June, and September 2013 (spring, summer, and fall 2013) and in January and March 2014 (winter 2013 and spring 2014). Procedures were approved by the Oklahoma State University Animal Care and Use Committee (ACUP AG-12-16). Refer to chapter III for a detailed description of small mammal sampling protocols.

Small Mammal Habitat Measurements

Habitat characteristics were divided between experiment-level characteristics and structural habitat characteristics. Experiment-level characteristics were related to the experimental designs. They included: treatment, i.e. low- vs high-BA (TRT), sampling period (Date), and individual stands (Stand).

In contrast, structural habitat characteristics were not part of the experimental design. They included: time since fire (TSF), BA of live trees (BA_live), BA of snags (BA_snags), CWD volume (CWD_vol), forest floor depth (FF = sum of litter and duff depths), DOV, and percent ground cover by functional group. Structural habitat characteristics were measured at every trapping station in summer 2013, except TSF which was recorded at the stand scale. The volume of CWD was measured within a circle of 6 m diameter centered on every trapping station. It included any piece of wood longer than 91cm, larger than 7.5cm, > 45° from vertical, and detached from a tree. The DOV was an index of vulnerability to predation and understory complexity. It was the minimum distance at which an object laid on the ground representing a small mammal was 100% obstructed from an observer's view, when the observer's eyes were 1 m from the ground. For the percent ground cover, the functional groups were: annual vegetation (GC_annual = sum of percent cover of graminoids, forbs, and legumes), live woody plants (GC_woody), litter (GC_litter), rocks (GC_rocks), bare ground (GC_bare), and down woody debris (GC_DWD). DWD included woody debris detached from a tree ≥ 6 mm (diameter) and > 45° from vertical. For a complete description of structural habitat measurement protocols, please refer to chapter II.

Data Analysis

Among the nine species caught in traps, only *P. leucopus* and *P. maniculatus* provided enough data for analysis with site occupancy models. Only data from Sherman traps was analyzed as these two species were never caught in a pitfall trap. I used logistic regression to model the probability of occurrence (P_{ijkl}) of each species individually:

$$Y_{ijk} \sim Bernoulli\ (P_{ijkl}) \qquad (1)$$

with the logit link function:

$$\text{Logit}\ (P_{ijkl}) = \mu + \text{TRT}_i + \text{Date}_j + \text{TRT}_i{*}\text{Date}_j + \text{Stand}_k + \sum_m \beta_m X_m \qquad (2)$$

where:

- Y_{ijk} was trap success for an individual species (1 = present, 0 = absent) at trapping station l;
- μ was the overall mean;
- TRT was an indicator variable representing treatment i (low- or high-BA);
- Date was an indicator variable representing sampling period j;
- Stand was an indicator variable representing stand k; and
- X_m were covariates representing structural habitat variables m with fitted regression coefficients β_m.

The assumptions included: (1) an equal detection probability among all traps; (2) independence among stands; and (3) a “closed” occupancy state, i.e., for each sampling period, occupancy did not change.

For comparison, different combinations of experimental covariates (TRT, Date, TRT*Date, and Stand) were fitted to the model. The best model was selected for the experiment-level covariates first, and then different combinations of structural habitat covariates were included in the best experimental model. To reduce the number of candidate models tested, and thus reduce the risks of generating spurious findings (Johnson and Omland 2004), structural habitat covariates were selected a priori based on the literature. Because previous research determined burning regime, tree density, complexity of the understory layer, volume of woody debris, and density of shrubs, graminoids, and forbs could influence habitat selection by *P. leucopus* (Kaufman et al. 1983, McMurry et al. 1996, Greenberg 2002, Masters et al. 2002, Anderson and Meikle 2006), the structural habitat covariates tested for *P. leucopus* were: TSF, BA_live, CWD_vol, GC_annual, GC_woody, GC_DWD, and DOV. For *P. maniculatus*, previous research determined that burning regime, tree density, light intensity, and amount of litter, bare soil, and graminoid influenced habitat selection (Pitts and Barbour 1979, Merkt 1981, Kaufman et al. 1988, Mayfield et al. 2000). Moreover, *P. maniculatus* is omnivorous, primarily feeding on insect, seeds, miscellaneous vegetation, and sometimes ripe-seeds (Kritzman 1974, Pitts and Barbour 1979, Whitaker, Jr. 1966). Snags, CWD, and DWD could provide food sources such as arthropods, and thus influence site occupancy. Thus, the structural habitat covariates tested for *P. maniculatus* were: TSF, BA_live, BA_snags, CWD_vol, FF, GC_annual, GC_litter, GC_bare, GC_DWD, and DOV. Because low- and high-BA stands were strikingly different in terms of habitat, I expected small mammal species to respond differently to structural habitat characteristics between treatments. For this reason, structural habitat covariates were standardized within a treatment (mean = 0, standard deviation = 1), and models were always fitted with a treatment interaction term.

