

8-1-2017

SUMMER HABITAT USE BY A MAMMAL COMMUNITY OF AN OAK-DOMINATED ECOSYSTEM IN THE CENTRAL HARDWOOD REGION

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SUMMER HABITAT USE BY A MAMMAL COMMUNITY OF AN OAK-DOMINATED
ECOSYSTEM IN THE CENTRAL HARDWOOD REGION

by

Brent S. Pease

B.S., Colorado State University, 2014

A Thesis

Submitted in Partial Fulfillment of the Requirements for the
Masters of Science Degree.

Department of Forestry
In the Graduate School
Southern Illinois University Carbondale
August 2017

THESIS APPROVAL

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A Thesis Submitted in Partial
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for the Degree of
Master of Science
in the field of Forestry

Approved by:

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April 8, 2017

AN ABSTRACT OF THE THESIS OF

Brent S. Pease, for the Masters of Science degree in Forestry, presented on April 13, 2017, at Southern Illinois University Carbondale.

TITLE: SUMMER HABITAT USE BY A MAMMAL COMMUNITY OF AN OAK-DOMINATED ECOSYSTEM OF THE CENTRAL HARDWOOD REGION

MAJOR PROFESSOR: Dr. Eric J. Holzmüller

In the greater Central Hardwood Region, advance regeneration of oak (*Quercus spp.*) and hickory (*Carya spp.*) has been in decline for several decades. Facilitated in part by an abrupt change in disturbance regime, coupled with an increase in herbivore density, the existing mid-successional, mast-producing species are being outcompeted by late-successional, mesophytic species. Oak-hickory forests provide keystone resources for a diverse forest wildlife community, and a decline in its dominance will likely impact habitat use and occupancy patterns in the mammal community, but to what extent is unclear. During May-August 2015-2016, I deployed 150 remotely-triggered camera traps in Trail of Tears State Forest (TTSF), Union County, Illinois to investigate single-season, site occupancy patterns and detection probabilities as a function of forest composition and structure for 3 mammals (eastern gray squirrel [*Sciurus carolinensis*], raccoon [*Procyon lotor*], and white-tailed deer [*Odocoileus virginianus*]). I collected microhabitat data at each camera-site and utilized a GIS application to estimate spatial relationships among anthropogenic features and camera-sites. I recorded 404 photographs of 11 endothermic species during 3927 days of survey effort, with white-tailed deer, raccoons, and eastern gray squirrels as the most detected species, respectively. Detection probability of eastern gray squirrels was best explained by the global detection model, indicating no covariate measured explained the variation in detection rates. Raccoon detection probability was best described by a negative relationship with the average temperature recorded during survey period. The best-fitting detection model for white-tailed deer indicated detection probabilities declined

throughout the sampling period and across seasons. Eastern gray squirrel site occupancy models received little support, however, ecological land type phase was the most supported model. The best fitting habitat model described a negative relationship between eastern gray squirrel site occupancy probability and coarse woody debris volume. For raccoons, no model with habitat covariates was better fitting than the null model. Raccoon occupancy probability increased with maximum DBH at a site, ground cover, and beech-maple importance values, but decreased with oak-hickory importance values. White-tailed deer occupancy was most positively influenced by ground cover and oak-hickory importance values, but decreased with distance to forest edge, number of understory stems, and beech-maple importance values. My research provides empirical evidence to predictions made regarding the impact of a decline in oak dominance across the Central Hardwood region on a portion of the region's mammal community. Shifts to late-successional conditions in the Central Hardwood region will likely continue and magnify if forest management approaches continue to minimize the frequency and occurrence of large, anthropogenic disturbances to the forest overstory. A mosaic of forest conditions will be needed to best support a diverse and complete mammal community across the region.

ACKNOWLEDGMENTS

First and foremost, sincere gratitude to my family for their continued support and encouragement during my professional development. Reanna, my life partner, endless thanks and love to you for your understanding, compassion, and encouragement during our time in Carbondale; I can't wait to begin our next chapter in Raleigh with Arlo! My parents, Bob and Brenda, as well as my brother, Bobby, were always available to chat and provide outlets from work – I wouldn't be here without your support!

This research could not have been completed without the financial and logistical support from the Department of Forestry in the College of Agricultural Sciences at Southern Illinois University in Carbondale. Additional support comes from the Illinois Department of Natural Resources and the staff at Trail of Tears State Forest. Advising and co-authorship from Eric Holzmueeller and Clayton Nielsen greatly improved this work and provided me with multiple perspectives on how to approach scientific investigation in ecology. Thank you, Eric, for your friendship and mentorship during the past two years; you allowed substantial freedom to explore ideas and develop professionally, all while providing sufficient resources and guidance when needed. Clay, your thoughtful comments were so helpful in improving my writing, and I cannot thank you enough for connections made during my time at SIU. Charles Ruffner was an irreplaceable asset to my committee and to my education while at SIU, for which I am grateful. In general, the Forestry Department was incredibly supportive - special thanks to: Patti Cludray, John Groninger, and Jim Zaczek. My officemate, Richard Nesslar, was a great motivation day in and out, and showed me the “forestry ropes” – thank you, Ricky! Lastly, a sincere thank you to the other students throughout the department that I shared conversations with or those who I was lucky enough to help out with their work.

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CHAPTER 1

INTRODUCTION

In the greater Central Hardwood Region, gradual decline of oak (*Quercus spp.*) in the overstory has been underway for several decades (Fralish and McArdle, 2009). Through changes in regional disturbance regimes, late-successional, shade-tolerant species such as American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) are outcompeting more desirable, shade-intolerant genera such as oak and hickory, leading to concerns regarding the future composition and structure of forests throughout the region (McShea and Healy, 2002; Ozier *et al.*, 2006). Additionally, current forest structure in many patches throughout the region is not providing spring and summer foraging suitability for a suite of silvicolous species due to light-limited conditions from a nearly completely closed overstory canopy (Johnson *et al.*, 1995; Gill *et al.*, 1996; Gillen and Hellgren, 2013). The decline of the ecologically important oak-hickory forest association, followed by subsequent compositional shifts throughout the region, will likely have an impact on the distribution of fauna dependent on its dominance (Rodewald, 2003). The impact of the subsequent loss of functional wildlife habitat in this region (Fralish and McArdle, 2009), which would otherwise provide high quality forage and a forest structure supporting cover and escape for prey species, is still unclear and has highlighted an area of study warranting research.

Trail of Tears State Forest (TTSF) in southwestern Illinois has been projected to be one of the first areas in the region to completely undergo a successional transition to beech-maple dominance (Fralish and McArdle, 2009). Monitoring trends in habitat use and microhabitat selection by the ground-dwelling silvicolous community currently utilizing the area is central to understanding the influence of shifting stand-level characteristics on mammal distribution and

identifying associations with key habitat components in mature oak-dominated ecosystems. Despite predictions and warnings of potentially negative impacts on wildlife (Rodewald, 2003; McShea *et al.*, 2007; Fralish and McArdle, 2009), few studies have attempted to quantify habitat associations of silvicolous species occurring in patches with shifting forest structure and composition (Gillen and Hellgren, 2013). Through the utilization of non-invasive, passive monitoring techniques, such as remotely triggered cameras, wildlife biologists can cheaply and efficiently estimate the spatial distribution in the mammal community, and simultaneously identify microhabitat characteristics associated with the distribution by the suite of vertebrates (O'Connell *et al.*, 2011; Rovero *et al.*, 2013; Meek *et al.*, 2014a; Lesmeister *et al.*, 2015). Understanding mammal response to shifting forest structure, composition, and spatial characteristics is one step towards supporting researchers' and practitioners' goal of retaining the oak-hickory forests in the Central Hardwood Region.

Literature Review

Oak-Hickory Forests

Oak-hickory forests provide irreplaceable resources to the forest community in which they exist through added richness and structure (Fralish, 2004), and to the substantial number of wildlife species that are dependent for food and other sustenance (Van Dersal, 1940; Martin *et al.*, 1951; Rodewald, 2003). These mast-producing species are paralleled by few in their ability to perpetuate and maintain a diverse forest wildlife community, and a decline in their dominance will likely create novel conditions for those dependent on the resource (McShea and Healy, 2002; McShea *et al.*, 2007). It is now widely accepted that disturbance is essential to the maintenance of this desirable community, and a lack thereof can have threatening consequences to their establishment and persistence (Abrams, 1992; Lorimer, 1993; Nowacki and Abrams, 2008;

Holzmueller *et al.*, 2014).

Oak-dominated Ecosystems in the Central Hardwood Region

Oak species make up the *Quercus* genus, a member of the beech family (*Fagaceae*). *Quercus* is arguably the most ecologically significant tree genus found in North America (Johnson *et al.*, 2009; Dey *et al.*, 2010). With 400-600 species globally and over 75 species in North America, this genus is continentally ubiquitous and is found in a wide range of environmental conditions (Smith, 1992; Johnson *et al.*, 2009). Indeed, the Forest Resources of the United States report (2007) documents the oak-hickory forest association as the most abundant forest cover type in the United States, comprising over 30% of the North region's forest cover, or totaling over 132 million acres (Smith *et al.*, 2009). Oak species are common associates in many forest cover types, with the genus often found coupled with hickory species in the Central Hardwood Region of the United States (Smith *et al.*, 2001; Hutchinson *et al.*, 2005; Johnson *et al.*, 2009). The Ozark Highlands section of the Central Hardwood Region, with its most easterly reach to southwestern Illinois, makes up one of the largest contiguous areas dominated by oak-hickory forests (Johnson *et al.*, 2009).

Despite the nomenclature for this cover type, Braun (1972) described a small fraction of the canopy to consist of hickories in a mature forest. Accordingly, the percentage of the canopy dominated by hickories is determined by site conditions, but generally with oaks occupying more than 50% of the canopy stocking (McWilliams *et al.*, 2002; Johnson *et al.*, 2009). Nonetheless, hickory species are important members of the forest community and are persistently found in association with oaks throughout the Central Hardwoods (Johnson *et al.*, 2009).

Oak-hickory forests are typically upland bound and are commonly found on south-facing slopes with dry-to-mesic conditions (McWilliams *et al.*, 2002; Johnson *et al.*, 2009; Dey *et al.*,

2010). The species' physiological characteristics contribute to their resiliency to drought conditions, as well as their inability to persist in shaded environments (Johnson *et al.*, 2009; Dey *et al.*, 2010). Additionally, the oak species found on sites exhibiting these characteristics tend to be able to withstand nutrient poor growing mediums (Abrams, 1992).

Oak-Wildlife Relationships

No other tree genera in North America contributes more to the persistence of wildlife species in deciduous forests than the *Quercus-Carya* association (Miller and Lamb, 1984; McShea and Healy, 2002; McShea *et al.*, 2007). Indeed, Martin *et al.* (1951) reported that 96 North American vertebrate species, 49 of those occurring in Eastern United States (Miller and Lamb, 1984), utilize acorns alone, with heavy emphasis during the fall and winter seasons. Another report stated that 186 different birds and mammal species feed on at least one component of the oak tree (Van Dersal, 1940). Despite the range in reports, it is evident that wildlife are heavily dependent oak and hickory as a source of hard mast. Additionally, in light of the near disappearance of American chestnut (*Castanea dentata*), even more pressure has been placed on oak species across the landscape to provide sustenance for wildlife species (Healy *et al.*, 1997). Considering the amount of land covered by oaks in North America, special care to maintain these populations is needed as the distribution and abundance of many wildlife species is intrinsically linked to these forests.

Oak and hickory presence in a forest creates a community structure that provides direct and indirect functional necessities to a substantial number of both exothermic and endothermic species (McShea and Healy, 2002; McShea *et al.*, 2007). Directly, the production and annual variation of acorns, the hard-shelled seed crop produced by oak species (Johnson *et al.*, 2009), influences the decision making of wildlife populations so extensively that they are considered

among many as the most important wildlife food resource in North America (Van Dersal, 1940; Miller and Lamb, 1984; McShea and Healy, 2002; McWilliams *et al.*, 2002; McShea *et al.*, 2007). Indeed, the distribution and abundance of silvicolous species is directly linked to the annual variation of the seed crop (McShea and Schwede, 1993; Wolff, 1996). Community dynamics can also be mediated indirectly by annual variation in mast production, in that increased population densities of small mammals due to acorn abundance can have multitrophic impacts. McShea (2000) reported that songbird nest success declines during heavy mast production years as a result of predation from the increased rodent population responding to the seed crop.

Wildlife communities reciprocally benefit the genus through dispersion mechanisms and vegetation propagation (Steele and Smallwood, 2002; Brose *et al.*, 2014). That is, acorn dispersal is highly dependent on wildlife (Johnson *et al.*, 2009). Acorns, as a highly digestible and nutritious food source to seed predators, serve as an advantage to the genus, in that the likelihood of being transported to another location via wildlife is most certain (Steele and Smallwood, 2002; Johnson *et al.*, 2009).

The movement of acorns by the silvicolous community can also propel or hinder the germination of oak species (Steele and Smallwood, 2002). While many acorns are immediately consumed or cached in locations unsuitable for germinations, some birds and mammals assist propagation through a process known as scatter-hoarding (Jenkins and Peters, 1992; Wauters and Casale, 1996). Scatter-hoarding is a dispersion mechanism that involves moving the seed to a location away from predator-competition that is often suitable for germination, and then caching the crop for propagation (Price and Jenkins, 1986). It is these complex interactions that have created lasting relationships between oak species and the wildlife that inhabit these ecosystems.

Species-specific Relationships to Oak Ecosystems

White-tailed Deer

White-tailed deer are the most populous species of cervid in North America and the most economically important game species in the Central Hardwood Region (Feldhamer, 2002; VerCauteren and Hygnstrom, 2011). Perhaps no other wildlife species has such profound, disproportional impacts on an ecosystem as White-tailed deer; their ability to alter both overstory and ground cover composition through browsing, ultimately creating indirect effects on similar herbivorous species as well as other trophic levels has led to their classification as a keystone species (Waller and Alverson, 1997; Rooney and Waller, 2003). Directly, their browsing of preferred advanced oak regeneration is contributing to the overall reduction of the genus in the Central Hardwood Region (VerCauteren and Hygnstrom, 2011). White-tailed deer have long been credited with decreases in browse-sensitive, herbaceous plant species richness as well as long-term shifts in compositional and structural diversity through modulating successional processes (DeCalesta, 1997; Feldhamer, 2002).

Much of white-tailed deer distribution overlaps with that of oaks, creating an intricate relationship between the species and the oak seed crop. White-tailed deer in the Central Hardwood Region have exhibited a preference for acorns more than other food resources (Korschgen, 1962; Korschgen *et al.*, 1980), which can cause direct, seasonal shifts in home-range sizes and habitat use by deer (Feldhamer, 2002). Given seasonal availability, acorns can constitute up to 90% of autumn diets of white-tailed deer (McShea and Schwede, 1993), and up to 50% of their winter diets (Torgerson and Porath, 1984).