I evaluated competing models with Akaike's Information Criterion (AIC) (Johnson and Omland 2004). For each model, ΔAIC (difference in AIC values between a given model and the best model) was provided. In addition, a null model (i.e., intercept-only model) was fitted for comparison. All models were fitted using SAS v.9.3 PROC GENMOD (SAS Institute 2012). Prior to evaluating competing models, I calculated Pearson correlation coefficients to assess correlations among habitat covariates (SAS PROC CORR, SAS Institute 2012). As several covariates were correlated, I did not use model averaging, because the interpretation of the results would depend on the combination of covariates used in the models (Stoddard and Hayes 2005).

A site occupancy model was not fitted for *R. fulvescens* because it was only caught in three low-BA stands (L2: n = 1; L3: n = 30; L4: n = 2). Instead, because most individuals were caught on L3, I described how this stand was different in terms of structural habitat characteristics. To do this, a one-way ANOVA with Tukey groupings was performed (SAS PROC GLM, SAS Institute 2012) to determine differences in structural habitat variables among low-BA stands.

RESULTS

Small Mammal Sampling

A total of 272 small mammals from nine different species were captured in Sherman traps during 4161.5 adjusted trap nights (Please see Chapter III)[1]. Only data for *P. leucopus* (n = 176), *P. maniculatus* (n = 32), and *R. fulvescens* (n = 33) were analyzed for habitat preferences, as these species were the only ones caught in sufficient numbers to provide meaningful results.

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[1] Data for Sherman traps only.

Correlation among Covariates

Many habitat variables showed significant correlation within low- and within high-BA stands (Tables 1, 2; Figure 2). For example, GC_annual and DOV were negatively correlated. These correlations should trigger caution when building and interpreting models, as correlated variables may interfere with one another.

Occupancy Model: *Peromyscus leucopus*

All models tested were better predictors of *P. leucopus* occupancy than the null model (Table 3). A model including TRT and Date as the only covariates explained occupancy considerably better than other experiment-level models. This model explained 7.4 % of the residual deviance compared to the null model. Holding other parameters at a fixed value, it predicted an odds ratio of 2.6 for low-BA stands. Therefore, when other variables were held constant, the probability of occupancy in low-BA stands was higher than in high-BA stands. The odds of occupancy also varied with seasons and years (winter 2013 < summer 2013 < fall 2013 < spring 2013 < spring 2014).

Adding structural habitat covariates to the best experiment-level model further improved occupancy prediction. The logit equation for the best model with experimental and structural habitat covariates was:

$$\text{Logit}\,(P_{ijkl}) = \mu + \text{TRT}_i + \text{Date}_j + \text{CWD\_Vol}_l{*}\text{TRT}_i + \text{GC\_DWD}_l{*}\text{TRT}_i + \text{DOV}_l{*}\text{TRT}_i \qquad (3)$$

This model explained 9.9 % of the residual deviance compared to the null model and 2.7 % compared to the best experiment-level model. According to this model, *P. leucopus* preferentially selected different habitat variables in low- and high-BA stands (Table 4). The model predicted that, in low-BA stands, the odds of occupancy increased by a multiplicative factor of 1.2 for every one standard deviation increase in CWD volume (17.0 m^3ha^{-1}). However, it did not predict that an increase in CWD volume significantly changed the odds of occupancy in high-BA stands.

In high-BA stands, when the ground cover of DWD increased by one unit of standard deviation (4.1 %), the odds of occupancy increased by a multiplicative factor of 1.4. However, an increase in the ground cover of DWD in low-BA stands did not significantly change the odds of occupancy. When the DOV increased by one unit of standard deviation (1.4 m in low-BA stands or 2.6 m in high-BA stands), the model further predicted an increase in the odds of occupancy by a multiplicative factor of 1.2 in low-BA stands or 1.3 in high-BA stands.

Occupancy Model: *Peromyscus maniculatus*

Not all models tested were better predictors of *P. maniculatus* occupancy than the null model. A single experiment-level habitat model including TRT and Date could fit the data (convergence was not attained for at least one side of the likelihood confidence interval for other experiment-level models). This model explained 5.9 % of the residual deviance compared to the null model. Holding other parameters at a fixed value, it predicted an odds ratio of 3.0 for low-BA treatment. Therefore, when other variables were held constant, the probability of occupancy in low-BA stands was higher than in high-BA stands. The odds of occupancy also varied with seasons and years (winter 2013 < summer 2013 < fall 2013 < spring 2013 < spring 2014).

With the addition of structural habitat characteristics to this model, only four models improved occupancy prediction (Table 5). The logit equation for the best model was:

$$\text{Logit}\,(P_{ijkl}) = \mu + \text{TRT}_i + \text{Date}_j + \text{DOV}_l{*}\text{TRT}_i \tag{4}$$

This model explained 7.5 % of the residual deviance compared to the null model and 1.7 % compared to the best experiment-level model. The odds of occupancy increased by a multiplicative factor of 1.8 for every one standard deviation decrease in DOV in low-BA stands (1.4 m), but a decrease in DOV in high-BA stands did not significantly change the odds of occupancy (Table 6).

Habitat preferences: *Reithrodontomys fulvescens*

A site occupancy model was not fitted for *R. fulvescens*, because it was only caught in three low-BA stands (L2: n = 1; L3: n = 30, L4: n = 2). Because the majority of animals were caught on L3, we determined how L3 was different from other stands in terms of structural habitat characteristics (Table 7). Compared to all other low-BA stands, the mean DOV was significantly shorter in L3. The rocky ground cover in L3 was also significantly different from other stands: it was higher than in L1 and L2, but lower than in L4.