Beyond mast availability, structure of oak-dominated stands plays an important role in habitat use by white-tailed deer, which is often dictated through food availability (Gill *et al.*, 1996). During spring and summer, prior to mast production and availability of agricultural crops,

white-tailed deer rely heavily on a variety of herbaceous forbs as well as reachable leaves and twigs of palatable species (Korschgen, 1962). However, in areas void of recent forest management practices, such as overstory manipulations, ground cover in mature forests is often lacking abundant, desirable forage (Gill *et al.*, 1996), reducing the suitability and use of the stand.

Year-round use of a stand by white-tailed deer requires a mosaic of varying stand characteristics that provide essential mast during the critical autumn and winter seasons (VerCauteren and Hygnstrom, 2011), sufficient amounts of spring and summer herbaceous forage (Korschgen, 1962), and suitable cover for reproduction and survival (Harlow, 1984). Unfortunately, land managers too often place emphasis on one habitat aspect and neglect the other basic needs of an organism (Fulbright and Ortega-Santos, 2006), ultimately leading to unsuitable wildlife habitat sparsely used by species of interest.

Eastern Wild Turkey

Eastern Wild turkeys (*Meleagris gallopavo silvestris*) are omnivorous opportunists and are associated with a variety of habitats, where habitat selection is subspecies specific (Steffen *et al.*, 2002). The eastern subspecies (*M. g. silvestris*) is the most prominent and extensively distributed turkey in North America, where it is abundant in the Central Hardwood Region (Vangilder and Kurzejeski, 1995; Steffen *et al.*, 2002). The importance of oak presence to eastern wild turkeys is particularly evident in diet studies of the species. Acorns are the primary food source for the species during spring, fall, and winter seasons, where their percent composition of overall diet is on average 20.5%, 20.4%, and 33.2%, respectively (Steffen *et al.*, 2002). Further, contrary to white-tailed deer and other mast consumers, wild turkeys do not exhibit a preference of white- versus red-oak mast, but rather size of nut determined preference

(Minser *et al.*, 1995). However, in accordance with their opportunistic nature, overall food accessibility and availability most dictate resource selection, and if agricultural crops are more easily acquired, then the species will equally utilize the resource (Minser *et al.*, 1995).

Forest structure tends to weigh equally with food resources in selection and preference decisions made by wild turkeys. Predator avoidance cannot be ignored, nor can the biomechanics of the species, as their ability to rapidly escape is limited by their biology. The species tends to utilize mature, closed-canopy oak-dominated forests void of thick understory growth, as those stand conditions are often most conducive to predators such as bobcats or raccoons (Steffen *et al.*, 2002). Additionally, forest composition and structure contributes to likelihood of use by wild turkeys, pending available escape-cover, roosting sites, and potential for brood rearing, thus these characteristics cannot be ignored when evaluating suitability and probability of use of a stand (Steffen *et al.*, 2002).

Carnivorous Mammals

The mesocarnivore guild common to this region can occur sympatrically and includes species such as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and bobcats (*Lynx rufus*) (Lesmeister *et al.*, 2015). Carnivore existence in oak-dominated landscapes is often mediated through trophic cascades via predation of silvicolous species dependent on resources endemic to these ecosystems (Gillen and Hellgren, 2013; Lesmeister *et al.*, 2015), though generalists common to the Central Hardwood Region, such as raccoons, rely on mast production of these ecosystems (Chamberlain *et al.*, 2003). Indeed, abundant mast production can cause direct trophic interactions and cascading effects due to the ecological significance of the resource (Gillen and Hellgren, 2013), expanding the consequences of the composition shift currently

underway in the Central Hardwood Region (Fralish and McArdle, 2009).

Species in this guild utilize a variety of habitats, food resources, and operate under varying methods of resource allocation (Lesmeister *et al.*, 2015). All species use forested habitats, with striped skunks, raccoons, and red foxes often being associated with forest edges consisting of brushy characteristics and closer to agricultural lands or other human-derived foods. Coyotes are associated with open habitats and fragmented forests while species such as gray foxes and bobcats are mature forest specialists and thrive in rocky, topographically rough areas (Lesmeister *et al.*, 2015). Resource allocation methods, or strategies for hunting, dictate habitat selection for many species and often vary by taxonomic families, such as canids contrasted with felids. The stalking tendencies of felids lend well to horizontally and vertically heterogeneous landscapes and vegetation structure while canids broadcasted approach of group, or social hunting lends well to mature, closed-canopy forests with vacant ground cover, or non-forested open habitats (Lesmeister *et al.*, 2015).

Raccoons' generalist nature suits the species for a variety of habitats and food sources. In forested areas, the species' habitat selection is associated with proximity to streams or other water sources to presumably satisfy daily metabolic demands (Wilson and Nielsen, 2007), while den site abundance and forest patch size are other important factors dictating use (Henner *et al.*, 2004). Outside of the forest, however, daytime resting sites (Wilson and Nielsen, 2007) can be a number of human resources such as trash receptacles or vacant buildings (Prange *et al.*, 2003).

Raccoon use of aquatic areas is prevalent in diet studies of the species where crayfish have been found to make up nearly 60% of their food intake (Hamilton Jr, 1936). Additional foods used by the species includes berries, commercial fruits, mast, grains, fish, insects, and small mammals (Hamilton Jr, 1936). Further, raccoons are also key predators of economically-

important game species such as eastern wild turkeys in forested habitats (Chamberlain *et al.*, 2003). The overlap of the species' preference for oak acorns indeed adds to the already intense competition for the resource, but also situates raccoons in habitats rich with prey during mast production.

Camera Trapping Sampling Technique

Monitoring fluctuations, behaviors, and interactions of wildlife populations has long been of interest to researchers, ecologists, and scientists. Until recently, options for studying wildlife were generally hands-on, expensive, and mostly inefficient (Meek *et al.*, 2014a). However, through widespread advances in technology, remotely-triggered cameras are now a viable sampling technique to efficiently survey a variety of taxa (O'Connell *et al.*, 2011; Meek *et al.*, 2012; Rovero *et al.*, 2013). Coupled with existing theoretical and analytical approaches, “camera-trapping” is now one of the most widely used wildlife research applications (Rovero *et al.*, 2013).

Camera trapping is a passive, non-invasive sampling technique that utilizes remotely-triggered cameras to capture images and/or videos of individuals passing in front of them (Swann *et al.*, 2011; Rovero *et al.*, 2013). There are different types of camera trap systems, but currently the most common is a triggered [vs. non-triggered, i.e., set to record at regular intervals (Swann *et al.*, 2011)] passive infrared system; these systems utilize heat from endothermic species to detect changes in the camera capture zone (Rovero *et al.*, 2013).

While the upfront cost of camera traps can be greater relative to other wildlife detection devices, camera traps have operational advantages over other survey methods such as track-plate surveys or transect sightings (Trollet *et al.*, 2014). For example, camera traps do not require daily monitoring, require fewer person-hours to deploy and maintain, and are well-suited for a

wide range of climatic conditions (Nielsen and McCollough, 2009; Rovero *et al.*, 2013). Camera traps are also an ideal detection survey method for community studies because they can capture wildlife occurrence patterns across multiple species simultaneously (Bridges and Noss, 2011). Further, camera traps can detect cryptic, nocturnal, or otherwise uncommon and elusive species with greater rates compared to other types of animal observation methods, thereby improving detection rates of imperfectly detected wildlife (Nielsen and McCollough, 2009). Cumulatively, the reasons listed place camera traps as the most appropriate detection device for studies of medium-to-large mammals across environmental conditions (Lesmeister *et al.*, 2015).

Occupancy Modeling Framework

While study designs that utilize cameras are varied, of particular interest to this research is the occupancy-modeling analytical framework. MacKenzie *et al.* (2002) describe occupancy as the fraction of sampling units in a landscape where a target species [or suite of species] is present. As found in many sampling techniques, it is well agreed that a species may go undetected in a survey of a sampling unit despite the species' actual presence, or occupancy, of the sampling unit. To account for this imperfect detection, a likelihood-based method developed by MacKenzie *et al.* (2002) provided a viable way to estimate site occupancy and detection probability based on repeated spatial and temporal surveys. Occupancy modeling framework has two parameters of interest, ψ – the probability a site is occupied by the target species and p – the probability of detecting the species during the survey, given it is present (MacKenzie *et al.*, 2002; MacKenzie *et al.*, 2003; MacKenzie *et al.*, 2006).

In keeping with the basic sampling scheme, cameras are deployed across an area of interest and programmed to run for a defined amount of time, thus creating multiple sampling units. Continuous data recorded by cameras are then binned into discrete time intervals, such as

days or weeks, to mimic the “multiple visit” requirement of occupancy methods (MacKenzie *et al.*, 2006). Satisfying both the spatial and temporal requirements, this sampling design can then answer questions related to faunal checklists, relative abundance and density of populations, species distributions, or to track behavioral changes as a result of management practices (O'Connell and Bailey, 2011; Rovero *et al.*, 2013).

Detectability

Most ecological studies are impacted by false-negative measurement error when an individual is unobserved or a species is recorded as absent at a site where it occurs (Gu and Swihart, 2004; MacKenzie *et al.*, 2006; Kéry and Royle, 2016). To account for this ubiquitous false-negative measurement error and achieve unbiased estimates of species-specific site occupancy, it has been demonstrated that in many cases it is necessary to explicitly model the measurement error process that underlie a matrix of presence/absence data (MacKenzie *et al.*, 2002; Gu and Swihart, 2004; Lesmeister *et al.*, 2015; Kéry and Royle, 2016). MacKenzie *et al.* (2002) developed a framework to estimate species-specific probabilities of detection (p) and site occupancy (ψ) which accounts for imperfect survey detection and estimates the probability of a site being used – a reduced-information quantity derived from the true state of abundance, which is ultimately an areal summary of the underlying spatial point pattern process (Kéry and Royle, 2016).

The occupancy modeling framework relies on spatiotemporal measurements of incidence (e.g., presence/absence) to account for the imperfect detection of a species. Camera-sites of interest must be surveyed a minimum of two times per survey season within a time period where the probability of a site being occupied does not change. During the surveys the target species is either detected with probability p which occurs with probability $\psi \times p$, or not detected ($1-p$)

which arises when either the species was present but undetected [$\psi \times (1 - p)$] or when it was truly absent ($1 - \psi$). When a species is detected during a visit, j , the visit is assigned a value of “1” and when non-detection occurs, it is denoted with a “0”; a vector of 1s and 0s is developed from multiple visits and sites to determine a species’ encounter history - a matrix used to inform maximum likelihood estimates (MacKenzie *et al.*, 2006). This framework allows parameters to be fit on a logit link scale that permits p or ψ to be a function of covariates that are hypothesized to influence the measurement process and the latent state variable. Likewise, a suite of site-specific biotic or abiotic habitat conditions (e.g., habitat type, topographic characteristics) that may influence the distribution of target species in an area of interest can be expressed in the modeling process (MacKenzie *et al.*, 2002).

Justification

There is an ever-increasing amount of literature discussing shifts in forest composition and structure in the Central Hardwood Region as a result of a combination of many factors (McEwan *et al.*, 2011), particularity due to widespread changes in the disturbance regime of the region (Abrams, 1992; Fralish and McArdle, 2009; Holzmüller *et al.*, 2014). The changing disturbance region is contributing to mesophication of forest stands across the area, with shade-tolerant, late-successional maple and beech species out-competing disturbance-dependent, shade-intolerant oak and hickory species (Ozier *et al.*, 2006). Given this, many agencies are working to implement regenerative forest management practices aimed at securing oak regeneration throughout the Central Hardwood Region.

A number of studies have considered avian and small mammal responses to regenerative forest management practices (Annand and Thompson, 1997; Urban and Swihart, 2011; Raybuck *et al.*, 2012; Kellner *et al.*, 2013), but few publications (Gill *et al.*, 1996) have studied responses

of medium-to-large mammals to such activities. Additionally, despite predictions and warnings of potentially negative impacts on wildlife (Rodewald, 2003; McShea *et al.*, 2007; Fralish and McArdle, 2009), few publications have attempted to quantify responses of silvicolous species to shifting forest structure and composition (Gillen and Hellgren, 2013).

Coupling the lack of empirical evidence on mammal habitat use in these shifting forests with the urgency many researchers have voiced towards the oak regeneration problem, a study such as mine is imperative to progress the comprehensive understanding of the state of forests throughout the region. My study on how habitat use by a silvicolous vertebrate community in the Central Hardwood Region, with special attention to economically important game species such as white-tailed deer and eastern wild turkey, will be one of few, if any others, to approach this problem. Additionally, few studies have measured as extensive microhabitat covariates that I am collecting, which will provide novel information in identifying which characteristics are most important for management practices to retain at the stand-level.

Specific Objective

Specific objective of this research project is to identify key microhabitat covariates contributing to the distribution and use of TTSTF during May-August 2015-2016. The following chapter describes the results of the field surveys conducted at Trail of Tears State forest to address this objective.

CHAPTER 2

EFFECTS OF FOREST CONDITIONS ON SITE OCCUPANCY PATTERNS IN A CENTRAL HARDWOOD MAMMAL COMMUNITY

Introduction

Throughout many hardwood forests in Eastern United States, oaks (*Quercus* spp.) have been a dominant genus for millennia (Abrams, 1992; Johnson *et al.*, 2009) but are currently facing a decline in dominance across this region (Lorimer, 1984; Abrams, 1992, 2003; Ozier *et al.*, 2006). Oak-dominated hardwood ecosystems were primarily maintained in mid-successional conditions through periodic natural and anthropogenic disturbances from forest fire, livestock grazing, disease and pest outbreak, and even-aged commercial timber harvesting (Abrams, 2003; McEwan *et al.*, 2011). Important changes to the disturbance regime in the United States during the 20th century, however, have encouraged the growth of shade-tolerant mesic species such as maple (*Acer* spp.) and beech (*Fagus* spp.; van de Gevel *et al.*, 2003; Ozier *et al.*, 2006; McEwan *et al.*, 2011). Over time, these species controlled the mid-story canopy and are becoming more abundant in the overstory as they fill in gaps following the death of mature oak species, most notably red and black oak (Groninger *et al.*, 2003; Ozier *et al.*, 2006; Holzmüller *et al.*, 2012).

Shifts from mid- to late-successional forest conditions will likely have an impact on plant-animal interactions due to the role of oak as a keystone and foundation species in ecosystems (Rodewald, 2003; Fralish, 2004; Ellison *et al.*, 2005; McShea *et al.*, 2007). Oak species have a disproportionally large influence on ecosystem communities due primarily to their mast (tree seed crops) production, which during dormant conditions in hardwood forests has documented consumption by over 100 wildlife species. (Van Dersal, 1940; Martin *et al.*, 1951). Further, research indicates that acorn production can influence foraging behavior (Johnson *et al.*,

1995; Feldhamer, 2002), distribution and home range sizes of white-tailed deer (*Odocoileus virginianus*; McShea and Schwede, 1993), and wildlife community dynamics and trophic relationships among small mammals and predators (Ostfeld, 2002), further supporting their unique role in Eastern hardwood forests. Physiognomy features (e.g., leaf and bark structure) of oaks also serve a critical role in harboring vital arthropod communities, which provide necessary food resources for bird and mammal communities (Rodewald and Abrams, 2002; Rodewald, 2003). The evidence supporting the importance of forest structure and composition in wildlife distribution suggests changes in forest composition will likely have impacts on wildlife-habitat relationships, but to what extent is still unclear.

While much is known about wildlife's dependence on oak mast and the multitrophic interactions that can result from acorn production (Van Dersal, 1940; McShea and Healy, 2002), a paucity of empirical information to evaluate the implications of shifts in forest composition and structure exists (Rodewald, 2003; McShea *et al.*, 2007). Rodewald and Abrams (2002) found evidence suggesting a shift from oak-dominated to maple-dominated forests may alter avian communities, which in turn may influence small mammal populations through nest predator dynamics. Gillen and Hellgren (2013), however, failed to find differences in small mammal-carnivore dynamics among oak-dominated and beech-maple dominated stands. Clearly, approaches to forest management in the 21st century are impacting wildlife communities differently, and research across functional and taxa groups is needed to refine ecological understanding and resulting policies. Understanding the relationships of wildlife communities to forest composition and structure can aid in adaptive forest management strategies aimed to promote complete ecosystem well-being (Kohm and Franklin, 1997). However, without detailed understanding of these ecological relationships, improving approaches to ecosystem management

may be hindered. To date, research on how key game species, such as white-tailed deer, respond to regional shifts in forest composition and structure is lacking, highlighting an economically important area of study in need of investigation. Indeed, over a 5 year study Grado *et al.* (2007) reported an economic impact of white-tailed deer hunting ranging up to \$1.03 billion.

Understanding how changes in 21st century forest management regimes may impact white-tailed deer distribution and habitat use, among other species, is of great importance to state and regional economies, and such an investigation will provide timely baseline information regarding wildlife management in Eastern forests. The objective of this study was to investigate how habitat use of multiple mammal functional groups are influenced by forest structure and composition in a Central Hardwood Forest. I compared microhabitat use across mixed hardwood compartments during late spring and summer seasons. Because of the concern over the gradual loss of oak from Central Hardwood Forests I focused on the relationship between oak dominance and mammal distribution.

Materials and Methods

Study Area

This study was conducted at Trail of Tears State Forest (37° 22' N, 89° 22' W; TTTSF), in Union County, Illinois (Figure 2.1). Situated in the easternmost section of the Ozark Plateau and consists of 2088 ha, TTTSF is one of the largest blocks of contiguous forest in the lower Midwest. The topography of TTTSF is primarily comprised of long and flat, narrow forested ridge tops and steep slopes (10-42%) leading to ravine bottoms. Elevation ranges from 140 m – 213 m above sea level and site aspect is most frequently S-SW. Overstory forest cover is a mosaic of mature oak-dominated patches with components of hickory (*Carya* spp.) and sweetgum (*Liquidambar styraciflua*) while midstory and understory are dominated by sugar maple (*Acer saccharium*) and

American beech (*Fagus grandifolia*) on upland sites, and mature mixed hardwoods at lower elevations including a significant component of yellow poplar (*Liriodendron tulipifera*) (van de Gevel *et al.*, 2003; Ozier *et al.*, 2006). During spring and summer, mean sum of weekly precipitation is 0.75 ± 0.03 (SE) cm (range 0 - 3.3 cm) and weekly temperature averages 30 ± 0.05 (SE) °C.

Site Selection

Using ArcGIS software 10.3 (Environmental Systems Research Institute, Redlands, CA), I established 150 sampling points (herein, camera-sites) within the 375-ha study area at TTSF (Figure 2.1). Using the ArcGIS function ‘Generate Random Points’, I randomly selected 150 camera-sites from a previously established systematic grid of camera-sites which had a minimum spacing of 60 m² and were stratified by ecological land types (Fralish and McArdle, 2009). Camera-sites had a mean distance to forest edge of 925 ± 33 (SE) m and water source of 206 ± 11 (SE) m. Because of the relatively consistent canopy cover at TTSF, I did not eliminate sites due to a lack of forest cover nor were any sampling sites placed within anthropogenic features.

Remote Camera Surveys

During May-August 2015 ($n = 50$ sites sampled) and 2016 ($n = 100$ additional sites sampled), I deployed one remotely-triggered camera (herein, camera trap; Cuddeback E2 [20.0 megapixel], Attack IR [5.0 megapixel], or Ambush Black Flash [5.0 megapixel], Non Typical, Inc., Park Falls, WI) equipped with passive infrared sensors and infrared or white flash at each camera-site that were triggered when changes in surface temperature of objects were detected (Welbourne *et al.*, 2016). At each camera-site, I mounted camera traps to trees approximately 40 - 50 cm above ground using steel mounts and nylon strapping. No bait or lure was used at the camera-sites (Meek *et al.*, 2014b). Cameras were set to be active 24-hours each day with 30-

second delays between photographs. Cameras recorded one image per trigger and each photo recorded the date, time, and geographic coordinates of the event. Upon retrieval I identified species present in each photo. I used a threshold of 60 minutes to temporally distinguish independence of unique photographic events of the same species (Cusack *et al.*, 2015).

Habitat Characteristics

During May-August 2015 and 2016, I surveyed forest composition and structure characteristics at all camera sites using standard measurements (McShea and Healy, 2002; VerCauteren and Hygnstrom, 2011; Lesmeister *et al.*, 2015). At each site, I measured all woody overstory stems ≥ 7.6 cm diameter at breast height (dbh) within a variable-radius plot (10-factor prism) to determine species-specific density and basal area. From these density and basal area estimates, I calculated species-specific and forest association (e.g., oak-hickory or beech-maple) importance values. Importance values represent relative basal area and relative tree density, allowing for a more thorough description of forest conditions at a site (Skeen, 1973). To estimate woody understory, I established four 1.6 m fixed-radius plots at each site that were located 7.9 m from plot center in cardinal directions. Within the four plots, I tallied all woody understory taller than 1 m with diameter of 2.5 – 7.6 cm to estimate species-specific understory stem density. Ground vegetation cover was recorded using ocular estimation of vegetation cover in two 1 m² plots located 5 m from plot center in opposite directions. Ground cover included graminoid, herbaceous and woody vegetation. I also estimated volume of coarse woody debris (m³ ha⁻¹) within an 8 m fixed-radius plot using methods described by Jenkins *et al.* (2004). Briefly, I measured tree length and dbh at the midpoint of a downed tree, and classified each downed tree into a decay stage based on bark, wood staining, tree branching formation, and primary surface substrate (Jenkins *et al.*, 2004). Trees classified in decay stage 5 (most decayed)

were not included in analyses as the majority of the tree at this decay stage is sunken into the ground and almost fully decomposed (Jenkins *et al.*, 2004). To assess the influence of topographic characteristics on mammal distribution, I calculated an ecological land type phase (sensu Fralish and McArdle 2009; ELTP) for each camera-site. Ecological land type phases incorporate a site's aspect, slope, and slope position to calculate a nominal value thereby summarizing the topographic characteristics and reducing the number of covariates needed to represent topographic conditions in a model (Fralish and McArdle, 2009). I used ArcGIS 10.3 to measure distances from each camera-site to the nearest stream and forest edge.

Occupancy Modeling

To evaluate which habitat variables best supported the probability of camera-site use, I used single-season, species-specific site occupancy models developed by MacKenzie *et al.* (2002) to account for the observation process (p) in estimates of the latent state variable, site occupancy (ψ), among the mammal community. Using a 2-step process, I first modeled covariates that I predicted would influence species-specific detectability (p) while keeping site occupancy (ψ) constant. For example, temperature, precipitation, and temporal characteristics have been found to influence the detection of mammals (Rivrud *et al.*, 2010; Lesmeister *et al.*, 2015). Once I identified the model that best explained species-specific detection probabilities (p), I then compared support for *a priori* site occupancy (ψ) candidate models that incorporated covariates reflecting variation in habitat that I hypothesized to influence the distribution of the mammal community (Table 2.1). I conducted all analyses in Program R (R Core Team, 2015) using packages *unmarked* (Fiske and Chandler, 2011) and *AICcmodavg* (Mazerolle, 2011).

While modeling detection, I held site occupancy constant across sites [designated by ψ (.)], then fit species-specific p as a function of survey-specific covariates and

factors predicted to influence the probability a species will be detected a site, given it is present (Table 2.2). The covariates and factors used include both temporal and environmental characteristics such as month and year a survey occurred, sum of precipitation during a survey period, average temperature during a survey period, an interaction of precipitation and temperature, and a unique detection probability for each survey period that was not a function of covariates, but represented unknown variability in the detection process. I also offered models a covariate that reflected an animal's behavioral response – whether positive or negative - to the presence of cameras or other species at the site. Temperature and precipitation data were based on records at the nearest National Weather Service climatological station ([NOAA], 2010). The null detection model [$p(.)$ – detection held constant across surveys] was included in the candidate model set for comparison of the relative strength of models that included covariates used to model variation in the detection process. I retained the most parsimonious detection model ($\Delta AIC = 0$) for subsequent stages of occupancy modeling.

Once the most parsimonious species-specific p model was identified, I fit species-specific *a priori* site occupancy models to photographic encounter history data that incorporated site-specific habitat covariates. *A priori* occupancy models included combinations of habitat and topographic characteristics predicted to influence ψ (Table 2.3; Table 2.4; Table 2.5), and were developed for focal species with sufficient detections. Model sets of occupancy models included a null occupancy model [$\psi(.)p(pars)$] to compare parameter estimates and relative fit of models containing habitat covariates (Lesmeister *et al.*, 2015).

Models were developed to reflect 2 general hypotheses that may be influencing the distribution of mammals in the study area. Given that there is notable differences in the life histories of the mammal community in the Central Hardwood Region, I developed unique,

species-specific *a priori* candidate models to fit, thus the habitat covariates included in each model set varies among species (Table 2.3; Table 2.4; Table 2.5). The first hypothesis (Topographic) tested whether the distribution of mammals was driven by topographic characteristics and not the vegetative features in the area of interest. I expected mammal distribution patterns to be positively associated with water sources (e.g., streams, ponds) to fulfill basic metabolic requirements. I also expected white-tailed deer, raccoons, and eastern gray squirrels to be positively associated with forest edges (Zegers *et al.*, 2000; Chamberlain *et al.*, 2007; Ruzicka *et al.*, 2010). Ecological land type phases (Fralish and McArdle, 2009) were used to reflect a site's elevation, aspect, and slope position – all of which may influence the mammal community's distribution in the study area . The second hypothesis (Habitat) tested whether the forest composition and structure at a site influenced the presence/absence of an individual or a species. I predicted all species to have a positive relationship with oak - hickory importance values. Similarly, I expected sites with increasing beech – maple importance values to be less used by the mammal community. Given the increased food availability from higher insect community abundance and diversity, as well as adding vertical structure to a site, I expected raccoons and eastern gray squirrels to be positively associated with coarse woody debris (Jenkins *et al.*, 2004). I expected site occupancy for white-tailed deer and other herbivores to be unaffected to slightly negatively affected by the presence of coarse woody debris at a site; increased coarse woody debris volume at a site reduced the surface area where vegetation could potentially grow, and given that coarse woody debris can harbor rich rodent communities, these sites may also attract predators thus further deterring herbivores in the community. Species with arboreal locomotion (e.g., raccoons, eastern gray squirrels) were expected to be positively associated with the presence of tree snags at a site.

I ranked models based on their Akaike's Information Criterion (AIC) values and model weights (ω) (Burnham and Anderson, 2002; MacKenzie *et al.*, 2006). I considered all occupancy models composing 0.90 cumulative ω (i.e., the 90% confidence set) for interpretation. I model-averaged estimates of detection and site occupancy for each species. To avoid numerical problems within the maximum likelihood surface in *unmarked*, I standardized continuous covariates so that means were centered on zero and divided by the covariate sample standard deviation. When scaling a covariate with the observed data's standard deviation, I then interpret model β coefficients as the expected change in occupancy for 1 unit change in the scaled covariate, or 1 standard deviation change in the covariate from the original value (Kéry and Royle, 2016). Covariate effects were evaluated by whether the 95% confidence interval of a parameter included 0. If the CI did not include 0, a strong covariate effect was clear, however, if the interval included 0 but the majority of the parameter's distribution was either positive or negative, I concluded the effect to be less precise but supported.

Results

Habitat Characteristics

Thirty-one tree species were recorded and ELTP ranged from South (camera-sites with an aspect between 135° - 203° and 270° - 315°, mid- to high-slope positions) to Low Slope (all camera-sites with a low-slope position, regardless of aspect). Overall, overstory basal area was estimated at 24 ± 0.5 (SE) m² ha⁻¹ with a mean density of 406 ± 23 (SE) stems ha⁻¹ (Table 2.6). White oak (*Quercus alba*) made up the greatest amount of basal area (29%), with black oak (*Quercus velutina*) following second (13%; Table 2.6). Overstory stem density consisted of nearly 25% sugar maple despite this species only accounting for 8% of the basal area, with American beech (19%) and white oak (15%) as the second and third densest (Table 2.6). The

species-specific importance values resulting from relative basal area and density showed that white oak, sugar maple, and American beech were the 3 most dominant overstory species (Table 2.6). Twenty-five and 78 camera-sites had importance values $\geq 50\%$ of beech-maple and oak-hickory, respectively (Table 2.6). In general, overstory was a mixed matrix of composition and structure and only pockets of high importance values existed.

Understory density was estimated at 947 ± 67 (SE) stems ha^{-1} , with American beech accounting for over 50%, followed by sugar maple (18%), pawpaw (*Asimina triloba*; 8%), and ironwood (*Ostrya virginiana*; 4%; Table 2.7). Mean coarse woody debris volume per camera-site was $2,656 \pm 492$ (SE) $\text{m}^3 \text{ha}^{-1}$ and overall ground cover was estimated at $34\% \pm 1.3$ (SE), with 76% of ground cover recorded as woody vegetation and 24% herbaceous (Table 2.8).

Survey Effort and Wildlife Detections

Of the 150 camera traps deployed, 10 cameras malfunctioned and the remaining 140 cameras recorded 404 photographs of endothermic animals during 3-6 1-week surveys resulting in 3927 camera-days of survey effort, with a mean survey length of 28 days. After adjusting for unique photographic events, there were 320 photographs used in subsequent analyses (Table 2.9). Among the photographs used in analyses were 30% white-tailed deer, 29% eastern gray squirrels and raccoons, respectively, 5% coyotes, 4% nine-banded armadillos, 2% bobcats, and 1% Virginia opossums. The 3 most recorded species (eastern gray squirrels, raccoons, and white-tailed deer) had sufficient detection histories for occupancy analysis. Models for the remaining 4 species (bobcats, coyotes, nine-banded armadillos, and Virginia opossums) did not coverage due to sparse detection histories and thus were not considered further.