DISCUSSION

The major findings of this research were that *P. leucopus* and *P. maniculatus* occupied low- and high-BA stands, but their odds of occupancy were greater in low-BA stands. Moreover, in low-BA stands, *P. leucopus* preferentially selected sites with greater amount of CWD and longer DOV, while *P. maniculatus* preferentially selected sites with shorter DOV. In high-BA stands, *P. leucopus* preferentially selected sites with greater ground cover of DWD and longer DOV, while *P. maniculatus* did not appear to preferentially select sites. As for *R. fulvescens*, it more frequently occupied the low-BA stand with the shortest DOV. Furthermore, the results suggested the DOV can help predict site occupancy and habitat preference in small mammal species.

Through occupancy modeling, I determined the habitat variables most likely responsible for changes in the habitat occupancy of two small mammal species, *P. leucopus* and *P. maniculatus*. Seasonal variation in their odds of occupancy was reflected in the models tested; odds of occupancy were highest in spring and lowest in winter. It is likely that survival and reproductive rates were lower in winter because of food scarcity and harsh weather conditions, and higher in spring because of more favorable conditions.

Habitat Preferences – *Peromyscus leucopus*

Peromyscus leucopus is typically associated with woodlands and avoids grassland (Kamler and Pennock 2004). Therefore, I expected to find *P. leucopus* more often in high- than in low-BA stands. However, the odds of occupancy were 2.6 times greater in low-BA stands. Preference for low-BA stands may be partly induced by the diet of *P. leucopus*, primarily composed of seeds, lepidopterous larvae, and masts (Whitaker, Jr. 1966). Although masts would be more abundant in high-BA stands, the more productive ground layer in low-BA stands (chapter II) likely resulted in more seeds available for consumption, and potentially more larvae. Although my results were distinct from most studies, Clark et al. (1987) also commonly recorded *P. leucopus* in tallgrass prairies in Kansas.

Adding structural habitat covariates to the experiment-level occupancy model revealed that *P. leucopus* responded differently to structural habitat variables between low- and high-BA stands. The best model predicted that *P. leucopus* likely responded positively to increased CWD volume in low-BA stands but CWD volume did not affect occupancy in high-BA stands. In contrast, it predicted that *P. leucopus* would respond positively to higher ground cover of DWD in high-BA stands but would not respond significantly to the ground cover of DWD in low-BA stands. My results were consistent with previous studies that have shown that CWD and DWD can be used as runways by *P. leucopus* (M'Closkey 1975) and can locally increase capture rates

(Greenberg 2002), but not always (Greenberg et al. 2006). The best model also predicted higher occupancy probability in habitat with longer DOV, both in low- and high-BA stands. Therefore, *P. leucopus* was more likely to occupy sites with structurally less complex understories. Because habitats with longer DOV were more opened, *P. leucopus* potentially sought CWD or DWD as travelling routes or hiding grounds from predators.

CWD volume and percent ground cover of DWD were positively correlated with one another and negatively correlated with DOV. Nevertheless, the addition of CWD volume, percent ground cover of DWD, and DOV to the best experiment-level model increased its predictive power. However, it is also possible that the inclusion of the percent ground cover of DWD and DOV acted as surrogates for other variables with which they were correlated. The percent ground cover of DWD was positively correlated with forest floor depth in low-BA stands and with BA of snags in high-BA stands. The DOV was correlated with multiple structural habitat characteristics in low- and high-BA stands.

Habitat Preferences – *Peromyscus maniculatus*

Although I did find several models predicting occupancy better than the null model, some models did not fit the data. The lack of fit may have resulted from the low capture rate of *P. maniculatus*.

Peromyscus maniculatus is usually a grassland species, but will sometimes prefer woody or shrubby habitat over grasslands (Merkt 1981, Mayfield et al. 2000). As expected, at PWMA, *P. maniculatus* predominantly occupied low-BA stands, representative of oak-pine savanna ecosystems, although it also occupied forested habitat.

Of the different combinations of structural habitat variables added to the experiment-level model, the addition of the DOV increased the power of the model the most. However, *P.*

maniculatus seemed to only respond to changes in the DOV in low-BA stands. Lack of response in high-BA stands may have been due to the very high DOV found there being above a threshold for the species. It is also possible that the inclusion of the DOV to the best model acted as a surrogate for other variables with which the DOV was highly correlated.

Habitat Preferences – *Reithrodontomys fulvescens*

Because of the limited number of stands in which *R. fulvescens* was caught, a valid site occupancy model could not be built for the second most frequently captured species. Nevertheless, the unique characteristics of the stand where it was most frequently captured allowed some insight into its preferred habitat.

Previous studies showed *R. fulvescens* is typically associated with grasslands or savanna ecosystems (Kincaid et al. 1983, Spencer and Cameron 1988, Turner and Grant 1987). As expected, it was only caught in low-BA stands at PWMA. Moreover, it was primarily caught in a stand with a significantly shorter DOV than other low-BA stands. These results were consistent with a previous study by Kincaid et al. (1983) that determined a seasonal preference for productive grasslands with high cover.