Detection

Model-averaged estimates of detection probability ($\pm SE$) varied slightly among species (white-tailed deer: $\hat{p} = 0.21 \pm 0.05$; raccoons: $\hat{p} = 0.21 \pm 0.04$; eastern gray squirrels: $\hat{p} = 0.26 \pm 0.10$). Several detection covariates were considered to significantly - positively or negatively - impact detection probabilities across species (Table 2.10; **Error! Reference source not found.**). Detection model certainty was heterogeneous across species, ranging in magnitude from one substantially supported model for eastern gray squirrels to five models satisfying the selection criteria of ≤ 2 AIC of the top model for raccoons. The best-fitting detection model for each species consistently outcompeted the null model ($\Delta AIC \geq 4.37$; Table 2.11).

Detection probability varied significantly across years 2015-2016 for each focal species (Table 2.10). White-tailed deer detection was best explained by unique weekly intercepts without covariates and the best fitting raccoon detection model contained mean weekly temperatures, where a negative relationship was observed (Table 2.10; Table 2.11). The global model was the top-fitting detection model for eastern gray squirrels (Table 2.11). For squirrels, detection probability was positively associated with being previously detected at a site, while a negative relationship existed with topographic slope (Table 2.10).

Occupancy

Naïve and model-averaged estimates ($\pm SE$) of site occupancy varied by species. White-tailed deer were detected at 40/140 sites (naïve $\psi = 0.29$), raccoons at 54/140 (naïve $\psi = 0.39$), and eastern gray squirrels at 18/140 (naïve $\psi = 0.13$). Model-averaged white-tailed deer $\hat{\psi} = 0.51 \pm 0.15$, and the top-ranked habitat model received similar support as the null model ($\Delta AIC < 3.0$; Table 2.12). The best-fitting white-tailed deer ψ habitat model indicated positive, but imprecise, effects of ground cover ($\beta = 0.63 \pm 0.47$) and oak-hickory importance values

($\beta = 0.63 \pm 0.56$; Figure 2.2; Table 2.12; Table 2.13). A less supported white-tailed deer ψ habitat model indicated a negative effect of mesic (beech-maple) importance values at a site ($\beta = -0.28 \pm 0.28$; Table 2.12; Table 2.13; Figure 2.3).

Model-averaged raccoon $\hat{\psi} = 0.63 \pm 0.10$, with the null model receiving the most support in the model set indicating weak relationships among raccoon occupancy patterns and the habitat characteristics surveyed (Table 2.12). Models containing topographic characteristics and oak-hickory importance values had similar support to the top model ($\Delta AIC \leq 1.03$), where raccoon ψ was higher with increasing distance to forest edge ($\beta = 0.40 \pm 0.33$) and ephemeral streams ($\beta = 0.23 \pm 0.30$) but ψ decreased with oak-hickory importance ($\beta = -0.40 \pm 0.33$; Table 2.12; Table 2.13; Figure 2.4). Following in model support, raccoon ψ increased with maximum DBH at a site ($\beta = 0.34 \pm 0.38$), ground cover ($\beta = 0.23 \pm 0.29$), and mesic importance values ($\beta = 0.11 \pm 0.29$; Table 2.12; Table 2.13; Figure 2.5; Figure 2.6). All raccoon ψ models within the 90% confidence model set, however, had similar support ($AIC \leq 2.00$), thus no single covariate clearly described patterns in raccoon site occupancy (Table 2.12).

Eastern gray squirrel model-averaged $\hat{\psi} = 0.20 \pm 0.05$. Most models for eastern gray squirrel received little support ($w \leq 0.06$; **Error! Reference source not found.**). Ecological 1 and type phase was the best-fitting eastern gray squirrel ψ model, followed by the null occupancy model – the only models in the set with $AIC \leq 2$ (Table 2.12; Figure 2.7). No other models were considered due to lack of weight and inconclusive relationships observed between eastern gray squirrel occupancy patterns and covariates measured.

Discussion

Forest structure of TTSHF resembled sites in the Central Hardwood Region that have had little to no management over the past 40 years: mature oak-dominated overstory with a beech-

maple midstory and a lack of oak regeneration (Ozier *et al.*, 2006; Holzmüller *et al.*, 2011). It has long been known that mammal abundance and richness can fluctuate along a forest successional gradient, as changes in habitat structure and composition are associated with these shifts (Bormann and Likens, 1979; Irwin and Peek, 1983; Huntly and Inouye, 1987; Swanson *et al.*, 2011). However, changes in faunal communities have historically been thought to be most notable during shifts from early- to mid-successional forest conditions (Swanson *et al.*, 2011). With the exception of a few studies (Rodewald and Abrams, 2002; Gillen and Hellgren, 2013), changes in faunal abundance and distribution following shifts from mid- to late-successional states in Eastern forests has been less studied, thus limiting discussion until now mostly to predictions (Rodewald, 2003; McShea *et al.*, 2007). The overall lack of definitive relationships between occupancy patterns and forest characteristics observed are in part a tribute to the generalist nature of the focal species and their ability to adapt to a myriad of environmental conditions, and suggests the consequences of the successional shifts underway across eastern North American forests will vary in severity across wildlife taxa, may be mediated by homogenous forest conditions, or may not be evident during spring and summer seasons.

My camera trap survey resulted in the detection of 4 non-targeted bird species and 7 targeted mammals during 3927 days of survey effort. This is comparable to other regional camera trap surveys, where 9 - 28 species were detected, suggesting sufficient survey effort (Cove *et al.*, 2012; Lesmeister *et al.*, 2015). Overall, I observed relatively low albeit consistent model-averaged detection rates across the focal species despite stark differences in body mass and size. Though their life histories vary, the focal species are similar in their ubiquitous distribution across the region, which may contribute to comparable probabilities of detection. The consistent detection probabilities observed may also be due to the relatively homogeneous

environmental and habitat characteristics across camera-sites (Gu and Swihart, 2004). Nonetheless, the observed detectability is comparable to similar regional and international mammal occupancy studies. O'Connell *et al.* (2006) found white-tailed deer and raccoon null detection probabilities to be 0.16 and 0.38, respectively. Likewise, detection probabilities ranged from 0.11 – 0.51 across tropical mammals (Rovero *et al.*, 2014). More survey effort per camera-site may be necessary to increase detection probabilities, as numerous factors including species-specific behavioral differences, sampling design, and environmental factors, among others, can influence detection rates (MacKenzie *et al.*, 2006; Pease *et al.*, 2016).

I observed strong yearly temporal effects on detection probability across all focal species, but temporal variation did not clearly correlate with environmental factors (e.g., precipitation) recorded at this scale. While the duration and scope of this study likely limited inference to yearly variation in detection, there were clear within-season trends. Detection rates for raccoons and squirrels were negatively, but imprecisely, related to month of survey, where detection was highest in May and lowest during August. Temperature is known to influence home range and activity patterns across many mammals, particularly in the extremes of summer and winter, which likely contributed to decreased detection rates (Elbroch and Rinehart, 2011). Doebel and Mcginnes (1974) found a negative effect of temperature on gray squirrel activity, while Elbroch and Rinehart (2011) reported squirrel activity to nearly cease during warmest temperatures. The dry conditions of late-summer in upland forests of this region may have contributed to declines in detection for raccoons, a species associated with water sources (Baldwin *et al.*, 2006; Wilson and Nielsen, 2007).

While topographic slope is often considered a factor contributing to habitat use patterns (Apps *et al.*, 2004; Creel *et al.*, 2005), few have incorporated its effect into detection models. I

hypothesized that the rugged topography of TTSF would have a negative effect on detection probabilities, particularly in smaller mammals. While efforts were made to avoid slopes that obstructed camera views, there were few occurrences of flat camera-sites across TTSF. I observed a strong negative relationship between topographic slope and eastern gray squirrel detection probability, and the same trend with white-tailed deer although a weaker relationship was observed. Camera trap placement, in regards to deployment height, distance to detection zone, and camera trap orientation, can impact detection rates across focal species, and suboptimal deployment often results from studies targeting a variety of species (Meek *et al.*, 2014b). Coupled with steep slopes (up to 42%), camera trap deployment for this study may have benefited by placing camera traps closer than 50cm to the ground, though more research on optimizing camera trap deployment in rugged terrain is warranted.

A rich literature supports the observed successional shifts taking place across eastern North American forests, where a number of factors are thought to contribute to these compositional changes (Ozier *et al.*, 2006; Holzmüller *et al.*, 2011; McEwan *et al.*, 2011). Across this region, forested areas are largely homogenous in structure, where a relatively uniform and dense canopy cover with negligible ground cover exists (Lashley *et al.*, 2011). Although widespread, the compositional shifts underway are not uniform, but rather appear to be related to topographic characteristics such as slope position and aspect (Ozier *et al.*, 2006). In unglaciated, topographically rough areas, such as TTSF, variability in environmental conditions lends to mixed compositional characteristics, where an oak-dominated camera-site can be situated adjacent to another comprised mostly of mixed mesophytic species, both being well within a mammal's home range. Thus, the interspersed patchwork of successional stages and species composition may explain the lack of clear relationships in occupancy and forest

composition and structure observed. However, barring significant changes to current forest management regimes, coupled with a consistent shift in composition and structure, changes in mammal occupancy may become evident with time. The following, then, discusses the nonsignificant occupancy trends observed across the focal species.

While I found no strong relationships between occupancy and the habitat characteristics surveyed, directional trends in the data were apparent. White-tailed deer occupancy was negatively related to beech and maple importance values while a positive relationship existed with ground cover and oak-hickory importance values (Figure 2.2). This may be due to food availability at sites with high beech-maple importance values (Rodewald and Abrams, 2002; MacKenzie *et al.*, 2006). Given this study took place in late-spring and summer when few to no acorns were available from the previous year's crop, food availability in this region, then, is primarily limited to forbs, grasses, fungi, or green leaves from tree species (Johnson *et al.*, 1995). Canham *et al.* (1994) found that the most shade-tolerant species (e.g., American beech) cast the deepest shade contributing to a spare ground layer, while mid-successional oak species allowed greater light penetration and presumably higher forage quality and availability. As the successional shift continues, the differences in spring and summer ground cover will likely exacerbate, potentially contributing to differences in white-tailed deer habitat use patterns.

I also saw a negative trend in deer occupancy with increasing distance to forest edge, which is consistent with a large body of literature (Waller and Alverson, 1997). Low forage quality and availability during spring and summer seasons in closed canopy forests, among other pressures such as predation and competition, can push deer to edge habitats to meet caloric demands (Williamson and Hirth, 1985; Alverson *et al.*, 1988; Gill *et al.*, 1996). Though creating challenges of connectivity and movement, ever-increasing fragmentation in Midwestern United

States has provided abundant edge habitat (Lindenmayer and Fischer, 2013). If metabolic demands are being met in edge habitat, then less reliance may be placed upon forests to provide food resources, shifting behavioral cues to identifying sites for resting and thermal relief from structural cover (Beier and McCullough, 1990; Mysterud and Ostbye, 1999). Thus, when foraging demands are met elsewhere, the homogenous forest structure may make it difficult to identify trends in habitat use, which potentially contributed to my failing to observe strong habitat use relationships.

Raccoon habitat use analysis revealed positive relationships with mesic importance values, suggesting habitat use by raccoons will increase as successional shifts to mesophytic conditions persist. This may be due to the physiology of beech and maples as these species tend to have greater rates of cavity abundance, providing shelter for small- to medium-sized mammals (Carey, 1983). Pedlar *et al.* (1997) found raccoon habitat use to be positively associated with sugar maple abundance, likely due to tree cavities associated with this species. In a comparison study of oak-hickory forest types and beech-maple forest types, Gysel (1961) found that raccoons displayed higher use of beech-maple sites due to the significantly higher number of tree cavities available at these sites. Additional corroboration comes from Wilson and Nielsen (2007), where they found raccoon daytime resting site selection during both breeding and cub-rearing seasons was best described by the number of available dens, although species distinction was not noted. The raccoon-mesic relationship observed could also possibly be attributed to differences in ground-dwelling small mammal prey abundance. However, Gillen and Hellgren (2013) found little evidence of differences in ground-dwelling prey communities across oak-dominated and beech-maple sites, further supporting the den availability hypothesis. Raccoons are well known predators of cavity-nesting songbirds and my findings may provide support for an expected

increase in nest predation rates at sites where beech and maple are the dominant species (Schmidt, 2003).

Beech-maple importance values had a positive influence on gray squirrel habitat use, while a negative relationship with oak-hickory importance values was observed. A seasonal diet study of gray squirrels in the Central Hardwood Region found hickory flowers and oak acorns and flowers to be the principal food items consumed in late spring (April-May), while mulberries, hickory nuts and black walnuts were the most consumed items during June – August (Korschgen, 1981); my findings suggest that food availability may not be the primary driver of gray squirrel distribution at TTSF. Rather, gray squirrel distribution may be a function of forest structure. While hickories can be vital food resources for gray squirrels, unlike American beech and sugar maple, they do not provide the same quality and quantity of nesting sites due to differences in morphology (Brown and Yeager, 1945; Gysel, 1961). Further, gray squirrel habitat use has been positively associated with understory density, providing additional support for the forest structure hypothesis. These findings suggest gray squirrels are responding well to successional shifts, but given their dependence on oaks and hickories for food resources during the dormant season, it is unlikely this species will use areas completely composed of late-successional, mesophytic species.

Providing diverse forest structure and composition to meet habitat requirements of multiple functional groups can be difficult without regional cooperation and collective efforts to increase diversity on a landscape-scale (Petit *et al.*, 1995). Areas such as TTSF whose goals include timber production are ideal for maintaining a shifting mosaic of wildlife habitat, particularly stages of forest development that often absent such as early-successional habitat (Askins, 2001). Societal demands for continuous canopy cover and low-intensity silvicultural

options, however, can limit management practices carried out and influence forest composition and wildlife habitat. Research that creates a link between wildlife abundance, particularly highly-valued game species such as white-tailed deer, and forest management practices has the potential to show the importance of actively managing forested patches to create desirable wildlife habitat, and public education efforts to elucidate this relationship should be emphasized. For example, in oak-dominated systems management actions that are known perpetuate oak dominance such as prescribed fire, thinning, or overstory removal may also improve wildlife habitat for some species and should be further explored (Lashley *et al.*, 2011).

Management Implications

Forests in eastern United States are changing in composition and structure due primarily to historically different management and societal values in the late 20th to early 21st century. The resulting forest composition and structure does not appear to be significantly impacting within-home range habitat use decisions by small-to-large mammals, although imprecise positive and negative trends were identified. Shifts to late-successional conditions in the central hardwood Region will likely continue and magnify if forest management approaches continue towards partial, uneven-aged cutting schemes, which may create unsuitable conditions for a variety of wildlife taxa. Creating a patchwork of differing forest composition and structure through active management will likely maintain components needed for year-round patch use by the mammal community and can aid wildlife adaptation to an increasingly anthropogenic landscape.

While no clear link between site occupancy and habitat characteristics surveyed was revealed, I suspect this would be less so if research were carried out during peak hard-mast availability. The effects of hard-mast availability on wildlife behavior is well documented across many taxa (McShea and Healy, 2002), and future research efforts should include this vital

component into analyses. If limitations, however, require wildlife surveys to be conducted during spring and summer, I suggest concentrating effort to the earlier portion of this period, as I saw within-season decreases in detection with time across all focal species. Additionally, avoiding sites with topographic slopes $\geq 20\%$ should help alleviate the decrease detections rates I experienced at steeper camera-sites. If the study area is topographically rough, then accounting for the effect of slope in detection models is suggested. Addressing the imperfect detection of mammals can greatly improve the inference made, and incorporating detection into statistical analyses through an occupancy modeling framework should continue to be instituted. Further, increasing per-unit sampling effort may be another option to improve detection rates which has also been shown to improve occupancy model performance, though logistical constraints can limit this option (Pease *et al.*, 2016).

Several have raised concerns regarding the impending successional shift underway and its impacts on wildlife communities (Rodewald, 2003; McShea *et al.*, 2007), however I found little evidence exists to support these claims across focal game species. Our research corroborates the findings of Gillen and Hellgren (2013), where they failed to see differences in tropic relationships among mammals across an oak-dominated gradient. However, Rodewald and Abrams (2002) provided support for these impacts in a bird community, indicating the impacts may be limited to avian and insect communities in current forest conditions. Nonetheless, maintaining a forest overstory of $\geq 50\%$ oak and other mast producing species will likely support fall and winter habitat use by white-tailed deer and other mammal species, and if patches of increased ground vegetation are available then higher rates of occupancy can be expected.

CHAPTER 3

SUMMARY AND CONCLUSION

This research examined how mammal distribution and habitat use has been affected by shifting forest composition structure in Trail of Tears State Forest (TTSF) – a portion of the Central Hardwood Region in southwestern Illinois. My study provided empirical evidence to address predictions about the impacts of late-successional, mesophytic forest conditions on habitat use patterns by a silvicolous community. Specific objectives of this research were to (1) quantify spatial distribution of ground-dwelling silvicolous species utilizing TTSF, and to (2) identify key microhabitat covariates contributing to the distribution and use of TTSF. Below, I briefly discuss the findings of my study designed to better understand how shifts in forest composition and structure, due in part to changes in forest management practices during the 20th century, is influencing mammal habitat use in TTSF.

In Chapter 2, I used non-invasive wildlife survey techniques with an occupancy modeling framework to account for imperfect wildlife detection while quantifying habitat associations and mammal distribution in TTSF. Results for two of the three species modeled indicate a neutral to positive response to late-successional forest conditions and a reduced probability of use in oak-dominated patches, although nonsignificant and often imprecise estimates were produced. These results were unanticipated due to oak's keystone role in ecosystem function and are contrary to several of the predictions made in the past decade. Results of this study have provided us with a baseline understanding of how forest management in the 21st century might impact the distribution of mammal communities across eastern United States. My findings suggest shifting forest composition and structure will likely have a varied response across wildlife species, although increased study longitude will be needed to fully evaluate the consequences.

Nonetheless, mitigation of the potentially negative effects will likely require a mosaic of conditions to maintain stable and complete mammal communities throughout the region. Forest management in the 21st century will need to find a balance among the social demands for recreation and aesthetics while maintaining a supply of timber to meet the commodity needs of expanding economies.

Table 2.1. Survey and camera-point explanatory variable codes, descriptions, and expected influence (positive +, negative -, no effect 0, not applicable n/a) on detectability or occupancy of bobcat, coyote, eastern gray squirrel, nine-banded armadillo, raccoon, Virginia opossum, and white-tailed deer during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Variables included informed detection probability (p) and occupancy (ψ) models.

Variable	Description	Expected Result						
		Armadillo	Bobcat	Coyote	Eastern Gray Squirrel	Raccoon	Virginia Opossum	White-tailed deer
PRECIP ^a	Sum of precipitation recorded during survey period at nearest NOAA station	-	-	-	-	-	-	-
PRECIP ^{2a}	Squared value of the sum of precipitation recorded during survey period at nearest NOAA station	-	-	-	-	-	-	-

Table 2.1 continued

TEMP ^a	Average temperature recorded during survey period at nearest NOAA station	-	-	-	-	-	-	-
TEMP ^{2a}	Squared value of average temperature recorded during survey period at nearest NOAA station	-	-	-	-	-	-	-
PRECIP X TEMP ^a	Interaction of sum of precipitation and average temperature recorded during survey period at nearest NOAA station	-	-	-	-	-	-	-
INT ^a	Survey period-specific intercept; unique detection probability calculated for each survey occasion	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Table 2.1 continued

MONTH ^a	Month survey was conducted (May was reference); months for comparison: June, July, August	-	-	-	-	-	-	-
YEAR ^a	Year survey was conducted (2015 was reference); 2016 year was used for comparison	0	0	0	0	0	0	0
CWD ^b	Volume of coarse woody debris recorded within 8-m radius of remote camera	+	+	+	+	+	+	-
GRCOV ^b	Percentage of vegetative ground cover recorded within 2 1-m ² plots at remote camera	+	+	-	+	+	+	+
SNAG ^b	Number of standing, dead tree stems ≥ 1.3 m tall and ≥ 7.6 cm in diameter recorded at remote camera	0	+	+	+	+	+	0

Table 2.1 continued

UNDERST ^b	Number of woody stems ≥ 1 m tall with diameter ≥ 2.5 cm but \leq 7.6 cm recorded within 4 1.7-m ² plots at remote camera	+	+	-	+	+	+	+
MESIC ^b	Importance value of American beech and sugar maple in overstory trees recorded at remote camera	-	-	-	-	-	-	-
MID ^b	Importance value of oak and hickory spp. in overstory trees recorded at remote camera	+	+	+	+	+	+	+
MAXDBH ^b	Maximum tree dbh recorded at remote camera	0	0	0	+	+	+	0
ELTP ^c	Ecological Land Type Phase. Categories describing combinations of aspect, elevation, and slope	+	+	+	+	+	+	+

Table 2.1 continued

DTEG ^c	Distance (m) to forest edge	-	+	+	-	-	-	-
DTST ^c	Distance (m) to nearest stream	-	-	-	-	-	-	-

^aSurvey-specific variable used in detection probability models

^bField-measured habitat variable for camera-point occupancy models

^cVariable derived from Digital Elevation Models

Table 2.2. Structure of a priori models used to evaluate detection probability (p) heterogeneity for eastern gray squirrel, raccoon, and white-tailed deer during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Models are presented by the primary hypotheses thought to influence species-specific detection probabilities. See Table 2.1 for factor and covariate descriptions and expected direction of variable effect on species-specific detection probability.

Hypothesis	Model ^a
Temporal	1. $\beta_0 + \beta_1(\text{Int})$
Temporal	2. $\beta_0 + \beta_1(\text{Month})$
Temporal	3. $\beta_0 + \beta_1(\text{PrevDet})$
Temporal	4. $\beta_0 + \beta_1(\text{Year})$
Temporal	5. $\beta_0 + \beta_1(\text{Month}) + \beta_2(\text{Year})$
Environmental	6. $\beta_0 + \beta_1(\text{Slope})$
Environmental	7. $\beta_0 + \beta_1(\text{Precip})$
Environmental	8. $\beta_0 + \beta_1(\text{Precip}) + \beta_2(\text{Precip}^2)$
Environmental	9. $\beta_0 + \beta_1(\text{Temp})$
Environmental	10. $\beta_0 + \beta_1(\text{Temp}) + \beta_2(\text{Temp}^2)$
Environmental	11. $\beta_0 + \beta_1(\text{Temp}) + \beta_2(\text{Precip})$
Environmental	12. $\beta_0 + \beta_1(\text{Temp}) + \beta_2(\text{Precip}) + \beta_3(\text{Temp} \times \text{Precip})$
Global	13. $\beta_0 + \beta_1(\text{Month}) + \beta_2(\text{Year}) + \beta_3(\text{Slope}) + \beta_4(\text{PrevDet}) + \beta_5(\text{Temp}) + \beta_6(\text{Precip}) + \beta_7(\text{Temp} \times \text{Precip})$
Null	14. β_0 (Intercept only)

Table 2.2 continued

^aModels with covariates were fit using the logit link function: $\hat{p} = (\exp(\beta_1 + \beta_2 + \cdots + \beta_k)) / (1 + \exp(\beta_1 + \beta_2 + \cdots + \beta_k))$, where \hat{p} = estimated detection probability and k = number of model covariates.

Table 2.3. Structure of a priori models used to evaluate occupancy (ψ) for white-tailed deer during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Models are presented by the primary hypotheses thought to influence species-specific occupancy probabilities. See Table 2.1 for covariate and factor codes, descriptions, and expected direction of variable effect on species-specific habitat occupancy.

Hypothesis	Model ^a
Topographic	1. $\beta_0 + \beta_1(\text{DTEG})$
Topographic	2. $\beta_0 + \beta_1(\text{ELTP})$
Topographic	3. $\beta_0 + \beta_1(\text{DTST})$
Topographic	4. $\beta_0 + \beta_1(\text{DTEG}) + \beta_2(\text{DTST})$
Habitat	5. $\beta_0 + \beta_1(\text{GRCOV})$
Habitat	6. $\beta_0 + \beta_1(\text{MESIC})$
Habitat	7. $\beta_0 + \beta_1(\text{MID})$
Habitat	8. $\beta_0 + \beta_1(\text{UNDERST})$
Habitat	9. $\beta_0 + \beta_1(\text{MESIC}) + \beta_2(\text{GRCOV})$
Habitat	10. $\beta_0 + \beta_1(\text{MID}) + \beta_2(\text{GRCOV})$
Global	11. $\beta_0 + \beta_1(\text{DTST}) + \beta_2(\text{ELTP}) + \beta_3(\text{DTEG}) + \beta_4(\text{GRCOV}) + \beta_5(\text{UNDERST})$
Null	12. β_0 (Intercept only)

^aModels with covariates were fit using the logit link function: $\hat{\psi} = (\exp(\beta_1 + \beta_2 + \dots + \beta_k)) / (1 + \exp(\beta_1 + \beta_2 + \dots + \beta_k))$, where $\hat{\psi}$ = estimated occupancy probability and k = number of model covariates.

Table 2.4. Structure of a priori models used to evaluate occupancy (ψ) for raccoon during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Models are presented by the primary hypotheses thought to influence species-specific occupancy probabilities. See Table 2.1 for covariate and factor codes, descriptions, and expected direction of variable effect on species-specific habitat occupancy.

Hypothesis	Model ^a
Topographic	1. $\beta_0 + \beta_1(\text{ELTP})$
Topographic	2. $\beta_0 + \beta_1(\text{DTST})$
Topographic	3. $\beta_0 + \beta_1(\text{DTEG})$
Topographic	4. $\beta_0 + \beta_1(\text{DTEG}) + \beta_2(\text{DTST})$
Habitat	5. $\beta_0 + \beta_1(\text{CWD})$
Habitat	6. $\beta_0 + \beta_1(\text{GRCOV})$
Habitat	7. $\beta_0 + \beta_1(\text{MESIC})$
Habitat	8. $\beta_0 + \beta_1(\text{MID})$
Habitat	9. $\beta_0 + \beta_1(\text{UNDERST})$
Habitat	10. $\beta_0 + \beta_1(\text{SNAG})$
Habitat	11. $\beta_0 + \beta_1(\text{SNAG}) + \beta_2(\text{CWD})$
Habitat	12. $\beta_0 + \beta_1(\text{MESIC}) + \beta_2(\text{CWD})$
Habitat	13. $\beta_0 + \beta_1(\text{MID}) + \beta_2(\text{CWD})$
Global	14. $\beta_0 + \beta_1(\text{DTST}) + \beta_2(\text{ELTP}) + \beta_3(\text{DTEG}) + \beta_4(\text{CWD}) + \beta_5(\text{GRCOV}) + \beta_6(\text{SNAG}) + \beta_7(\text{UNDERST}) + \beta_8(\text{MAXDBH})$
Null	15. β_0 (Intercept only)

Table 2.4 continued

^aModels with covariates were fit using the logit link function: $\hat{\psi} = (\exp(\beta_1 + \beta_2 + \dots + \beta_k)) / (1 + \exp(\beta_1 + \beta_2 + \dots + \beta_k))$, where $\hat{\psi}$ = estimated occupancy probability and k = number of model covariates.

Table 2.5. Structure of a priori models used to evaluate occupancy (ψ) for eastern gray squirrel during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA.

Models are presented by the primary hypotheses thought to influence species-specific occupancy probabilities. See Table 2.1 for covariate and factor codes, descriptions, and expected direction of variable effect on species-specific habitat occupancy.

Hypothesis	Model ^a
Topographic	1. $\beta_0 + \beta_1(\text{ELTP})$
Topographic	2. $\beta_0 + \beta_1(\text{DTST})$
Topographic	3. $\beta_0 + \beta_1(\text{DTEG})$
Topographic	4. $\beta_0 + \beta_1(\text{DTEG}) + \beta_2(\text{DTST})$
Habitat	5. $\beta_0 + \beta_1(\text{CWD})$
Habitat	6. $\beta_0 + \beta_1(\text{GRCOV})$
Habitat	7. $\beta_0 + \beta_1(\text{MESIC})$
Habitat	8. $\beta_0 + \beta_1(\text{MID})$
Habitat	9. $\beta_0 + \beta_1(\text{UNDERST})$
Habitat	10. $\beta_0 + \beta_1(\text{SNAG})$
Habitat	11. $\beta_0 + \beta_1(\text{SNAG}) + \beta_2(\text{CWD})$
Habitat	12. $\beta_0 + \beta_1(\text{MESIC}) + \beta_2(\text{CWD})$
Habitat	13. $\beta_0 + \beta_1(\text{MID}) + \beta_2(\text{CWD})$
Habitat	14. $\beta_0 + \beta_1(\text{MESIC}) + \beta_2(\text{GRCOV})$
Habitat	15. $\beta_0 + \beta_1(\text{MID}) + \beta_2(\text{GRCOV})$
Global	16. $\beta_0 + \beta_1(\text{DTST}) + \beta_2(\text{ELTP}) + \beta_3(\text{DTEG}) + \beta_4(\text{CWD}) + \beta_5(\text{GRCOV}) + \beta_6(\text{SNAG}) + \beta_7(\text{UNDERST}) + \beta_8(\text{MAXDBH})$

Table 2.5 continued

Null 17. β_0 (Intercept only)

^aModels with covariates were fit using the logit link function: $\hat{\psi} = (\exp(\beta_1 + \beta_2 + \dots + \beta_k)) / (1 + \exp(\beta_1 + \beta_2 + \dots + \beta_k))$, where $\hat{\psi}$ = estimated occupancy probability and k = number of model covariates.