The percent cover of rocks in the stand where *R. fulvescens* was caught the most frequently was also significantly different from other low-BA stands. Although it is possible that *R. fulvescens* preferentially chose intermediate rock cover at PWMA, it is unlikely because the DOV and rocky ground cover are negatively correlated.

CONCLUSION

For *P. leucopus* and *P. maniculatus*, significant differences in occupancy were modeled between low- and high-BA stands, i.e., between oak-pine savannas and oak-pine forests. In low-BA stands, *P. leucopus* preferentially selected trap sites with higher CWD volume and longer DOV, while *P. maniculatus* preferentially selected shorter DOV. In high-BA stands, *P. leucopus* preferentially selected sites with higher ground cover of DWD and longer DOV, while *P. maniculatus* did not appear to respond to those characteristics. Although a site occupancy model was not fitted for *R. fulvescens*, I did find it significantly more often in the low-BA stand with the shortest DOV.

The overall objective of this study was to understand why low-BA practices favored some species, but not others. The results showed different species responded to different structural habitat characteristics. Knowing the habitat preferences of these species can help inform land managers on how to manage for small mammal diversity by altering habitat structure.

DOV helped predict site occupancy for three small mammal species. It was a cost-effective index of vulnerability to predation and understory complexity that provided significant new information. DOV could be measured at different heights to account for aerial and terrestrial predators of different sizes. However, predators can also rely on auditory, thermal, and olfactory cues to detect preys, which cannot be accounted for with the DOV. Moreover, the DOV may act as a surrogate for other variables with which it is highly correlated. Although I recommend using the DOV to explain preferences in small mammal habitat, results should be interpreted cautiously.

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TABLES

Pearson Correlation Coefficients, N = 148											
Prob > |r| under H0: Rho=0											
	BA_live	**BA_snags**	**CWD_vol**	**FF**	**GC_woody**	**GC_litter**	**GC_rocks**	**GC_bare**	**GC_DWD**	**GC_annual**	**DOV**
BA_live		-0.20*	-0.04	-0.01	0.14	0.12	-0.25*	0.17*	-0.14	-0.25*	0.39*
BA_snags	0.01		0.17*	0.11	-0.12	-0.12	-0.04	-0.11	0.16	-0.01	-0.18*
CWD_vol	0.61	0.03		0.07	-0.04	-0.04	-0.04	-0.04	0.40*	0.06	-0.18*
FF	0.95	0.18	0.42		0.07	0.06	-0.17*	-0.11	0.16*	0.05	-0.04
GC_woody	0.10	0.14	0.66	0.40		0.17*	0.19*	0.01	0.00	-0.34*	0.04
GC_litter	0.15	0.16	0.62	0.44	0.04		-0.08	0.10	0.14	-0.21*	0.22*
GC_rocks	<0.01	0.62	0.63	0.04	0.02	0.31		-0.12	-0.02	-0.07	-0.20*
GC_bare	0.04	0.18	0.61	0.19	0.94	0.24	0.15		0.14	-0.48*	0.32*
GC_DWD	0.09	0.05	<0.01	0.05	0.98	0.09	0.82	0.08		-0.15	-0.11
GC_annual	0.00	0.89	0.45	0.56	<0.01	0.01	0.39	<0.01	0.07		-0.37*
DOV	<0.01	0.03	0.03	0.60	0.60	0.01	0.01	<0.01	0.18	<0.01	

Table 1: Pearson correlation coefficients for structural habitat variables in low-BA stands. The diagonal separates coefficients (above) from *P*-values (below). Asterisks indicate significant correlation ($P < 0.05$). BA_live: BA of live trees, BA_snags: BA of snags, CWD_vol: CWD volume, FF: forest floor depth, GC_woody: percent cover of live woody plants, GC_litter: percent cover of litter, GC_rocks percent cover of rocks, GC_bare: percent cover of bare ground, GC_DWD: percent cover of DWD, GC_annual: percent cover of annual plants, DOV: distance of vulnerability.

Pearson Correlation Coefficients, N = 148											
Prob > |r| under H0: Rho=0											
	BA_live	**BA_snags**	**CWD_vol**	**FF**	**GC_woody**	**GC_litter**	**GC_rocks**	**GC_bare**	**GC_DWD**	**GC_annual**	**DOV**
BA_live		0.04	0.01	0.11	0.00	0.41*	-0.25*	-0.13	-0.05	-0.42*	0.19*
BA_snags	0.67		0.15	-0.08	-0.05	-0.15	0.06	-0.01	0.19*	0.04	-0.15
CWD_vol	0.89	0.08		-0.07	-0.04	-0.13	0.06	0.00	0.41*	0.02	-0.25*
FF	0.19	0.36	0.37		0.29*	-0.01	-0.07	-0.09	0.03	-0.05	-0.10
GC_woody	0.95	0.54	0.63	<0.01		0.08	-0.11	-0.04	0.08	-0.20*	-0.24*
GC_litter	<0.01	0.07	0.13	0.90	0.31		-0.35*	-0.11	-0.14	-0.72*	0.46*
GC_rocks	<0.01	0.49	0.43	0.37	0.17	<0.01		0.07	0.06	0.19*	-0.12
GC_bare	0.10	0.91	0.98	0.26	0.59	0.18	0.40		0.12	-0.07	0.02
GC_DWD	0.51	0.02	<0.01	0.75	0.36	0.09	0.47	0.16		0.05	-0.22*
GC_annual	<0.01	0.66	0.80	0.52	0.02	<0.01	0.02	0.41	0.55		-0.44*
DOV	0.02	0.06	<0.01	0.20	<0.01	<0.01	0.16	0.84	0.01	<0.01	