Table 2.6. Basal area, density, and importance values of the most frequently occurring overstory tree species (> 7.6 cm dbh) and forest associations recorded during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Only forest association importance values are presented.

Species	Importance Value ^a		Basal Area (m ² ha ⁻¹)		Density (Stems ha ⁻¹)	
	MEAN	SE	MEAN	SE	MEAN	SE
Overall	-	-	24	0.5	406	23
White oak	26	1.7	7	0.5	61	6
Sugar maple	16	1.5	2	0.2	95	12
American beech	12	1.4	2	0.2	79	13
Black oak	9	1.1	3	0.3	15	2
Yellow poplar	7	1.1	2	0.3	20	6
Northern red oak	6	0.8	2	0.3	13	2
Mockernut hickory	5	0.8	1	0.2	29	7
Sweetgum	3	0.6	1	0.2	14	4
Bitternut hickory	2	0.6	1	0.1	13	4
Forest Association						
Oak-hickory	53	2.3				
Beech-maple	27	1.7				
^a $\frac{(Relative\ Basal\ Area + Relative\ Density)}{2} * 100$						

Table 2.7. Density estimates of the most frequently occurring understory tree species (dbh 2.5-7.6 cm and >1 m height) recorded during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA.

Species	Density (Stems ha ⁻¹)	
	MEAN	SE
Overall	947	67
American beech (<i>Fagus grandifolia</i>)	554	47
Sugar maple (<i>Acer saccharum</i>)	171	24
Pawpaw (<i>Asimina triloba</i>)	72	21
Ironwood (<i>Ostrya virginiana</i>)	39	11
Elm spp (<i>Ulmus spp.</i>)	33	9
Flowering dogwood (<i>Cornus florida</i>)	23	7
Sassafras (<i>Sassafras albidum</i>)	14	7
Mockernut hickory (<i>Carya alba</i>)	10	5
Yellow poplar (<i>Liriodendron tulipifera</i>)	8	4
Blackgum (<i>Nyssa sylvatica</i>)	8	5
Sweetgum (<i>Liquidambar styraciflua</i>)	8	5
Red maple (<i>Acer rubrum</i>)	2	2
Shagbark hickory (<i>Carya ovata</i>)	2	2
White oak (<i>Quercus alba</i>)	2	2

Table 2.8 Ground layer estimates recorded during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA.

Attribute	MEAN	SE
Coarse woody debris ($\text{m}^3 \text{ ha}^{-1}$)	2656	492
Ground cover (%)	34	1.3
Woody	18	1.5
Seedling	8	0.5
Herbaceous	8	0.6

Table 2.9. The total number of bobcat, coyote, eastern gray squirrel, nine-banded armadillo, raccoon, Virginia opossum, and white-tailed deer detections during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA.

Species	Count
Bobcat	7
Coyote	16
Eastern gray squirrel	92
Nine-banded armadillo	12
Raccoon	93
Virginia opossum	4
White-tailed deer	96
Total photographs ^a	404
Analysis photographs ^b	320
Length of survey (days) ^c	28 (range 16-45)
Camera days	3927
Total photographs/camera day	0.103
Analysis photographs/camera day	0.081

^aTotal number of photographs (detections) recorded of each species

^bTotal number of photographs (detections) used in detection and occupancy modeling after removing photographs taken within 60 minutes of another photograph of the same species at the same camera-point

^cMean number of survey days per station

Table 2.10. Model-averaged estimates of covariate coefficients (β), standard errors (SE), and 95% confidence intervals from detection probability (p) models within ≤ 2 AIC points of best fitting model for white-tailed deer, raccoons, and eastern gray squirrels during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA.

Species		95% Confidence Interval		
Covariate	$\hat{\beta}$	\widehat{SE}	Lower	Upper
White-tailed deer				
INTERCEPT	-1.33	0.28	-1.88	-0.78
INT*	-0.42	0.17	-0.76	-0.09
MONTH	-0.22	0.20	-0.61	0.17
YEAR*	-0.41	0.19	-0.77	-0.05
PREVDET	-0.13	0.15	-0.43	0.17
SLOPE [†]	-0.26	0.17	-0.60	0.07
PRECIP	-0.02	0.20	-0.40	0.37
PRECIP ²	-0.10	0.16	-0.42	0.22
TEMP	-0.17	0.18	-0.53	0.18
TEMP ^{2†}	-0.26	0.17	-0.59	0.06
TEMP x PRECIP	0.32	0.31	-0.29	0.93
Raccoon				
INTERCEPT	-1.34	0.25	-1.82	-0.85
INT	0.14	0.15	-0.14	0.43
MONTH [†]	-0.29	0.17	-0.62	0.04
YEAR*	0.35	0.17	0.01	0.69
PREVDET	0.06	0.14	-0.21	0.33

Table 2.10 continued

SLOPE	-0.07	0.15	-0.36	0.21
PRECIP	-0.11	0.19	-0.48	0.27
PRECIP ²	-0.12	0.15	-0.41	0.17
TEMP*	-0.36	0.17	-0.69	-0.04
TEMP ²	0.02	0.13	-0.25	0.28
TEMP x PRECIP [†]	0.39	0.27	-0.14	0.92

Eastern gray squirrel

INTERCEPT	-1.05	0.51	-2.04	-0.05
INT	0.37	0.30	-0.22	0.95
MONTH [†]	-0.72	0.37	-1.45	0.01
YEAR*	0.96	0.45	0.08	1.84
PREVDET*	0.47	0.22	0.04	0.90
SLOPE*	-1.05	0.43	-1.88	-0.21
PRECIP	-0.04	0.34	-0.72	0.63
PRECIP ²	0.17	0.25	-0.33	0.67
TEMP	0.53	0.42	-0.29	1.34
TEMP ²	0.06	0.22	-0.38	0.49
TEMP x PRECIP [†]	1.32	0.69	-0.03	2.66

*Designates statistically significant detection covariates, as determined by whether the 95% confidence interval contains 0.

[†]Designates an imprecise but supported covariate effect, as determined by parameters whose 95% confidence interval contained 0, but the bulk of the parameter's distribution was either positive or negative.

Table 2.11. Most supported (≤ 2 AIC of top model) models (plus the null model (.) for comparison of covariate effects) related to detection probabilities (p) for white-tailed deer, raccoons, and eastern gray squirrels during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. To estimate p for each species I held occupancy constant [$\psi(.)$] and fit encounter history data from 6 1-week surveys at 140 remote camera-sites into the candidate model set described in Table 2.2. See Table 2.1 for measured parameter codes and descriptions and Appendix A for complete model sets.

Species					
Model Name	AIC ^a	Δ AIC ^b	ω^c	K ^d	-2Log(L) ^e
White-tailed deer					
INT	339.40	0.00	0.37	3	333.40
YEAR	340.49	1.09	0.22	3	334.49
MONTH + YEAR	341.28	1.88	0.15	4	333.28
(.)	343.77	4.37	0.04	2	339.77
Raccoon					
TEMP	419.15	0.00	0.22	3	413.15
TEMP + PRECIP + TEMP x PRECIP	419.28	0.13	0.21	5	409.28
TEMP + PRECIP	419.52	0.37	0.18	4	411.52
MONTH + YEAR	420.20	1.06	0.13	4	412.20
TEMP + TEMP ²	421.13	1.98	0.08	4	413.13
(.)	424.25	5.10	0.02	2	420.25
Eastern gray squirrel					
MONTH + YEAR + SLOPE + PREVDET + TEMP + PRECIP + TEMP x PRECIP	193.85	0.00	0.71	9	175.85

Table 2.11 continued

(.)	202.33	8.48	0.01	2	198.33
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^aAkaike Information Criterion

^bDifference of AIC points in current model from the top model

^cModel weight, interpreted as model probability

^dNumber of model parameters

^e-2Log(Likelihood), interpreted as a measure of model fit

Table 2.12. Habitat occupancy results in the 90% confidence model set (cumulative $\omega \geq 0.90$) for white-tailed deer, raccoon, and eastern gray squirrels during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. I fit encounter history data from 3-6 1-week surveys at 140 remote camera-sites into the candidate model set described in Table 3. For all models, the probability of detection (p) was the most parsimonious model from detectability modeling process for each species (Table 2.11). The null (.) model (occupancy held constant across all camera-sites) is included to assess relative support for habitat covariates. See Table 2.1 for measured parameter codes and descriptions and Appendix B for full model sets.

Species					
Model Name	AIC ^a	Δ AIC ^b	ω^c	K ^d	-2Log(L) ^e
White-tailed deer					
MID + GRCOV	336.59	0.00	0.32	5	326.59
GRCOV	338.12	1.53	0.15	4	330.12
MID	338.72	2.13	0.11	4	330.72
MESIC + GRCOV	338.99	2.40	0.10	5	328.99
(.)	339.40	2.81	0.08	3	333.40
DTEG	339.78	3.19	0.07	4	331.78
MESIC	340.46	3.87	0.05	4	332.46
UNDERST	341.16	4.57	0.03	4	333.16
Raccoon					
(.)	419.15	0.00	0.13	3	413.15
DTEG	419.34	0.20	0.12	4	411.34
MID	419.42	0.27	0.11	4	411.42
DTST	420.17	1.03	0.08	4	412.17

Table 2.12 continued

MAXDBH	420.18	1.03	0.08	4	412.18
GRCOV	420.51	1.36	0.07	4	412.51
UNDERST	420.60	1.45	0.06	4	412.60
ELTP	420.64	1.65	0.06	4	412.64
SNAG	420.86	1.71	0.06	4	412.86
CWD	420.98	1.83	0.05	4	412.98
MESIC	420.98	1.83	0.05	4	412.98
DTEG + DTST	421.05	1.90	0.05	5	411.05
Eastern gray squirrel					
ELTP	192.24	0.00	0.27	10	172.24
(.)	193.85	1.61	0.12	9	175.85
CWD	195.15	2.92	0.06	10	175.15
MID	195.16	2.93	0.06	10	175.16
DTEG	195.23	2.99	0.06	10	175.23
UNDERST	195.71	3.47	0.05	10	175.71
GRCOV	195.71	3.47	0.05	10	175.71
MAXDBH	195.76	3.53	0.05	10	175.76
SNAG	195.78	3.54	0.05	10	175.78
MESIC	195.84	3.60	0.04	10	175.84
DTST	195.85	3.61	0.04	10	175.85
MID + CWD	196.38	4.15	0.03	11	175.38
SNAG + CWD	197.06	4.83	0.02	11	175.06

^aAkaike Information Criterion

^bDifference of AIC points in current model from the top model

Table 2.12 continued

^cModel weight, interpreted as model probability

^dNumber of model parameters

^e-2Log(Likelihood), interpreted as a measure of model fit

Table 2.13. Model-averaged estimates of covariate coefficients (β), standard errors (SE), and 95% confidence intervals from site occupancy (ψ) models within 90% confidence interval of best fitting model for white-tailed deer, raccoons, and eastern gray squirrels during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA.

Species		95% Confidence Interval		
Covariate	$\hat{\beta}$	\widehat{SE}	Lower	Upper
White-tailed deer				
INTERCEPT	-0.07	0.38	-0.81	0.67
ELTP	0.00	0.26	-0.50	0.51
DTST	0.01	0.29	-0.57	0.58
DTEG	-0.33	0.27	-0.85	0.19
GRCOV	0.63	0.47	-0.29	1.55
UNDERST	-0.15	0.28	-0.70	0.39
MESIC	-0.28	0.28	-0.84	0.28
MID	0.63	0.56	-0.48	1.74
Raccoon				
INTERCEPT	0.51	0.44	-0.36	1.37
ELTP	-0.21	0.31	-0.82	0.39
DTST	0.23	0.30	-0.35	0.82
DTEG	0.40	0.33	-0.25	1.05
CWD	0.13	0.40	-0.65	0.90
GRCOV	0.23	0.29	-0.33	0.80
UNDERST	0.21	0.31	-0.39	0.81
MESIC	0.11	0.29	-0.46	0.69
MID	-0.40	0.33	-1.05	0.24

Table 2.13 continued

MAXDBH	0.34	0.38	-0.40	1.08
SNAG	0.15	0.29	-0.41	0.72
Eastern gray squirrel				
INTERCEPT	-1.41	0.34	-2.07	-0.74
ELTP [†]	-0.53	0.29	-1.09	0.03
DTST	-0.01	0.30	-0.60	0.58
DTEG	0.24	0.31	-0.36	0.84
CWD	-0.49	0.76	-1.98	1.00
GRCOV	0.12	0.31	-0.50	0.73
UNDERST	0.09	0.24	-0.39	0.57
MESIC	0.04	0.28	-0.52	0.60
MID	-0.25	0.29	-0.82	0.33
MAXDBH	-0.09	0.30	-0.67	0.49
SNAG	-0.07	0.27	-0.60	0.46

[†]Designates an imprecise but supported covariate effect, as determined by parameters whose 95% confidence interval contained 0, but the bulk of the parameter's distribution was either positive or negative.

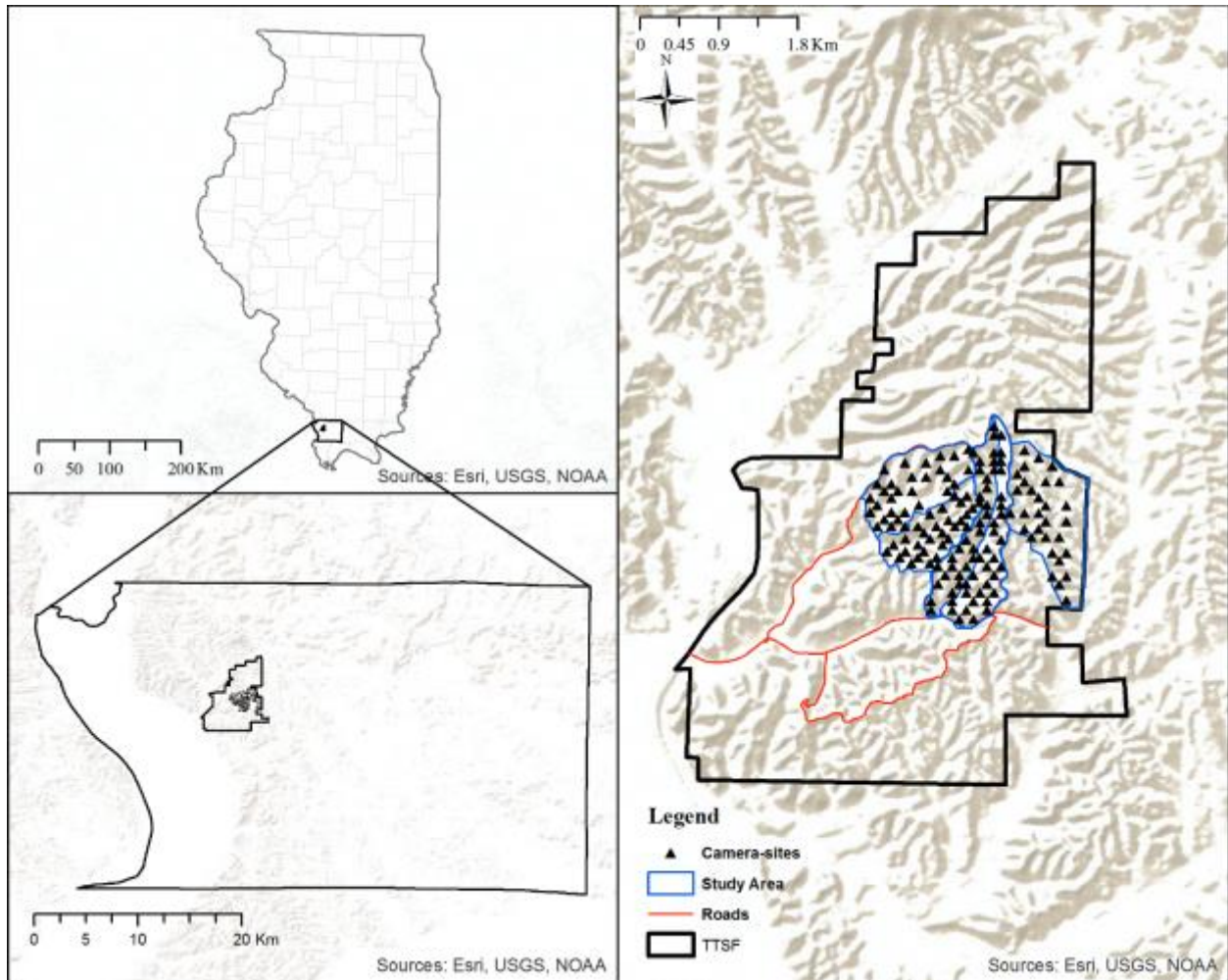


Figure 2.1. Study Area in Trail of Tears State Forest, Union County, Illinois, USA. Top left: Overview of Illinois depicting the location of Union County. Bottom left: Union County with Trail of Tears State forest outlined. Right: Study area at Trail of Tears State Forest with camera-sites.

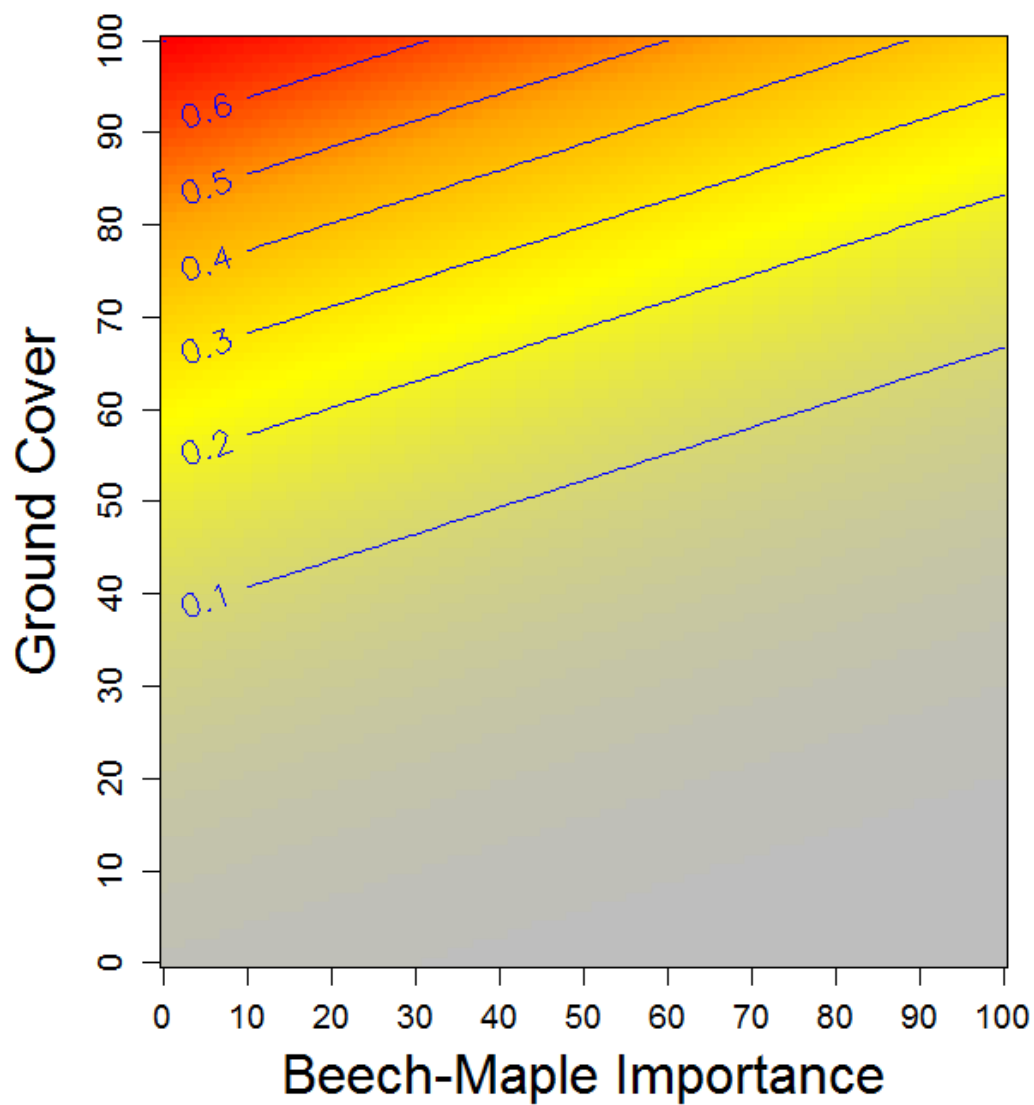


Figure 2.2. Two-dimensional predictions of the joint relationship of occupancy with ground cover and beech-maple importance value for white-tailed deer during May-August 2015-2016, Trail of Tears State Forest, Union County, Illinois, USA.

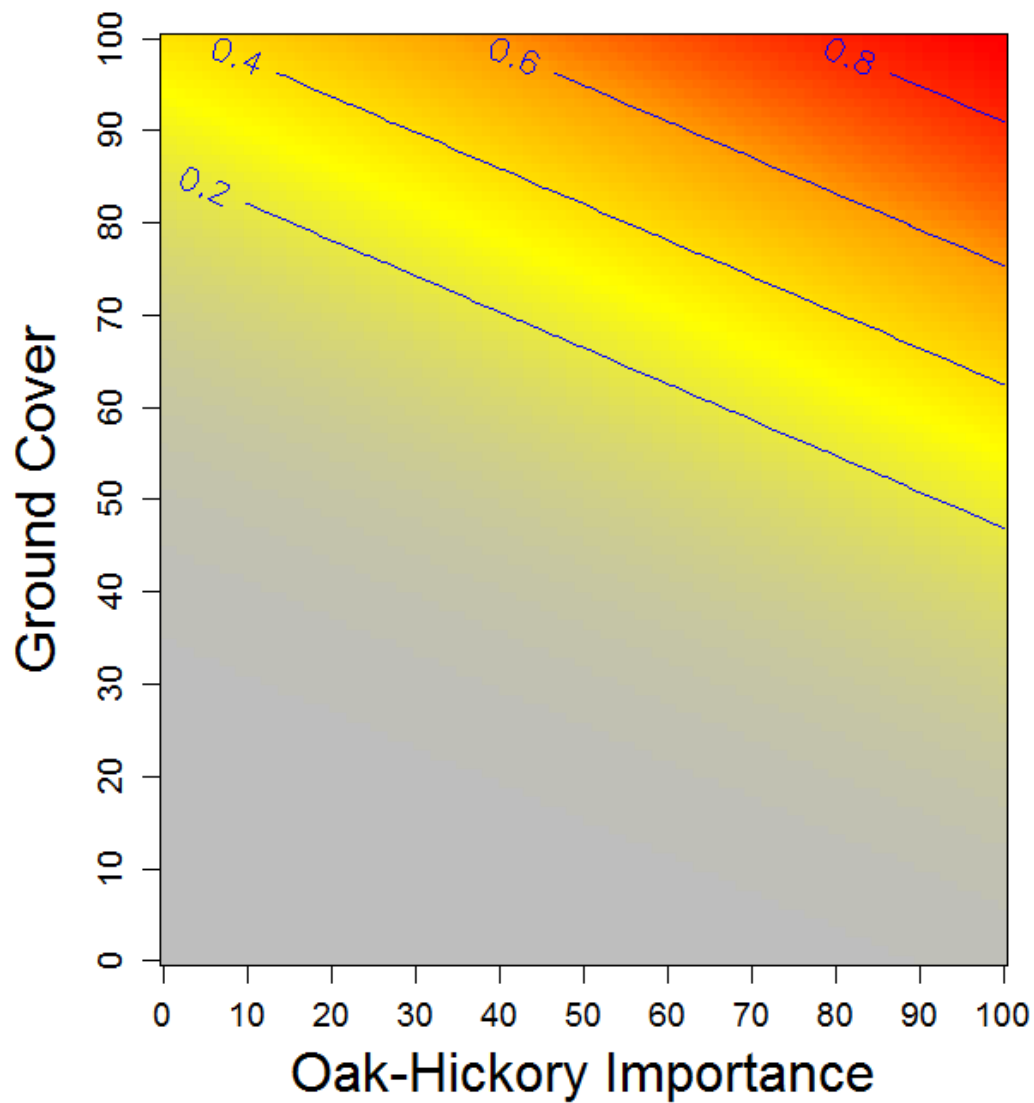


Figure 2.3. Two-dimensional predictions of the joint relationship of occupancy with ground cover and oak-hickory importance value for white-tailed deer during May-August 2015-2016, Trail of Tears State Forest, Union County, Illinois, USA.

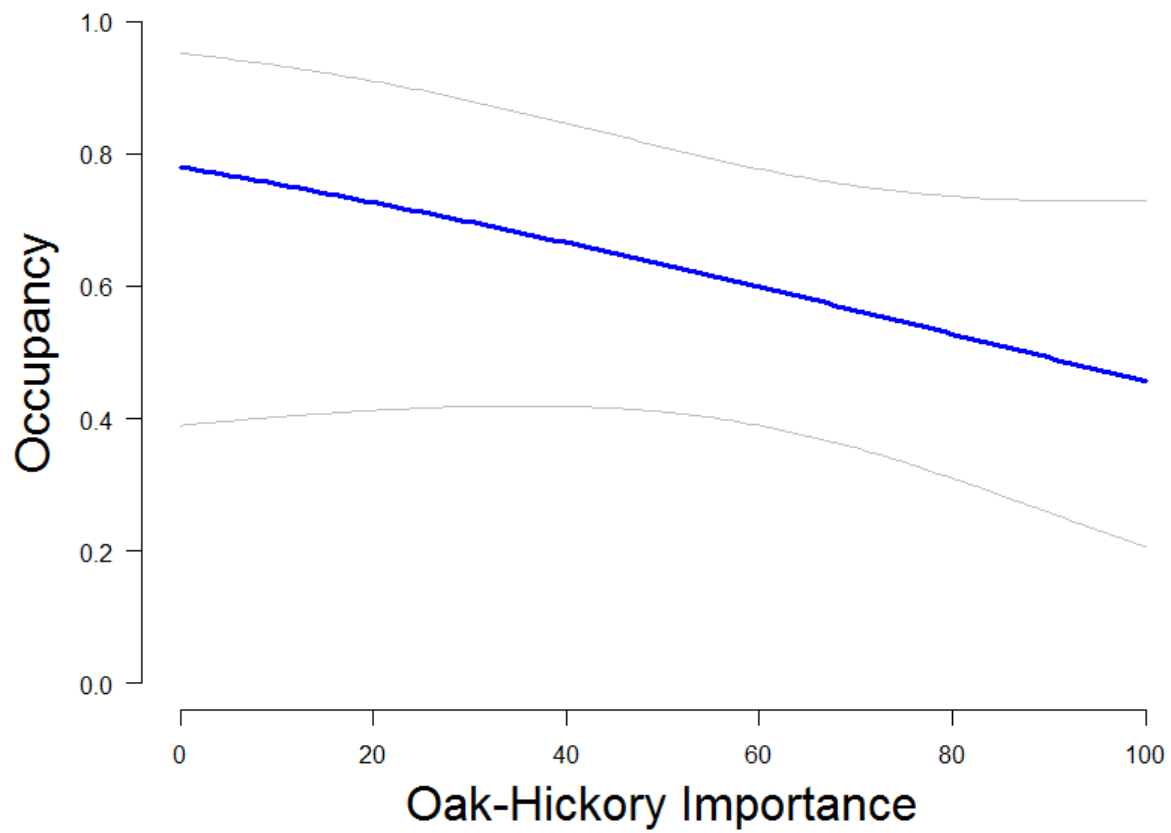


Figure 2.4. Estimated relationship between raccoon occupancy and oak-hickory importance value during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Grey lines show 95% CIs.

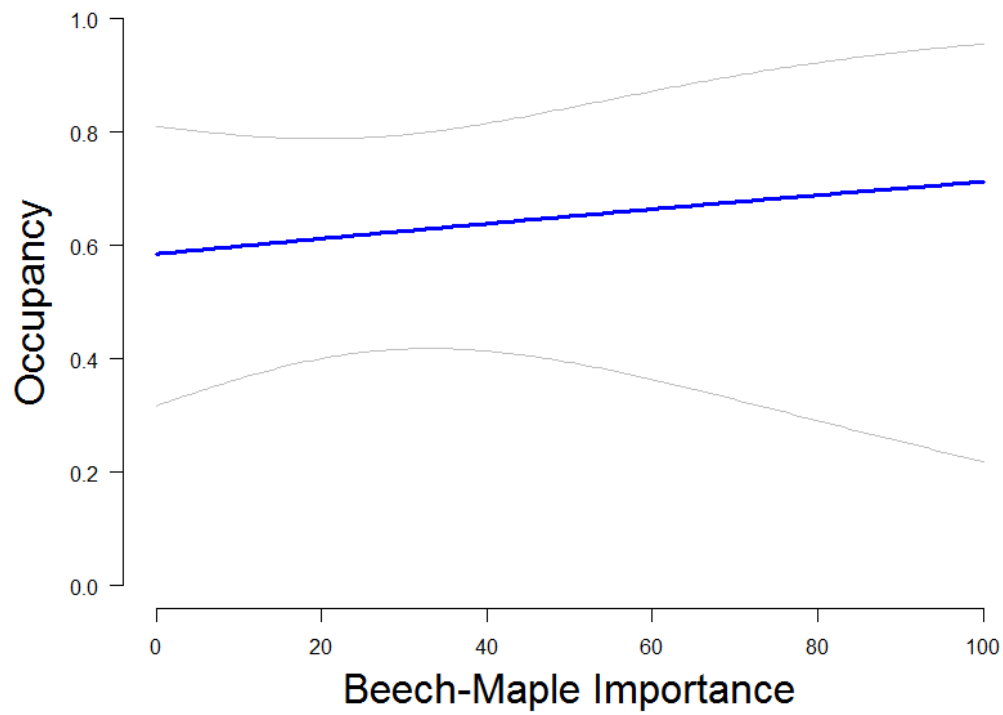


Figure 2.5. Estimated relationship between raccoon occupancy and beech-maple importance value during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Grey lines show 95% CIs.