Table 2: Pearson correlation coefficients for structural habitat variables in high-BA stands. The diagonal separates coefficients (above) from *P*-values (below). Asterisks indicate significant correlation ($P < 0.05$). BA_live: BA of live trees, BA_snags: BA of snags, CWD_vol: CWD volume, FF: forest floor depth, GC_woody: percent cover of live woody plants, GC_litter: percent cover of litter, GC_rocks percent cover of rocks, GC_bare: percent cover of bare ground, GC_DWD: percent cover of DWD, GC_annual: percent cover of annual plants, DOV: distance of vulnerability.

Experiment-level covariates	Structural habitat covariates							ΔAIC¥	Akaike weight¥
	TSF	BA_live	CWD_vol	GC_annual	GC_woody	GC_DWD	DOV		
Null model								114.75	0.0000
TRT + Date								15.47	0.0001
TRT + TRT*Date								21.69	0.0000
TRT + TRT*Date + Stand								26.55	0.0000
TRT + Date + Stand								20.55	0.0000
TRT + Date	Note 1		ns(H) +(L)			+(H) ns(L)	+ (H) + (L)	0.00	0.2289
	Note 1		ns(H) + (L)	ns(H) - (L)		+(H) ns(L)		0.18	0.2092
	Note 1		ns(H) +(L)		+(H) ns(L)	+ (H) ns(L)	+ (H) + (L)	0.73	0.1589
	Note 1		ns(H) +(L)			+(H) ns(L)		1.90	0.0885
	Note 1					+(H) + (L)		2.08	0.0809
	Note 1	ns(H) s(L)	ns(H) +(L)			+(H) ns(L)	+ (H) ns(L)	2.23	0.0751
	Note 1		ns(H) +(L)					3.32	0.0435

Table 3: Occupancy models for *P. leucopus*. The table includes: valid models with experiment-level covariates (above the double line) and models with experiment-level and structural habitat covariates with ΔAIC < 4 (below the double line). Positive and negative signs indicate the presence of a structural habitat variable in a model (row) and the sign of its coefficient in high-BA stands (H) and in low-BA stands (L). "ns" indicates non-significance at α = 0.1. TRT: treatment (low- or high-BA), Date: sampling period, Stand: stand where the sampling took place, TSF: time since fire, BA_live: BA of live trees, CWD_vol: CWD volume, GC_annual: percent cover of annual plants, GC_woody: percent cover of live woody plants, GC_DWD: percent cover of DWD, DOV: distance of vulnerability. Note 1: TSF was tested as a categorical variable, with years as categories.

Parameter			DF	Estimate	Standard Error	Likelihood Ratio 95% Confidence Limits		Wald Chi-Square	Pr > ChiSq
Intercept			1	-5.5564	0.7632	-7.212	-4.1395	53	<.0001
TRT	High-BA		1	-0.6	0.4415	-1.525	0.2253	1.85	0.1741
TRT	Low-BA		0	0	0	0	0	.	.
Date	Fall	2013	1	0.9923	0.3586	0.318	1.7381	7.66	0.0056
Date	Spring	2013	1	1.238	0.3493	0.5864	1.9693	12.56	0.0004
Date	Spring	2014	1	1.8889	0.3799	1.1671	2.6706	24.72	<.0001
Date	Summer	2013	1	0.6577	0.3764	-0.0608	1.431	3.05	0.0806
Date	Winter	2013	0	0	0	0	0	.	.
TSF	0		1	1.5179	0.6966	0.2335	3.0647	4.75	0.0293
TSF	1		1	1.9022	0.7559	0.492	3.5404	6.33	0.0119
TSF	10		1	0.8492	0.7815	-0.6581	2.5129	1.18	0.2772
TSF	11		1	2.0159	0.6616	0.8313	3.5176	9.28	0.0023
TSF	2		1	1.1965	0.6706	0	2.7136	3.18	0.0744
TSF	3		0	0	0	0	0	.	.
CWD_vol*TRT	High-BA		1	0.0862	0.1039	-0.1619	0.2669	0.69	0.407
CWD_vol*TRT	Low-BA		1	0.1836	0.0743	0.0275	0.3223	6.1	0.0135
GC_DWD*TRT	High-BA		1	0.3231	0.1263	0.063	0.562	6.55	0.0105
GC_DWD*TRT	Low-BA		1	0.1014	0.0916	-0.0839	0.2763	1.23	0.2683
DOV*TRT	High-BA		1	0.2567	0.1488	-0.0396	0.5456	2.98	0.0845
DOV*TRT	Low-BA		1	0.1631	0.0931	-0.0216	0.3439	3.07	0.0799

Table 4: Parameter estimates for the best model predicting *P. leucopus* occupancy with a logistic regression. TRT: treatment (low- or high-BA), Date: sampling period, TSF: time since fire, CWD_vol: CWD volume, GC_DWD: percent cover of DWD, DOV: distance of vulnerability. CWD_vol, GC_DWD, and DOV were standardized.

Experiment-level covariates	Structural habitat covariates			AIC	ΔAIC	Akaike weight
	BA_snags	GC_DWD	DOV			
Null model				380.60	14.47	0.00
TRT + Date				368.33	2.20	0.10
TRT + Date			ns(H) -(L)	366.13	0.00	0.29
TRT + Date	ns(H) ns(L)		ns(H) -(L)	367.54	1.41	0.14
TRT + Date		ns(H) ns(L)	ns(H) -(L)	367.94	1.81	0.12
TRT + Date	ns(H) +(L)			368.28	2.15	0.10
TRT + Date		ns(H) +(L)		368.98	2.85	0.07
TRT + Date	ns(H) ns(L)	ns(H) ns(L)	ns(H) -(L)	369.83	3.70	0.05
TRT + Date	ns(H) +(L)	ns(H) +(L)		369.90	3.77	0.04

Table 5: Occupancy models for *P. maniculatus*. The table includes: valid models with experiment-level covariates (above the double line) and models with experiment-level and structural habitat covariates with ΔAIC < 4 (below the double line). Positive and negative signs indicate the presence of a structural habitat variable in a model (row) and the sign of its coefficient in high-BA stands (H) and in low-BA stands (L). "ns" indicates non-significance at α = 0.1. TRT: treatment (low- or high-BA), Date: sampling period, BA_snags: BA of snags, GC_DWD: percent cover of DWD, DOV: distance of vulnerability. Note 1: TSF was tested as a categorical variable.

Parameter			DF	Estimate	Standard Error	Likelihood Ratio 95%		Wald Chi-Square	Pr > ChiSq
						Confidence Limits			
Intercept			1	-5.8257	0.7258	-7.6435	-4.6506	64.42	<.0001
TRT	**High-BA**		1	-0.9514	0.4264	-1.8434	-0.1439	4.98	0.0257
TRT	**Low-BA**		0	0	0	0	0	.	.
Date	**Fall**	**2013**	1	0.9161	0.8387	-0.6229	2.8619	1.19	0.2748
Date	**Spring**	**2013**	1	1.4086	0.7928	0.0192	3.3025	3.16	0.0756
Date	**Spring**	**2014**	1	1.9716	0.7583	0.6905	3.8257	6.76	0.0093
Date	**Summer**	**2013**	1	0.4018	0.9148	-1.399	2.4316	0.19	0.6605
Date	**Winter**	**2013**	0	0	0	0	0	.	.
DOV*TRT	**High-BA**		1	-0.0078	0.3552	-0.7439	0.6543	0	0.9826
DOV*TRT	**Low-BA**		1	-0.5757	0.2483	-1.0955	-0.116	5.37	0.0204

Table 6: Parameter estimates for the best model predicting *P. maniculatus* occupancy with a logistic regression. TRT: treatment (low- or high-BA), Date: sampling period, DOV: distance of vulnerability (standardized).

	BA_live	BA_Snags	CWD_vol	FF	GC_woody	GC_litter	GC_rocks	GC_bare	GC_DWD	GC_annual	DOV
L1	A	A	A	A,B	A,B	A,B	C	A	A	B	A
L2	A	B	A	A	A	A	C	A	A	A	A
L3	B	A	A	A,B	B	B	B	A	A	A	B
L4	A, B	B	A	B	A	A,B	A	A	A	B	A

Table 7: Differences in structural habitat variables among low-BA stands (Tukey groupings). For each variable, stands that are not significantly different share the same letter. BA_live: BA of live trees (m^2ha^{-1}), BA_snags: BA of snags (m^2ha^{-1}), CWD_vol: CWD volume (m^3ha^{-1}), FF: forest floor depth (cm), GC_woody: percent cover of live woody plants (%), GC_litter: percent cover of litter (%), GC_rocks percent cover of rocks (%), GC_bare: percent cover of bare ground (%), GC_DWD: percent cover of DWD (%), GC_annual: percent cover of annual plants (%), DOV: distance of vulnerability (m).