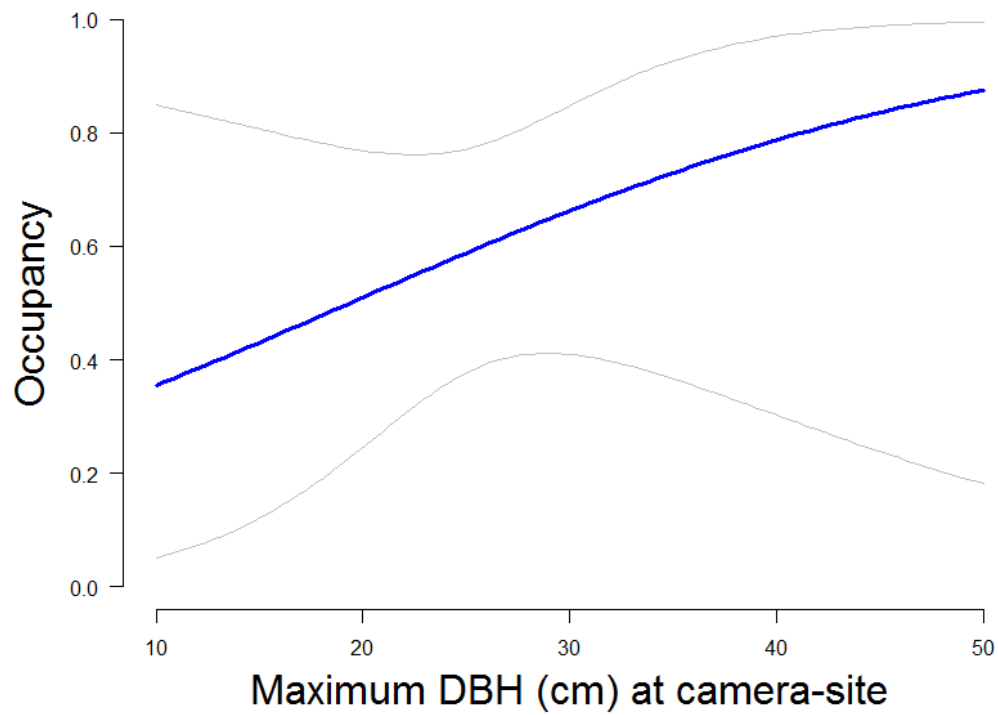


Figure 2.6. Estimated relationship between raccoon occupancy and maximum DBH during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Grey lines show 95% CIs.

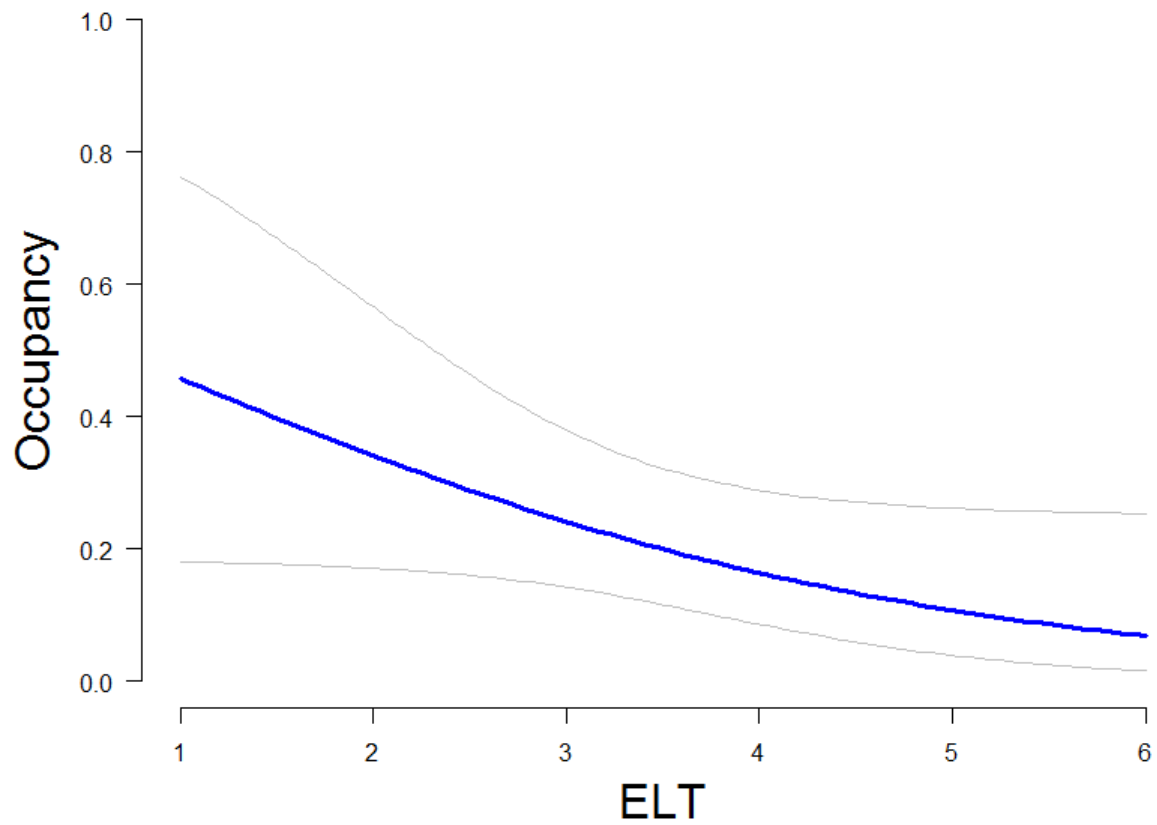


Figure 2.7. Estimated relationship between eastern gray squirrel occupancy and ecological land type (ELT) during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. Grey lines show 95% CIs.

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APPENDICES

APPENDIX A

Evaluation of survey covariates related to detection probabilities (p) for eastern gray squirrel, raccoon, and white-tailed deer during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. To estimate p for each species I held occupancy constant [(.)] and fit encounter history data from 6 1-week surveys at 150 remote camera-sites into the candidate model set described in Table 2. See Table 1 for measured parameter codes and descriptions.

Species					
Model Name	AIC ^a	Δ AIC ^b	ω^c	K ^d	-2Log(L) ^e
White-tailed deer					
INT	339.40	0.00	0.37	3	333.40
YEAR	340.49	1.09	0.22	3	334.49
MONTH + YEAR	341.28	1.88	0.15	4	333.28
SLOPE	343.37	3.97	0.05	3	337.37
(.)	343.77	4.37	0.04	2	339.77
TEMP + TEMP ²	343.94	4.54	0.04	4	335.94
MONTH	343.97	4.57	0.04	3	337.97
TEMP	344.57	5.17	0.03	3	338.57
PREVDET	344.95	5.55	0.02	3	338.95
PRECIP	345.77	6.37	0.02	3	339.77
TEMP + PRECIP	346.31	6.91	0.01	4	338.31
TEMP + PRECIP + TEMP x PRECIP	346.78	7.38	0.01	5	336.78
PRECIP + PRECIP ²	347.40	8.00	0.00	4	339.40

MONTH + YEAR + SLOPE + PREVDET + TEMP + PRECIP + TEMP x PRECIP ($\hat{c} =$ 0.54, $\chi^2 = 46.09, p = 0.83$)	348.58	9.18	0.00	9	330.58
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Raccoon

TEMP	419.15	0.00	0.22	3	413.15
TEMP + PRECIP + TEMP x PRECIP	419.28	0.13	0.21	5	409.28
TEMP + PRECIP	419.52	0.37	0.18	4	411.52
MONTH + YEAR	420.20	1.06	0.13	4	412.20
TEMP + TEMP ²	421.13	1.98	0.08	4	413.13
MONTH + YEAR + PREVDET + SLOPE + TEMP + PRECIP + TEMP x PRECIP ($\hat{c} =$ 1.24, $\chi^2 = 116.06, p = 0.20$)	422.30	3.16	0.05	9	404.30
MONTH	422.48	3.34	0.04	3	416.48
YEAR	422.58	3.43	0.04	3	416.58
(.)	424.25	5.10	0.02	2	420.25
INT	425.29	6.15	0.01	3	419.29
SLOPE	426.16	7.01	0.01	3	420.16
PRECIP	426.21	7.06	0.01	3	420.21
PREVDET	426.23	7.08	0.01	3	420.23
PRECIP + PRECIP ²	427.55	8.41	0.00	4	419.55

Eastern gray squirrel

MONTH + YEAR + PREVDET + SLOPE + TEMP + PRECIP + TEMP x PRECIP ($\hat{c} =$ 0.67, $\chi^2 = 65.78, p = 0.68$)	193.85	0.00	0.71	9	175.85
PREVDET	197.48	3.63	0.11	3	191.48

YEAR	198.61	4.76	0.07	3	192.61
MONTH + YEAR	200.08	6.23	0.03	4	192.08
SLOPE	201.09	7.24	0.02	3	195.09
PRECIP	201.40	7.55	0.02	3	195.40
(.)	202.33	8.48	0.01	2	198.33
INT	202.89	9.04	0.01	3	196.89
PRECIP + PRECIP ²	202.96	9.11	0.01	4	194.96
TEMP + PRECIP	203.31	9.46	0.01	4	195.31
TEMP	203.53	9.68	0.01	3	197.53
TEMP + PRECIP + TEMP x PRECIP	203.55	9.70	0.01	5	193.55
MONTH	204.30	10.45	0.00	3	198.30
TEMP + TEMP ²	205.46	11.61	0.00	4	197.46

^aAkaike Information Criterion

^bDifference of AIC points in current model from the top model

^cModel weight, interpreted as model probability

^dNumber of model parameters

^e-2Log(Likelihood), interpreted as a measure of model fit

APPENDIX B

Complete habitat occupancy (ψ) results for eastern gray squirrel, raccoon, and white-tailed deer during May-August 2015-2016 in Trail of Tears State Forest, Union County, Illinois, USA. I fit encounter history data from 6 1-week surveys at 150 remote camera-sites into the candidate model set described in Table 3 for each species. For all models, the probability of detection (p) was the most supported model from detectability modeling process for each species (Appendix A). See Table 1 for measured parameter codes and descriptions.

Species					
Model Name	AIC ^a	Δ AIC ^b	ω^c	K ^d	-2Log(L) ^e
White-tailed deer					
MID + GRCOV	336.59	0.00	0.32	5	326.59
GRCOV	338.12	1.53	0.15	4	330.12
MID	338.72	2.13	0.11	4	330.72
MESIC + GRCOV	338.99	2.40	0.10	5	328.99
(.)	339.40	2.81	0.08	3	333.40
DTEG	339.78	3.19	0.07	4	331.78
MESIC	340.46	3.87	0.05	4	332.46
UNDERST	341.16	4.57	0.03	4	333.16
DTST	341.39	4.80	0.03	4	333.39
ELTP	341.40	4.81	0.03	4	333.40
DTEG + DTST	341.72	5.13	0.03	5	331.72
ELTP + DTST + DTEG + GRCOV +	343.17	6.58	0.01	8	327.17
UNDERT ($\hat{c} = 0.60, \chi^2 = 55.45, p =$ 0.65)					

Raccoon

(.)	419.15	0.00	0.13	3	413.15
DTEG	419.34	0.20	0.12	4	411.34
MID	419.42	0.27	0.11	4	411.42
DTST	420.17	1.03	0.08	4	412.17
MAXDBH	420.18	1.03	0.08	4	412.18
GRCOV	420.51	1.36	0.07	4	412.51
UNDERST	420.60	1.45	0.06	4	412.60
ELTP	420.64	13.50	0.06	4	412.64
SNAG	420.86	1.71	0.06	4	412.86
CWD	420.98	1.83	0.05	4	412.98
MESIC	420.98	1.83	0.05	4	412.98
DTEG + DTST	421.05	1.90	0.05	5	411.05
MID + CWD	421.36	2.21	0.04	5	411.36
SNAG + CWD	422.62	3.47	0.02	5	412.62
MESIC + CWD	422.87	3.72	0.02	5	412.87
ELTP + DTST + DTEG + CWD + GROUND + UNDERST + MAXDBH + SNAG ($\hat{c} =$ $0.93, \chi^2 = 99.63, p = 0.34$)	428.75	9.61	0.00	13	402.75

Eastern gray squirrel

ELTP	192.24	0.00	0.27	10	172.24
(.)	193.85	1.61	0.12	9	175.85
CWD	195.15	2.92	0.06	10	175.15
MID	195.16	2.93	0.06	10	175.16
DTEG	195.23	2.99	0.06	10	175.23

UNDERST	195.71	3.47	0.05	10	175.71
GRCOV	195.71	3.47	0.05	10	175.71
MAXDBH	195.76	3.53	0.05	10	175.76
SNAG	195.78	3.54	0.05	10	175.78
MESIC	195.84	3.60	0.04	10	175.84
DTST	195.85	3.61	0.04	10	175.85
MID + CWD	196.38	4.15	0.03	11	175.38
SNAG + CWD	197.06	4.83	0.02	11	175.06
MESIC + CWD	197.10	4.86	0.02	11	175.10
DTEG + DTST	197.19	4.95	0.02	11	175.19
MESIC + GRCOV	197.70	5.46	0.02	11	175.70
MID + GRCOV	197.70	5.46	0.02	11	175.70
ELTP + DTST + DTEG + CWD + GROUND + UNDERST + MAXDBH + SNAG ($\hat{c} =$ $0.60, \chi^2 = 58.32, p = 0.76$)	205.10	12.86	0.00	17	171.10

^aAkaike Information Criterion

^bDifference of AIC points in current model from the top model

^cModel weight, interpreted as model probability

^dNumber of model parameters

^e-2Log(Likelihood), interpreted as a measure of model fit

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