FIGURES

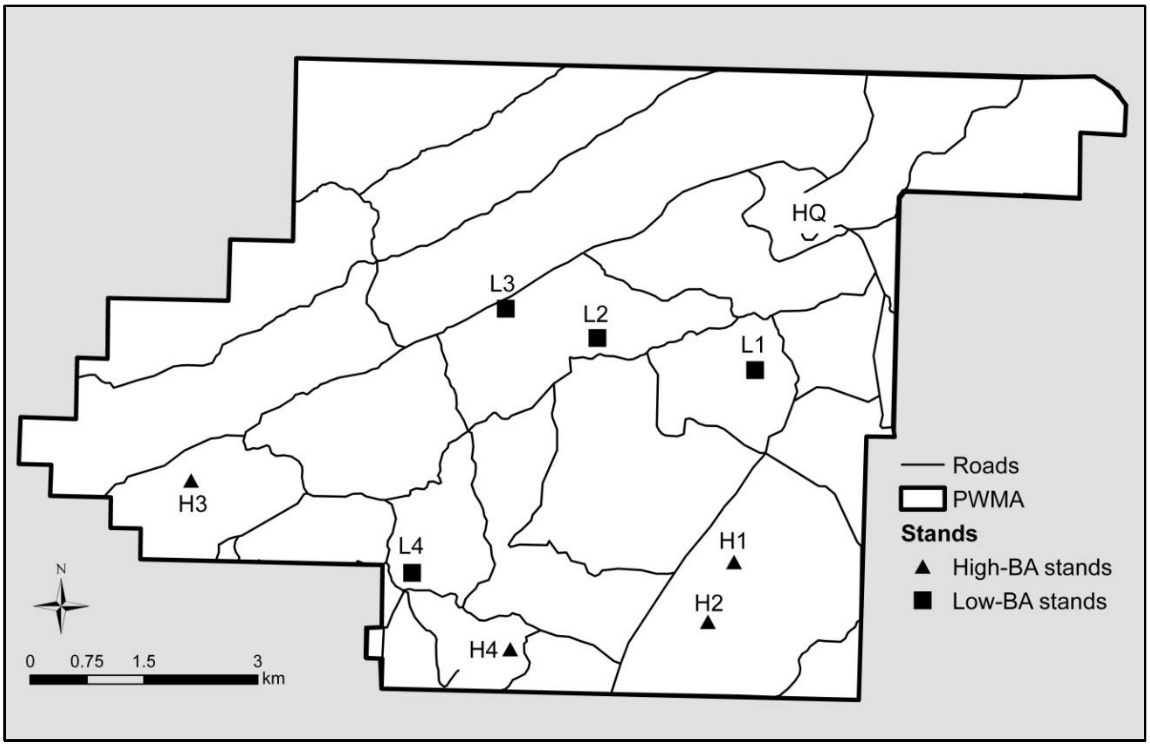

Figure 1: Stand location at PWMA. Roads were fire breaks and treatment boundaries.

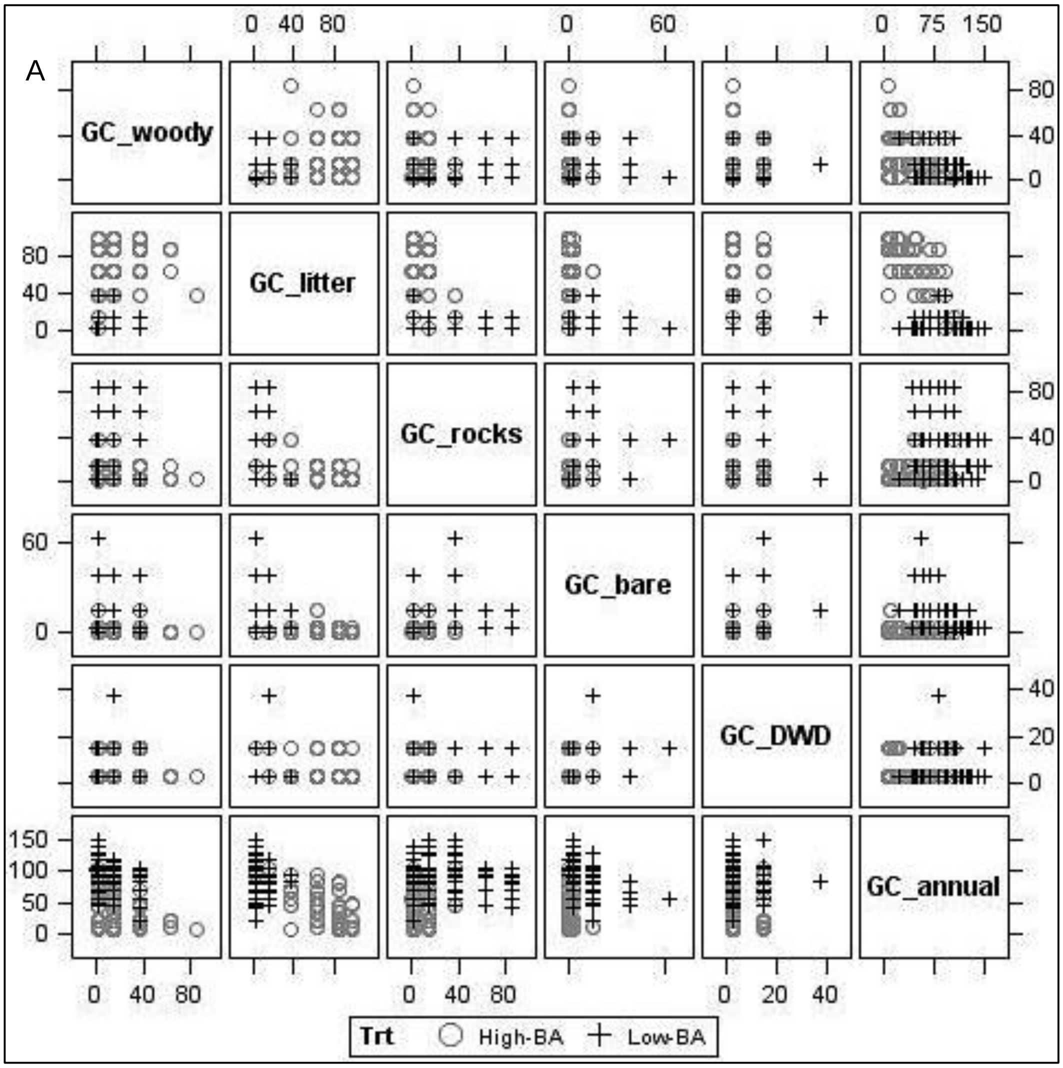

Figure 2: Matrices showing correlation among structural habitat variables. High-BA: open circle; low-BA: cross. Graphs above and below the diagonal are mirrored images. (A) GC_woody: percent ground cover of live woody plants (%), GC_litter: percent ground cover of litter (%), GC_rocks: percent ground cover of rocks (%), GC_bare: percent cover of bare ground (%), GC_DWD: percent ground cover of DWD (%), GC_annual: percent ground cover of annual plants (%). (B) BA_live: BA of live trees (m^2ha^{-1}), BA_snags: BA of snags (m^2ha^{-1}), CWD_vol: CWD volume (m^3ha^{-1}), DOV: distance of vulnerability, FF: forest floor depth (cm).

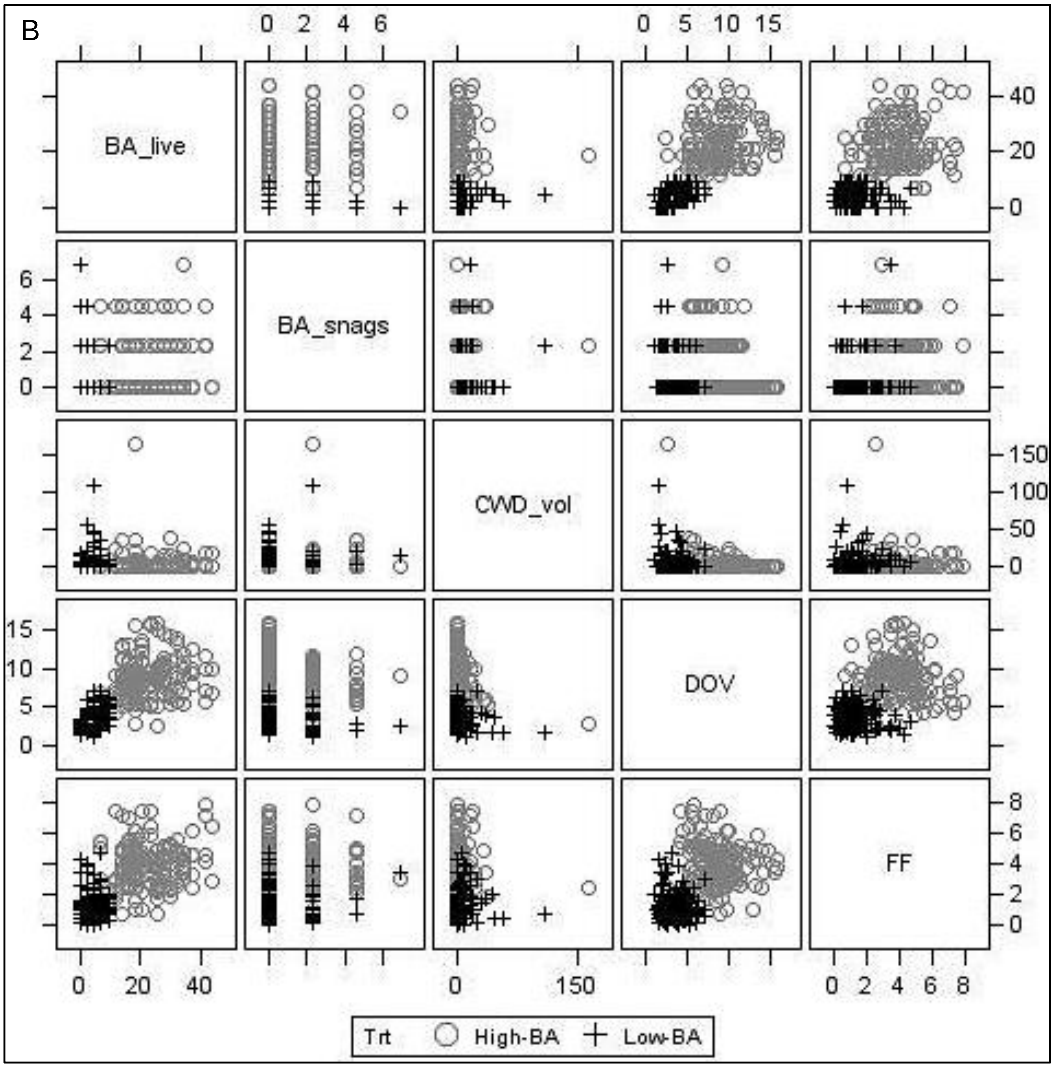

Figure 2 (continued).

VITA

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Candidate for the Degree of

Master of Science

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